

Influence of benthic invertebrates on phosphorus flux at the sediment–water interface in the easternmost Baltic Sea

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ABSTRACT: Since the late 2000s, 2 sediment-dwelling invertebrates, the polychaete *Marenzelleria arctia* and the oligochaete *Tubificoides pseudogaster*, have established populations in the Gulf of Finland (Baltic Sea). This article focuses on the effects of these and other benthic species on sediment–water phosphate flux in the easternmost part of the gulf. We estimated total phosphate (soluble reactive form, P-PO₄³⁻) fluxes (P_{flux}), the benthic biomass in intact sediment cores and the phosphate excretion (P_{exc}) by abundant benthic animals at 4 sites ranging in depth from 20–50 m in the gulf during the Catamaran ‘Centaurus-II’ cruise in August 2015. We found significant positive correlations between P_{exc} and benthic biomass (especially *M. arctia* and *Monoporeia affinis*) and negative correlations between P_{flux} and benthic variables (biomass and abundance). P_{flux} in intact sediment–water cores containing various benthic animals ranged from –2890 to +1180 μmol m⁻² d⁻¹. Mass-specific P_{exc} in *M. arctia* was at least 4 times higher than in other species (*Limecola balthica*, *Saduria entomon*, *M. affinis* and *T. pseudogaster*). Total benthic excretion rates varied from 320 to 3460 μmol m⁻² d⁻¹; 79–98 % of which was released by *M. arctia*. This work reveals a direct effect of benthic animals (via excretion) on phosphate dynamics at the sediment–water interface in the marine environment.

KEY WORDS: Benthic–pelagic coupling · Benthic fluxes · Bioturbation · Excretion · Phosphorus cycling · Invasive species · Functional group · Gulf of Finland

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1. INTRODUCTION

Nitrogen (N) and phosphorus (P) are needed for syntheses of proteins, RNA, DNA and energy transfer, and are the key limiting nutrients for primary production in most marine ecosystems. Human-mediated input of nutrients to coastal areas has led to eutrophication, harmful algal blooms and ‘dead hypoxic zones’ at the sea floor (Rabalais et al. 2009). In the Baltic Sea, the effects of eutrophication are also associated with the most important changes in the ecosystem (Andersen et al. 2015). In this regard, many countries along the Baltic Sea shore have sought to reduce external N and P loads into the sea. Trends for the whole Baltic Sea show that, due to the

efforts and actions taken by these countries, flow-normalized inputs of total N and P to the Baltic Sea from 1994 to 2010 decreased by 16 and 18 %, respectively (HELCOM 2015). Despite this nutrient management strategy (including a target to reduce external nutrient loads by 40–50 % compared to the late 1980s), the Gulf of Finland (the easternmost part of the Baltic Sea) still contains large amounts of nutrients (Raateoja & Setälä 2016).

Significant progress has been made by the scientific community in understanding the mechanisms of water eutrophication in the marine environment (Howarth et al. 2011). In the Baltic Sea, N is the nutrient that limits spring phytoplankton production; the sinking spring bloom provides organic matter to bot-

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tom waters, resulting in bottom hypoxia (Vahtera et al. 2007, Savchuk 2010). Deterioration of the oxygen regime leads to intensive P release from the sediments to the water. The lowering of the N:P ratio then stimulates a summer bloom of cyanobacteria, which fix N_2 and therefore increase N in surface waters (Funkey et al. 2014). This 'new' N helps to sustain further algae production, causing the next algae bloom (Vahtera et al. 2007). The development of N-fixing cyanobacteria during summer is therefore supported by internal P sources: rapidly recycled within the water column or released from sediments.

Diffusive molecular P fluxes with pore water at the sediment–water interface are strongly dependent on oxygen conditions in the sediments and water near the bottom. Hypoxia increases the P release rate from the sediment to the water, while normoxia decreases the rate or even reverses this process (Lehtoranta 1998, Clavero et al. 2000, Conley et al. 2002). P is a redox-sensitive nutrient, and dissolved phosphates released into the pore water may be adsorbed onto ferric iron under oxic conditions. The Fe (oxy)-hydroxide and Mn–Fe oxide/hydroxide particles in the oxygenated sediment surface act as a trap for phosphate diffusing upwards (Dellwig et al. 2010). For example, in the eastern part of the Gulf of Finland in the 1990s, the positive diffusive P flux for reduced sediments with oxygen $<3 \text{ mg l}^{-1}$ reached $+387 \mu\text{mol m}^{-2} \text{ d}^{-1}$, while the P flux for surface oxygenated sediments was low, averaging $+16 \mu\text{mol m}^{-2} \text{ d}^{-1}$ (Lehtoranta 1998).

