Journal of
Marine Science and Engineering

Article

Polychaete Invasion May Lead to Biogeochemical Change in Host Marine Environment

Cintia O. Quintana * and Erik Kristensen

Department of Biology, University of Southern Denmark, Campusvej 55, Odense M, 5230 Odense, Denmark; ebk@biology.sdu.dk
* Correspondence: cintia@biology.sdu.dk

Received: 6 August 2020; Accepted: 18 November 2020; Published: 19 November 2020

Abstract: Marine invasive species may modify their host environment by altering ecosystem biogeochemistry. We hypothesized that the invasive polychaete *Marenzelleria viridis* in Baltic Sea areas increases sulfate reduction (SR) in sediment micro-zones surrounding its burrow. Consequently, higher free porewater sulfide (H_2S) is expected in sediments dominated by *M. viridis* than in corresponding sediments inhabited by the native polychaete *Hediste diversicolor*. In a thin-aquaria experiment, we found high SR rates (220 to 539 nmol cm^{-3} d^{-1}) around the burrow walls of *M. viridis* as well as in surface and subsurface sediments with overall rates 2-fold higher than in defaunated control sediment. Similarly, an in situ survey revealed subsurface porewater H_2S peaks moving upward towards the sediment surface in *M. viridis* inhabited areas. Accordingly, 50–85% higher porewater H_2S was found almost year-round in these areas compared with *H. diversicolor* inhabited areas, suggesting that the invasion of *M. viridis* probably led to a substantial change in sediment biogeochemistry. In conclusion, *M. viridis* stimulates SR in sediment micro-zones and increases H_2S in coastal sediments. Such change to more reducing conditions after the invasion may have critical environmental implications on, e.g., the distribution of H_2S intolerant flora and fauna species.

Keywords: *Marenzelleria viridis*; sulfate reduction; sediment biogeochemistry; estuarine sediments; North Sea; Baltic Sea

1. Introduction

Major impacts of invasive species in host environments are often related to biodiversity loss, predation and competition for space or food [1]. However, invasive species of benthic infauna living within the bottom of marine ecosystems can alter the biogeochemistry of the habitat, and ultimately affect carbon mineralization, nutrient regeneration, larval recruitment and distribution of flora and fauna [2]. Three species of the invasive polychaete genus *Marenzelleria* are found in Europe along the North Sea and Baltic Sea coasts [3]. *M. viridis* is the only *Marenzelleria* species found in high salinity coastal areas of Denmark with current abundances ranging from 200 to 1200 ind m^{-2} in sandy sediments [4]. The invasion of this species has shifted the dominance of benthic infauna and introduced a new functional niche through the formation of narrow (3 mm), but deep (up to 40 cm) "J"-shaped and blind-ended burrows [4,5]. Bioturbation by *M. viridis* is known to increase sulfate reduction (SR) in contrast to native species, such as *Hediste diversicolor* that increase aerobic processes in the sediment [6]. This ability of *M. viridis* is explained by its burrow ventilation behavior. Cilia covering the dorsal gills in the anterior part of the body are in constant movement creating a head-tail inflow of water, while muscular body undulations sporadically pump anoxic water out of the burrow [7]. The ventilation rate is not high, but the associated bioirrigation is sufficient to stimulate SR by forcing DOC- and sulfate-rich water across the walls of the blind ended burrow [7]. Therefore, the production of free sulfide (henceforth referred as $H_2S = H_2S + HS^-$), the end-product of SR, may reach levels in the sediment above those observed before the *M. viridis* invasion [8]. Additionally, redox oscillations may affect the sediment capacity to store H_2S by precipitation with Fe^{2+}, which affects the pools and partitioning of AVS (acid volatile sulfur = H_2S + FeS) and CRS (Chromium Reducible Sulfur = S° + FeS_2) in zones surrounding *M. viridis* burrows. Higher H_2S levels in sediment near the surface may influence the recruitment of H_2S intolerant macrophytes and benthic fauna species [9,10], and can potentially hamper management efforts to recover ecosystems from eutrophication. However, there is limited knowledge on the exact spatial pattern of SR stimulation by *M. viridis* in sediment micro-zones and to which extent high porewater H_2S levels prevail in sediments where this species occurs.

