EFFECTS OF THE DENSITY OF CO-OCCURING BIVALVES (*MYA ARENARIA)* AND DEEP-BURROWING POLYCHAETES (*NEREIS VIRENS)* ON BENTHIC FLUXES AND THE CONCENTRATIONS OF AMMONIUM AND SOLUBLE SULFIDES IN SEDIMENT POREWATER

A Thesis

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Master of Science

by

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May 2009

ABSTRACT

Increases in the frequency and severity of disturbance events, such as periodic hypoxia and trawling, have caused dramatic changes in benthic invertebrate communities in many coastal regions. In order to predict the effects of disturbance on ecosystem function, it is necessary to improve understanding of how changes in invertebrate density and species composition affect benthic geochemical cycling. I used laboratory microcosms to test the effects of recolonization of previously defaunated sediments by deep-burrowing polychaetes (*Nereis virens*) and suspension-feeding bivalves (*Mya arenaria*) on porewater ammonium and soluble-sulfide concentrations as well as benthic fluxes of oxygen and nutrients: dissolved inorganic nitrogen (ammonium and nitrate + nitrite, or DIN), dissolved silicate (Si), and soluble reactive phosphorus (SRP). I added single and two-species treatments including a range of densities comparable to densities common for shallow estuaries. I sampled porewater and measured fluxes under both dark and light conditions one month after organism addition. Effects of *N. virens* on porewater chemistry were significantly greater than *M. arenaria*, but even the lowest density of each organism lowered porewater ammonium and soluble-sulfide concentrations significantly relative to defaunated controls. However, increasing density had little additional effect on porewater. Benthic oxygen and nutrient fluxes generally increased between low and high densities. However fluxes of DIN and SRP were higher in controls than in low-density treatments and fluxes of SRP were significantly lower in *N. virens* treatments than *M. arenaria* treatments. This suggests that whether organisms would increase or decrease nutrient availability depends on density and that the ratio of DIN:SRP release depends on species composition. Macrofaunal respiration and excretion of ammonium and SRP appeared to account for most of the increased nutrient flux. *Mya* arenaria

also stimulated significant increases in benthic gross primary production (GPP) and corresponding decreases in ammonium, SRP, and Si fluxes in the light relative to the dark. *N. virens* had no effect on GPP but enhanced both nitrate and Si flux significantly in the light, probably by increasing ventilation. Changes in porewater solute concentrations and benthic flux rates in two-species treatments were generally greater than expected based on single-species treatments, and the deviation of observed from expected values increased with density. This suggests that niche complimentarity could influence the effects of these organisms on elemental cycling and that effects become more important with increasing density.

BIOGRAPHICAL SKETCH

Ursula H Mahl was born and raised in San Francisco, California. She graduated from Lowell High School in 1999, after which she began her undergraduate work at University of California, Davis. While at UC Davis, she focused primarily on wildlife medicine and ecology. Through coursework and involvement with various research projects ranging from population monitoring for Brown pelicans to water quality monitoring at a local Super Fund site, she developed a particular interest in the effects of human activities on ecosystem function. Her senior thesis work related to strategies for controlling California Ground Squirrel populations that minimize risks to non-target species. In 2004, she received a B.S. in Animal Biology with high honors.

After graduation, Ursula worked as a technician in the Grosholz Laboratory at UC Davis on an NSF-funded biocomplexity project examining the impacts of cordgrass (*Spartina alterniflora*) invasion on lower trophic levels and biogeochemical cycling in tidal estuaries. During field trips to San Francisco Bay, CA and Willapa Bay, WA, she fell in love with the estuary and developed a fascination with feedbacks between biogeochemical processes and community structure. This project also provided her a model for collaborative science and an opportunity to gain experience with methods development and advising undergraduate interns, all of which fomented her interest in continuing on an academic path.

Ursula met Robert W Howarth in 2005 at a biennial meeting of the Estuarine Research Federation. She applied to work with Professor Howarth shortly after, and in 2006, enrolled as a graduate student at Cornell University in the field of Natural Resources. She designed her dissertation to complement Professor Howarth's ongoing biocomplexity project examining non-linear feedbacks in coupled-elemental cycling during eutrophication of shallow estuaries. She completed her master's work at the Marine Biological Laboratory in Woods Hole, MA.

ACKNOWLEDGMENTS

I would like to thank my advisor, Robert W. Howarth, for all of his help in the development of my research project and for the opportunity to be involved with his NSF-funded biocomplexity project, which has provided a context for my work. I would also like to thank him for the time he has spent helping me to refine my understanding of processes that control elemental cycles in my study system, particularly the nuances that may be neglected in the community-based approach to ecosystem science in which I am rooted. I also thank the other members of my committee, Clifford Kraft, Drew Harvell, and Anna-Christina Tyler for their support. In particular, Anna-Christina Tyler played an integral role in the development of my scientific interests during my time at UC Davis; her continued involvement with my work and her friendship have been invaluable to me over the last two years.

I would also like to acknowledge Ted Grosholz and his lab group for their role in the development of my interests and the scientific communities at Cornell and the Marine Biological Laboratory for helping to maintain and refine these interests. Anne Giblin, Roxanne Marino, Tom Duncan, Peter Berg, Natalie McLengehan, and Melanie Hayn all helped with the execution of this project or provided input as I was refining the story that my data tells. In particular, collaboration with McLengehan made long days in the lab – that would have otherwise been spent alone – a pleasure. Interactions with students in Natural Resources, E&EB, and the biogeochemistry program, particularly S. Romaniello, L. Martin, and C. Turner, have also been an important part of my graduate experience. Finally, thanks to my family for their love and support.

Funding was provided for by the NSF Biocomplexity grant (BE-0420575), NSF IGERT (DGE0221658), NSF Predoctoral Fellowship (2006043892), and the department of E&EB at Cornell University. Thanks also to the Marine Biological Laboratory for lab space and to Salem State University for provision of organisms.

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ANOVA	analysis of variance
DIN	dissolved inorganic nitrogen (ammonium + nitrate + nitrite)
DNRA	dissimilatory nitrate reduction to ammonium
DO	dissolved oxygen
GPP	gross primary production
Ha	hectares
LOI	loss on ignition
MBL	Marine Biological Laboratory, Woods Hole, MA
N	nitrogen
OM	organic matter
ppt	parts per thousand
SE	standard error
Si	Silicate
SOD	sediment oxygen demand
spp	species
SRP	Soluble reactive phosphorus
WFH	West Falmouth Harbor, MA

INTRODUCTION

Benthic invertebrates can play an important role in benthic processes which may influence broader ecosystem function (Rhoads 1974, Lohrer et al. 2004, Meysman et al. 2006). There is also growing evidence that functional differences in organism behavior (Francois et al. 2002, Mermillod-Blondin et al. 2004b, Michaud et al. 2006), density-dependent processes (Marinelli 1994, Marinelli & Williams 2003, Nordstrom et al. 2006, Karlson et al. 2007, Nizzoli et al. 2007), and interactions between species (Waldbusser et al. 2004, Mermillod-Blondin et al. 2005) could contribute significantly to geochemical variability in sediments. However, the results of studies evaluating the relationship between biodiversity and ecosystem function have been idiosyncratic (Emmerson et al. 2001) and surprisingly few studies have incorporated density into their design. A better understanding of how diversity and functional differences between faunal species affect the relationship between biogeochemical cycling and invertebrate abundance is needed in order to predict how changes in invertebrate distributions will affect ecosystem function.

An invertebrate's feeding and burrowing behaviors determine how it will affect the distribution of porewater solutes and the form and amount of nutrients released to the overlying water (Aller 1982, Francois et al. 2002, Michaud et al. 2006). Burrow ventilation decreases concentrations of reduced porewater solutes both by direct transport of reduced chemical species to the water column and by increasing the supply of oxidized compounds to deeper sediments (Kristensen & Hansen 1999, Berg et al. 2003). This can stimulate chemical oxidation of reduced sulfides (eg. FeS, pyrite, H_2S, HS^-, S^{2-}) (Hansen et al. 1996, Banta et al. 1999) and redox sensitive metals (Rhoads 1974, Thayer 1979, Sun & Torgersen 2001). Intermittent ventilation can also create oscillating redox conditions that promote removal of nitrogen from the

system through coupled nitrification-denitrification (Pelegri & Blackburn 1995). Though poorly studied in the context of bioturbation, the secondary effects of oxidation and subsequent decrease in pH could increase sorption of phosphate (Krom & Berner 1980, Sundby et al. 1986, Howarth et al. 1995) and ammonium (Morse & Morin 2005) to sediments and decrease rates of dissimilatory nitrate reduction to ammonium (DNRA) by reduced sulfur (Burgin & Hamilton 2007).

Burrow ventilators could also enhance benthic fluxes directly through respiration and excretion (of ammonium and phosphate) or indirectly by stimulating microbial remineralization through secretion of mucus into the burrow lining, removal of inhibitory metabolites (Rowe & Howarth 1985, Aller & Aller 1998) and promotion of redox oscillations that favor more complete and rapid organic matter decomposition than is possible under unidirectional redox change (Aller 1994).

Suspension feeding bivalves generally have a weaker effect on physical transport of solutes and oxidation-reduction reactions than burrow-ventilators (Pelegri & Blackburn 1995a, Francois et al. 2002) because they pump water through their body cavity without direct contact with the surrounding porewater (Forster & Zettler 2004). However, bivalves can stimulate oxidation reactions by mixing labile organic matter and oxidized solid-phased compounds such as oxidized manganese, Fe(III) oxides, and hydroxides from the surface to greater depths (Aller 1982, 1990). They can also greatly accelerate the transfer of pelagic carbon to the sediments relative to deposit feeders through biodeposition (Amouroux et al. 1990) which can stimulate remineralization and recycling of nutrients to the water column.

Within the range of densities commonly observed in the field, the effects of abundance on nutrient flux (Gallepp 1979) can be additive, but most studies that have included density in their design have demonstrated non-linear relationships between organism density and benthic flux rates (Marinelli & Williams 2003, Nordstrom et al.

2006, Karlson et al. 2007, Nizzoli et al. 2007, Tang & Kristensen 2007). Transport-reaction models predict that porewater profiles for solutes subject to zero-order reactions, such as the production of ammonium and soluble sulfides by remineralization, will be highly sensitive to changes in abundance when densities are low but that the effects of ventilation will saturate as the diffusion path-length between burrows decreases (Aller 1980). These models demonstrate that, when invertebrates affect porewater exchange but do not alter net-production, fluxes of remineralization-produced solutes will be relatively independent of density, while fluxes of solutes subject to first-order reactions, such as silica dissolution, will be highly sensitive to density (Aller 1980). Model experiments simulating diffusive exchange have demonstrated that density-dependent changes in remineralization (Aller & Aller 1998) and nitrification coupled with denitrification (Gilbert et al. 2003) can also alter porewater solute concentrations and fluxes. Invertebrates could also alter their feeding modes (Marinelli & Williams 2003), rates of irrigation (Woodin and Marinelli, 1991), and respiration (Kristensen 1983b, 1989) in response to changes in the sediment environment that accompany increasing density. It is not clear how these behavioral changes or functional differences between species will alter the relationship between sediment chemistry and density that would be predicted by physical models.

Invertebrate diversity can influence sediment processes by niche complimentarity (eg. more effective partitioning of sediment habitat and use of different food resources) or through interspecific facilitation (Emmerson et al. 2001, Waldbusser et al. 2004, Mermillod-Blondin et al. 2005), and results from one study suggest that the effects of diversity may depend upon invertebrate density (Emmerson & Raffaelli 2000). Some organisms may also alter their burrowing behaviors when co-occurring with other species (Hill & Elmgren 1987). Other studies have shown that community effects may be largely determined by the most dominant organisms

and that effects of diversity loss on ecosystems can result from the increased probability of extinction of the dominant species (Cardinale et al. 2006).

Changes in the distribution of macroinvertebrates could strongly influence temporal and spatial patterns of phytoplankton production and subsequent organic matter supply to the sediments. In shallow estuaries, regeneration of nutrients from the benthos can provide up to 80% of phytoplankton nutrient demand (Nixon 1981, Fisher et al. 1982) and 30 to 60% of the ammonium release may be due to invertebrates (Blackburn & Henriksen 1983). Macroinvertebrate distributions can change regularly due to seasonal changes in primary production that can alter species composition and abundance (Duplisea 1998, Diaz & Rosenberg 2008) and periodic disturbances that can completely defaunate patches of sediment such as severe anoxic events, resuspension by storms, and trawling (Pearson 1978, Hall 1994, Thrush et al. 2001). Particularly in estuaries with high nutrient loading, high rates of remineralization and sulfide production following spring blooms can lead to a decline in the abundance of deeper burrowing species while dominance of phytoplankton may favor suspension feeders over deposit feeders and grazers (Pearson 1978, Gray 1989). Over small spatial scales, invertebrate distributions are controlled by biological interactions (Woodin 1974, Davey & George 1986, Kristensen 1988), and competition for food and space can drive recolonization of defaunated sediments as primary production declines in the fall. Recolonization could potentially facilitate the return to pre-bloom conditions by decreasing concentrations of toxic metabolites (e.g. solubule sulfides) in sediment porewater, accelerating the removal of excess sediment organic matter, and stimulating removal of remineralized DIN through denitrification relative to recycling to the water column. However, rapid flushing of reduced metabolites (i.e. soluble sulfides, ammonium and soluble reactive phosphorus (SRP) from sediment porewater immediately following recolonization and enhanced remineralization

(Hansen & Kristensen 1997) could also favor a temporary shift back towards hypoxic conditions by promoting pelagic primary production and increasing benthic oxygen demand. The abundance and identity of the recolonizing organisms will likely determine the magnitude of these effects.