It is well known that the activity of benthic animals in the sediment, such as bioturbation (the stirring of sediment by living organisms due to burrowing, ingestion and defecation of sediment grains) and bioirrigation (burrow ventilation), may be important factors affecting P fluxes as in the Baltic and other seas (Karlson et al. 2007, Kristensen et al. 2012, Carstensen et al. 2014). Burrowing organisms (oligochaetes, polychaetes and chironomids) are able to alter biogeochemical cycling within surface sediments by increasing solute fluxes, mixing solid sediment and upward-bio-conveying of sediment particles (Hölker et al. 2015). At the same time, P flux from benthic animals, including excretion as a direct source of dissolved nutrients, has received little attention in the marine environment (Vink & Atkinson 1985, Johannes 2003). In other ecosystems (mostly freshwater lakes), benthic animals have been shown to be important heterotrophs, releasing soluble reactive phosphates from oxygenated sediment through their excretory activity (Devine & Vanni 2002, Ji et al. 2011, Berezina et al. 2017, Vanni et al. 2017). Bottom

animals contribute about 20% to the total P content in European lakes (Vanni et al. 2017), and their role in P cycling might be comparable to other sources known to be important, such as P inputs from watersheds and release from sediments via microbial processes. For example, in oxygenated sediments of Lake Acton, OH, USA, the soluble reactive P flux was $13.7 \mu\text{mol P m}^{-2} \text{ d}^{-1}$ by direct release from sediments and $81.1 \mu\text{mol P m}^{-2} \text{ d}^{-1}$ by benthic invertebrate excretion (Devine & Vanni 2002).

Benthic animals excrete P, originating from the consumption of detritus and sediment particles, directly into the water column, almost completely in the form of soluble (dissolved) reactive orthophosphate, which is considered to be completely available for producers (algae, cyanobacteria). They release particulate P with feces and dissolved P with urine, so that P excretion rates relate functionally with the body mass and food habits of consumers (Golubkov & Berezina 2012, Vanni & McIntyre 2016). In addition, it had been shown that benthic animals (including amphipods) can influence the activity of alkaline phosphatase, a hydrolase enzyme which is responsible for removing phosphates from many types of molecules and may be an important means for cyanobacteria and algae to generate free phosphate groups for uptake and use as an additional source of free P in the case of low availability of phosphates in the water (Berezina et al. 2017).

Ekeröth et al. (2016) revealed that benthic animals may shift chemical processes at the water–sediment interface by colonization of previously anoxic bottom sediment (in an example from the Western Gotland Basin). Several non-indigenous species, including the polychaete *Marenzelleria arctica* and the oligochaete *Tubificoides pseudogaster*, have actively colonized the bottom environment in the Gulf of Finland (Maximov 2015). In the Baltic Sea, *Marenzelleria* spp. have the potential to affect sediment nutrient dynamics and conditions on the seafloor due to their abundance, the deep burrows they dig (25–35 cm into the sediment) and their clear resilience to challenging environmental conditions such as low oxygen concentrations (Hietanen et al. 2007). The quantitative influence of benthic animals on various processes in the P cycle is not fully understood (Carstensen et al. 2014). These processes are species-specific (Karlson et al. 2007) and density-dependent (Hietanen et al. 2007, Norkko et al. 2012). It has been shown that *Marenzelleria* spp. can influence nutrient fluxes at the sediment–water interface by bioturbation (Hietanen et al. 2007) and bioirrigation (Maximov et al. 2015). The potential impact of these ani-

mals on P cycling was estimated using a spatially explicit model, comparing estimates of expected sediment-to-water P fluxes from a biophysical model to ecologically relevant experimental measurements of benthic P flux (Sandman et al. 2018). At the same time, there have been no quantitative field estimates of P excretion rates by these species, which are new to the Gulf of Finland, and other abundant benthic animals; the role of macrofauna in the P cycling therefore remains unclear.

