



ORIGINAL RESEARCH ARTICLE

# Context-dependent consequences of *Marenzelleria* spp. (Spionidae: Polychaeta) invasion for nutrient cycling in the Northern Baltic Sea<sup>☆</sup>

Alexey Maximov<sup>a,\*</sup>, Erik Bonsdorff<sup>b</sup>, Tatjana Eremina<sup>c</sup>, Laura Kauppi<sup>d</sup>, Alf Norkko<sup>d</sup>, Joanna Norkko<sup>d</sup>

<sup>a</sup> Zoological Institute Russian Academy of Sciences, St. Petersburg, Russia

<sup>b</sup> Environmental and Marine Biology, Faculty of Science and Engineering, Åbo Akademi University, Åbo, Finland

<sup>c</sup> Russian State Hydrometeorological University, St. Petersburg, Russia

<sup>d</sup> Tvärminne Zoological Station, University of Helsinki, Hanko, Finland

Received 12 January 2015; accepted 17 June 2015

Available online 14 July 2015

## KEYWORDS

Bioturbation;  
Bioirrigation;  
Nutrient fluxes;  
Macrozoobenthos;  
Non-indigenous species

**Summary** *Marenzelleria* spp. are among the most successful non-native benthic species in the Baltic Sea. These burrowing polychaetes dig deeper than most native Baltic species, performing previously lacking ecosystem functions. We examine evidence from experiments, field sampling and modelling that the introduction of *Marenzelleria* spp. affects nutrient cycling and biogeochemical processes at the sediment–water interface. Over longer time scales, bioirrigation by *Marenzelleria* spp. has the potential to increase phosphorus retention in bottom deposits because of deeper oxygen penetration into sediments and formation of a deeper oxidized layer. In contrast, nitrogen fluxes from the sediment increase. As a consequence of a decline of the phosphate concentration and/or rising nitrogen/phosphorus ratio, some Northern Baltic ecosystems may experience improvement of the environment because of mitigation of eutrophication and harmful cyanobacteria blooms. Although it is difficult to unambiguously estimate the ecosystem-level consequences of invasion, in many cases it could be considered as positive due to increased structural and functional diversity. The long-term interactions with the native

<sup>☆</sup> The present study was supported by BONUS project COCOA, Russian Foundation for Basic Research (grant 14-04-91721), Russian Geographical Society (grant 13-05-41464) and Government Target Project N°2014/166 of the Ministry of Education and Science of the Russian Federation.

\* Corresponding author at: Zoological Institute Russian Academy of Sciences, Universitetskaya nab. 1, 199034 St. Petersburg, Russia. Tel.: +7 8123281311; fax: +7 8123282941.

E-mail address: [alexeymaximov@mail.ru](mailto:alexeymaximov@mail.ru) (A. Maximov).

Peer review under the responsibility of Institute of Oceanology of the Polish Academy of Sciences.



Production and hosting by Elsevier

fauna still remain unknown, however, and in this paper we highlight the major knowledge gaps.  
 © 2015 Institute of Oceanology of the Polish Academy of Sciences. Production and hosting by Elsevier Sp. z o.o. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

## 1. Introduction

Annelid worms are well known habitat modifiers. In terrestrial ecosystems, the key role of earthworms was first recognized by Darwin (1881). He stated “It may be doubted whether there are many other animals which have played so important a part in the history of the world...” (Darwin, 1881). The earthworms function as ecosystem engineers by modifying the physical, chemical and biological characteristics of soil (Straube et al., 2009). In marine sediments, analogical roles are played by polychaete worms. Through bioturbation and bioirrigation they affect the physical structure of sediments and exchange processes at the sediment–water interface (Berke, 2010; Kristensen et al., 2012; Meysman et al., 2006; Quintana et al., 2011). Although experimental studies of the effects of burrowing animals on marine sediment biogeochemistry are numerous (e.g. Caliman et al., 2011; Hedman et al., 2011; Karlson et al., 2007b; Norling et al., 2007), ecosystem-level biogeochemical consequences of this activity still remain poorly understood. A recent large-scale invasion of bioturbating polychaetes of the genus *Marenzelleria* to the species-poor benthic communities of the Northern Baltic Sea (Maximov, 2011; Norkko and Jaale, 2008; Villnäs and Norkko, 2011) has provided the opportunity to study the role of worm-induced processes in the ecosystem.

*Marenzelleria* spp. are among the most successful non-native benthic species in the Baltic Sea during recent decades. They first appeared in 1985 and quickly colonized the entire sea, occupying a dominant position in the zoobenthos (Ezhova et al., 2005; Kauppi et al., 2015; Villnäs and Norkko, 2011; Zettler et al., 2002). Initially the introduced polychaetes were identified as the North American *Marenzelleria viridis* (Verrill). During the subsequent revision of the genus the polychaetes from the eastern Baltic Sea were described as a different species, namely *Marenzelleria neglecta*, also originating from North America (Sikorski and Bick, 2004). In the mid-2000s the occurrence of three sibling *Marenzelleria* species in the Baltic Sea was confirmed by molecular methods: *M. viridis*, *M. neglecta* and *M. arctica* (Chamberlin) (Bastrop and Blank, 2006; Blank et al., 2008). The last species was known earlier only from the Arctic Basin (Sikorski and Buzhinskaya, 1998). According to recent studies, polychaetes dominating in the deep open areas of northern Baltic Sea belong to *M. arctica* (Kauppi et al., 2015).