In order to examine the relationship between macroinvertebrate community structure and benthic biogeochemical cycling, I created laboratory microcosms in which I varied the density of two co-occurring species with similar body sizes but different feeding and burrowing behaviors: the marine worm *Neries virens* and the soft-shelled clam *Mya arenaria*. I measured the effects of organisms on porewater ammonium and soluble-sulfide concentrations and exchange of oxygen and nutrients between sediments and the water column one month after recolonization.

Neries virens (Polychaeta) primarily deposit feeds on surface sediment, and constructs deep (12 to 15 cm) u-shaped burrows which it irrigates intermittently (Kristensen 2000). Because it is highly mobile and its distribution is strongly influenced by competitive interactions with other *Nereids* (Kristensen 1988, Miron & Kristensen 1993b), it is likely to either emigrate when conditions are poor or to recolonize. Typical densities range from 150 to 1400 individuals m^{-2}, but *N. virens* can be found in very low densities in shallower systems because fluctuations in temperature and salinity often restrict it to deeper waters (Kristensen, 2000; Table 1).

Mya arenaria (Bivalvia) is a large, high volume suspension feeder which burrows to a depth of approximately 7 to 25 cm (Henriksen et al. 1983, Mermillod-Blondin et al. 2004a). These organisms move vertically in response to high sulfide concentrations and are less likely to recolonize than *N. virens*. However, organisms up to the 1-year age class used in this experiment may move through active resuspension and bedload transport (LeBlanc and Miron, 2006). Distributions are typically patchy and mean densities range from 75 to 400 individuals m^2 (Table 1).

Table 1. Typical *N. virens* and *M. arenaria* densities in estuarine sediment.

Species	Mean Density (Individuals m-2)	Site	Source
N. virens	150 - 800	Norsminde (Kysing) Fjord	Kristensen 1984
	175 - 250	Kertinge Nor, Denmark	Nielson et al. 1995
	500 - 1000	N. European Coast (review)	Kristensen 2000
	1400	St. Lawrence River, Estuary, Quebec Canada	Mermillod-Blondin et al. 2004
M. arenaria	75 - 325	Halifax Harbor, Nova Scotia	Emerson et al. 1987
	420	St. Lawrence River, Estuary, Quebec Canada	Mermillod-Blondin et al. 2004
	250	German coast of southern Baltic	Forster et al. 2004

I predicted that:

(1) *Neries virens* would lower porewater ammonium and soluble sulfide concentrations and alter oxygen and nutrient flux rates more than *M. arenaria* because burrowing and ventilation of burrows by *N. virens* would enhance exchange of oxygen and dissolved constituents between sediment porewater and the overlying water more than burrowing and filter feeding by *M. arenaria*.

(2) Changes in porewater ammonium and soluble-sulfide concentrations and benthic flux rates would be density dependent and that the effects of *N. virens* would approach a maximum at lower densities than *M. arenaria* because the stronger effects of the polychaete would result in greater intraspecific interference (eg. overlap in sediment volume affected by burrows).

(3) The difference between single species and two species treatments would be greater at higher densities because interspecific interference is less than intraspecific interference due to complementarity of species resource use and spatial distribution.

METHODS.

Site description- I conducted microcosm experiments at the Marine Biological Laboratory (MBL) in Woods Hole, MA using sediments collected from an intertidal zone in the outer harbor of West Falmouth Harbor (WFH), MA. WFH is a small, shallow estuary that is divided into an inner harbor with muddy, organic sediments and an outer harbor with sandier less organic sediments (Figure 1). At mean high tide, the mean surface area is 79 ha and the mean depth is 1.54 m (Hayn *unpub*). Inputs of nitrate from a contaminated aquifer that feeds the inner harbor have doubled nitrogen (N) load to WFH over the past 5 years; given transit times in the groundwater, N loads should decline within the next 6 to 10 years due to pollution control measures that are already in place at the source in the watershed (Foreman and Giblin, pers. Comm).

I designed this study to compliment an ongoing research project funded by the National Science Foundation Biocomplexity Grant (BE-0420575) examining biogeochemical and biotic feedbacks that occur among coupled elemental cycles during eutrophication. Preliminary analyses from the biocomplexity project suggest that, similar to other shallow estuaries, the distribution of macroinvertebrates in the harbor is patchy and that abundance of macroinvertebrates in the inner harbor declines dramatically during the summer following peak primary production (Duncan, pers. Comm.). The overall abundance of deeper burrowing species in the inner harbor is extraordinarily low in comparison to otherwise similar areas that are not subject to high levels of N loading (Duncan pers. Comm). It is not clear how seasonal and long term changes in invertebrate abundance and community composition will alter benthic-pelagic coupling. I approached this question by comparing the effects of invertebrate density on porewater chemistry and benthic fluxes in microcosms with deep-burrowers or suspension feeders to microcosms with both functional groups.

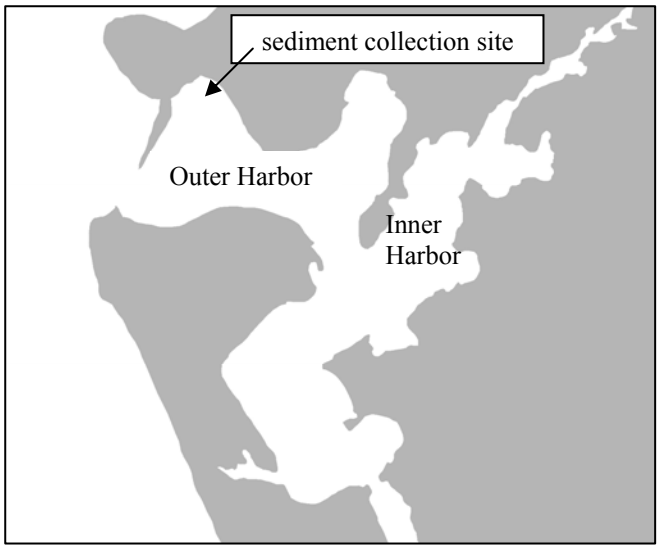

Figure 1. West Falmouth Harbor, MA.

Microcosm set-up- I collected sediment cores from the outer harbor in WFH, sectioned cores by depth (0-2 cm, 2-5 cm, and 5-15 cm), and defaunated sediments by sieving (1 mm mesh). I then filled experimental cores (9.5 cm ID x 30 cm tall clear polycarbonate tube sealed at the base with a rubber stopper) with homogenized sediment from each depth range. This ensured homogeneity of initial conditions between microcosms and removed macrofauna while minimizing disruption of the vertical distribution of organic matter and minerals. I wrapped the lower 15 cm of each core with aluminum foil to prevent exposure of sediments at depth to light.

I incubated the microcosms for 54 days during June/July 2007, in a tank supplied constantly with sea water from Woods Hole Harbor (18-23°C, 30 ppt salinity). I used full spectrum fluorescent lights to augment natural light and maintain light intensity above saturation for primary production at the sediment surface (10 hour dark, 14 hour light, 250-350 μEinsteins m^{-2} s^{-1}). Each core was aerated with an upward-curved tube 3 cm above the sediment surface to ensure circulation between microcosms and the overlying water (depth 40 cm above the sediment surface).

I allowed sediments to acclimate for three weeks prior to organism addition. After 14 days, I added 0.6 g of dried, ground macroalgae (*Gracilaria vermiculophylla*) to the sediment surface in each microcosm to simulate conditions that lead to seasonal decline of macroinvertebrates in the inner harbor. This was comparable to organic matter loading from an intermediate-sized algal bloom (Hauxwell et al. 1998).

Experimental treatments were established at the end of the three-week acclimation period and consisted of a control with no macroinvertebrates and 8 macroinvertebrate treatments (n=5; Figure 2). Macroinvertebrate treatments varied in density (1, 2, and 4 individuals per core (68 cm^2) and species composition (*N. virens, M. arenaria* or both species in combination). Densities were comparable to 141, 282, and 564 individuals m^{-2} and were within the range of common field densities (Table 1). The addition of organisms was staggered over a three-day period (day 21, 22, and 23) to allow for sampling over a three day period. Treatments were assigned to cores in a completely randomized design. *Neries virens* were collected from an estuary in Maine by Aquatic Research Organisms. *Mya arenaria* were from a year 1 cohort raised by Salem State Aquaculture. I allowed organisms to acclimate to laboratory conditions in a tub of fresh sediments from WFH for four days prior to adding them to microcosms. I measured the initial biovolume of each organism by displacement.

Sediment property measurement- I estimated organic matter (OM) content for freshly sieved sediments prior to microcosm construction, for three microcosms sampled at the time of organism addition, and for all experimental microcosms at the termination of the experiment. I sectioned microcosms by depth (0-2 cm, 2-5 cm, 5-10 cm), dried a subsample of sediment from each depth at 60°C for 48 hours and estimated sediment OM as the loss of weight on ignition (LOI) after 4 hours at 500°C. I also calculated porosity as the difference between wet and dry weights divided by sediment volume.

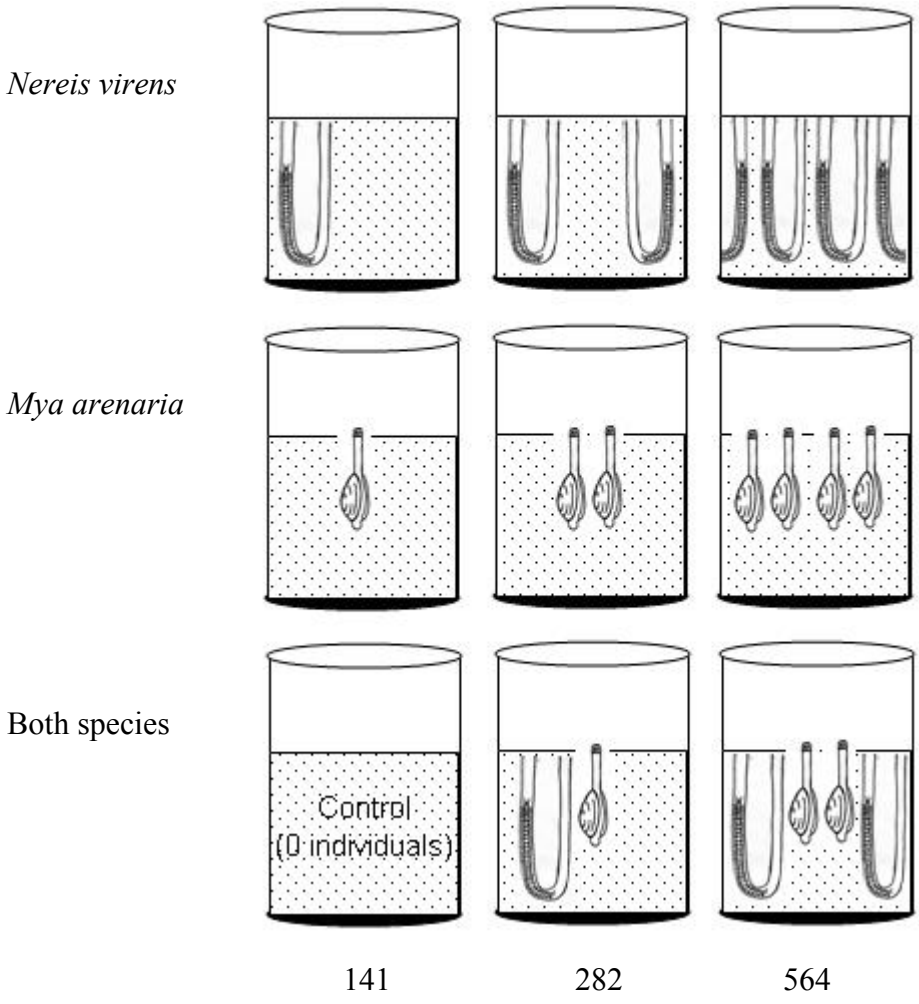

Figure 2. Experimental design (n=5).

Sediment Porewater Measurements- I sampled porewater from three intact cores from the sediment collection site, three microcosms at the time of organism addition and from experimental microcosms 33 days after organism addition. I extracted two ml of porewater from each of four depths (2, 4, 7, 10 cm) using suction probes as described by Berg and McGlathery (2001). I analyzed porewater immediately for ammonium by the phenol hypochlorite method (Solorzan.L 1969). I fixed 250 µL of porewater with 6 mL of 2% ZnAc and, after storage for 2-3 days at 3°C, analyzed samples according

to Howarth and Jorgensen (1984). I standardized samples by subtracting the absorbance in blanks containing ZnAc and deionized water from absorbance of the sample and dividing this difference by a conversion factor derived from methylene blue standards checked against polarographic measurements.

$$concentration = \frac{(abs_{sample} - abs_{blank})}{0.542}$$

Benthic Flux Measurements- I measured fluxes of dissolved oxygen and nutrients (ammonium, nitrate, silicate (Si), and SRP) between sediments and overlying water 26 days after organism addition (days 47, 48, 49) according to Tyler et al. (2001). Prior to initiating flux measurements, I replaced the overlying water in each core with unfiltered water from Woods Hole Harbor and sealed each core with a clear lid. Magnetic stir bars suspended over the sediment surface gently mixed water (60 rpm) to prevent the development of concentration gradients that could interfere with diffusion across the sediment-water interface. I incubated cores in an environmental chamber (CONVIRON^{TM}) at 19°C for 6 hours (3 h dark, 3 h light). Sodium halogen, metal halide, and full spectrum fluorescent lights maintained a light intensity of 175 to 250 μEinsteins m^{-2} h^{-1} at the sediment surface. Every 1.5 hours I fitted a sampling port in the lid with a WTW 330i galvanic sampling probe with a magnetic stir bar and measured dissolved oxygen concentrations after 2 to 3 minutes equilibration. I then took a 35 ml water sample for nutrient analysis. I replaced the sample volume carefully to ensure that air bubbles were not introduced to microcosms.