In this study, we hypothesized that *Marenzelleria viridis* increases SR in sediment surrounding its burrow walls. Accordingly, we expected that H_2S concentrations in sediment porewater is higher in coastal areas dominated by *M. viridis* when compared with areas dominated by the native polychaete *Hediste diversicolor*. To test this hypothesis, we performed a laboratory experiment with thin-aquaria to assess two-dimensional depth patterns of SR in sandy sediments with and without *M. viridis*. In addition, seasonal sediment cores were collected from a shallow coastal lagoon where *M. viridis* and *H. diversicolor* dominates to follow the year-round in situ development of H_2S.

2. Materials and Methods

Sandy sediment and *M. viridis* individuals were collected during winter at shallow water in Bregnør Bay, Odense Fjord, Denmark. The sediment had a median grain size of 170 µm and low organic matter content (~0.5%). The sediment and worms were stored in a temperature-controlled room (15 °C) for three days to acclimatize. A series of five thin-aquaria (20 × 30 × 1 cm) were filled with homogenized sediment to 27 cm depth leaving 3 cm of water phase (electronic supplementary material, Figure S1A). The aquaria were transferred to a 90 L tank with local seawater maintained at 15 °C, salinity 20 and 12 h light/12 h dark cycles to assure microphytobenthos production as food source [5,6]. Water circulation and aeration was maintained by air stones placed on the bottom of the tank. After one day of sediment compaction, one *M. viridis* individual (216–228 mg wet weight) was introduced to each of four aquaria leaving one without fauna as control. After two weeks for settling and burrow construction, we only obtained two functional aquaria inhabited by *M. viridis* (Aq. 1 and Aq. 2), i.e., with visible established burrows near one of the aquarium walls. We assumed that *M. viridis* individuals were inactive or died in the other two aquaria without visible burrows. The rates of sulfate reduction (SR) and associated sediment pools of AVS (Acid Volatile Sulfur = H_2S+ FeS) and CRS (Chromium Reducible Sulfur = S° + FeS_2) were measured by the ^{35}S-radiotracer and two-step distillation technique [11,12]. Five µL of $^{35}S\text{-}SO_4{}^{2-}$ (60 kBq) was injected into the sediment through silicon-filled ports distributed in a 2 cm grid along one side of the aquaria (electronic supplementary material, Figure S1B). Three horizontal profiles at 0, 2, 4, and 6 cm radial distance on both sides of the burrow were injected at 4, 10 and 16 cm depth (electronic supplementary material, Figure S1A). In addition, one full vertical profile was injected from the upper 0.5 cm sediment and at 2 cm intervals down to 16 cm at a distance of 6 cm from the burrow in each *M. viridis* aquarium. Two full vertical profiles were injected 8 cm apart in the control aquarium following the same procedure. Thus, total vertical and horizontal injected intervals in all aquaria summed up to 87 samples (see Figure S1A for details). The $^{35}S\text{-}SO_4{}^{2-}$ labelled aquaria were incubated in darkness at 15 °C for 5–7 h. After incubation, the aquaria were opened, and 1 mL sediment samples from injected intervals were collected with cut-off syringes, transferred to centrifugation tubes containing 5 mL of 20% zinc acetate for fixing and stored frozen until analysis. The activity of ^{35}S in the supernatant, as well as AVS and CRS distillates was measured on a Tri-Carb 2200 CA Liquid Scintillation Analyzer for the determination of SR. Concentrations of total AVS and CRS were determined spectrophotometrically based on the H_2S in the distillates [12,13]. No thin-aquarium experiment was done with the native *H. diversicolor*, because it is well -documented that this species increases rates of aerobic processes and lowers rates of sulfate reduction (SR) [6,14]. Instead, we used results from a previous laboratory experiment conducted in similar sediment and incubation conditions for comparison [14].

Three sediment cores (5 cm i.d., 30 cm long) were sampled at each of two areas in Bregnør Bay during spring, summer, autumn and late winter to examine in situ H_2S profiles. One area was dominated by *M. viridis* (220–310 ind m^{-2}) at a water depth of 0.5–1.0 m and never exposed during low tide. The other area was populated by *H. diversicolor* (1900–2200 ind m^{-2}) at a water depth of 0.2–0.5 m and exposed two times per day during low tide. Sediment cores were sliced immediately after return to the laboratory into 0–0.5, 0.5–1, 1–2, 2–3, 3–4, 4–6, 6–8, 8–10, 12–14 and 16–18 cm while intervals 10–12 and 14–16 cm were discarded due to limited solute changes in deeper sediment zones and to simplify analytical procedures [5]. Porewater was extracted from the sediment by centrifugation at 500× *g* for 15 min. The porewater was retrieved with a syringe and H_2S samples were fixed in 20% zinc acetate (9:1 volume ratio) and analyzed as described previously.

