RESEARCH ARTICLE

Effects of an invasive polychaete on benthic phosphorus cycling at sea basin scale: An ecosystem disservice

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Abstract Macrofaunal activities in sediments modify nutrient fluxes in different ways including the expression of species-specific functional traits and density-dependent population processes. The invasive polychaete genus *Marenzelleria* was first observed in the Baltic Sea in the 1980s. It has caused changes in benthic processes and affected the functioning of ecosystem services such as nutrient regulation. The large-scale effects of these changes are not known. We estimated the current *Marenzelleria* spp. wet weight biomass in the Baltic Sea to be 60–87 kton (95% confidence interval). We assessed the potential impact of *Marenzelleria* spp. on phosphorus cycling using a spatially explicit model, comparing estimates of expected sediment to water phosphorus fluxes from a biophysical model to ecologically relevant experimental measurements of benthic phosphorus flux. The estimated yearly net increases (95% CI) in phosphorous flux due to *Marenzelleria* spp. were 4.2–6.1 kton based on the biophysical model and 6.3–9.1 kton based on experimental data. The current biomass densities of *Marenzelleria* spp. in the Baltic Sea enhance the phosphorus fluxes from sediment to water on a sea basin scale. Although high densities of *Marenzelleria* spp. can increase phosphorus retention locally, such biomass densities are uncommon. Thus, the major effect of *Marenzelleria* seems to be a large-scale net decrease in the self-cleaning capacity of the Baltic Sea that counteracts human efforts to mitigate eutrophication in the region.

Keywords Benthic–pelagic coupling · Ecosystem services · Eutrophication · Invasive species · Nutrient cycling

INTRODUCTION

Effective integration of ecosystem services in marine management involves spatial planning and decision making, identification, mapping and quantification of the relationship between ecosystem characteristics and their associated functions and services (de Groot et al. 2010). However, there are few examples of ecosystem services mapping in marine environments and the quality of available data (such as habitat maps) is often inadequate (Maes et al. 2012).

Deep soft-substrate sediments (sand and mud) cover approximately 80% of the Baltic Sea seafloor (Al-Hamdani and Reker 2007) and these habitats, including the organisms living there, provide ecosystem services such as the remineralization of nutrients through decomposition of organic matter. Benthic fauna enhance transport of materials and affect fluxes of oxygen and nutrients (Carstensen et al. 2014), but these processes are species-specific (Karlson et al. 2007, 2011; Norling et al. 2007) and density-dependent (Hietanen et al. 2007; Norkko et al. 2012). The quantitative influence of benthic fauna on various processes in the nitrogen and phosphorus cycles is not fully understood (Carstensen et al. 2014). *Marenzelleria* (Polychaeta) was first observed in the southern Baltic Sea in 1985 (Bick and Burckhardt 1989) and was likely introduced via ballast water. Three species of *Marenzelleria* have been identified in the Baltic Sea: *M. viridis*, *M. neglecta* and *M. arctia* (Blank et al. 2008). In their native waters (North American East coast and Russian Arctic

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Ocean), *Marenzelleria* spp. are relatively uncommon and their populations are limited by predation (Virnstein 1977; Sarda et al. 1995). The highly invasive *Marenzelleria* species complex is now an important component of the benthic community throughout the Baltic Sea (Leppäkoski and Olenin 2000; Zettler et al. 2002). Densities of several thousand individuals m^{-2} are often found in soft seafloor substrates (e.g. Kotta et al. 2001; Kauppi et al. 2015) but this genus is rarely a major component of the total biomass (Kauppi et al. 2015; Gogina et al. 2016).