I filtered water samples (0.45 micron supor GFF filters) and measured ammonium immediately using the phenol hypochlorite method (Solorzan.L 1969). I fixed a portion of the sample using 10 μL of 6N HCl and stored it for 3 to 5 days at 3

°C prior to analysis for SRP by the molybdate blue method (Murphy & Riley 1962). The remaining sample was frozen and analyzed later for Si by the metol-sulfite method (Parsons 1984) and for nitrate + nitrite with an ALPKEM autoanalyzer.

Benthic flux calculations- I estimated hourly flux rates by calculating the slope change in concentration versus time for each pair of successive sampling points and calculating the average of the slopes for the entire flux period:

$$J = \frac{V}{A}\left(\frac{(C_2 - C_{1-diluted})}{(t_2 - t_1)} + \frac{(C_3 - C_{2-diluted})}{(t_3 - t_2)}\right)\frac{1}{2}$$

where J is the flux rate in μmol m^{-2} h^{-1}, A is the core area, V is the water volume, C_1, C_2 and C_3 are concentrations for successive samples, and t is time. Concentrations at each time point were corrected for dilution after sampling based on the concentration and volume of water used to refill each microcosm. To account for the effects of water column processes on benthic fluxes, I multiplied head space volume by the slope change in concentration measured in blanks containing water without sediment and subtracted this from the measured flux. I multiplied hourly rates by the number of daylight and dark hours per day to estimate daily flux rates. I calculated ratios of dissolved inorganic nitrogen (the sum of nitrate + nitrite and ammonium, or DIN), SRP and Si release from the sediment using average daily rates.

I estimated the hourly rate of benthic gross primary production (GPP) rates by calculating the difference between the change in oxygen concentration measured in the light and the change in oxygen concentration in the dark ($GPP = \Delta DO_{light} - \Delta DO_{dark}$). Changes in DO in the dark are due to respiration and chemical oxidation alone while the change in the light would be due to primary production and respiration and chemical oxidation. Although this is a commonly used method for estimating GPP

(Howarth and Michaels, 2000), some error may be associated with this calculation because microbial respiration is likely to be higher in the light than in the dark (Roberts et al. *in press*) and both macrofaunal respiration and faunal stimulation of sediment oxygen consumption are influenced by diel changes in invertebrate behavior (Scott et al. 1976, Wenzhofer & Glud 2004, Tang & Kristensen 2007).

Invertebrate Respiration- At the termination of the experiment, I placed individuals in microcosms filled to 15 cm with sediments ashed at 500°C for 6 hours (*N. virens* n=2*, M. arenaria* n=3). I allowed organisms to acclimate for 13 hours during which time *N. virens* established and began ventilating burrows and *M. arenaria* burrowed and resumed suspension feeding. I measured the change in oxygen concentration over a 3 hour period in the dark according the flux method described above and estimated respiration as the change in oxygen divided by the wet weight of the organism (mmol O_2 g^{-1} h^{-1}). This estimate of respiration integrated both active ventilation and rest periods for *N. virens*.

Organism respiration is influenced by environmental conditions and by the nutritional state and level of activity of the organisms (Kristensen 1983b, 1983c, 1983a, 1989). By measuring respiration at the end of the experiment using experimental flux methods, I ensured that the nutritional state of the organisms and the effects of time of day, temperature and salinity on behaviors and physiology were similar for respiration fluxes and experimental fluxes. The measurement of respiration rates for organisms in sediments also provided a more realistic estimate of respiration than measurement in free water or in polyethylene tubes in which increased motor activity and decreased resistance to flow can cause as much as a 6 fold overestimation of metabolism (Kristensen 1989). Sediment oxygen consumption should have been negligible because the incubation time was too short for re-

establishment of microbes or for the reformation of reduced metabolites oxidized during ashing. However, macrofaunal metabolism would likely differ from experimental conditions due to the absence of soluble sulfides and higher oxygen tension in ashed sediments. Under anoxic conditions, *Nereis* species can increase fractional extraction of oxygen as oxygen tension declines (Kristensen 1983c) and can reduce metabolic requirements for oxygen by switching from aerobic respiration during active ventilation to anaerobic respiration during rest periods (Scott et al. 1976). In contrast, increasing ventilation to flush soluble sulfides from burrows would increase metabolism (Kristensen 1989). Bivalve respiration is less well studied.

Statistical analysis- For benthic fluxes, I used JMP software to perform a 1-way analysis of variance (ANOVA) followed by Tukey's post hoc multiple comparisons analysis for all nine treatments; treatment was defined by both the species (defaunated control (0), *N. virens, M. arenaria* or both species) and the density (0, 141, 282 or 564 individuals m^{-2}). Because the unbalanced design did not allow me to distinguish between the effects of species and density when all treatments were included in the model, I also performed a 2-way ANOVA for a subset of the data with species (*N. virens* or *M. arenaria*), density (141, 282, or 564 individuals m^{-2}), and the interaction between species and density as separate fixed effects. Porewater concentration measurements were repeated at multiple depths within each core. Therefore, I analyzed porewater data using mixed models in which I included depth as a fixed effect in addition to the fixed effects used in flux analyses and included core as a random effect. The random effect accounted for correlations between concentrations measured at different depths within a single core. Data that did not meet equal variance or normality assumptions were square root transformed and equal variance was verified using Bartell's test.

To determine whether *N. virens* and *M. arenaria* have different effects on porewater solute concentrations and benthic fluxes in treatments with both species versus single species treatments, I calculated the proportional deviation of the concentrations and fluxes measured in microcosms containing both species from the predicted concentrations and fluxes estimated based on single-species measurements (as in Emmerson & Raffaelli 2000). The proportional deviation is calculated as:

$$D_T = \frac{M_D - E_T}{E_T}$$

Where M_D is the measured concentration or flux for a given community density and E_T is the estimated concentration or flux calculated as:

$$E_T = C + \Sigma(E_i)d$$

where C is the concentration or flux in controls without macroinvertebrates, E_i is the concentration or flux attributable to each organism of each species, and d is the density of each species within the mixed species treatment. The change in concentration or flux attributable to each organism was calculated based on single species treatments with the same total number of organisms as the multiple species treatment:

$$E_i = (M_D - C)/D$$

where C is the measurement in microcosms in which organisms were absent and D is the total number of organisms.

I then tested for significance of the proportional deviation using a rank sum test comparing D to zero. A proportional deviation less than zero implies interference; a deviation greater then zero implies complementarity (Loreau & Hector 2001).

RESULTS.

Initial conditions- Microcosm sediments were initially dark, silty and moderately organic-rich near the surface and lighter grey, sandier and less organic-rich at depth (Table 2). Microalgae formed at the sediment surface, and deeper sediments darkened over the experimental period. Addition of labile OM on day 13 to simulate the effects of a macroalgal bloom increased surface OM by approximately 35% (Table 2). Although field concentrations of ammonium and soluble sulfides were relatively low when sediments were collected (early June), porewater ammonium and soluble-sulfide concentrations in microcosms doubled over the acclimation period, and ranged from approximately 330 μM (SE 51) to 833 μM (SE 87) ammonium and 300 μM (SE 101) to 1450 μM (SE 98) soluble-sulfide when organisms were added (Figure 3).

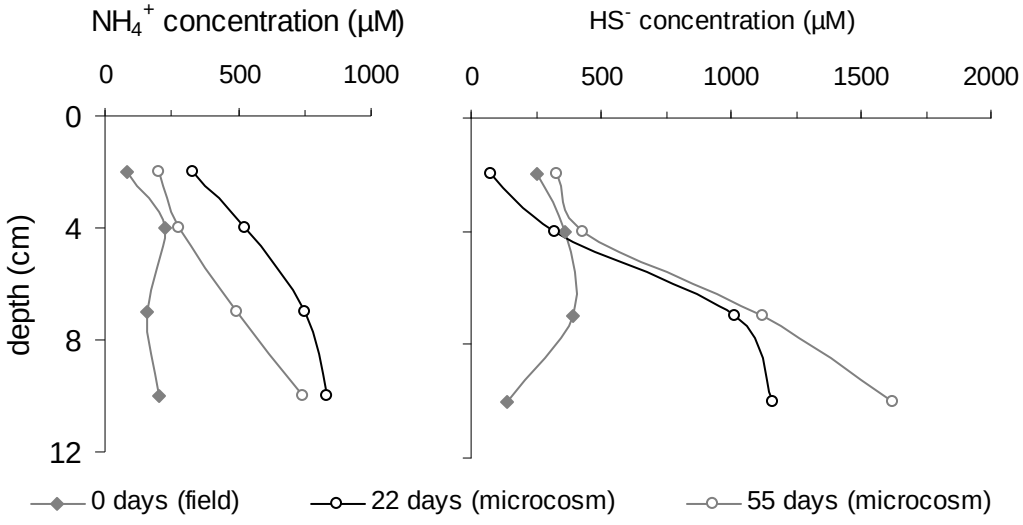

Figure 3. Porewater ammonium and soluble-sulfide concentrations versus depth. Values are given for profiles measured in the field (0 days) and for microcosms sampled at the time of organism addition (22 days) and at the end of the experiment (55 days).

Table 2. Sediment organic matter (OM) and porosity for sediments used to fill microcosms (0 days) and for microcosms without macroinvertebrates. Microcosms were sampled prior to organism addition (22 days) and at the end of the experiment (55 days). OM (0.6 g) was added to the surface of each microcosm on day 14.

Depth	Organic Matter (%LOI)									Porosity		
	0 d			22 d			55 d			55 d		
0 - 2 cm	1.4	(SE	0.03)	1.9	(SE	0.09)	2.1	(SE	0.08)	0.53	(SE	0.04)
2 - 5 cm	1.2	(SE	0.03)	1.1	(SE	0.09)	1.0	(SE	0.04)	0.39	(SE	0.01)
5 - 10 cm	0.86	(SE	0.07)	0.78	(SE	0.08)	0.71	(SE	0.06)	0.34	(SE	0.01)

General observations- Both *M. arenaria* and *N. virens* burrowed within a few hours after they were added to microcosms (22 d). However, during the first week following organism addition, *M. arenaria* periodically moved upward so that the apex of the shell was between a few cm below and a few mm above the sediment surface. *Nereis virens* constructed and began ventilating burrows within 24 hours but periodically emerged and laid on the sediment surface. A white film, probably elemental sulfur also formed in microcosms to which macroinvertebrates were added. This film began to disappear shortly before the emergence behavior ceased.

Mya arenaria typically aggregated near the center of the microcosm and were all recovered between 3 to 7 cm depth when microcosms were deconstructed. *Mya arenaria* did not visibly alter sediments. In contrast, *N. virens* appeared to avoid each other, building burrows that extended 8 to 12 cm into the sediment on opposite sides of the microcosms. Sediments within a few mm to 4 cm from the burrow wall were light brown, suggesting less iron monosulfide due to increased supply of oxidized compounds to the sediments, while sediments further from the burrow were a dark grey similar to that in control and *M. arenaria* treatments. Black patches of sediments pigmented by FeS also formed along the edge of the light brown sediment in some microcosms. All organisms were recovered alive at the termination of the experiment.

Porewater profiles- Concentrations of porewater ammonium and soluble sulfides in sediments without macroinvertebrates were high and increased with depth. Ammonium ranged from 199 μM (SE 50) at 2 cm below the surface to 700 μM (SE 88) at 10 cm depth, and soluble sulfides ranged from 243 μM (SE 30) to 1592 μM (SE 172). Recolonization decreased the concentrations of dissolved ammonium and soluble sulfide significantly relative to controls for all species-density combinations except for the lowest density *M. arenaria* treatment (Figure 4, Table 3).

Similar to controls, porewater ammonium and soluble-sulfide concentrations in microcosms containing *M. arenaria* increased steeply with depth. The lowest density of *M. arenaria* (141 individuals m^{-2}) decreased ammonium concentrations by approximately 40% over all depths (i.e. between 50 to 100 μM from 2 to 10 cm) and decreased soluble sulfide concentrations by 30 to 60% (80 to 400 μM) depending upon depth. *Nereis virens* had a similar effect near the surface (2 and 4 cm), but concentrations of ammonium and soluble sulfide were 70 to 90% less than controls at lower depths and concentrations did not increase significantly with depth.

Table 3. Results of Tukey's Test comparing porewater ammonium and soluble-sulfide concentrations for all species + density combinations. Treatments that do not share a common letter differ significantly.