The native benthic macrofauna of the Northern Baltic Sea is low in diversity and thus strongly dominated by a few key species. Examples of the most common sediment-dwelling invertebrate species in the area are the bivalve *Macoma balthica*, and the crustaceans *Monoporeia affinis*, *Pontoporeia femorata* and *Saduria entomon* (Bonsdorff, 2006; Elmgren, 1984; Villnäs and Norkko, 2011). Polychaete worms in the Northern Baltic Sea are, as a rule, not abundant with a complete absence of large burrowing forms. In this paper we

provide an overview of evidence from experiments, field sampling and modelling that the introduction of *Marenzelleria* spp. affects sediment-water fluxes and nutrient cycling in a region that was previously practically devoid of worms. Here we discuss patterns emerging from reviewed studies on direct worm-induced effects on nutrient fluxes, highlighting perspectives for future research and important implications of the *Marenzelleria* spp. invasion for ecosystem services and management.

## 2. Experimental studies

A substantial amount of experimental data about the influence of *Marenzelleria* spp. on exchange processes between sediments and the water column exists in the literature. In all these studies worm activity enhanced fluxes of nitrogen (Bonaglia et al., 2013; Quintana et al., 2013; Renz and Forster, 2014; Urban-Malinga et al., 2013). For phosphorus, however, results are somewhat more contradictory and appear to depend on experimental design. In several cases the sediments used in experiments were sieved to remove other fauna and reduce background variability. In such experiments *Marenzelleria* spp. increased the fluxes of both phosphorus and nitrogen to the water column (Hietanen et al., 2007; Renz and Forster, 2014; Urban-Malinga et al., 2013; Viitasalo-Frösén et al., 2009). In two studies defaunated sediments were obtained from anoxic sites. In one of these studies using intact sediments, no significant effects on phosphorus fluxes were found (Karlson et al., 2005). The results of another study indicated that polychaete activity stimulated the opposite processes, i.e. uptake of phosphorus by sediments (Bonaglia et al., 2013). There are no indications that *Marenzelleria* spp. can stimulate processes leading to nitrogen removal from the aquatic ecosystem. On the contrary, experimental studies suggest that these polychaetes do not influence (Hietanen et al., 2007; Karlson et al., 2005; Kristensen et al., 2011) or even reduce denitrification (Bonaglia et al., 2013). It is surprising as bioturbation and bioirrigation by sediment-burrowing macrofauna are usually recognized as stimulating benthic denitrification because of increased nitrate flux to anoxic sediment layers (Stief, 2013). For example, from studies in the Northern Baltic Sea region, Gran and Pitkänen (1999) found that benthic denitrification was stimulated in the eastern Gulf of Finland, which was previously dominated by the amphipods *M. affinis* and *P. femorata*. The reason for such impact of *Marenzelleria* spp. on nitrogen cycling is still not fully understood. It seems possible that excessive aeration of sediments by worms negatively impact on microbial anaerobic processes such as denitrification.

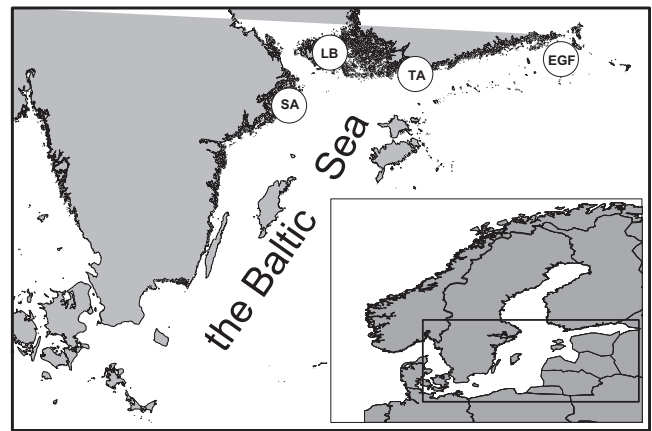
Recent laboratory experiments indicated differences between *Marenzelleria* species, referring to burrow morphology, burrowing depth, and bioturbation pattern (Renz

and Forster, 2013). It is concluded that effects of shallow-burrowing (down to 11 cm) *M. arctia* on the sediments and benthic nutrient fluxes will be less dramatic and different from the deep-burrowing (26 and 35 cm, respectively) *M. neglecta* and *M. viridis*, which are similar in many bioturbation characteristics (Renz and Forster, 2013, 2014). The worms from shallow sandy sites in the Southern Baltic Sea used in experiments of Quintana et al. (2013) and Kristensen et al. (2011) were represented by *M. viridis*. Other authors refer to experimental worms as *Marenzelleria* spp. because definite identification of polychaetes of this genus requires molecular methods (Blank et al., 2008). However the studies from the Northern Baltic Sea used polychaetes collected at deep (>35 m) muddy bottoms that most probably belonged to *M. arctia* (Bonaglia et al., 2013; Hietanen et al., 2007; Karlson et al., 2005; Viitasalo-Frösén et al., 2009). All studied *Marenzelleria* spp. stimulated the release of nitrogen and phosphate in experiments with sieved sediments. However, the only studies with intact defaunated sediments (Bonaglia et al., 2013; Karlson et al., 2005) were carried out most probably with *M. arctia*. The different species of *Marenzelleria* seem to prefer different habitats (Blank et al., 2008). *M. viridis* and likely *M. neglecta* prefer shallow sandy sediments with low organic content (Kube et al., 1996; Quintana et al., 2007). In contrast, *M. arctia* are most abundant at the deeper and more organic-rich muddy bottoms both in the Baltic, as well as, in its native Arctic areas (Jirkov, 2001). Also the arctic *M. arctia* is evidently better adapted to the low temperature of deep sub-thermocline waters of the Northern Baltic Sea than other congeners. These features appear to allow *M. arctia* to occupy the more extensive bottom areas in comparison with *M. viridis* and *M. neglecta*. It is hypothesized that colonization of vast expanses with more nutrient-rich substrates by *M. arctia*, which commonly occurs in higher numbers than *M. viridis* and *M. neglecta*, can lead to more pronounced changes in nutrient cycling despite lower bioturbation activity of this species. The species-specific and context-dependent (e.g. sediment type) effects of *Marenzelleria* on nutrient cycling, however, require further experimental and field-based evidence.