The introduction of *Marenzelleria* spp. into the highly eutrophied Baltic Sea has probably changed important benthic processes across the entire region but the specific large-scale consequences of its introduction on the benthic ecosystem are poorly understood. Norkko et al. (2012) and Maximov et al. (2015) suggested that *Marenzelleria* spp. can improve insufficient oxygen conditions on the seafloor and thus enhance long-term phosphorus retention. They also suggested that this effect is probably density-dependent. *M. arctia* have been shown to significantly increase the resource use efficiency of freshly deposited organic matter in a typical Baltic Sea sediment community (Karlson et al. 2011). This suggests that organic matter deposition in the benthic community likely decreases when *Marenzelleria* spp. are present, enabling more nutrients to be assimilated in secondary production or remineralized. All three *Marenzelleria* species are mobile as sub-adults and adults and disperse over large distances in the planktonic larval phase. Adult individuals burrow deeper and are less sensitive to oxygen deficiency in sediments than native species such as *Limecola balthica*, *Monoporeia affinis* and *Pontoporeia femorata* (Hietanen et al. 2007; Karlson et al. 2011; Renz and Forster 2013). As hypoxia increases the benthic efflux of phosphate (Conley et al. 2002; Reed et al. 2011), an increase in oxidized sediments due to high abundances of *Marenzelleria* spp. could increase phosphorus retention across the entire Baltic Sea. Oxygenation of sediments per se, does not guarantee phosphorus retention. Increased phosphorous remineralization due to a higher utilization rate of deposited organic matter could further decrease phosphorus retention. High rates of phosphorus release from sediments occur even under oxic conditions, which have been observed in the Baltic Sea (Conley et al. 1997; Lehtoranta and Heiskanen 2003; Kauppi et al. 2017). *Marenzelleria* spp. increased phosphorus retention in one experimental study (Bonaglia et al. 2013) while other have reported decreased phosphorous retention (Hietanen et al. 2007; Viitasalo-Frösén et al. 2009; Renz and Forster 2014), or no distinguishable effect due to large variation among replicates (Karlson et al. 2005; Norling et al. 2007; Urban-Malinga et al. 2013).

A decrease in phosphorus recycling due to *Marenzelleria* spp. could benefit ocean water quality by increasing the

self-cleaning capacity of the sea. More of the phosphorus in the sea would be buried in the sediments (Norkko et al. 2012), counteracting eutrophication and its associated ecosystem damage. This suggests the possibility that certain targets on maximum phosphorus pools in the marine basin, such as the HELCOM (2013a) targets, may be obtained at a lower cost, as an increase in the ocean's self-cleaning capacity would decrease the cost of necessary human interventions such as pollution abatement measures in agriculture, industry or sewage (Gren et al. 2013). In contrast, an increase in phosphorus recycling may raise the cost of achieving maximum phosphorus pool targets because of the need for more phosphorus reduction at the sources. Thus, a quantification of the possible Baltic-wide influence of *Marenzelleria* spp. on phosphorus cycling is important for several stakeholders. From a management perspective, it would be desirable to have more complete data of the effects of non-indigenous marine species on relevant spatial and temporal scales in order to calculate costs and benefits from preventive actions, such as regulations on exchange of ballast water in international shipping. Since eradicating established invasive marine species is next to impossible, we should aim to reduce the risk of introducing additional species and mitigate the negative effects of existing invaders. Additional measures will be needed to achieve the aims of the EU Marine Strategy Framework Directive, and it is important for decision makers to have information on associated costs and benefits. The topic of potential large-scale effects of *Marenzelleria* spp. on Baltic Sea nutrient dynamics is also relevant to several international environmental commitments, e.g. the HELCOM Baltic Sea Action Plan and the EU Water Framework Directive.

This study provides basin scale quantifications of the potential net contribution of current *Marenzelleria* spp. biomass densities on phosphorous fluxes from the benthic to the pelagic ecosystem compartments in the Baltic Sea.