Treatment	NH_4^+ Tukey's results					HS⁻ Tukey's results					
Control	A					A					
M. arenaria L		B				A	B				
M. arenaria M		B	C				B	C			
M. arenaria H		B	C				B	C	D		
N. virens L			C	D				C	D		
N. virens M			C	D					D	E	
N. virens H				D	E						F
Both M		B	C				B	C	D		
Both H				D	E					E	F

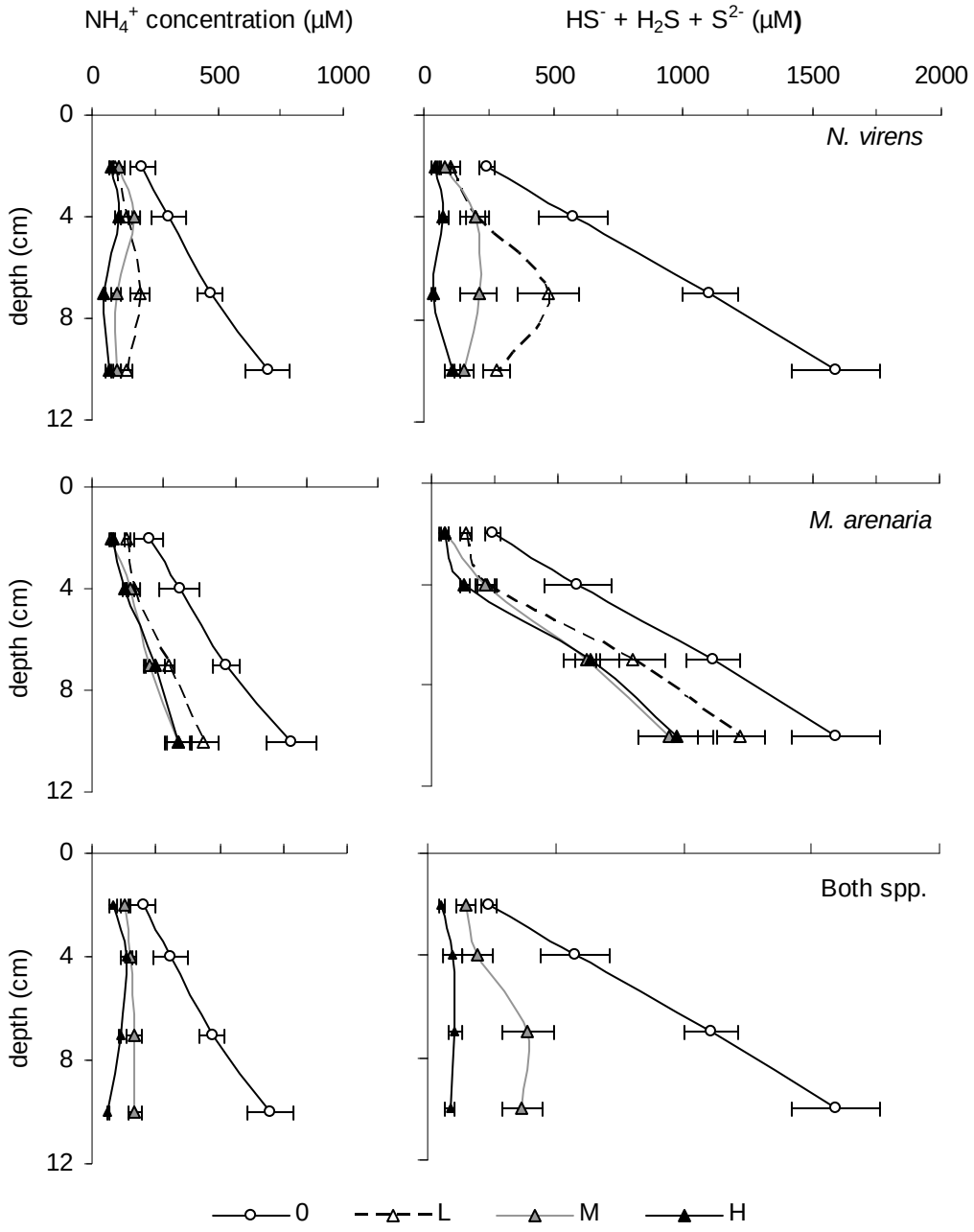

Figure 4. Vertical profiles of ammonium (left) and soluble sulfides (right) for day 55 (means ± SE, n=5). Profiles for controls without macroinvertebrates (0) are repeated in each panel for comparison with microcosms containing *M. arenaria* (top), *N. virens* (middle), or both species together (bottom). Separate profiles are shown for each organism density (L = 141, M = 282, H = 564 individuals m^{-2}).

Dissolved ammonium and soluble-sulfide concentrations decreased with increasing invertebrate density. However, this additional change was 2- to 8- times less than the decrease in concentrations between controls and the lowest density treatments. Dissolved ammonium and soluble-sulfide concentrations in low-density *M. arenaria* treatments were 40 to 90 μM higher than concentrations in medium and high-density treatments. For microcosms containing *N. virens*, porewater ammonium concentrations were 15 to 150 μM less and soluble-sulfide concentrations were 60 to 450 μM less in the high-density treatments than in the low-density treatments. Post hoc tukey tests indicated that profiles differed significantly between the low and high densities (Table 3).

A mixed model excluding controls and testing the effects of density (141, 282 and 564 individuals m^{-2}), species (*M. arenaria* or *N. virens*) and depth (2, 4, 7 and 10 cm) confirmed that porewater ammonium and soluble-sulfide concentrations depended on density and that *N. virens* had a stronger effect than *M. arenaria.* Significant interaction terms also indicated that porewater profile shape and the strength of the density response depended on which species was present (Table 4).

Table 4. Results of 3-way ANOVA analyses of the effects of species (*N. virens, M. arenaria*), density (141, 282, 564 individuals m^{-2}) and depth (2, 4, 7, 10 cm) on porewater ammonium and soluble sulfide concentrations.

	NH_4^+		TRS	
Source	F	P	F	P
density	13.6	0.0001*	23.3	<.0001*
species composition	64.0	<0.0001*	72.7	<.0001*
Depth	19.1	<.0001*	55.5	<.0001*
spp comp*density	3.2	0.0598	3.7	0.0276*
spp comp*Depth	25.4	<.0001*	15.5	<.0001*
density*Depth	1.9	0.0887	1.0	0.4545
density*spp comp*Depth	2.3	0.0397*	2.3	0.0426*

* Indicates significant results (p*<0.05)

Similar to microcosms with *N. virens* alone, dissolved ammonium and soluble-sulfide concentrations were roughly the same at all depths when both *N. virens* and *M. arenaria* were present. Concentrations measured in medium-density two-species treatments (141 *N. virens* + 141 *M. arenaria* m^{-2}) were roughly equal to concentrations that would be expected based on medium-density single-species treatments. In high-density two-species treatments, measured and expected concentrations were similar near the surface (2 and 4 cm) but concentrations deeper in the sediment were much less than expected (Figure 5). When concentrations in high density treatments were pooled over all depths, the deviation of measured from expected concentrations was significant for soluble sulfides and marginally significant for ammonium (Table 5).

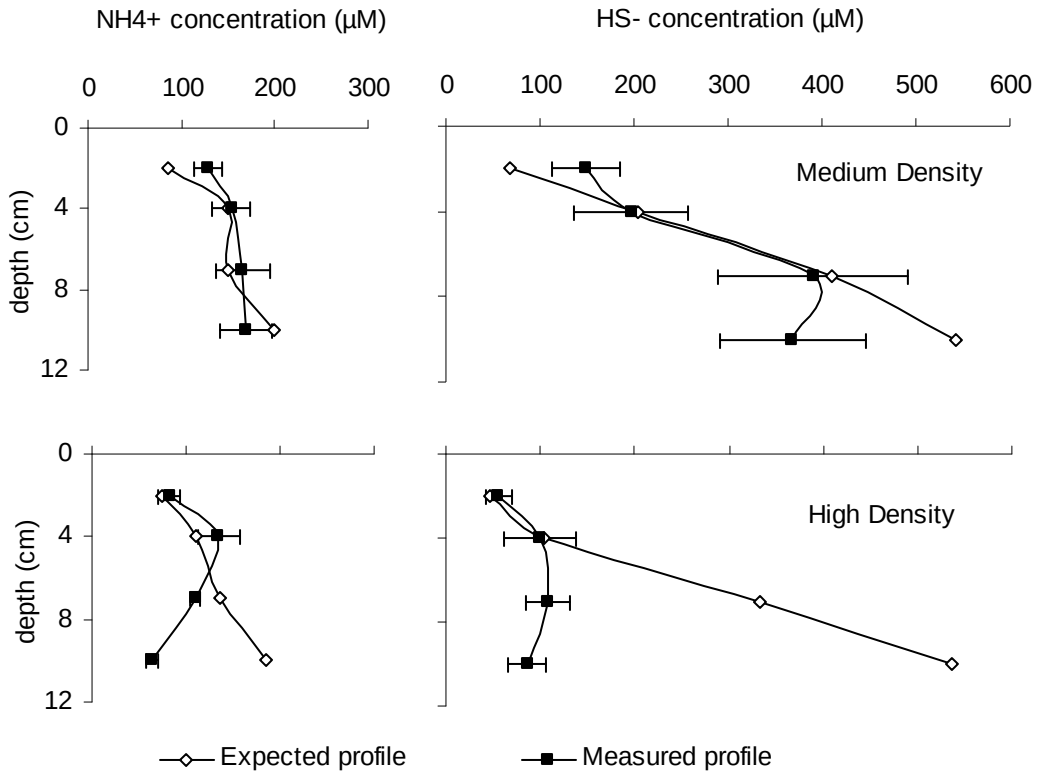

Figure 5. Porewater ammonium and soluble-sulfide concentrations measured in two-species treatments versus concentrations expected based on single-species treatments.

Table 5. Comparison of porewater ammonium and soluble-sulfide concentrations pooled over all depths in two-species treatments (M_T) versus concentrations expected based on single-species treatments (E_T).

	NH_4^+ (umol)		HS^- (umol)	
	medium density	high density	medium density	high density
MD	158 (SE 9.0)	106 (SE2.6)	296 (SE 58)	95 (SE 15)
ET	149	129	314	264
DT	-0.06 (SE 0.07)	0.18 (SE 0.07)	0.14 (SE 0.21)	1.1 (SE 0.26)
P > t	0.41	0.06	0.5	0.03*

*Indicates that the proportional deviation ($D_T=(E_T-M_D)/E_T$) differs significantly from zero.

Benthic oxygen consumption- Animals clearly increased benthic oxygen consumption relative to controls, but there were no obvious differences between species (Figure 6). Oxygen consumption rates in all of the highest density treatments were approximately twice the rates in controls (1.6 mmol O_2 m^{-2} h^{-1} (SE 0.15). The positive relationship between density and oxygen consumption was confirmed by a 2-WAY ANOVA comparing *M. arenaria* and *N. virens* at densities from 121 to 564 individuals m^{-2} (ANOVA, p=0.0008). Oxygen consumption rates in two-species treatments did not deviate from rates expected based on single species treatments (Table 6).

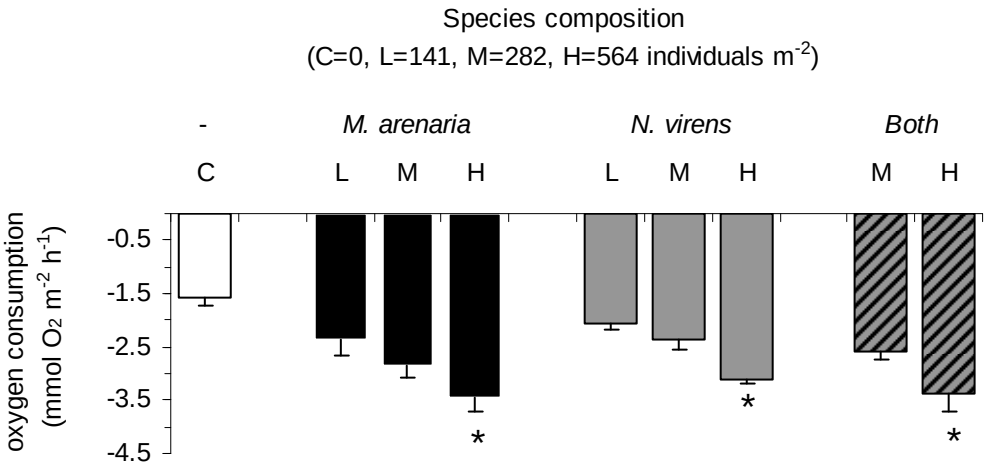

Figure 6. Effects of species composition and density on benthic oxygen demand (mean – SE). * Indicates significant differences from controls.

Table 6. Dark oxygen consumption and benthic GPP measured in treatments with both *N. virens* and *M. arenaria* (M_T) versus expected fluxes (E_T).

	O_2 (mmol)		GPP (mmol)	
	medium density	high density	medium density	high density
M_D	-2.6 (SE 0.2)	-3.5 (SE 0.4)	1.6 (SE 0.2)	1.8 (SE 0.2)
E_T	-2.6	-3.2	1.8	2.3
D_T	0.001 (SE 0.07)	0.18 (SE 0.23)	-0.11 (SE 0.21)	-0.43 (SE 0.17)
p-value	0.88	0.63	0.63	0.03*

* Indicates that the proportional deviation ($D_T=(E_T-M_D)/E_T$) differs significantly from zero.