The major focus of this study was to understand how benthic animals can affect biochemical processes in the sediment and P cycle in the marine ecosystem. Our hypothesis is that P flux from oxygenated sediments to the water, mediated by benthic animals via excretion (urine production) and together with other mechanisms (bioturbation, bioirrigation), can be an important mechanism of nutrient translocation from the sediments to the water in the marine environment. We addressed this question by studying the composition and biomass of zoobenthos, P excretion rates by abundant benthic species and total P fluxes at the sediment–water interface at various sites in the easternmost part of the Gulf of Finland. P excretion rates were further compared between various benthic animals with different modes of feeding and physical activity in sediments, in order to compare the effects on P fluxes by the recently established and very abundant species in the gulf (the polychaete *M. arctia* and the oligochaete *T. pseudogaster*) and local species. Our results further contribute to an explanation of the mechanism of water eutrophication and the factors causing cyanobacterial blooms in marine coastal ecosystems.

2. MATERIALS AND METHODS

2.1. Study area

The Gulf of Finland (29 700 km²) comprises 7% of the total area of the Baltic Sea. The study location is in the gulf area, situated east of Gogland Island and commonly referred to as the ‘Eastern part of the Gulf of Finland’ (EGoF) (12 500 km²). The EGoF is strongly influenced by the rivers flowing into the gulf, primarily the Neva River (Fig. 1). The Neva River forms one of the largest estuaries in the Baltic Sea, with a gradient of water salinity from fresh to 8.5. Neva Bay (400 km²), the easternmost freshwater part of the EGoF, is separated from the open gulf by St. Petersburg’s storm-surge dike (Neva Bay was not included in this study).

Four study sites with various communities of zoobenthos were selected along the central transect (Fig. 1); Sites 1 (17F) and 2 (2ugms) were located in the open marine areas in the EGoF, while Sites 3 (4F) and 4 (2F) were in the Neva River estuarine zone. According to A. Maximov (unpubl. data), 5 species (the polychaete *Marenzelleria arctia*, the oligochaete *Tubificoides pseudogaster*, the bivalve mollusk *Limecola balthica*, the isopod *Saduria entomon* and the amphipod *Monoporeia affinis*) were the most abundant taxa at these sites in 2015. The biomass of *M. arctia* achieved 20–23 g wet weight (WW) m⁻² at Sites 1–3 and 40 g WW m⁻² at Site 4. The biomass of *L. balthica* was highest at Site 1 (up to 26 g WW m⁻²), while *T. pseudogaster* (up to 20 g WW m⁻²) and *S. entomon* (13 g WW m⁻²) were the leading taxa at Site 2. The native amphipod *M. affinis* was a common species at Sites 1–3 but its biomass was not high (<3 g WW m⁻²). The invasive annelids and *M. affinis* also dominated in abundance (see Table 1).

2.2. Sampling and laboratory procedures

All sampling of sediment, water and benthos, as well as incubations of the sediment–water cores and direct measurements of P excretion, was carried out during the research cruise of the R/V Catamaran ‘Centaurus II’ in early August 2015. All chemical analyses were conducted immediately after sampling or during experiments in the ship-board laboratory.

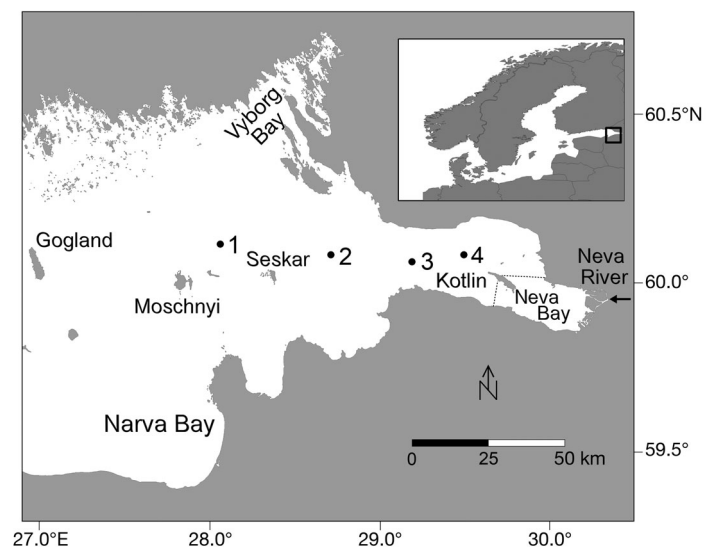


Fig. 1. Eastern Gulf of Finland with study site locations 1–4 marked (dark circles). Arrow: storm surge artificial barrier

CTD and Rosette samplers were used to collect deep water samples for experiments and to measure salinity and temperature. The Winkler method was used to determine the level of dissolved oxygen in the water. Phosphates in the water were estimated using the molybdenum blue method; the detection limit of this method is 5–100 $\mu\text{g l}^{-1}$ (Murphy & Riley 1962).