MATERIALS AND METHODS

A Random Forest model of *Marenzelleria* spp. biomass, based on relationships to environmental variables, was used to predict *Marenzelleria* spp. biomass across the entire Baltic Sea at a 200 m horizontal grid cell resolution. Random Forest is a machine-learning algorithm that utilizes many small classification or regression tree models to produce a combined result (i.e. the forest) for prediction (Breiman 2001). This method can quickly analyse very large datasets, automatically fit complex interactions between predictor variables, and estimate predictor variable importance. Cutler et al. (2007) provided a description

of Random Forest algorithms and their ecological applications.

The model was fit with randomForest for R (version 4.6-12) (Breiman 2001; Liaw and Wiener 2002; R Core Team 2014) using biomass data of *Marenzelleria* spp. from benthic grab samples from across the entire Baltic Sea. Data from the Helsinki Commission (2013b, c) were complemented with data from Finland (OIVA database, Finnish Environment Institute), Denmark (MADS database, National Environmental Research Institute MADS, mads-en.dmu.dk) and Sweden (SHARK database, Swedish Meteorological and Hydrological Institute). A total of 18 412 samples taken between 2000 and 2015 were collated. In most of the Baltic Sea area, environmental monitoring did not differentiate between the different species of *Marenzelleria*, which are known to hybridize (Götting et al. 2011). Therefore, species level data were aggregated to genus. As the grab sampling area varied among samples, all biomasses are expressed in g m^{-2} . Abundance information was only available for about 25% of the samples (mainly from archipelago areas in southern Sweden and Finland, where biomass data were scarce) and a conversion factor of $16.52 \text{ mg ind}^{-1}$ (the mean individual weight in Swedish monitoring data) was used to estimate wet weight biomass. To reduce autocorrelation bias in densely sampled areas, a 100 m buffer zone was created around each sampling location and whenever these buffer zones overlapped only the most recent sample was used. If there were several samples from the same year, one sample was selected at random. This method yielded a total of 8962 samples for use in the modelling. A total of 7962 samples were used to train the model, and 1000 randomly selected samples were set aside for subsequent (external) validation.

Environmental predictors covering depth, slope, halocline, salinity, temperature, Secchi depth, seafloor currents and wave exposure were available. Collinearity among predictors was tested using variance inflation factors (VIFs; Quinn and Keough 2002), and predictors with $\text{VIF} > 3$ were excluded from further analysis to facilitate model interpretation. The final model included a spatial layer derived from geographical latitude/longitude coordinates, depth, seafloor slope, standard deviation of salinity, Secchi depth, near-bed current speed and wave exposure. Details of the predictors used are shown in Table 1.

The model was used to predict *Marenzelleria* spp. biomass for the entire Baltic Sea at 200 m horizontal resolution. Confidence intervals were calculated using randomForestCI 1.0.0 (Wager et al. 2014; Wager 2016) for R (R Core Team 2014). Spatially explicit phosphorus fluxes were calculated using two different approaches: (i) based on the biophysical model by Norkko et al. (2012), and (ii) based on measured fluxes at naturally varying densities of *Marenzelleria* spp. (Norling 2007, see

Table 1 Environmental variables used in the analysis (1–7) and for exclusion of areas (8–10)

Environmental variables	Description	Sources
1 Depth	Interpolated depth, 200 m resolution	EMODnet
2 Slope	Seabed slope	BALANCE
3 Salinity	Standard deviation of seafloor salinity	EUSEaMap
4 Secchi depth	Modelled Secchi depth	EUSEaMap
5 Seafloor currents	Seafloor current speed	EUSEaMap
6 Wave exposure	Wave energy, log transformed	EUSEaMap
7 Coordinate layer	Latitude * longitude (decimal degrees)	
8 Substrate	Benthic marine landscapes, reclassified to rock, hard bottom complex, sand and mud + clay	BALANCE
9 Photic zone	Modelled photic zone	BALANCE
10 Oxygen depletion	Oxygen concentrations at seafloor, reclassified to $<$ or $> 2 \text{ ml l}^{-1}$	BALANCE