Benthic gross primary production (GPP)- In contrast to oxygen consumption, benthic GPP depended upon which species was added to microcosms (p=0.0003) but did not relate generally to organism density (ANOVA, p=0.495). *Mya arenaria* enhanced production by up to 120% relative to basal rates of 1.3 mmol O_2 m^{-2} h^{-1} (SE 0.2) in controls while *N. virens* had no clear effects on GPP (Figure 7). Benthic GPP in microcosms containing both species was approximately 10 to 30% lower than would be expected based on single species treatments. Similar to porewater profiles, the proportional deviation of observed from expected values could only be confirmed statistically for higher densities (p=0.03; Table 6).

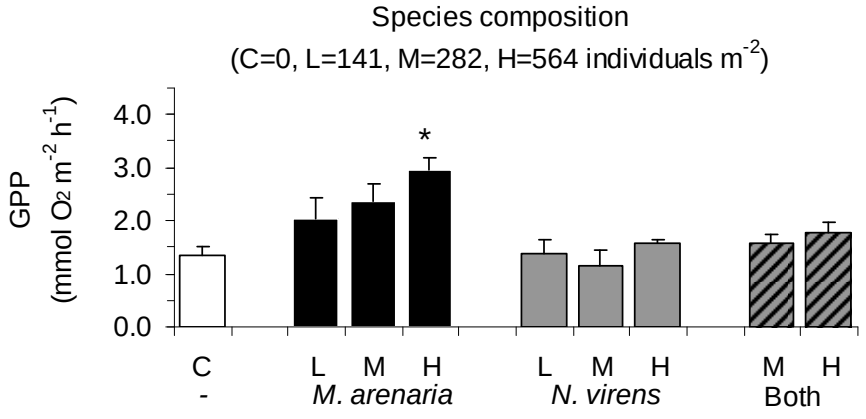

Figure 7. Effects of species composition and density on benthic GPP.
* Indicates significant differences from the control.

Benthic nutrient flux in the dark- Flux rates depended both upon which species was present and its density. However, in contrast to porewater profiles, the rate of nutrient (ammonium, SRP, nitrate and Si) flux from sediments without macroinvertebrates generally did not differ significantly from flux rates in microcosms containing macroinvertebrates (Figure 8).

Under dark conditions, ammonium was released from sediments without macroinvertebrates at a rate of 173 µmol m^{-2} d^{-1} (SE 13). Whether macroinvertebrates enhanced or depressed flux rates relative to controls depended upon density. The lowest density of *N. virens* depressed fluxes by nearly 40% relative to controls, but fluxes increased by approximately 70% (77 µmol m^{-2} h^{-1} (SE) between the lowest and highest densities. Fluxes in *M. arenaria* treatments were significantly higher (20 to 30%) than in *N. virens* treatments (Table 7), and the increase in flux rates between the lowest and highest densities of *M. arenaria* (134 µmol m^{-2} h^{-1} (SE)) was nearly twice that for *N. virens*. The highest density of *M. arenaria* enhanced fluxes significantly relative to controls (Tukey *p=0.05).

Nitrate was generally released from sediments under dark conditions and flux rates ranged from -12 (SE 34) to 41 (SE 7) µmol m^{-2} h^{-1}. Increasing *M. arenaria* density had a weak negative effect on nitrate release. However, neither density nor species composition significantly affected dark flux rates (Figure 8, Table 7).

Table 7. Results of 2-WAY ANOVA for effects of density and species (*M. arenaria* and *N. virens)* on dissolved oxygen consumption and nutrient flux in the dark.

	DO		NH_4^+		NO_3^-		Si		PO_4^{3-}	
Source	F	P	F	P	F	P	F	P	F	P
species	3.5	0.08	10.7	0.004*	2.0	0.17	0.57	0.46	12	.003*
Density	9.1	0.001*	16.8	<.0001*	0.7	0.53	0.97	0.40	2.1	0.15
species*Density	0.1	0.94	0.9	0.40	0.4	0.66	0.01	0.99	1.1	0.36

* Indicates significant results.

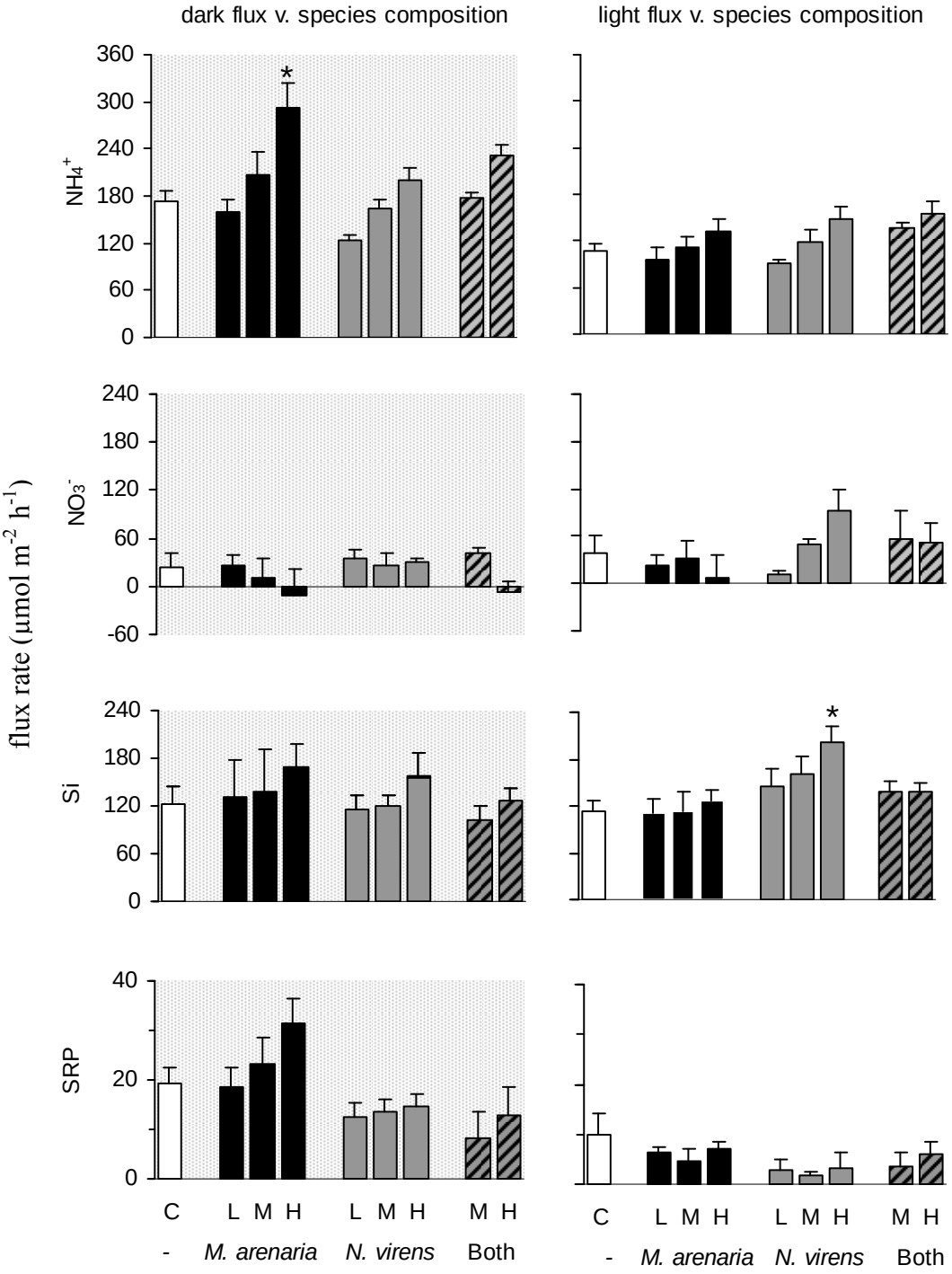

Figure 8. Flux of ammonium, nitrate, Si and SRP across the sediment water interface in microcosms under dark (left) and light (right) conditions. The figure shows mean flux rates + SE (n=4) measured on day 48 for multiple densities of each species (0=zero, L=141, M=282, H=564 individuals m^{-2}). * indicates significant differences from the control.

Si flux in the dark ranged from 103 (SE 17) to 175 (SE 29). There was a weak positive relationship between density and flux. However, fluxes were highly variable and there were no significant differences between treatments (Figure 8, Table 7).

SRP was released from control microcosms at a rate of 193 μmol m^{-2} h^{-1} (SE 3) in the dark (Figure 8). There was a weak (20%) increase in SRP fluxes between the lowest and highest densities of *N. virens* but SRP fluxes were lower in all *N. virens* treatments than in controls. Similar to ammonium, *M. arenaria* enhanced SRP fluxes in the dark relative to controls and rates ranged from 5% below control rates in the lowest density treatment to 60% above control rates in the highest density treatments. However, macroinvertebrate treatments and controls did not differ significantly (Tukey, *p=0.05). A two-way ANOVA excluding controls confirmed that there were significant differences between species, but the effects of density were not significant (Table 7).

Rates of ammonium, Si and SRP flux measured in two-species treatments were similar to flux rates in *N. virens* treatments and were generally lower than rates that would be expected based single-species treatments. However, the deviation of measured from expected rates could not be confirmed statistically (Table 8).

Table 8. Comparison of measured (M_D) versus expected (E_T) nutrient fluxes in the dark for medium (M) and high (H) density two-species treatments.

	NH_4^+ (umol)		NO_3^- (umol)		Si (umol)		PO_4^{3-} (umol)	
	M	H	M	H	M	H	M	H
M_D	177	232	41	-6	103	127	8.3	13
	(SE 9)	(SE 15)	(SE 7.3)	(SE 11)	(SE 17)	(SE 15)	(SE 5.1)	(SE 6)
E_T	185	246	19	9	132	165	19	23
D_T	-0.05	-0.12	1.2	-3.4	-0.20	-0.44	-0.55	-0.89
	(SE 0.1)	(SE 0.1)	(SE 0.4)	(SE 2.6)	(SE 0.5)	(SE 0.2)	(SE 0.3)	(SE 0.5)
p > |t|	0.63	0.44	0.13	0.31	0.25	0.13	0.25	0.31

Fluxes in the light- To determine how benthic primary producers and diel changes in invertebrate behavior could affect nutrient release, I also measured nutrient flux rates in the light (Figure 7). Ammonium and SRP fluxes were 50 to 90% lower in the light than in the dark and ranged from 91 (SE 5) to 155 (SE 16) μmol m^{-2} h^{-1} for ammonium and 3.4 (SE 2.8) to 10.0 (SE 4.3) μmol m^{-2} h^{-1} for SRP. In contrast to fluxes in the dark, increasing *M. arenaria* density did not enhance light ammonium and SRP flux rates significantly relative to controls and there were no obvious differences between *M. arenaria* and *N. virens* treatments (Table 9). Fluxes of nitrate and Si in the light increased with *N. virens* density. Fluxes of nitrate and silicate were respectively 140% and 90% higher in treatments with the highest density of *N. virens* than in controls. In treatments containing *M. arenaria* silicate fluxes were slightly lower in the light than in the dark and nitrate fluxes were slightly higher in the light. A two way ANOVA confirmed that both nitrate and Si fluxes were significantly higher when *N. virens* was present than when *M. arenaria* was present (Table 9).

Fluxes of ammonium, nitrate Si and SRP flux in the light were similar to flux rates in *N. virens* treatments. However, in contrast to dark fluxes, rates in two-species treatments were generally greater than expected. However, these deviations could not be confirmed statistically (Table 10).

Table 9. Results of 2-WAY ANOVA for effects of density and species (*M. arenaria* and *N. virens)* on dissolved oxygen consumption and nutrient flux in the light.

	GPP		NH_4^+		NO_3^-		Si		PO_4^{3-}	
Source	F	P	F	P	F	P	F	P	F	P
species	20	0.0002*	0.0	0.96	4.8	0.04*	12	0.003*	2.3	0.14
density	2.2	0.13	3.0	0.07	0.7	0.51	2.2	0.14	0.2	0.79
species*Density	0.86	0.44	0.1	0.91	3.0	0.07	0.6	0.61	0.0	0.95

* Indicates significant results ($p^*<0.05$).

Table 10. Comparison of measured (M_D) versus expected (E_T) nutrient fluxes in the light for medium (M) and high (H) density treatments with both *N. virens* and *M. arenaria*.

	NH_4^+ (umol)		NO_3^- (umol)		Si (umol)		PO_4^{3-} (umol)	
	M	H	M	H	M	H	M	H
M_D	136 (SE 7)	155 (SE 16)	56 (SE 37)	53 (SE 23)	137 (SE 15)	134 (SE 11)	3.4 (SE 2.8)	6.2 (SE 2.4)
E_T	114	128	41	51	140	168	3.5	5.2
D_T	0.19 (SE 0.07)	0.42 (SE 0.25)	0.37 (SE 1.0)	0.09 (SE 0.9)	-0.02 (SE 0.12)	-0.31 (SE 0.17)	-0.02 (SE 0.91)	0.38 (SE 0.92)
$p > \|t\|$	0.13	0.19	0.88	0.81	1	0.19	1	1

Daily flux rates- Daily DIN flux rates, estimated for a 14 h light and 10 h dark cycle, increased as a function of increasing invertebrate density (ANOVA, p=0.003) but was not significantly affected by species composition (ANOVA, p=0.69; Table 11). The rate of DIN flux was 4.0 (SE 1.9) mmol m^{-2} d^{-1} in controls and ranged from approximately 25% below controls in the lowest density treatments to 30% above controls in the highest density treatments. SRP was released from control sediments at a rate of 0.33 mmol m^{-2} d^{-1} and increased with density from rates 18% below the control to rates 24% above the control for *M. arenaria* and from rates 51% below the control to rates 41% above the control for *N. virens*. Si fluxes also increased with density and were enhanced by as much as 65% by *N. virens* and by approximately 30% by *M. arenaria* relative to basal rates of 2.7 (SE 0.2) µmol m^{-2} d^{-1} in controls.