Muddy sediments were collected by gravity cores (Fig. 2). The amount of total organic carbon in the sediment was measured by coulometric titration on an AN-7529M carbon express-analyzer; with a detection limit of 0.03–9.999%.

Benthic animals in the sediment cores were counted and weighted after total flux measurement. Sediments were passed through a 0.125 mm sieve, and all animals were picked out of the samples and identified with a microscope to the highest taxon separation before being counted and weighted on a torsion balance with a precision of ± 0.01 mg. Prior to evaluation of WW, water was removed from the animal's body using filter paper (the shell of mollusks was included). To obtain dry weight (DW), animals were dried to a constant weight at 60°C for 96 h.



Fig. 2. Gravity corer used for collection of intact sediment–water cores

2.3. P fluxes in cores

The direct method, based on experimental incubation of intact sediments with water collected in the field, was used to evaluate total P flux. A total of 8 intact sediment–water columns were collected from each sampling site by a gravity corer (Fig. 2) equipped with four 40 cm Plexiglas columns (3 cm internal diameter), 6 of which were used for exposition and 2 to measure initial concentration. The collected sediment layer was approximately 10 cm in height with 30 cm of water. These sealed cores were incubated in dark conditions and at temperatures of 12–15°C for 4 h (time of exposure was the same for the excretion experiments). This water temperature corresponds to the 20 m depth isobath in the gulf during the period of study. Final dissolved phosphates in the water overlying the cores were measured after incubation, and changed by 25–40%. Oxygen varied from 4.2 to 3.9–4.0 ml $\text{O}_2 \text{l}^{-1}$ in cores from Site 1 (5%); this level was reduced by 20–30% in the other cores during incubation.

Total dissolved phosphate fluxes (P_{flux}) across the sediment–water interface were calculated as the difference between the initial and final concentrations in the overlying water according to formula $P_{\text{flux}} = M A^{-1} T^{-1}$, where P_{flux} is the phosphate flux ($\mu\text{mol m}^{-2} \text{d}^{-1}$), $M = V(C_t - C_{t_0})$, where V is the total volume of overlying water in the core (in l), C_t and C_{t_0} are the dissolved phosphate concentrations at times t and t_0 , respectively in the water ($\mu\text{mol l}^{-1}$), A is the surface of the sediment enclosed by the flux corer (m^2) and T is exposure time (in days).

2.4. P excretion experiments

The excretion rates of dissolved orthophosphates P-PO_4^{3-} (soluble reactive phosphorus, SRP) were estimated by the direct method as previously described (Devine & Vanni 2002, Ji et al. 2011). According to metabolic ecology predictions, many biological rates, including nutrient excretion, are power functions of body mass/size (Gillooly et al. 2001). This dependence is usually captured in the formula $B = B_0 M^b$, where B is the individual's metabolic rate (e.g. P excreted $\text{ind.}^{-1} \text{unit}^{-1} \text{time}$), B_0 is a 'normalization constant', M is body mass, and b is the scaling coefficient.

For this study, P excretion rates were measured experimentally in 5 taxa of benthic animals from at Sites 2 and 3. Animals were collected carefully (with a pipette or spoon) from the surface water of sedi-

ment and placed into clean bottom water from the study sites (at a temperature of 15°C) for several minutes to remove silt particles. Then the animals were moved to 100 ml glass vials (acid cleaned) that had been 90%-filled with filtered bottom water (0.45 µm pore size filter). As the study animals were adapted to live close to the bottom, artificial substrate was not added, since particles can affect the accuracy of measurements. From 1 to 50 individuals of each species were used for exposition (separately for each taxon), increasing the number from larger to smaller animals, i.e. 1 ind. vial⁻¹ of *S. entomon*, 2–4 ind. of *L. balthica*, 5–15 ind. of *M. arctia*, 5–10 ind. of *M. affinis* and 40–50 ind. of *T. pseudogaster*. The individual DW (around 20% of WW) ranged from 0.015–0.208 g for *L. balthica*, 0.03–0.3 g for *S. entomon*, 0.02–0.15 g for *M. affinis*, 0.003–0.02 g for *M. arctia* and 0.001–0.005 g for *T. pseudogaster*.