Appendix S1 for a summary). The shallow coastal zone (assumed to be equivalent to the BALANCE model of the photic zone, Al-Hamdani and Reker 2007) was excluded from the phosphorus calculations, as phosphorus dynamics in this zone are more complex due to uptake from primary producers, larger abundance of hard substrates, and proximity to anthropogenic phosphorus sources. The differentiation between shallow coastal and deep-water sites is supported by Kauppi et al. (2017), where phosphorous flux dynamics was compared. Anoxic or hypoxic (suboxic) areas in the Baltic (i.e. with bottom oxygen concentrations $< 2 \text{ mg l}^{-1}$) have no long-term occurrence of macroscopic fauna, including *Marenzelleria* spp., and were also excluded.

Measured phosphorus fluxes from intact sediment cores at different densities of *Marenzelleria* spp. from Norling (2007, Appendix S1, Table S1, Fig. S1) were used to derive a linear relationship between *Marenzelleria* spp. biomass and phosphorus flux between sediment and water (Table S2). We used the slope of the relationship as a model for the additional effect of *Marenzelleria* spp. in the presence of other species. Norkko et al. (2012) found that the depth-integrated phosphorus content of the sediment was a sigmoidal function of faunal density, with a net release of phosphorus for densities below ca. 3269 ind m^{-2} and a net burial at higher densities. As the function was only defined for values greater than 1000 ind m^{-2} , we extrapolated the phosphorous flux between 0 and 1000 ind m^{-2} using a quadratic polynomial function

($y = -0.0024x^2 + 0.1207x$). Since most samples lacked adequate sediment information (either missing or classified using very different methods), substrate was not used in the biomass model, although phosphorus cycling probably differs between sandy and muddy substrates. On sandy erosion bottoms, the phosphorus content in the upper 3 cm of the sediment was about half of that on silty-muddy accumulation bottoms (Viktorsson et al. 2013). In the model, we parameterized this and the typically lower average biomass in sand compared to mud (which is not accounted for in the biomass model, as substrate was not included as a predictor) through a phosphorus flux that was assumed to be 50% lower in sand (sediment type according to EUSeaMap, Table 1) compared to muddy sediments. For the linear function based on the Norling data ($y = 12.613x$), we assumed the phosphorous flux calculations to be representative of the summer, during which recently deposited organic material is available (Kauppi et al. 2017). The phosphorous flux values were therefore adjusted to be representative of 4 months during a typical year. The annual change in phosphorus flux was calculated for each grid cell and aggregated for each type of substrate and sea basin.

Table 2 Statistics for the *Marenzelleria* spp. biomass prediction including root-mean-square error (RMSE) and normalized root-mean-square error (NRMSE)

	Train	Test
RMSE	5.746	4.917
NRMSE	0.041	0.069
Mean	1.515	1.191
r^2	0.447	0.239

Sample sizes were $n_{\text{train}} = 7962$, $n_{\text{test}} = 1000$

RESULTS

The *Marenzelleria* spp. biomass model explained 57% of the sample variance. The normalized root-mean-square deviation (NRMSE) for observed versus predicted was 4% for training data and 7% for test data; r^2 was 0.45 and 0.24, respectively (Table 2). The model is of acceptable quality according to benchmarks described by Bučas et al. (2013). The model predicted a total average biomass of 73.4 kton *Marenzelleria* spp. in the Baltic Sea (Table 3) with a 95% CI of 60–87 kton.

The highest *Marenzelleria* spp. biomasses were predicted in the Gulf of Finland, Gulf of Riga, and along the Swedish Bothnian Sea coast. The maximum predicted wet weight biomass was 28.3 g m^{-2} , similar to the 99th percentile obtained from the experimental data (29.7 g m^{-2} ; Fig. 1a). Maps of confidence intervals, which provide measures of uncertainty, show that areas with larger uncertainties are Western Bothnian Sea as well as Eastern and Western Baltic Proper (Fig. 1b).