To compare *M. viridis* and *H. diversicolor* profiles, a bioturbation zone of 10 cm depth was used for depth-integrating in situ porewater H_2S, since this is the typical summer bioturbation depth limit for the latter species [15]. The difference in depth-integrated in situ porewater H_2S in seasonally sampled *M. viridis* and *H. diversicolor* sediment cores and interactions between these factors were tested by two-way ANOVA. All tests were performed after normality and homogeneity were verified and with significance level of $\alpha = 0.05$ using the software SigmaPlot 14.0.

3. Results

M. viridis individuals were recovered intact from the two functional thin-aquaria at the end of the experiment. The burrows were "J"- shaped, had one opening with a diameter of 2–3 mm and depth between 17 and 25 cm. *Beggiatoa* spp. mats were observed around the burrow openings and at the sediment surface of the two *M. viridis* aquaria. Hotspots of SR ranging from 220 to 539 nmol cm^{-3} d^{-1} were identified in the center along the burrow walls of the two aquaria with *M. viridis* down to 16 cm depth (Figure 1A,B). A SR plume of similar magnitude was found from 4–8 cm depth at 2–6 cm distance to the right of the burrow walls while SR in surrounding sediment was low (39 to 141 nmol cm^{-3} d^{-1}, Figure 1A,B). The overall rates of SR in *M. viridis* aquaria was about 2-fold higher than the control aquarium (Figure 1C). The concentrations of AVS (0.05–1.1 µmol cm^{-3}) were generally much lower than those of CRS (2.0–52.3 µmol cm^{-3}) in the aquaria (Figure 1D–I). The AVS pool showed in Aq. 1 a pattern that was inverse of SR with lowest concentrations immediately around the burrow followed by 2–4-fold increased levels in zones 2–6 cm away from the burrow walls, while Aq. 2 had highest concentrations on the left side of *M. viridis* burrow (Figure 1D,E). AVS concentrations were lower in the control, with highest levels near the outer left perimeter. The CRS pool, on the other hand, was in Aq. 1 enriched far from the burrow walls (i.e., 6 cm), but otherwise not different from the more homogeneous concentrations in Aq. 2 and higher than the control. The averaged vertical pattern of SR in the thin-aquaria showed higher rates at almost all depths in *M. viridis* treatments compared with the control and with the *H. diversicolor* (previous published data) (Figure 2). Accordingly, depth integrated SR from these vertical profiles was 42–114% higher in *M. viridis* aquaria (13.1–19.8 mmol m^{-2} d^{-1}) than in the control (9.2–10.0 mmol m^{-2} d^{-1}) and both of them were 2- to 5-fold higher than the *H. diversicolor* (3.6 ± 1.0 mmol m^{-2} d^{-1}).

The bottom water temperature at Bregnør Bay was 2–3-fold higher during summer than the other seasons in both the *M. viridis* and *H. diversicolor* areas (Table 1). However, temperature levels were generally higher in the *H. diversicolor* area where the water was shallower and exposed twice every day. The temperature difference was particularly large during summer as the average water depth was only 10 cm in the *H. diversicolor* area. In situ profiles in the area dominated by *M. viridis* showed subsurface porewater H_2S peaks (2.0–5.0 nmol cm^{-3}) at sediment depths of 4–10 cm in all seasons. High levels of in situ H_2S were observed at shallow depths (0.4–1.0 nmol cm^{-3} at 0–2 cm) in *M. viridis* sediment from spring to autumn. Porewater H_2S in *H. diversicolor* sediment increased gradually with depth from 0.0–0.1 nmol cm^{-3} near the surface to 0.2–1.3 nmol cm^{-3} at 3–10 cm depth, except during the warm summer where H_2S reached very high levels below the bioturbation zone (Figure 3). The depth-integrated in situ H_2S levels were 2–6 times higher in *M. viridis* than *H. diversicolor* sediment within the bioturbation zone ($p = 0.019$) in all seasons, except for summer where the generally high levels were more than two times higher in *H. diversicolor* than *M. viridis* sediment ($p = 0.001$). No interaction was detected between the factors seasons and depth-integrated H_2S levels in the bioturbation zone of *M. viridis* and *H. diversicolor*.