The daily ratio of DIN to SRP release was approximately 12:1 in sediments without macroinvertebrates. The ratio of DIN:SRP more than doubled between controls and the highest density *N. virens* treatment but *M. arenaria* had little effect on this ratio. Neither species had a strong effect on the ratio of DIN to Si release from sediments (Table 11).

Table 11. Daily nutrient flux estimated assuming 10 hours dark and 14 hours light. Nutrient release ratios are also given for daily flux rates and for fluxes in the dark.

Treatment		daily nutrient flux (mmol m^{-2} d^{-1})			daily flux ratio		dark flux ratio	
		DIN	SRP	Si	N:P	N:Si	N:P	N:Si
Control	0	4.0 (1.9)	0.33 (0.1)	2.7 (0.2)	12	1.5	10	1.6
M. arenaria	L	3.5 (0.5)	0.27 (0.1)	2.9 (0.6)	13	1.2	10	1.4
	M	4.2 (0.9)	0.30 (0.1)	3.1 (0.8)	14	1.4	9	1.5
	H	4.8 (0.7)	0.41 (0.04)	3.5 (0.4)	12	1.4	9	1.6
N. virens	L	3.0 (0.2)	0.16 (0.1)	3.2 (0.4)	18	0.9	13	1.4
	M	4.3 (0.3)	0.17 (0.1)	3.5 (0.3)	25	1.2	14	1.6
	H	5.3 (0.6)	0.19 (0.1)	4.5 (0.5)	28	1.2	16	1.5
Both spp.	M	4.9 (0.6)	0.13 (0.1)	2.9 (0.2)	37	1.7	26	2.1
	H	5.2 (0.7)	0.21 (0.1)	3.2 (0.3)	24	1.6	18	1.8

Macroinvertebrate respiration and excretion- Macroinvertebrate respiration rates measured at the termination of the experiment were 0.0014 mmol O_2 g $tissue^{-1}$ h^{-1} (SE 0.0003) for *N. virens* and 0.0011 mmol O_2 g $tissue^{-1}$ h^{-1} (SE 0.0001) for *M. arenaria*. These rates were within the range of published literature values for both *N. virens* (0.0008 to 0.0063 mmol g^{-1} h^{-1}; Theede et al. 1973, Kristensen 1983b, 1983c, 1983a, 1989, Nielson 1995, Christensen et al. 2000) and *M. arenaria* (0.0003 to 0.001 mmol g^{-1} h^{-1}; Kristensen 1987, MacDonald et al. 1998). The contributions of macrofaunal respiration to benthic oxygen demand in high density treatments were 1.5 and 1.3 mmol m^{-2} h^{-1} for *N. virens* and *M. arenaria* respectively (Table 12).

The ranges of published excretion rates were 0.11 to 0.69 µmol NH_4^+ g $tissue^{-1}$ h^{-1} for *N. virens* (Henriksen et al. 1983, Kristensen 1985, Christensen et al. 2000) and 0.02 to 0.14 µmol NH_4^+ g $tissue^{-1}$ h^{-1} for *M. arenaria* (Emerson 1969, MacDonald et al. 1998). I estimated the contribution of macrofaunal excretion to benthic ammonium fluxes based on this range of excretion rates. However, because *N. virens* excretion can be up to four times higher during active ventilation than during rest periods, I

adjusted excretion rates according to Emmerson (1985) to account for both active ventilation and rest periods. This yielded a range of excretion rates from 0.11 to 0.35 µmol NH_4^+ g^{-1} tissue h^{-1}. Converted to ammonium production per m^{-2}, rates of ammonium excretion for the high-density treatments could have ranged from 109 to 343 µmol NH_4^+ m^{-2} h^{-1} for *N. virens* and from 25 to 160 µmol NH_4^+ m^{-2} h^{-1} for *M. arenaria* (Table 12).

Estimated SRP excretion for *N. virens* was 0.0006 µmol g $tissue^{-1}$ h^{-1} (Henriksen et al., 1983). Based on this rate, excretion was approximately 6 µmol m^{-2} h^{-1} for the high-density treatment. Published phosphate excretion rates were not available for *M. arenaria*.

Table 12. Macrofaunal biomass, respiration and excretion expressed as a rate per fresh tissue weight (g) and as a rate per m^2 for the total population at each density. Respiration rates were measured at the termination of the experiment. Excretion rates were estimated based on a range of published values.

	Density	Biomass	Respiration	Excretion	
	individ. m^{-2}	g (wet)	(mmol O_2 m^{-2} h^{-1})	(µmol NH_4^+ m^{-2} h^{-1})	(µmol PO_4^{3-} m^{-2} h^{-1})
M. arenaria		2.2 g $individual^{-1}$	0.0011 mmol O_2 g^{-1} h^{-1}	0.02 - 0.14 µmol NH_4^+ g^{-1} h^{-1}	-
	141	314	-0.35	6 - 40	-
	282	661	-0.72	13 - 85	-
	564	1250	-1.3	25 - 160	-
N. virens		1.9 g $individual^{-1}$	0.0013 mmol O_2 g^{-1} h^{-1}	0.11 - 0.35 µmol NH_4^+ g^{-1} h^{-1}	0.0006 µmol PO_4^{3-} g^{-1} h^{-1}
	141	264	-0.37	28 - 88	0.16
	282	500	-0.77	57 - 179	0.30
	564	1007	-1.5	109 - 343	0.60

DISCUSSION

Porewater ammonium and soluble sulfide profiles- The concentrations of porewater ammonium and soluble sulfides in microcosms without macroinvertebrates were high and within the range measured in shallow estuaries with very organic-rich sediments during the late summer when remineralization rates are high and invertebrate abundance is low (Table 13). Porewater ammonium and soluble-sulfide concentrations in recolonized sediments were also within the range of concentrations commonly observed in the field but were 40 to 90% lower than in defaunated sediments (Table 13). This indicates that the presence of deep burrowing invertebrates was a dominant factor controlling concentrations of these metabolites in sediments.

Table 13. Range of ammonium and soluble-sulfide concentrations in porewater profiles for low (L) and high (H) density treatments compared to the range of concentrations measured in the field in low and high OM sediments. Concentration ranges matches depth ranges or are pooled over all depths.

Species (abundance)	depth (cm)	%OM %C	NH_4^+ (µM)	HS^- (µM)	Site	Source
no macrofauna	2 - 10	1.3 %OM	200 - 700	210-1600	microcosm	Figure 4
M. arenaria (L)	2 – 10	1.2 %OM	120– 390	140-1200	microcosm	Figure 4
(H)	2 - 10		75 - 300	51 - 960		
N. virens (L)	2 – 10	1.3 %OM	89 – 190	100 – 480	microcosm	Figure 4
(H)	2 - 10		48 - 110	38 - 110		
no macrofauna	1 - 15	1– 4 %OM	50 - 600	50 - 1500	WFH, MA inner harbor	Giblin unpubl.
L	2 - 10	1.3%OM	30 - 120	60 - 250	WFH, MA outer harbor	Figure 3.
no macrofauna	0-15	3%C	0 – 3000	0 – 4500	Boston Harbor, MA	Giblin et al. 1997
H	0-15	0.4%C	< 500	< 100		
no macrofauna	0 - 16	3-5 %C	-	1000 - 3000	Cape Bight, NC	Chanton and Martens 1987
Nereis (L)	Pooled	2%C	-	81 (SE 41)	Kentridge Nor	Miron and Kristensen 2003
(H)	(0-15)	1%C	-	14 (SE 2)		
Nereis, Mercenaria	0 - 17	1 – 2 %OM	100 - 400	-	Barnstable Harbor, MA	Aller and Yingst 1978
Nereis, Macoma	0 – 10	1.3 %OM	0 – 700	-	Kysing fjord	Henriksen et al. 1983

The observation that ammonium and soluble-sulfide concentrations were significantly lower in microcosms with *N. virens* than in the controls and that the concentrations of these chemical species did not increase with depth is indicative of greater rates of transport and oxidation at lower depths where remineralization rates are lower (Aller 1982, Kristensen & Hansen 1999, Berg et al. 2003). Similar displacement of porewater profiles has been observed in other studies for high densities (>600 m^{-2}) of *N. virens* (Christensen et al. 2000) and other *Nereid* species (eg Banta et al. 1999, Kristensen & Hansen 1999). Results from my study suggest that, for sediments with relatively low organic matter (2% LOI), the presence of very low densities of organisms will strongly affect porewater profiles but that further variation in porewater chemistry will be modest over the density range typical for this species (150 to 1400 individuals m^{-2}).

The observed relationship between *N. virens* density and concentrations of ammonium in sediment porewater is generally consistent with results from Aller's (1980) transport-reaction model for organisms with a similar burrow size (0.5 cm) (Figure 9). However, the change in concentration due to increasing abundance appeared to plateau at a lower density in this experiment (<141 individuals m^{-2}) than in Aller's model for which concentrations leveled off somewhere between 200 to 500 individuals. Because porewater solute concentrations depend on the balance between solute production and transport, less ventilation would be required to flush the majority of porewater ammonium from the sediments if remineralization rates in my microcosms were lower than modeled rates. Although remineralization rates for microcosms were unknown, that porewater ammonium concentrations in defaunated microcosms were lower than in the model suggests that lower remineralization was lower. This could account, in part, for the lower threshold for density dependence.

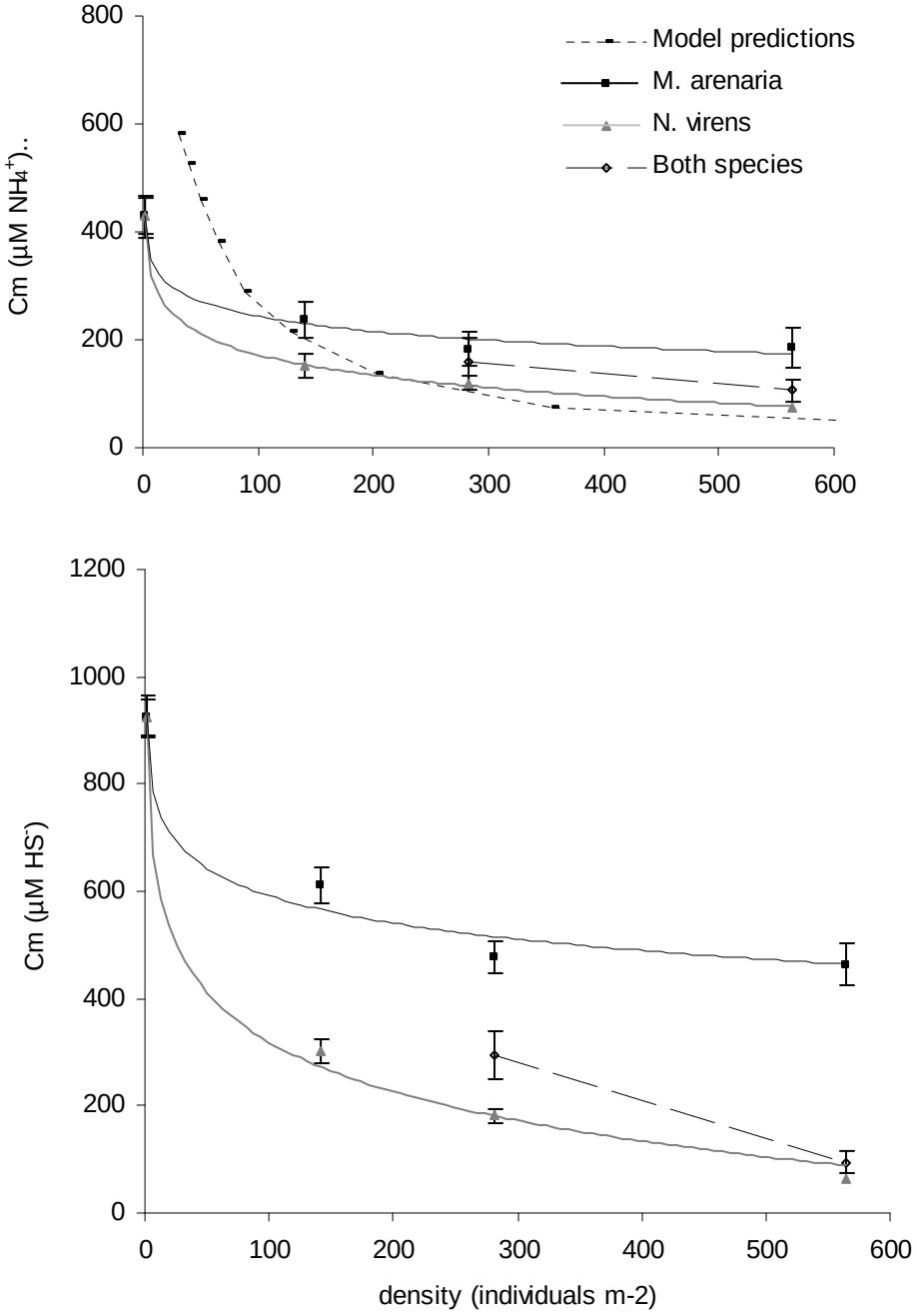

Figure 9. Effect of increasing *N. virens* and *M. arenaria* density on dissolved ammonium and soluble-sulfide concentrations pooled over all depths. The concentrations predicted by Aller (1980) for a polychaete with a similar burrow size to *N. virens* are also plotted for comparison.