The average net change in phosphorus flux from sediment to water due to the presence of *Marenzelleria* spp. in the Baltic Sea was $7.7 \text{ kton year}^{-1}$ (95% CI of $6.3\text{--}9.2 \text{ kton year}^{-1}$) based on measured fluxes in sediment (Table 3; Fig. 1c). The corresponding average net change in phosphorus flux was $5.2 \text{ kton year}^{-1}$ (95% CI of $4.2\text{--}6.1 \text{ kton year}^{-1}$) based on the biophysical model (Table 3; Fig. 1d). The basins with the highest estimated increase in phosphorus flux was the Bothnian Sea and the Baltic Proper (Table 3; Fig. 1c, d). High expected increases in phosphorus flux were observed in archipelago areas in Sweden and Finland and in the Gulf of Riga (Fig. 1c, d). Maps of expected increases in phosphorus flux are available as electronic supplementary material in geo-referenced tiff format (Figs. S2 and S3).

Table 3 Average biomass of *Marenzelleria* spp. and average net phosphorous (P) flux per year, based on measured experimental data and biophysical model data

Basins	Biomass			P-flux (measured data)			P-flux (model data)		
	Average	Min	Max	Average	Min	Max	Average	Min	Max
Baltic Proper	21.1	15.7	26.9	2.2	1.6	2.8	1.5	1.1	1.9
Gulf of Riga	6.0	5.3	6.7	0.7	0.7	0.8	0.5	0.4	0.6
Gulf of Finland	15.9	14.5	17.4	1.6	1.5	1.8	1.1	1.0	1.2
Bothnian Sea	23.7	19.7	27.7	2.6	2.1	3.0	1.7	1.4	2.0
Bothnian Bay	6.6	4.9	8.3	0.6	0.4	0.7	0.4	0.3	0.5
Total	73.4	60.0	87.1	7.7	6.3	9.2	5.2	4.2	6.1

Sums are expressed in kton per basin. Min and max are based on 95% confidence intervals

Fig. 1 Baltic Sea maps of predicted *Marenzelleria* spp. biomass (a), its 95% confidence interval (b) and expected phosphorous release due to *Marenzelleria* spp. at a 200 m horizontal resolution, based on experimental data (c) and biophysical model data (d). White areas in the Baltic Sea are anoxic or hypoxic areas, which were excluded from the study as they have no long-term occurrence of macroscopic fauna. Maps of expected increases in phosphorus flux are available as electronic supplementary material in tiff format (Figs. S2 and S3). Figure colours used are taken from a palette developed for colour-blind people (<http://jfly.iam.u-tokyo.ac.jp/color/>)

DISCUSSION

Our results show that the current biomass densities of *Marenzelleria* spp. in the Baltic Sea increase the sea basin scale release of phosphorous from sediment to water. Although the activities of *Marenzelleria* spp. may potentially enhance long-term sedimentary phosphorus retention locally, the *Marenzelleria* spp. biomass densities needed to achieve this positive effect rarely occur. On the contrary, given the predicted biomasses, the recycling of phosphorus from Baltic Sea sediments to water is likely to increase, leading to higher dissolved concentrations and thus increased abatement costs for achieving internationally agreed reductions in phosphorus (HELCOM 2013a). Eutrophication is a severe problem in the Baltic Sea and all processes influencing nutrient cycling and availability need to be quantified. Although *Marenzelleria* spp., at high densities, could potentially provide a valuable ecosystem service by reducing phosphorous availability, in the current situation the opposite seems to be the case.

The invasion by *Marenzelleria* spp. followed a typical pattern for invasive species. The highest abundances occurred in 2005–2006 followed thereafter by decreased densities (Kauppi et al. 2015). As the data used in this study cover the time period 2000–2015, the temporal pattern was not resolved in our analysis. However, lower densities of *Marenzelleria* spp. than those found in this study would not contribute to a net burial of phosphorus according to our models. Gustafsson et al. (2012) estimated the release of phosphorus from Baltic Sea sediments at 229 kton year⁻¹ during 1997–2006 based on physical variables. Compared to this amount, the presence of *Marenzelleria* spp. increases recirculation of phosphorus from the sediments by 2–4%. Our current results, with their assumptions and uncertainties, give an indication of the large-scale effects of one genus and the potential magnitude of its influence on these processes.