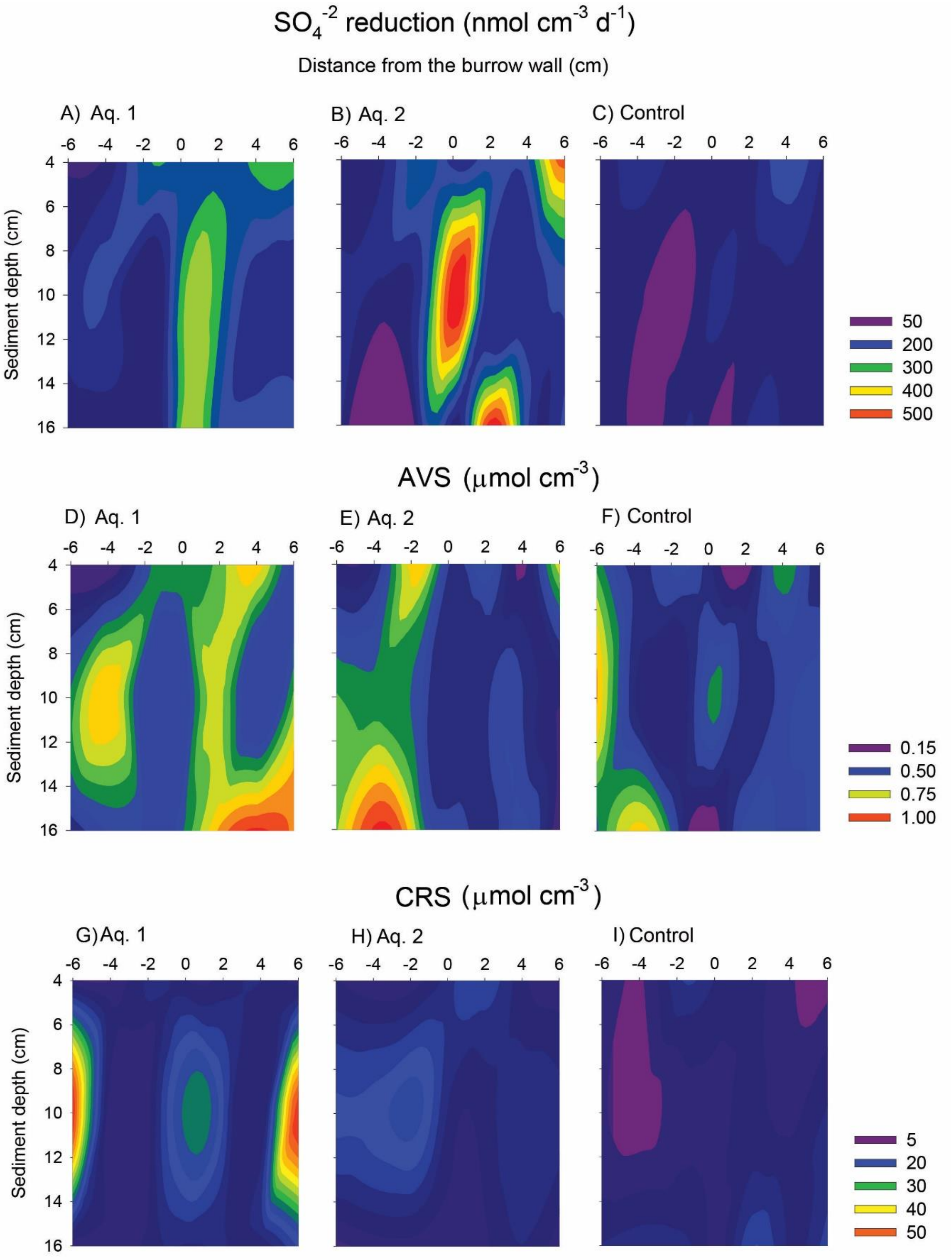

Figure 1. Contour plots of average sulfate reduction rates (**A**–**C**), AVS (Acid Volatile Sulfur, (**D**–**F**) and CRS (Chromium Reducible Sulfur, **G**–**I**) sediment pools in thin-aquaria inhabited by *M. viridis* (Aq. 1 and Aq. 2) and defaunated aquarium (Control).