### 3. Field studies

There are only a few field studies using site-specific long-term data to examine nutrient cycling in the Northern Baltic Sea ecosystems before and after *Marenzelleria* spp. invasion (Fig. 1). In the Stockholm archipelago, which had suffered from seasonal hypoxia for several decades, an increase in polychaete abundances in the mid-2000s coincided with marked improvements in bottom-water oxygen conditions (Karlsson et al., 2010). Since phosphorus cycling is strongly related to oxygen conditions, phosphate concentration declined resulting in decreasing chlorophyll-*a* levels and mitigation of eutrophication. It is thus possible that bioirrigation by the polychaetes resulted in enhanced phosphorus retention in the sediments, although these changes were partly also explained by reduction of external nutrient loads because of improvement of sewage treatment (Karlsson et al., 2010; Norkko and Reed et al., 2012).

In the eutrophied eastern Gulf of Finland invasion of *M. arctia* was not followed by improvement of oxygen



**Figure 1** Map of the Baltic Sea with case study areas mentioned in the text. SA, Stockholm area; LB, Lumparn basin; TA, Tvärminne area; EGF, eastern Gulf of Finland.

conditions, which are strongly modulated by large-scale hydrographic phenomena in this area (Eremina et al., 2012; Maximov, 2006). However mass development of polychaetes in 2008–2009 coincided with changes in the concentration of nutrients in near-bottom waters (Maximov et al., 2014). Under similar oxygen conditions, the pre-invasion years were characterized by higher phosphate concentrations than post-invasion years. In contrast, the concentration of inorganic nitrogen compounds (nitrites and nitrates) increased markedly. The opposite trends in the dynamics of nitrogen and phosphorus levels resulted in changes in the ratio between the compounds of these nutrients in the bottom waters. Evidently the rise of the N/P ratio was the reason for the observed cascading changes in the planktonic communities (Maximov et al., 2014). Under these new conditions of high nitrogen availability the cyanobacteria, especially nitrogen-fixing species, lost their competitive advantage. The disappearance of large cyanobacterial blooms resulted in a sharp decrease in the phytoplankton biomass and chlorophyll-*a* level (Maximov et al., 2014). This seemingly paradoxical effect of increasing nitrogen level in the eastern Gulf of Finland is in agreement with numerous field and laboratory studies, as well as with practical experience of fertilizing of fish-farming ponds, which suggest that raising the N/P ratio because of nitrogen application suppresses the development of cyanobacteria (Bulgakov and Levich, 1999; Levich, 1996). In the western Gulf of Finland and the coastal Tvärminne area, marked opportunistic increases in *Marenzelleria* spp. densities were observed in 2006 (Kauppi et al., 2015), but no change in N and P could be observed following this marked change in abundance of the polychaetes. Concurrently, a dramatic increase in *Marenzelleria* abundance in the Lumparn basin in the Åland archipelago over a ten-year period (2001–2011) was paralleled by an increase in nutrient levels as well as a decrease in oxygen levels (Bonsdorff et al., unpublished data). Hence the effects of the establishment of *Marenzelleria* are idiosyncratic, with both increases and decreases in nutrients. Neither Tvärminne nor the Lumparn area in the Åland archipelago, have experienced severe oxygen depletion although the trend in the Åland-case is decreasing. A potential explanation for these idiosyncratic effects may be due to area-specific differences

**Table 1** Studies highlighting the influence of *Marenzelleria* spp. on nutrient cycling at the sediment–water interface in the Baltic Sea.

Process	Research approach			
	Experiments with sieved sediment	Experiments with intact sediment	Field measurements	Models
Phosphate release	Hietanen et al. (2007), Renz and Forster (2014), Viitasalo-Frösén et al. (2009) and Urban-Malinga et al. (2013)			
Phosphate retention		Bonaglia et al. (2013)	Maximov et al. (2014) and Karlsson et al. (2010)	Norkko and Reed et al. (2012)
Nitrogen release	Hietanen et al. (2007), Quintana et al. (2013), Renz and Forster (2014), Viitasalo-Frösén et al. (2009), Kristensen et al. (2011) and Urban-Malinga et al. (2013)	Karlson et al. (2005) and Bonaglia et al. (2013)	Maximov et al. (2014)	

in e.g. oxygen levels, sediment type and organic content, but could partly also be attributed to different polychaete species, with contrasting bioturbation potential (Renz and Forster, 2014) dominating in different areas, although such information is lacking, and thus offering another open field for research.