Behavioral responses to the concentration of toxic metabolites in sediment porewater could also have lowered the threshold for density-dependence. It has been suggested that macroinvertebrates aggregate in high densities during recolonization in order to reduce individual irrigation requirements (Rhoads 1974, Aller 1982). Some species of polychaetes increase ventilation when concentrations of toxic metabolites are high (Woodin and Marinelli, 1991) and Miron and Kristensen (1993a) found that *N. virens* may exhibit this behavior at soluble-sulfide concentrations exceeding 100 μM. Total ventilation could have been similar for all populations regardless of density if individual *N. virens* increased ventilation at low densities in order to keep soluble sulfides in the burrow low. This could explain why all *N. virens* densities maintained soluble-sulfide concentrations around 100 μM (Figure 9).

As expected based on its shallower burrow and weaker effects on transport and oxidation, *M. arenaria* had much less effect on porewater ammonium and soluble-sulfide concentrations at lower depths. However, it was surprising to see that *M. arenaria* lowered concentrations to a similar degree as *N. virens* near the sediment surface. Studies measuring the effects of bivalves on porewater are limited. With the exception of a few studies in which clams lowered porewater ammonium concentrations slightly (Marinelli & Williams 2003), past work has generally focused on mussels, which occupy the sediment surface and can increase porewater ammonium and SRP concentrations through excretion (Reusch et al. 1994, Reusch 1998, Peterson & Heck 2001). Infaunal bivalves such as *M. arenaria* would be expected to have an effect more similar to burrowing polychaetes because diffusion of oxygen through a gape in the base of the siphon and influx of water to the burrow space during extension and retraction of the siphon could introduce oxygen to the deeper sediments (Henriksen et al. 1983, Forster & Zettler 2004). Previous work has shown that *M. arenaria* can decrease soluble-sulfide concentrations in porewater

surrounding the siphon (Hansen et al. 1996) and stimulate nitrification though to a lesser degree than *N. virens* (Henriksen et al. 1983, Pelegri & Blackburn 1995).

Also contrary to my expectation, *M. arenaria* reached a maximum effect at a lower density than *N. virens,* despite its weaker effects on porewater (Figure 7). The tendency of *M. arenaria* to aggregate near the center of the core could have reduced the effect of each burrow by decreasing the distance between burrows. This would cause overlap in the volume of ventilated sediments, lowering the supply of reduced metabolites compared to what would be expected if the M. arenaria were distributed evenly in the core. Though I did not quantify the effects of density on the distance between burrows, this observation agrees with past work that has shown that very small-scale variation in aggregation patterns can have significant effects on processes due to short (scale of a few cm) diffusional path lengths (Marinelli 1992, Aller & Aller 1998, Marinelli & Williams 2003).

In contrast to single-species treatments, in which density had little effect on the concentrations of ammonium and soluble sulfides in porewater, concentrations of porewater solutes decreased significantly between medium and high densities for two-species treatments (Table 3, Figure 9). This suggests that niche complimentarity reduced interference at high densities. The observation that solute concentrations measured in high-density, two-species treatments were similar to expected concentrations in the shallower depths occupied by both species but deviated strongly from expected concentrations below *M. arenaria's* burrowing depth suggests that niche complimentarity was due to decreased overlap in burrow space. Although the effects of niche complimentarity are expected to increase with density due to increased intraspecific interference, it is surprising that the number of species did not affect porewater chemistry significantly at medium densities given that the relatively small

changes in concentrations between low and medium-density treatments suggest that interference was high even at low densities.

At all organism densities used, the porewater soluble-sulfide concentrations in the surface sediments were decreased to a sufficiently low level to make sediments habitable for other organisms (Pearson 1978). However, the high ammonium and soluble-sulfide concentrations below 7 cm in *M. arenaria* microcosms (> 600 μM) suggest that this species would be less effective than *N. virens* in facilitating the survival of deeper-dwelling organisms. A simple comparison of the percentage area in which each species is present versus the area in which each species is absent might yield some insight into the effects of these species over broader scales.

The low threshold for density dependence and high within-treatment variability could make it difficult to predict how variation in invertebrate density might influence porewater ammonium and soluble-sulfide concentrations in the field. However, relatively small changes in porewater ammonium and soluble sulfides, such as those observed in my study, could determine community succession by significantly altering establishment of larval recruits (Cuomo 1985, Woodin et al. 1998), competitive interactions that may lead to the exclusion of a particular species (Miron & Kristensen 1993b), and behaviors that may affect susceptibility of organisms to predation (Pearson 1978). In addition, high soluble-sulfide concentrations (> 100 μM) can severely inhibit nitrification (Gould & McCready 1982, Jensen & Cox 1992, Joye & Hollibaugh 1995) and denitrification (Senga et al. 2006) while at the same time enhancing dissimilatory nitrate reduction to ammonium (Brunet & GarciaGil 1996, Burgin & Hamilton 2007). This suggests that both biological structure and the balance between nitrogen recycling and nitrogen removal from the system might shift at intermediate densities for each of these species.

Benthic oxygen demand and macrofaunal respiration- The observed increase in benthic oxygen demand in recolonized sediments was likely due to macrofaunal respiration and faunal stimulation of sediment oxygen demand (SOD), which typically includes some aerobic respiration but is driven primarily by re-oxidation of reduced metabolites in near shore sediments (Howarth 1984). Specific respiration rates were approximately 0.001 (SE 0.0001) mmol g^{-1} h^{-1} for both *N. virens* and *M. arenaria* and accounted for up to 50% of benthic oxygen demand in experimental microcosms. Macrofaunal respiration accounted more than 100% of the stimulation of benthic oxygen demand by *N.* virens and up to 70 % of benthic oxygen demand stimulated by *M. arenaria*. The remainder of the flux enhancement, which could be attributed to change in SOD, ranged from 0.42 to 0.50 mmol m^{-2} h^{-1} for *M. arenaria* and from -0.02 to 0.07 mmol m^{-2} h^{-1} for *N. virens* (Figure 9). Behavioral and physiological responses of macroinvertebrates to soluble-sulfides in experimental microcosms could have created some error in these estimates by altering macrofaunal metabolism (Kristensen 1983b, 1989). However, the finding that macrofaunal respiration was the dominant mechanism controlling faunal effects on benthic oxygen demand is consistent with the observations that the relationship between benthic oxygen demand and density was roughly additive and that species composition had little effect on benthic oxygen demand despite strong differences in ventilation behavior.

The effects of *M. arenaria* on benthic oxygen demand were similar to effects observed in another study comparing *N. virens* and *M. arenaria* in which the total organism biomass was comparable to the biomass of high-density treatments in my study (Michaud et al. 2005). However, in contrast to my results, Michaud et al. (2005) found that *N. virens* had a significantly (45%) greater effect on benthic oxygen demand than *M. arenaria*. Also in contrast to this study, other studies involving *N. virens* found that macrofaunal respiration accounted for less than 30% of faunal

effects on benthic oxygen demand (Andersen & Kristensen 1988, Kristensen 1993, Christensen et al. 2000). However, in sediments with relatively low organic content, similar to my study, respiration can dominate faunal effects on sediments and deposit feeders can depress SOD due to competition with microbes for organic matter (Kristensen et al. 1992). Competition for limited sediment OM could explain the minor decreases in SOD in *N. virens* treatments. *M. arenaria* likely stimulated SOD despite the relatively low sediment OM because it feeds on OM in the water column and enhances OM deposition to sediments rather than competing with microbes.

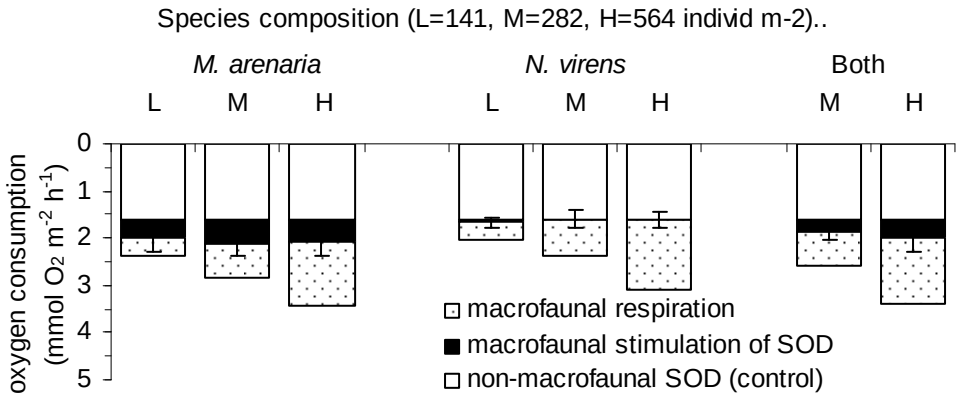

Figure 9. Effects of *M. arenaria* and *N. virens* density on benthic oxygen demand. Benthic oxygen demand is partitioned into 3 components: SOD in controls without macroinvertebrates, macrofaunal respiration and macrofaunal stimulation of SOD. SE's (n=4) shown for macrofaunal stimulation of SOD do not account for error in respiration estimates.

Laboratory artifacts associated with sediment manipulation (Porter et al., 2006) could also contribute to differences between studies. Reduced compounds produced by microbial metabolism tend to accumulate in microcosms with homogenized sediments during acclimation. Immediately following organism addition, SOD can increase dramatically due to rapid flushing of reduced metabolites to the surface and oxidation of solid reduced compounds along the burrow wall. Rates typically decline after 1 to 2 weeks (Hansen & Kristensen 1997, Bartoli et al. 2000). This porewater

flushing most likely did not affect fluxes in this study because the initial build-up of reduced metabolites due to sediment disturbance was likely minimized by sediment stratification and fluxes were measured 4 weeks after recolonization. The formation of white elemental sulfur at the sediment surface following recolonization could have been the result of porewater flushing resulting in increased sulfide oxidation of the surface. The disappearance of the white film 1 week after recolonization could indicate that, as expected based on previous work, initial increases in SOD due to porewater flushing declined long before fluxes were measured (day 48).

Although faunal stimulation of SOD appeared to be negligible for *N. virens* and accounted for less than 20% of benthic oxygen demand in *M. arenaria* treatments, stimulation of SOD by the later species was roughly 2- to 6- times higher than the rate of decrease in the soluble-sulfide pool in sediments averaged over the recolonization period and was similar in magnitude to increases in nutrient flux. This suggests that fauna had a strong effect on oxidation-reduction chemistry. Increase in SOD could be the result of increased anaerobic metabolism and subsequent re-oxidation of metabolites or a decrease in solid and dissolved reduced metabolites stored in sediments. These results suggest that the presence of organisms could decrease organic matter inventory in sediments by enhancing metabolism or affect seasonal variation in oxygen consumption by flushing reduced metabolites that would otherwise be stored in sediments during the summer and released slowly, enhancing SOD in the fall. Further, benthic oxygen demand can drive hypoxia in estuaries less than 5 m deep during the spring and summer when production is high and the water column is often stratified (Kemp et al. 1992). The observation that invertebrates accounted for up to 50% of benthic oxygen demand in microcosms suggests that changes in invertebrate distributions should not be neglected in modeling the effects of the benthos on bottom water oxygen depletion and development of hypoxia.

Benthic primary production- In contrast to expectations that *N. virens* would have stronger effects on benthic gross primary production (GPP) because it feeds directly on the sediment surface while *M. arenaria* feeds on phytoplankton, I found that *N. virens* had no obvious effects on GPP while *M. arenaria* stimulated primary production by as much as two fold. Previous studies have shown that macrofaunal excretion and increased nutrient release from sediments can enhance GPP (Hall et al. 200, Hillebrand et al. 2004). However, *Mya arenaria* stimulated GPP at all densities but only increased ammonium and SRP flux at higher densities. This suggests that other mechanisms also influenced GPP. Suspension feeders can also enhance benthic primary production by decreasing pelagic chlorophyll standing stock during suspension feeding which can reduce light limitation for benthic algae (Newell et al., 2002). This, however, would have been unimportant in my microcosms as water was well mixed within the tanks and light at the sediment surface was saturating.

Changes in macrofaunal respiration between light and dark periods could have confounded estimates for GPP. *N. virens* increases ventilation in the light (Scott et al. 1976), which could enhance both macrofaunal metabolism and chemical oxidation causing underestimation of GPP. *Mya arenaria* generally filters continuously during the day and rests at night. However, *M. arenaria* will also decrease or cease filtration during the day if pelagic chl *a* becomes low (Forster & Zettler 2004). The change in metabolism that would accompany changes in filtration rates, however, is small relative to stimulation of benthic GPP by this organism (Grant & Thorpe 1991).

Benthic GPP in microcosms containing both species was lower than expected based on single species treatments suggesting that interference between *N. virens* and *M. arenaria* counteracted the positive effects of *M. arenaria* on primary production. There was a greater than expected decrease in SRP release from sediments when both species were present. This suggests that reduction in intraspecific interference

between *N. virens* could have lowered benthic GPP by increasing SRP retention in sediments. *N. virens* can also decrease benthic GPP directly by disturbing the sediment surface during feeding and burrow construction (Eckman et al, 1981) and through direct consumption of microphytes (Andersen & Kristensen 1988).