Research on larvae of Chironomidae (Diptera) in lakes (Gallepp 1979; Chaffin and Kane 2010) have demonstrated release of phosphorus from sediments and this release is directly related to larval density. The maximum density (6585 larvae m⁻² = 28 g m⁻²) corresponded to a release of soluble reactive phosphorus of 2.8 g m⁻² year⁻¹ (Gallepp 1979), which is similar to our results (Fig. 1c, d). According to the function derived by Norkko et al. (2012), an abundance of 3269 ind m⁻², corresponding approximately to a biomass of 54 g m⁻², is necessary to reach the tipping point between net release and burial of phosphorous. Thus, if all the currently oxygen-depleted areas of the Baltic were to be oxygenized and colonized by *Marenzelleria* spp., a biomass of more than 54 g m⁻² would be required, according to the model, to counteract the stimulating effect of *Marenzelleria* spp. on phosphorus efflux

from the oxygenated sediments. The difference in *Marenzelleria* spp. densities that were applied in our model could be the main reason why the results from this study, that focus on larger scales, differ from the results of Norkko et al. (2012) who applied an equivalent model on a local and near-coastal scale. In coastal areas of Finland, Kauppi et al. (2015) found a maximum biomass of 57.73 g m⁻² which is sufficient to cause a net burial of phosphorous. However, in the open sea, they found a maximum biomass of only 26.86 g m⁻². Since we did not include the photic zone in the present study, the total effect of *Marenzelleria* spp. might differ from the results presented here. The open sea constitutes 90% of the area of the Baltic Proper and Gulf of Finland, and 80% of the area of the Gulf of Riga. Open Sea sediment processes are thus likely to dominate the overall effect of *Marenzelleria* spp. on larger scales. The Bothnian Sea and Bothnian Bay have, in comparison to the other sea basins, generally sandier substrates with lower organic content (Borg and Jonsson 1996; Leipe et al. 2011), and a higher iron availability (Borg and Jonsson 1996). Therefore, the phosphorous flux estimates for these basins are more uncertain and may likely be overestimated.

Ecologically relevant data on phosphorous fluxes across substrates, species, sea basins, seasons and a gradient of *Marenzelleria* spp. densities are unavailable so our study results are dependent upon several assumptions which contribute varying degrees of uncertainty. Different *Marenzelleria* species likely have different impacts on the Baltic Sea ecosystem as they vary in bioturbation activity (Renz and Forster 2013). Norkko et al. (2012) based the model on measured fluxes from Quintana et al. (2013), who studied *M. viridis*. Using this function we also inherit any assumptions they made and assume that the three *Marenzelleria* species have the same bioturbation activity. This may not be true, as the species vary in their functional ecology (Renz and Forster 2013), but due to the lack of distribution data on the individual *Marenzelleria* species, this assumption was necessary. Renz and Forster (2014) found clear differences among the *Marenzelleria* species when expressing phosphorous fluxes and water exchange rates per individual. However, due to the lighter individual biomass of *M. arctica*, the differences were small or indistinguishable when comparing wet weight rates across species. For the predominant muddy and deeper areas of the Baltic Sea, *M. arctica* is the most common of the three sibling species (Blank et al. 2008; Kauppi et al. 2018). The function based on measured flux data of *M. arctica* is thus more representative for most of the Baltic and is similar to the situation in the Gulf of Finland (Isaev et al. 2016). The substrate maps available on Baltic Sea are of poor quality, but are generally more accurate in deeper, homogenous areas, which were the main focus of this study. We accounted for seasonality in the model calculations and our