#### 4. Models

The only model study that demonstrates that colonization by *Marenzelleria* spp. over longer time scales (several years), potentially has a marked, density-dependent impact on phosphorus cycling is by Norkko and Reed et al. (2012). A reactive-transport model was modified to represent a seasonally hypoxic muddy site in the inner Stockholm archipelago. The results suggest that these polychaetes have the potential to enhance long-term phosphorus retention in muddy sediments, thus reducing phosphorus release from bottom waters that might contribute to surface water eutrophication and hypoxia (Norkko and Reed et al., 2012). However, the modelling was based on mechanistic studies of bioirrigation by *M. viridis*, i.e. another species than the ones present in the northern Baltic, so it can only be used to illustrate that polychaetes have a real potential to influence nutrient cycling. An analogical modelling approach is being applied in the eastern Gulf of Finland (Eremina et al., 2014). Also here preliminary results show a significant worm-induced increase in phosphorus content of sediments, thereby reducing the contribution of bottom-water phosphorus to eutrophication. The importance of *Marenzelleria* spp. and other species/functional categories of zoobenthos for the general ecosystem productivity were also modelled in a study covering the entire Baltic Sea gradient by Timmermann et al. (2012), who showed that reductions in external nutrient loading would indeed lead to improved oxygen conditions and increased macrozoobenthic biomass, with potential subsequent effects on benthic nutrient cycling.

#### 5. Emerging patterns

All the reviewed studies demonstrate some effects of *Marenzelleria* on biogeochemical processes at the sediment–water interface in the Baltic Sea (Table 1). The nutrient fluxes from and/or to the sediments were, as a rule, significantly affected by the worms. Studies where nitrogen is considered, all show enhanced fluxes from sediments to the water column as a result of *Marenzelleria* spp. activity. It is known that in general benthic animals increase the nitrogen flux from sediments through excretion and bioturbation (Stief, 2013). Ammonium often accumulates in sediment pore-water. Physical mixing of sediments by benthic invertebrates can increase the rate at which pore-water nitrogen is released to overlying waters. This effect is especially evident during an initial stage of recolonization of defaunated anoxic bottoms (Karlson et al., 2007a).

In the case of phosphorus, there is contradiction between results of experiments with sieved sediments and results of studies employing other methodical approaches. Most laboratory experiments produce results identical to that for nitrogen compounds; phosphate release from sediments increases as a result of worm activity. However, transferring and up-scaling results from these experiments to real-life systems is still questionable. Under natural conditions, the phosphate-binding capacity of sediments depends on the thickness of the oxidized layer at the water–sediment interface. The oxygen penetration depth into sediments is naturally low. Therefore, only a small portion of the uppermost sediment layer is in contact with oxygen. In this case bioirrigation by polychaetes is significant because it increases the depth of oxygen penetration into sediments resulting in formation of a thicker oxidized layer and subsequently in increased phosphorus retention. It provides an explanation for the decrease of phosphate concentration, which is observed in field studies in areas suffering from seasonal or episodic hypoxia, as well as, in an experiment with intact

sediment cores (Bonaglia et al., 2013). The same pattern cannot be observed in laboratory studies using sieved sediments, because the sieving results in oxidation of the previously reduced compounds. In this case additional burrowing and sediment irrigation by worms is of little importance for aeration of sediments. Also, a modelling study demonstrates that short-term experiments reflect mainly the immediate effect on nutrient cycling and their results cannot be extrapolated to processes on longer time-scales in natural ecosystems (Norkko and Reed et al., 2012).

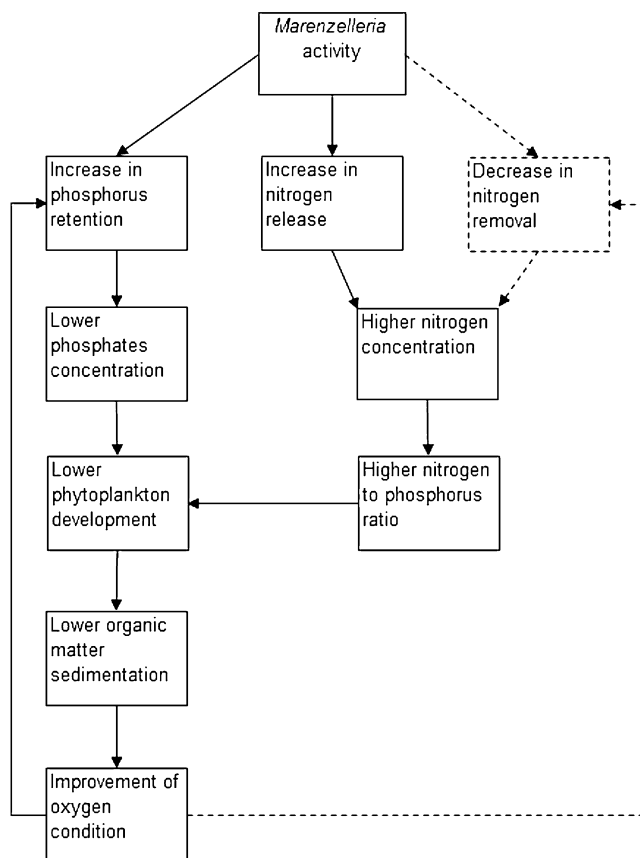
The potential main worm-induced effects on nutrient cycling in the Northern Baltic Sea ecosystem are summarized in Fig. 2. The history of oxygen deficiency (or lack thereof) has a pronounced effect on the role of the worms. Bioirrigation by *Marenzelleria* spp. increases the phosphorus retention in bottom deposits because of deeper oxygen penetration into sediments and formation of a deeper oxidized layer. This results in a declining phosphate concentration in the water column. In contrast, nitrogen fluxes from the sediment increase. In addition, it is known that several anaerobic biochemical processes (denitrification, anammox) result in the formation of nitrogen gas venting to the atmosphere (Conley et al., 2009; Savchuk, 2010; Vahtera et al., 2007). Therefore, improvement of oxygen conditions in sediments through bioirrigation can potentially inhibit these processes and prevent the loss of nitrogen compounds resulting in an increased nitrogen flux into the water column. The