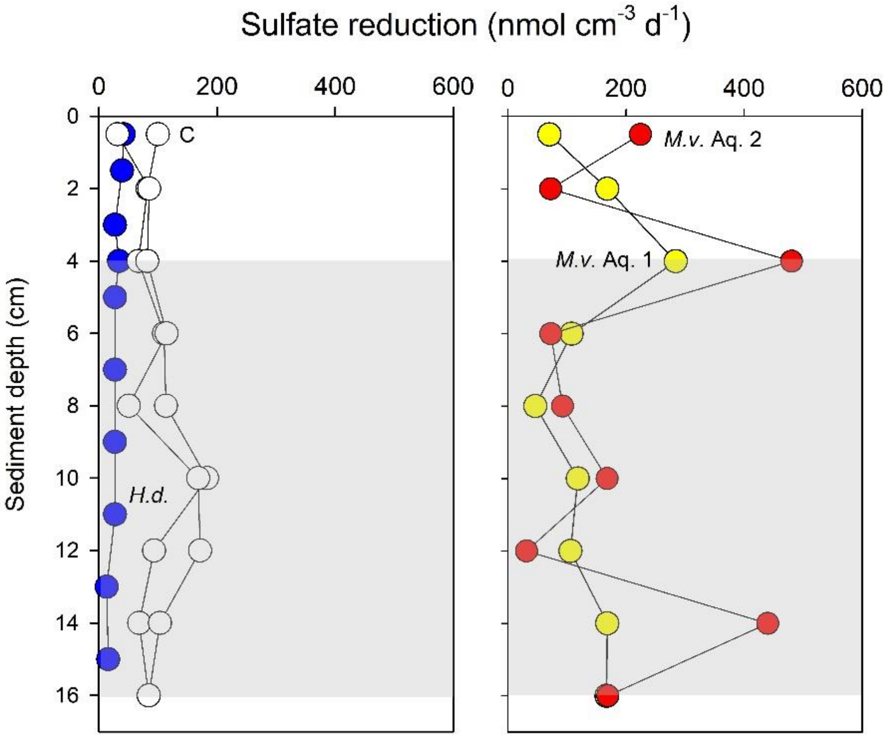

Figure 2. Vertical profiles of sulfate reduction rates in aquaria with *M. viridis* (*M. v.*); Aq 1. (yellow circles) and in Aq. 2 (red circles), and control aquarium (C, white circles). The rates obtained for similar sediment and experimental conditions in the presence of *H. diversicolor* (*H. d.*) from Banta et al. (1999) are shown for comparison (blue circles). The shaded grey box corresponds to the thin-aquaria zone shown in Figure 1.

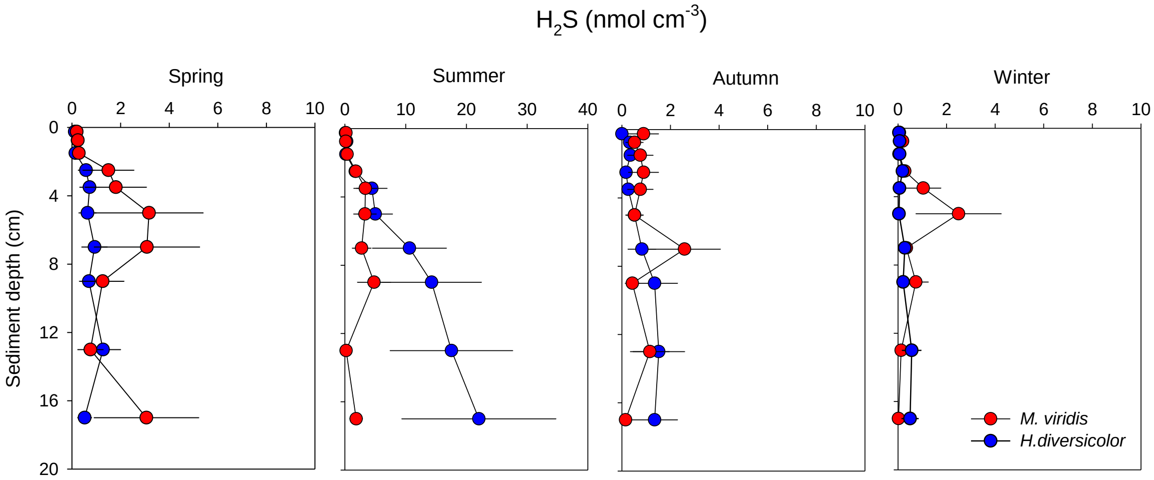

Figure 3. Vertical porewater profiles of H_2S in *M. viridis* and *H. diversicolor* dominated coastal sediment in spring, summer, autumn and late winter at Bregnør Bay. Values represent mean ± standard error ($n = 3$). Note the different *x*-axis scale for H_2S in summer.