assumption agrees well with field measurements from a 33 m site (Kauppi et al. 2017). The *Marenzelleria* spp. biomass model explains a relatively modest 57% of the variance, but on larger scales this result was adequate. Relatively high natural variance in the model is also expected, due to both local population dynamics and patch bias resulting from the relatively small sampling area in benthic grab samples. Effects of the differences in functional ecology among the three *Marenzelleria* species on the study results are unclear. Renz and Forster (2013, 2014) demonstrated that effects on phosphate fluxes are similar (per wet weight) among all three species and suggest that interspecific differences are not significant in this case. Our experimental data were similar to the data used in other studies (Renz and Forster 2014; Kauppi 2017) when normalizing phosphorous fluxes to wet weight, further validating our results. An unaddressed variable, due to lack of applicable data, was the potential sorption of phosphorous to iron oxides. This could be of relatively greater importance in the Bothnian Sea and Bothnian Bay but may also interact with species-specific effects. Renz and Forster (2014) found a stimulation of anaerobic bacterial processes around the burrows of *M. neglecta* and *M. viridis* but not for *M. arctica*. A further source of variation in estimates for the Bothnian Sea and Bothnian Bay results from relatively low primary production in these basins and production highly limited by the long winter. Therefore, smaller amounts of organic matter are deposited. Nonetheless, the final results in this study were similar regardless of using theoretical modelling or based on experimental data assuming comparability across species. We are confident that the estimates are valid, especially for the Baltic Proper and the Gulf of Finland. The results show that the potential effects on Baltic Sea phosphorous fluxes are of significance for eutrophication management in the Baltic Sea region. We recommend that all national monitoring programmes in the Baltic Sea should determine *Marenzelleria* spp. samples to species level when appropriate, as an identification key is available for use on intact adult and subadult individuals (width about > 1.2 mm) (Bick 2005). Further research, especially on substrate mapping and ecologically relevant measurements of phosphorous flux at varying biomasses of *Marenzelleria* spp. is needed to increase estimate accuracy and further reduce uncertainties. This would provide data helpful for improving eutrophication management of the Baltic Sea.

CONCLUSIONS

Marenzelleria spp. cannot be eradicated from the Baltic Sea, so management options are limited to considering the effects of *Marenzelleria* spp. in eutrophication abatement

plans and avoiding introduction and spread of other invasive non-indigenous species. The estimated yearly increase in fluxes of phosphorus from the sediments to the water in the Baltic Proper corresponds to about 12% of the yearly burial (Gren et al. 2013). This means a corresponding reduction in the self-cleaning capacity of the basin. Gren et al. (2013) found that a 10% decrease in the self-cleaning capacity of the Baltic Proper increases the cost of meeting HELCOM (2013a) targets, within 70 years, by approximately 45% or 6.42×10^9 Swedish kronor per year (ECB exchange rate 2nd January 2018 was 1 Euro = 9.8 SEK). The results of this study show the potential effects of one invasive genus on an ecosystem and illustrate the necessity of management programmes for preventing the introduction of potentially invasive non-indigenous species. This study covers only one aspect of the ecosystem services or disservices provided by *Marenzelleria* spp. Considering the large total biomass of *Marenzelleria* spp. in the Baltic Sea, the genus is also likely to influence other processes on large scale. Processes that may have been influenced includes nitrogen cycling (Hietanen et al. 2007), oxygenation (Bonaglia et al. 2013), re-activation of high priority contaminants from pulp fibre sediments in the Bothnian Sea and Bothnian Bay, release of contaminants in Baltic Sea Proper areas (Granberg et al. 2008), and food availability for fish such as cod (Winkler and Debus 1996). An ecological function (bioturbation by *Marenzelleria* spp.) that could be an ecosystem disservice in some situations might be a benefit in other conditions (Saunders and Luck 2016). The magnitude of these opposite impacts can be effectively weighted and considered, when appropriate knowledge is available, using cost–benefit analysis.

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