decrease in phosphorus concentration together with higher N/P ratio causes a decrease in phytoplankton biomass. The lower the phytoplankton production, the lower the sedimentation of organic matter, which subsequently results in improved near-bottom oxygen conditions. This leads to a positive feedback loop where the better oxygen conditions lead to greater phosphorus retention and probably to lesser nitrogen removing and further decreases in phytoplankton production (Fig. 2).

## 6. Prospects for future research and implications for the ecosystem

We have here illustrated the potential effect of *Marenzelleria* bioturbation and bioirrigation on sediment biogeochemistry in the Northern Baltic Sea. *Marenzelleria* spp. burrow deeper than most native Baltic species (Karlson et al., 2005), thus performing previously lacking ecosystem functions. The importance of benthic macrofauna for biogeochemical processes within the sediment is typically mentioned in the context of consequences of biodiversity loss for ecosystem functioning, especially as a result of hypoxia (Bouma et al., 2009; Solan et al., 2004). A disappearance of large deep-dwelling fauna is generally observed in hypoxic areas (Diaz and Rosenberg, 2001; Levin et al., 2009). The resultant reduced bioturbation adversely impacts the benthic habitats by disrupting biogeochemical processes (Middelburg and Levin, 2010; Steckbauer et al., 2011; Villnäs et al., 2012). Invasion of *Marenzelleria* spp. to the Baltic Sea is the rare, maybe unique, example of the opposite phenomenon resulting in an increase of functional diversity of the original ecosystem. It is notable that now the composition of soft-bottom macrofauna in the Northern Baltic Sea becomes practically identical to that of the Arctic estuaries where benthic communities are dominated by the polychaete *M. arctia*, crustaceans *S. entomon* and *M. affinis*, priapulid *Halicryptus spinulosus* and bivalve *M. balthica* (Denisenko et al., 1999). Until recently, *M. arctia* was the only species from this list that was absent in the Baltic Sea. This is in line with the concept of continuing postglacial succession of the Baltic Sea (Bonsdorff, 2006). The appearance of bioturbating polychaetes is consistent with the general model of zoobenthic succession in Baltic sedimentary habitats predicting a few successional stages ranging from dead anoxic bottoms to a diverse “climax community” dominated by deep-burrowing species (Rumohr et al., 1996).

The beneficial consequences of *Marenzelleria* spp. activity can, however, be offset by the potentially unpleasant side-effects. Burial and subsequent decomposition of fresh organic matter originated from settled phytoplankton can counteract the irrigation effects of *Marenzelleria* spp. (Josefson et al., 2012; Karlson et al., 2011). The beneficial effect of the polychaetes on phosphate removal can be counteracted by the concurrent increase of the nitrogen concentration in the water column. At present, in the eastern Gulf of Finland changes in nitrogen cycling seem positive because of mitigation of harmful cyanobacteria blooms during summer. However, it is possible that in other seasons and/or areas the increasing concentration of nitrogen can stimulate eutrophication. This problem calls for further investigation because primary production in open areas of the Baltic



**Figure 2** Potential effects of *Marenzelleria* spp. on nutrient cycling in the ecosystems of the Northern Baltic Sea. Dashed box and lines indicate a hypothesized process and effects with little data at this time.

Sea is mainly nitrogen-limited, especially during the spring phytoplankton bloom forming the biomass peak of the year (HELCOM, 2009). The potentially increased release of contaminants buried in the sediment (Granberg et al., 2008; Skei et al., 2000) further complicates assessing the ecosystem-level effects of the *Marenzelleria* invasion. Empirical, species- and context-specific, long-term field and laboratory studies are still needed to assess the real effect of the worms on the ecosystem.