Table 1. Bottom water temperature and average depth-integrated porewater H_2S (upper 10 cm) over the seasons in *M. viridis* and *H. diversicolor* dominated coastal sediments in Bregnør Bay. Porewater H_2S values represent mean ± standard error ($n = 3$). Porewater H_2S ranges are indicated for the two sediment core replicates sampled in Spring in *M. viridis* coastal sediments.

Temperature (°C)	**Spring**	**Summer**	**Autumn**	**Winter**
M. viridis	11.0	18.0	11.7	5.0
H. diversicolor	11.5	30.0	14.2	6.5
H_2S (µmol m^{-2})				
M. viridis	29.6 and 44.3	53.7 ± 10.9	24.8 ± 7.4	17.1 ± 6.5
H. diversicolor	12.0 ± 3.9	130.1 ± 45.6	12.4 ± 1.6	2.6 ± 0.4

4. Discussion

Two-dimensional spatial analysis showed that *M. viridis* bioturbation creates micro-zones of elevated SR along the burrow walls at 4–14 cm sediment depth. The tendency for slightly higher SR at the right side of the burrows in our aquaria may be due to porewater percolation generated in that direction forced by the J-shaped blind-ended burrow morphology (Figure S1A). The micro-zones of accumulated AVS observed 2–6 cm away from the burrow walls were displaced from the zones of high SR, while CRS was deposited even further away in Aq. 1 indicating radial transport of SR end-products. Similar radial redox transport has been observed recently around burrows of the polychaete *Chaetopterus variopedatus* [16]. The levels of AVS and CRS pools in our Fe-poor sediment (0.04 µmol cm^{-3}) were lower compared with sediments richer in Fe, suggesting a low H_2S buffer capacity in Bregnør Bay sediment [8]. The vertical SR profiles revealed that high SR levels may occur near the sediment surface in *M. viridis* sediments, as observed at 0–4 cm depth zone. The high SR in micro-zones around *M. viridis* burrows were 2-fold higher than the calculated average rates (Figure 2) and average rates previously found in sediment cores with *M. viridis* [6]. The higher resolution of the two-dimensional spatial analysis therefore provides a reliable tool to identify the location of stimulated SR in sediment inhabited by *M. viridis.* The depth integrated SR calculated here in the presence of *M. viridis* is 6 to 7-fold higher,, respectively, than the average rates previously found in similar sandy-sediments inhabited by *H. diversicolor* (Figure 3) and mud-shrimps [14,17]. Although *M. viridis* is tolerant to hypoxia and H_2S and can colonize hypoxic sediments [18], there is no current consensus on ecophysiological advantages by its SR stimulating behavior. *M. viridis* may benefit by grazing on chemoautotrophic sulfur oxidizing bacteria growing along the burrow walls and surface sediment [19]. However, chemoautotrophic bacteria are probably not a major food source for *M. viridis* in shallow coastal areas when abundant microphytobenthos is available [20].

The high in situ levels of H_2S found in sediment dominated by *M. viridis* were consistent with the sulfur dynamics observed in the thin-aquaria. The high H_2S levels recorded in deep sediment at the *H. diversicolor* area during summer was probably caused by the excessive stimulation of SR due to the very high temperatures in the shallow water (10 cm depth). Otherwise, the depth-integrated H_2S levels in the upper 10 cm bioturbation zone of *M. viridis* sediment was always consistently higher than the same zone in *H. diversicolor* sediment. This is somewhat surprising since ventilation by *M. viridis* in its blind-ended burrows forces porewater to percolate faster to the surface than diffusion-driven bioirrigation in open-ended burrows ventilated by *H. diversicolor* [7,21]. Accordingly, the introduction of a new functional trait by the *M. viridis* invasion, i.e., deep burrows and upward percolation of sulfidic porewater [7], may change the sediment biogeochemistry with consequences on recruitment and settlement of benthic flora and fauna. The shape of in situ H_2S profiles in *M. viridis* sediment was similar to that observed for SR in the thin-aquaria experiment. Subsurface peaks of H_2S within the bioturbation zone therefore suggests upward transport of this solute. This upward H_2S percolation may ultimately result in high concentrations at the sediment surface where sulfide-oxidizing sulfur bacteria typically proliferate at H_2S and O_2 interfaces [22]. The presence of *Beggiatoa* spp. mats at the sediment surface of *M. viridis* aquaria supports this contention. The low redox conditions and presence of H_2S at the sediment-water interface may prevent larval settlement of benthic fauna intolerant to H_2S and hypoxia, i.e., lugworms, bivalves and many crustaceans, while species such as opportunistic capitellid polychaetes can be attracted [9,23,24]. The presence of H_2S near the sediment surface may also decrease the fitness of eelgrass seedlings if they are exposed to H_2S levels above their growth and survival threshold (0.06–1.6 μmol cm^{-3}) [10,25]. The environmental effects of the biogeochemical changes induced by *M. viridis* may, together with other coastal ecosystem stressors such as nutrient loading and climate change, be detrimental to the ecological status of sandy coastal areas.