Benthic nutrient flux- The estimated daily release of DIN, SRP and Si to the water column increased with invertebrate density (Figure 6, Table 7). However, DIN and SRP flux rates were higher in sediments without macroinvertebrates than in sediments inhabited by low densities of macrofauna. This suggests that DIN and SRP fluxes were controlled by competing mechanisms and that the balance between production and consumption processes for these nutrients can shift with increasing density. The observed changes in flux rates were likely due to both the direct effect of macrofaunal excretion of ammonium and SRP and the indirect effects of faunal activities on transport and sediment processes (i.e. remineralization, oxidation-reduction reactions, sorption versus desorption, precipitation versus dissolution, and assimilation).

Nutrient flux in the dark: macrofaunal respiration and effects on sediment processes- To determine the net effect of invertebrates on sediments, I estimated the net release of nutrients produced through microbial pathways by subtracting estimated macrofaunal excretion from ammonium and SRP flux rates measured in the dark. I assumed that due to the highly advective nature of the burrow environment, 100% of the excretion was released to the water. To account for error inherent in this estimation, I estimated a range using the most extreme and the average excretion rates.

Though *N. virens* had only a weak effect on benthic nutrient fluxes measured in the dark, when excretion was accounted for it appeared that increasing *N. virens* density did have a strong effect on sediments. Even with the lowest estimated

excretion rates, increasing density appeared to decrease non-macrofaunal fluxes by up to 60% and the release of SRP by up to 50% (Figure 9). This indicates that the activities of this organism strongly favored processes that decrease concentrations of dissolved ammonium and SRP (eg. nitrification, adsorption and precipitation) over production processes (eg. remineralization, DNRA, desorption, and dissolution). Results suggested that, at low densities, effects on sediment processes could inhibit the return of both ammonium and SRP to the water column. At higher densities, SRP flux was lower in the presence of *N. virens* but increase in ammonium excretion appeared to outweigh effects on sediments resulting in a net increase in ammonium flux.

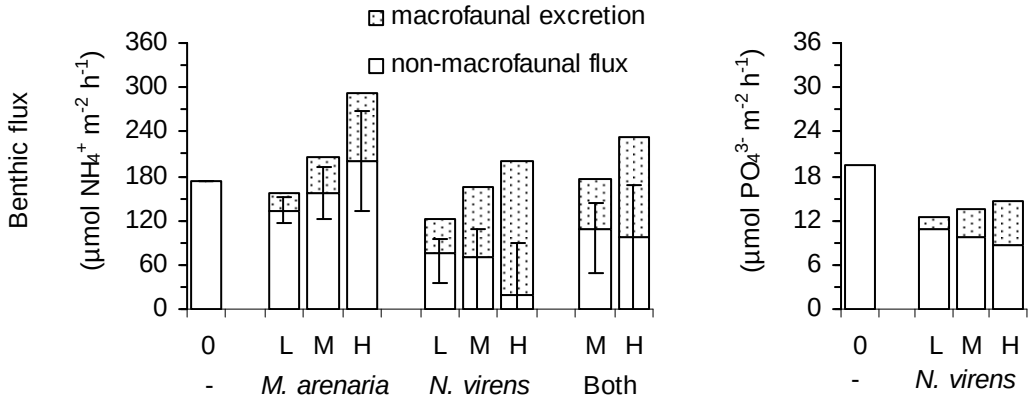

Figure 10. Ammonium and SRP flux partitioned into macrofaunal excretion and non-macrofaunal flux. The given excretion rates were calculated from the average of the published excretion rates. Non-macrofaunal fluxes estimated using average excretion are shown as white bars while the range bars show non-macrofaunal fluxes estimated using the lowest and highest published rates.

The observed effects of *N. virens* on nutrient flux differed from previous studies which have generally shown that high densities (>600 individuals m^{-2}) can significantly enhance efflux of ammonium, SRP and Si and uptake of nitrate by sediments (Henriksen et al. 1983, Kristensen 1985, Christensen et al. 2000, Michaud et al. 2006, Nizzoli et al. 2007). However, the effects of burrow ventilation on redox

sensitive processes would be expected to decrease non-macrofaunal sediment fluxes of ammonium and SRP. Similar to my results, Henriksen et al. (1983) found that several macroinvertebrate species that increase ammonium release in very organic rich sediments can depress flux rates in sediments with low organic matter (<2% LOI; similar to my microcosms) by stimulating rates of nitrification in excess of excretion. Surface deposit feeders, such as *N. virens*, could also have a negative effect on microbial remineralization either through competition with microbes for organic matter or direct consumption of microbes (Kristensen et al. 1992, Retraubun et al. 1996). In my study, the observation that *N. virens* did not increase nitrate efflux from sediments in the dark indicates either that increases in nitrification were coupled with denitrification or that the decrease in non-macrofaunal ammonium flux was primarily due to a shift from microbial to macrofaunal pathways for remineralization.

In contrast to *N. virens*, *M. arenaria* enhanced ammonium fluxes relative to controls but, regardless of the excretion rate, did not appear to have a strong effect on microbial regeneration of ammonium from the sediments (Figure 9). SRP fluxes mirrored the pattern for ammonium fluxes but excretion rates were not available for estimation of effects on sediment processes. Once again, these results differed from previous studies which have shown that *N. virens* can enhance flux rates to a greater degree than *M. arenaria* (Michaud et al. 2006) but were consistent with previous work that has demonstrated that *N. virens* has a stronger effect on sediment processes such as nitrification (Pelegri & Blackburn 1995) and oxygen uptake (Michaud et al. 2005). *Mya arenaria* could also have enhanced regeneration of nutrients to the water column through excretion and stimulation of microbial remineralization because suspension feeding accelerates the deposition of organic matter from the water to sediments rather than decreasing sediment organic matter inventory (Amouroux et al. 1990). The observation that *M. arenaria* had little effect on silicate flux is consistent with the

expectation that this bivalve would have only minor effects on transport while the weak effect on nitrate release suggests minor effects on oxidation-reduction cycling.

Dark flux rates in two-species treatments were lower than expected based on single species treatments. The deviation of observed from expected results also increased with density. In particular, depression of SRP flux was greater in two-species treatments than in either single species treatment. Given that excretion rates were likely unaffected by the number of species present, the observed deviations were likely due to the effects of niche complimentarity on sediment processes. Although changes in density had a stronger effect on flux rates than changes in the number of species present, results suggest that "diversity" could influence the effects of organisms on sediments at high densities.

Fluxes under light conditions: interactions with primary production and behavior- Changes in flux rates between light and dark conditions reflect interactions between primary producers and macroinvertebrates and diel changes in macroinvertebrate behavior. The observation that *N. virens* did not significantly affect benthic GPP suggests that the changes in nutrient flux rates between light and dark periods were due to changes in behavior. *N. virens* can decrease burrow ventilation by as much as 75% during the night relative to day-time rates (Scott et al. 1976). Because I began flux measurements in the morning just prior to the beginning of the light cycle, it is likely that ventilation was initially at a minimum and then increased when I began the light period. The increase in Si flux is indeed suggestive of increased transport while changes in nitrate, ammonium and SRP fluxes could be accounted for by the shift in oxidation-reduction status that would accompany increased ventilation. This suggests that *N. virens* density would determine the magnitude of daily oscillations in nutrient regeneration to the water column.

That increasing *M. arenaria* density did not enhance ammonium, SRP and Si fluxes significantly suggests that stimulation of benthic GPP by this organism was of sufficient magnitude to counteract the positive effects of *M. arenaria* on nutrient release under dark conditions. The diurnal change in flux rates could have been due to assimilation by photosynthetic microbes (Anderson et al., 2000; Tyler et al., 2001; McLeneghan, 2008) or increased sediment oxygen penetration which could stimulate nitrification (An & Joye 2001) and SRP adsorption, particularly if oxidation reactions decreased pH in the microlayer (Krom & Berner 1980, Howarth et al. 1995).

Fluxes in two-species treatments were generally greater than expected in the light and, similar to dark fluxes, the deviation of measured from expected flux rates increased with density. This could be explained by under yielding for GPP in two-species treatments which would result in lower benthic-microalgal demand than would be expected based on single species treatments. However, in contrast the GPP, deviations for fluxes were not statistically significant.

Daily fluxes: ecological implications- Past studies of the effects of invertebrates on benthic fluxes have generally been performed in the dark to eliminate the confounding effects of primary producers on processes. However, significant differences between dark and light periods in the relationship between faunal species composition, abundance, and flux rates emphasizes the importance of considering both interactions with primary producers and diel patterns in invertebrate behaviors when extrapolating microcosm results to the ecosystem. The observation that the DIN:SRP flux ratio in the dark was below Redfield composition (16:1) for all densities of *N. virens* and *M. arenaria* would suggest that nutrient release from the sediments would promote limitation of primary production by DIN (Howarth & Marino 2006) regardless of which species was present. However, the DIN:SRP ratio was greater than Redfield in

two-species treatments. This suggests that overlap in distributions is important (Table 7). Dark fluxes also suggest that nutrient availability for primary production would be higher in sediments inhabited by *M. arenaria* than sediments inhabited by *N. virens*.

Similarly, the DIN:SRP ratio for daily fluxes integrated over light and dark periods was close to 12:1 for sediments without macroinvertebrates and all *M. arenaria* treatments. However, increasing *N. virens* density increased the DIN:SRP ratio relative to controls by as much as a factor of 3, and DIN:SRP was greater than Redfield for all microcosms inhabited by *N. virens* indicating a shift towards limitation of primary production by SRP. When both species were present the DIN:SRP ratio was greater than for either single species treatment due to a lower rate of SRP release from sediments. The ratio of Si:DIN release in all microcosms was slightly below the 1:1 ratio that would favor diatoms (Cloern 2001). The increase in the DIN:SRP ratio (Cloern 2001, Carstensen & Heiskanen 2007) and the increase in the ratio of nitrate to ammonium observed for *N. virens* (Glibert et al. 2004, Heil et al. 2007), could favor growth of diatoms over cyanobacteria and dinoflagellates. This could increase efficiency of energy transfer to higher trophic levels (Ryther 1969). In contrast to fluxes in the dark, the daily rate of DIN release was similar for both species. That both species demonstrated a shift from negative effects on DIN release when densities were low to enhancement of DIN flux by the highest densities, suggests that whether the activities of these species stimulate or inhibit pelagic production could depend strongly upon density although availability of SRP could limit stimulation of production by DIN in sediments inhabited by *N. virens*. Feeding by *M. arenaria* could also maintain an extremely low standing stock of phytoplankton even if primary production were to increase (Nichols 1985). Heterogeneity of invertebrate distributions could have particularly strong effects on spatial and temporal patterns of pelagic primary production in shallow systems where regeneration of nutrients from

sediments can supply up to 75% of the nutrient requirements for growth of phytoplankton (Nixon 1981, Fisher et al. 1982, Blackburn & Henriksen 1983) and macro algae (Tyler et al. 2001).

Conclusions- The frequency of disturbance events that can alter benthic invertebrate community structure, such as periodic anoxia, has increased over the past decade (Diaz and Rosenberg, 2008). Being able to predict how these changes in benthic community structure could affect benthic biogeochemistry is particularly important for shallow estuaries where whole ecosystem function can be dominated by benthic processes and primary production.

Results from this study suggest that local variability in invertebrate densities could cause ecologically relevant changes in porewater chemistry, benthic GPP and availability of oxygen and nutrients in the overlying water. The density dependence of these changes was strongly influenced by species composition. The observed changes in porewater ammonium and soluble-sulfide concentrations agreed well with reaction-transport models which suggest that the deeper burrows and stronger ventilation of the *N. virens* should result in deeper anomalies in porewater solute distributions and that the effects of increasing abundance should plateau at fairly low densities (Aller, 1980). That the changes in porewater solute concentrations were greater than expected when both species were present suggests that niche complimentarity could influence community effects at higher densities. The spatial arrangement of organisms would therefore need to be accounted for in predictive models.

That variation in density influenced not only the magnitude but also the direction of faunal effects on fluxes underscores the need for a better understanding of competing mechanisms that control the balance between production and consumption processes for metabolites in sediments. My results suggest that faunal metabolism,

which is often ignored in models relating faunal activity to flux rates, had a dominant effect on both dark oxygen uptake and nutrient fluxes. Further, that the effects of macrofaunal abundance and species composition on nutrient release were strongly dependent on light conditions suggests that it is necessary to account for the effects of primary producers and changes in macroinvertebrate behavior in the light and raises serious questions regarding extrapolation of previous laboratory results to field conditions. That benthic GPP was significantly lower than expected in the presence of both organisms and that SRP and ammonium release were also slightly lower than expected when both species were present suggests that the spatial arrangement of organisms will also influence flux rates.

The thresholds at which the effects of increasing abundance on porewater concentrations began to level off and the balance between positive and negative effects of organisms on nutrient release from sediments shifted were well below the range of densities in this study. This suggests that, while the effects of combining species appeared to be important only at higher densities, intraspecific interference between organisms could be very important even at very low densities. Consequently, understanding of density-dependent processes is essential to the prediction of the effects of recolonization on the recovery of ecosystem function following disturbance events.

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