## References

- Bastrop, R., Blank, M., 2006. Multiple invasions – a polychaete genus enters the Baltic Sea. *Biol. Invasions* 8, 1195–1200, <http://dx.doi.org/10.1007/s10530-005-6186-6>.
- Berke, S.K., 2010. Functional groups of ecosystem engineers: a proposed classification with comments on current issues. *Integr. Comp. Biol.* 50 (2), 147–157, <http://dx.doi.org/10.1093/icb/iciq077>.
- Blank, M., Laine, A.O., Jürss, K., Bastrop, R., 2008. 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.* 62, 129–141, <http://dx.doi.org/10.1007/s10152-007-0081-8>.
- Bonaglia, S., Bartoli, M., Gunnarsson, J.S., Rahm, L., Raymond, C., Svensson, O., Shakeri Yekta, S., Brüchert, V., 2013. Effect of reoxygenation and *Marenzelleria* spp. bioturbation on Baltic Sea sediment metabolism. *Mar. Ecol. Prog. Ser.* 482, 43–55, <http://dx.doi.org/10.3354/meps10232>.
- Bonsdorff, E., 2006. Zoobenthic diversity-gradients in the Baltic Sea: continuous post-glacial succession in a stressed ecosystem. *J. Exp. Mar. Biol. Ecol.* 330, 383–391, <http://dx.doi.org/10.1016/j.jembe.2005.12.041>.
- Bouma, T.J., Olenin, S., Reise, K., Ysebaert, T., 2009. Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. *Helgol. Mar. Res.* 63, 95–106, <http://dx.doi.org/10.1007/s10152-009-0146-y>.
- Bulgakov, N.G., Levich, A.P., 1999. The nitrogen:phosphorus ratio as a factor regulating phytoplankton community structure. *Arch. Hydrobiol.* 146 (1), 3–22.
- Caliman, A., Carneiro, L.S., Bozell, R.L., Farjalla, V.F., Esteves, F.A., 2011. Bioturbating space enhances the effects of non-additive interactions among benthic ecosystem engineers on cross-habitat nutrient regeneration. *Oikos* 120, 1639–1648, <http://dx.doi.org/10.1111/j.1600-0706.2011.19362.x>.
- Conley, D.J., Björck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B.G., Hietanen, S., Kortekaas, M., Kuosa, H., Meier, H.E.M., Müller-Karulis, B., Kjell Nordberg, Norkko, A., Nürnberg, G., Pitkänen, H., Rabalais, N.N., Rosenberg, R., Savchuk, O.P., Slomp, C.P., Voss, M., Wulff, F., Zillén, L., 2009. Hypoxia-related processes in the Baltic Sea. *Environ. Sci. Technol.* 43 (10), 3412–3420, <http://dx.doi.org/10.1021/es802762a>.
- Darwin, C., 1881. *The Formation of Vegetable Mould through the Action of Worms with Observations on Their Habits*. Murray, London.
- Denisenko, S., Sandler, H., Denisenko, N., Rachor, E., 1999. Current state of zoobenthos in two estuarine bays of the Barents and Kara Seas. *ICES J. Mar. Sci.* 56 (Suppl.), 187–193, <http://dx.doi.org/10.1006/jmsc.1999.0633>.
- Diaz, R.J., Rosenberg, R., 2001. Overview of anthropogenically induced hypoxic effects on marine benthos. In: Rabalias, N.T., Turner, R.E. (Eds.), *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*, vol. 58. Am. Geophys. Union, Washington, 129–145.
- Elmgren, R., 1984. Trophic dynamics in the enclosed, brackish Baltic Sea. *ICES Rapp. Proc. Verb.* 183, 152–169.
- Eremina, T.R., Maximov, A.A., Voloshchuk, E.V., 2012. The influence of the climate's variability on the deep-water oxygen conditions in the east of the Gulf of Finland. *Oceanology* 52, 771–779, <http://dx.doi.org/10.1134/S0001437012060045>.
- Eremina, T., Voloshchuk, E., Maximov, A., Ryabchenko, V., 2014. Biogeochemical changes on the sediment-water interface due to *Marenzelleria* spp. invasion in the eastern Gulf of Finland. In: *Baltic Earth – Gulf of Finland Year 2014 Modeling Workshop. International Baltic Earth Secretariat Publication* 4, p. 11.
- Ezhova, E., Zmudzinski, L., Maciejewska, K., 2005. Long-term trends in the macrozoobenthos of the Vistula Lagoon, southern Baltic Sea. Species composition and biomass distribution. *Bull. Sea Fish. Inst.* 1 (164), 55–73.
- Gran, V., Pitkänen, H., 1999. Denitrification in estuarine sediments in the eastern Gulf of Finland, Baltic Sea. *Hydrobiologia* 393, 107–115.
- Granberg, M.E., Gunnarsson, J.S., Hedman, J.E., Rosenberg, R., Jonsson, P., 2008. Bioturbation-driven release of organic contaminants from Baltic Sea sediments mediated by the invading polychaete *Marenzelleria neglecta*. *Environ. Sci. Technol.* 42, 1058–1065, <http://dx.doi.org/10.1021/es071607j>.
- Hedman, J.E., Gunnarsson, J.S., Samuelsson, G., Gilbert, F., 2011. Particle reworking and solute transport by the sediment-living polychaetes *Marenzelleria neglecta* and *Hediste diversicolor*. *J. Exp. Mar. Biol. Ecol.* 407 (2), 294–301, <http://dx.doi.org/10.1016/j.jembe.2011.06.026>.
- HELCOM, 2009. Eutrophication in the Baltic Sea – an integrated thematic assessment of the effects of nutrient enrichment and eutrophication in the Baltic Sea region. In: *Baltic Sea Environ. Proc.* 115B. 1–148.
- Hietanen, S., Laine, A.O., Lukkari, K., 2007. The complex effects of the invasive polychaetes *Marenzelleria* spp. on benthic nutrient dynamics. *J. Exp. Mar. Biol. Ecol.* 352, 89–102, <http://dx.doi.org/10.1016/j.jembe.2007.07.018>.
- Jirkov, I.A., 2001. *Polychaetes of the Arctic Ocean*. Yanus-K, Moscow, (in Russian).
- Josefson, A., Norkko, J., Norkko, A., 2012. Burial and decomposition of plant pigments in surface sediments of the Baltic Sea: role of oxygen and benthic fauna. *Mar. Ecol. Prog. Ser.* 455, 33–49, <http://dx.doi.org/10.3354/meps09661>.
- Karlson, A.M.L., Näslund, J., Rydén, S.B., Elmgren, R., 2011. Polychaete invader enhances resource utilization in a species-poor system. *Oecologia* 166, 1055–1065, <http://dx.doi.org/10.1007/s00442-011-1936-x>.
- Karlson, K., Bonsdorff, E., Rosenberg, R., 2007a. The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediments. *AMBIO* 36 (2–3), 161–167.
- Karlson, K., Hulth, S., Ringdahl, K., Rosenberg, R., 2005. Experimental recolonisation of Baltic Sea reduced sediments: survival of benthic macrofauna and effects on nutrient cycling. *Mar. Ecol. Prog. Ser.* 294, 35–49.
- Karlson, K., Hulth, S., Rosenberg, R., 2007b. Density of *Monoporeia affinis* and biogeochemistry in Baltic Sea sediments. *J. Exp. Mar. Biol. Ecol.* 344, 123–135, <http://dx.doi.org/10.1016/j.jembe.2006.11.016>.
- Karlsson, O.M., Jonsson, P.O., Lindgren, D., Malmaeus, J.M., Stehn, A., 2010. Indications of recovery from hypoxia in the inner Stockholm archipelago. *AMBIO* 39, 486–495, <http://dx.doi.org/10.1007/s13280-010-0079-3>.
- Kauppi, L., Norkko, A., Norkko, J., 2015. Large-scale species invasion into a low-diversity system: spatial and temporal distribution of the invasive polychaetes *Marenzelleria* spp. in the Baltic Sea. *Biol. Invasions* 17, 2055–2074, <http://dx.doi.org/10.1007/s10530-015-0860-0>.
- Kristensen, E., Hansen, T., Delefosse, M., Banta, G.T., Quintana, C. O., 2011. Contrasting effects of the polychaetes *Marenzelleria viridis* and *Nereis diversicolor* on benthic metabolism and solute