We conclude that *M. viridis* stimulates the development of sediment micro-zones with high SR alongside their burrow walls. These high SR zones deliver H_2S to the porewater in iron-poor sandy sediments, which confirms our hypothesis. We are confident that the data collected support our conclusions, but the study would have been strengthened if all planned thin-aquaria replicates had been successful. Future studies should focus on investigating how changes in redox conditions at the sediment-water interface promoted by *M. viridis* affect recruitment success of other fauna and flora. More importantly, the SR patterns and H_2S levels found in this study should be integrated into ecological models used for planning of management actions in coastal ecosystems along the Baltic Sea.

Supplementary Materials: The following are available online at http://www.mdpi.com/2077-1312/8/11/940/s1.

Author Contributions: C.O.Q. wrote the manuscript. C.O.Q. and E.K. designed and conducted the experiment. Both authors edited the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the Danish Council for Independent Research (contract no. 12-127012).

Acknowledgments: We thank Lisbeth Elbek Carlsen and Thomas Valdemarsen for assistance with field and laboratory work.

Conflicts of Interest: The authors have no competing interests.

References

1. Katsanevakis, S.; Wallentinus, I.; Zenetos, A.; Leppäkoski, E.; Cinar, M.E.; Oztürk, B.; Grabowski, M.; Golani, D.; Cardoso, A.C. Impacts of invasive alien marine species on ecosystem services and biodiversity: A pan-European review. *Aquat. Invasions* **2014**, *9*, 391–423. [CrossRef]
2. Kristensen, E.; Delefosse, M.; Quintana, C.O.; Flindt, M.R.; Valdemarsen, T. Influence of benthic macrofauna community shifts on ecosystem functioning in shallow estuaries. *Front. Mar. Sci.* **2014**, *1*, 41. [CrossRef]
3. Blank, M.; Laine, A.O.; Jürss, K.; Bastrop, R. Molecular identification key based on PCR/RFLP for three polychaete sibling species of the genus *Marenzelleria*, and the species' current distribution in the Baltic Sea. *Helgol. Mar. Res.* **2008**, *62*, 129–141. [CrossRef]
4. Delefosse, M.; Banta, G.T.; Canal-Vergés, P.; Penha-Lopes, G.; Quintana, C.O.; Valdemarsen, T.; Kristensen, E. Macrobenthic community response to the *Marenzelleria viridis* (Polychaeta) invasion of a Danish estuary. *Mar. Ecol. Prog. Ser.* **2012**, *461*, 83–94. [CrossRef]
5. Quintana, C.O.; Raymond, C.; Nascimento, F.J.A.; Bonaglia, S.; Forster, S.; Gunnarsson, J.S.; Kristensen, E. Functional performance of three invasive *Marenzelleria* species under contrasting ecological conditions within the Baltic Sea. *Estuaries Coasts* **2018**, *41*, 1766–1781. [CrossRef]
6. Kristensen, E.; Hansen, T.; Delefosse, M.; Banta, G.; Quintana, C.O. Contrasting effects of the polychaetes *Marezelleria viridis* and *Nereis diversicolor* on benthic metabolism and solute transport in sandy coastal sediments. *Mar. Ecol. Prog. Ser.* **2011**, *425*, 125–139. [CrossRef]
7. Quintana, C.O.; Hansen, T.; Delefosse, M.; Banta, G.; Kristensen, E. Burrow ventilation and associated porewater irrigation by the polychaete *Marenzelleria viridis*. *J. Exp. Mar. Biol. Ecol.* **2011**, *397*, 179–187. [CrossRef]
8. Kristiansen, K.D.; Kristensen, E.; Jensen, M.H. The influence of water column hypoxia on the behaviour of manganese and iron in sandy coastal marine sediment. *Estuar. Coast. Shelf Sci.* **2002**, *55*, 645–654. [CrossRef]
9. Woodin, S.A.; Marinelli, R.L.; Lindsay, S.M. Process-specific cues for recruitment in sedimentary environments: Geochemical signals? *J. Mar. Res.* **1998**, *56*, 535–558. [CrossRef]