- transport in sandy coastal sediment. *Mar. Ecol. Prog. Ser.* 425, 125–139, <http://dx.doi.org/10.3354/meps09007>.
- Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O., Banta, G.T., 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Mar. Ecol. Prog. Ser.* 446, 285–302, <http://dx.doi.org/10.3354/meps09506>.
- Kube, J., Zettler, M.L., Gosselck, F., Ossig, S., Powilleit, M., 1996. Distribution of *Marenzelleria viridis* (Polychaeta: Spionidae) in the Southwestern Baltic Sea in 1993/94 – ten years after introduction. *Sarsia* 81, 131–142.
- Levich, A.P., 1996. The role of nitrogen-phosphorus ratio in selecting for dominance of phytoplankton by cyanobacteria or green algae and its application to reservoir management. *J. Aquat. Ecosyst. Health* 55–61.
- Levin, L.A., Ekau, W., Gooday, A.J., Jorissen, F., Middelburg, J.J., Naqvi, W., Neira, C., Rabalais, N.N., Zhang, J., 2009. Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences* 6, 2063–2098.
- Maximov, A., 2006. Causes of the bottom hypoxia in the eastern part of the Gulf of Finland in the Baltic Sea. *Oceanology* 46 (2), 185–191, <http://dx.doi.org/10.1134/S0001437006020056>.
- Maximov, A., 2011. Large-scale invasion of *Marenzelleria* spp. (Polychaeta; Spionidae) in the eastern Gulf of Finland, Baltic Sea. *Russ. J. Biol. Invasions* 2 (1), 11–19, <http://dx.doi.org/10.1134/S207511711010036>.
- Maximov, A.A., Eremina, T.R., Lange, E.K., Litvinchuk, L.F., Maximova, O.B., 2014. Regime shift in ecosystem of the eastern Gulf of Finland due to invasion of polychaetes *Marenzelleria arctica*. *Oceanology* 54 (1), 52–59, <http://dx.doi.org/10.1134/S0001437013060052>.
- Meysman, F.J.R., Middelburg, J.J., Heip, C.H.R., 2006. Bioturbation: a fresh look at Darwin's last idea. *Trends Ecol. Evol.* 21, 688–695, <http://dx.doi.org/10.1016/j.tree.2006.08.002>.
- Middelburg, J.J., Levin, L.A., 2010. Coastal hypoxia and sediment biogeochemistry. *Biogeosciences* 6, 1273–1293.
- Norkko, A., Jaale, M., 2008. Trends in soft sediment macrozoobenthic communities in the open sea areas of the Baltic sea. *MERI – Report Series of the Finnish Institute of Marine Research* 62, 73–79.
- Norkko, J., Reed, D.C., Timmermann, K., Norkko, A., Gustafsson, B. G., Bonsdorff, E., Slomp, C.P., Carstensen, J., Conley, D.J., 2012. A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biol.* 18 (2), 422–434, <http://dx.doi.org/10.1111/j.1365-2486.2011.02513.x>.
- Norling, K., Rosenberg, R., Hulth, S., Grémare, A., Bonsdorff, E., 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Mar. Ecol. Prog. Ser.* 332, 11–23.
- Quintana, C.O., Hansen, T., Delefosse, M., Banta, G., Kristensen, E., 2011. Burrow ventilation and associated porewater irrigation by the polychaete *Marenzelleria viridis*. *J. Exp. Mar. Biol. Ecol.* 397, 179–187, <http://dx.doi.org/10.1016/j.jembe.2010.12.006>.
- Quintana, C.O., Kristensen, E., Valdemarsen, T., 2013. Impact of the invasive polychaete *Marenzelleria viridis* on the biogeochemistry of sandy marine sediments. *Biogeochemistry* 115, 95–109, <http://dx.doi.org/10.1007/s10533-012-9820-2>.
- Quintana, C.O., Tang, M., Kristensen, E., 2007. Simultaneous study of particle reworking, irrigation transport and reaction rates in sediment bioturbated by the polychaetes *Heteromastus* and *Marenzelleria*. *J. Exp. Mar. Biol. Ecol.* 352, 392–406.
- Renz, J.R., Forster, S., 2013. Are similar worms different? A comparative tracer study on bioturbation in the three sibling species *Marenzelleria arctica*, *M. viridis*, and *M. neglecta* from the Baltic Sea. *Limnol. Oceanogr.* 58 (6), 2046–2058, <http://dx.doi.org/10.4319/lo.2013.58.6.2046>.
- Renz, J.R., Forster, S., 2014. Effects of bioirrigation by the three sibling species of *Marenzelleria* spp. on solute fluxes and porewater nutrient profiles. *Mar. Ecol. Prog. Ser.* 505, 145–159.
- Rumohr, H., Bonsdorff, E., Pearson, T.H., 1996. Zoobenthic succession in Baltic sedimentary habitats. *Arch. Fish. Mar. Res.* 44 (3), 179–214.
- Savchuk, O.P., 2010. Large-scale dynamics of hypoxia in the Baltic Sea. In: Yakushev, E.V. (Ed.), *Chemical Structure of Pelagic Redox Interfaces, Observation and Modeling*. Springer-Verlag, Berlin, Heidelberg, 137–160.
- Sikorski, A., Bick, A., 2004. Revision of *Marenzelleria* Mesnil, 1896 (Spionidae, Polychaeta). *Sarsia* 89, 253–275.
- Sikorski, A.V., Buzhinskaya, G.N., 1998. Genus *Marenzelleria* (Polychaeta, Spionidae) in the Russian Seas. *Zool. Zh.* 77 (10), 1111–1120, (in Russian).
- Skei, J., Larsson, P., Rosenberg, R., Jonsson, P., Olsson, M., Broman, D., 2000. Eutrophication and contaminants in aquatic ecosystems. *AMBIO* 29 (4), 184–194, <http://dx.doi.org/10.1579/0044-7447-29.4.184>.
- Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., Srivastava, D.S., 2004. Extinction and ecosystem function in the marine benthos. *Science* 306, 1177–1180, <http://dx.doi.org/10.1126/science.1103960>.
- Steckbauer, A., Duarte, C.M., Carstensen, J., Vaquer-Sunyer, R., Conley, D.J., 2011. Ecosystem impacts of hypoxia: thresholds of hypoxia and pathways to recovery. *Environ. Res. Lett.* 6, 025003, <http://dx.doi.org/10.1088/1748-9326/6/2/025003> 12 pp.
- Stief, P., 2013. Stimulation of microbial nitrogen cycling in aquatic ecosystems by benthic macrofauna: mechanisms and environmental implications. *Biogeosciences* 10, 7829–7846, <http://dx.doi.org/10.5194/bg-10-7829-2013>.
- Straube, D., Johnson, E.A., Parkinson, D., Scheu, S., Eisenhauer, N., 2009. Nonlinearity of effects of invasive ecosystem engineers on abiotic soil properties and soil biota. *Oikos* 118 (6), 885–896, <http://dx.doi.org/10.1111/j.1600-0706.2009.17405.x>.
- Timmermann, K., Norkko, J., Janas, U., Norkko, A., Gustafsson, B. G., Bonsdorff, E., 2012. Modelling macrofaunal biomass in relation to hypoxia and nutrient loading. *J. Mar. Syst.* 105, 60–69.
- Urban-Malinga, B., Warzocha, J., Zalewski, M., 2013. Effects of the invasive polychaete *Marenzelleria* spp. on benthic processes and meiobenthos of a species-poor brackish system. *J. Sea Res.* 80, 25–34, <http://dx.doi.org/10.1016/j.jseares.2013.02.005>.
- Vahtera, E., Conley, D.J., Gustafsson, B.G., Kuosa, H., Pitkänen, H., Savchuk, O.P., Tamminen, T., Viitasalo, M., Voss, M., Wasmund, N., Wulff, F., 2007. Internal ecosystem feedbacks enhance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic Sea. *AMBIO* 36 (2), 186–194.
- Viitasalo-Frösén, S., Laine, A., Lehtiniemi, M., 2009. Habitat modification mediated by motile surface stirrers versus semi-motile burrowers: potential for a positive feedback mechanism in a eutrophied ecosystem. *Mar. Ecol. Prog. Ser.* 376, 21–32, <http://dx.doi.org/10.3354/meps07788>.
- Villnäs, A., Norkko, A., 2011. Benthic diversity gradients and shifting baselines: implications for assessing environmental status. *Ecol. Appl.* 21, 2172–2186, <http://dx.doi.org/10.1890/10-1473.1>.
- Villnäs, A., Norkko, J., Lukkari, K., Hewitt, J., Norkko, A., 2012. Consequences of increasing hypoxic disturbance on benthic communities and ecosystem functioning. *PLoS ONE* 7 (10), e44920, <http://dx.doi.org/10.1371/journal.pone.0044920>.
- Zettler, M.L., Daunys, D., Kotta, J., Bick, A., 2002. History and success of invasion into the Baltic Sea: the polychaete *Marenzelleria cf. viridis*, development and strategies. In: Leppakoski, et al. (Eds.), *Invasive Aquatic Species of Europe*. Kluwer Academic Publishers, 66–75.