10. Mascaró, O.; Valdemarsen, T.; Holmer, M.; Pérez, M.; Romero, J. Experimental manipulation of sediment organic content and water column aeration reduces *Zostera marina* (eelgrass) growth and survival. *J. Mar. Exp. Biol. Ecol.* **2009**, *373*, 26–34. [CrossRef]
11. Jørgensen, B.B. A comparison of methods for the quantification of bacterial sulfate reduction in coastal marine sediments. *Geomicrobiol. J.* **1978**, *1*, 29–47. [CrossRef]
12. Quintana Fossing, H.; Jørgensen, B.B. Measurement of bacterial sulfate reduction in sediments: Evaluation of a single-step chromium reduction method. *Biogeochemistry* **1989**, *8*, 205–222.
13. Cline, J.D. Spectrophotometric determination of hydrogen sulfide in natural waters. *Limnol. Oceanogr.* **1969**, *14*, 454–458. [CrossRef]
14. Banta, G.T.; Holmer, M.; Jensen, M.H.; Kristensen, E. Effects of two polychate worms, *Nereis diversicolor* and *Arenicola marina*, on aerobic and anaerobic decomposition in sandy marine sediment. *Aquat. Microb. Ecol.* **1999**, *19*, 189–204. [CrossRef]
15. Muus, B.J. *The Fauna in Danish Estuaries and Lagoons: Distribution and Ecology of Dominating Species in the Shallow Reaches of a Mesohaline Zone*; Høst & Søn: Copenhagen, Denmark, 1967; 316p.
16. Aller, R.C.; Aller, J.Y.; Zhu, Q.; Heilbrun, C.; Klingensmith, I.; Kaushik, A. Worm tubes as conduits for the electrogenic microbial grid in marine sediments. *Sci. Adv.* **2019**, *5*, eaaw3651. [CrossRef]
17. Bertics, V.; Ziebis, W. Bioturbation and role of microniches for sulfate reduction in coastal marine sediments. *Environ. Microbiol.* **2010**, *12*, 3022–3024. [CrossRef]
18. Schiedek, D. *Marenzelleria* cf. *viridis* (Polychaete: Spionidae)—Ecophysiological adaptations to a life in the coastal waters of the Baltic Sea. *Aquat. Ecol.* **1997**, *31*, 199–210. [CrossRef]
19. Vasquez-Cardenas, D.; Quintana, C.O.; Meysman, F.J.R.; Kristensen, E.; Boschker, H.T.S. Species-specific effects of two bioturbating polychaetes on sediment chemoautotrophic bacteria. *Mar. Ecol. Prog. Ser.* **2016**, *549*, 55–68. [CrossRef]
20. Dauer, D. Functional morphology and feeding behavior of *Marenzelleria viridis* (Polychaete: Spionidae). *Bull. Mar. Sci.* **1997**, *60*, 512–516.
21. Hedman, J.E.; Gunnarsson, J.S.; Samuelson, G.; Gilbert, F. Particle reworking and solute transport by the sediment-living polychaetes *Marenzelleria neglecta* and *Hediste diversicolorI*. *J. Exp. Mar. Biol. Ecol.* **2011**, *402*, 294–301. [CrossRef]
22. Preisler, A.; de Beer, D.; Lichtschlag, A.; Lavik, G.; Boetius, A.; Jørgensen, B.B. Biological and chemical sulfide oxidation in a *Beggiatoa* inhabited marine sediment. *ISME J.* **2007**, *1*, 341–353. [CrossRef] [PubMed]
23. Groenendaal, M. Tolerance of the lugworm (*Arenicola marina*) to sulphide. *Neth. J. Sea Res.* **1980**, *14*, 200–207. [CrossRef]
24. Levin, L.A.; Ekau, W.; Gooday, A.J.; Jorisson FMiddelburg, J.J.; Naqvi, S.W.; Neira, C.; Rabalais, N.N.; Zhang, J. Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences* **2009**, *6*, 2063–2098. [CrossRef]
25. Pedersen, M.Ø.; Kristensen, E. Sensitivity of *Ruppia maritima* and *Zostera marina* to sulfide exposure around roots. *J. Exp. Mar. Biol. Ecol.* **2015**, *468*, 138–145. [CrossRef]

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© 2020 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (http://creativecommons.org/licenses/by/4.0/).