After the vials were completely filled with water they were tightly closed. For each species, 7 to 16 vials (see Table 2) containing animals and 3 controls without animals were run simultaneously under water in darkness for 4 h. Salinity, oxygen level and SRP concentrations in used bottom water were measured before exposure (see Table 1). Control vials contained the same water used for incubation of the animals, which allowed for identification of non-species-mediated changes in the SRP concentration. When the experiments were completed, SRP concentrations were measured in all vials to calculate the P excretion rate. In preliminary experiments, we found that oxygen levels in the vials with biomass did not decrease below 20% over 4 h (5% h⁻¹), thus there was no effect of hypoxia.

After the experiment was complete, all animals were carefully collected from the vials, counted and weighted with a torsion balance (precision: 0.01 mg) to obtain WW and DW (the same approach as with animals from cores). No animals died during the experiment.

The P excretion rate (P_{exc} ; µg P h⁻¹) was calculated as the difference between the SRP concentrations in treatments and controls divided by the experiment duration (4 h). Empirical data on P_{exc} values were obtained as a power function of individual DW. The mass-specific P excretion rate (P_{exc}/DW ; nmol mg⁻¹ h⁻¹; Fig. 3) of animals was further used for calculations of benthic P efflux rates (in cores). Units and exposition time used were as suggested by Vanni et al. (2017).

The total P efflux rate (µmol P m⁻² d⁻¹) for zoobenthos was calculated as a sum of the SRP released by each taxon over 24 h, multiplying its corresponding

biomass in the sediment cores at each site, and then re-calculating on 1 m² of bottom surface.

2.5 Statistics

All measured parameters are expressed as an arithmetical mean value and standard error (±SE). The relationships between measured phosphate sediment release and benthic excretion and biomass/abundance of benthos in the cores were analyzed using the nonparametric Spearman rank correlation, since the data were not normally distributed. Differences in mean values of biomass, abundance of benthic fauna, phosphate excretion rates and fluxes between sites were analyzed by ANOVA using the non-parametric Kruskal-Wallis *H*-test and the Mann-Whitney *U*-test for pair-wise comparisons. Differences in the relative rate of excreted SRP (i.e. P_{exc}) depending on DW of animals were analyzed by pair-wise comparison of slope/intercept of P_{exc}/DW regressions. Results were considered significant at $p < 0.05$. The software package STATISTICA v.10.0 was used.

3. RESULTS

3.1. Site characteristics

Coordinates, location and depths at the study sites, as well as salinity, oxygen and P concentrations of bottom water are presented in Table 1. Bottom sediments were mainly (60–70%) composed of pelitic (particle size <0.01 mm) and silt (0.01–0.05 mm) fractions, and showed high similarity between sites. The sand fraction (0.05–2 mm) ranged from negligible values (<3%) at Sites 1 and 4–8 to 13% at Sites 2 and 3. Anoxia at the sediment surface and hypoxia in the bottom water were not observed (Table 1). The depth of the oxygenated layer (grey colored sediments) was around 5 cm at Sites 2–4 but was <1 cm at Site 1. Total organic carbon in the sediments ranged from 1.2–4.1% (Table 1).

3.2. Benthic abundance and biomass in cores

The mean abundance and biomass of studied taxa varied significantly among sites (Kruskal-Wallis ANOVA, $p < 0.05$; Fig. 4). The abundance of *Marenzelleria arctia* was significantly higher in cores from Site 4 (12 857 ind. m⁻²) compared to the other sites

Table 1. Main physical, chemical and biotic characteristics of study sites in the eastern Gulf of Finland. Site name is used in local monitoring programs. D: site depth, S: salinity; P: soluble reactive phosphates ($P-PO_4^{3-}$); O_2 : oxygen concentration of water near the bottom; POC: particulate organic carbon in sediment; B and N: wet biomass and abundance of macrozoobenthos. % B and % N are percentage contributions of taxa to the total biomass and abundance, respectively. L.b.: *Limecola balthica*; Mar.: *Marenzelleria arctica*; M.a.: *Monoporeia affinis*; S.e.: *Saduria entomon*; T.p.: *Tubificoides pseudogaster*

Site no.	Site name	Coordinates	D (m)	Bottom water					Sediment		
				S (ppt)	P ($\mu\text{mol l}^{-1}$)	O_2 (ml l^{-1})	POC (%)	B (g m^{-2})	% B	N (ind. m^{-2})	% N
1	17F	60° 06.91' N, 28° 04.00' E	51	5.2	1.45	4.02	4.1	51.2	50 (L.b.), 45 (Mar.)	2160	52 (Mar.), 45 (M.a.)
2	2ugms	60° 05.01' N, 28° 43.00' E	37	4.5	1.51	3.83	3.1	63.5	31 (Mar.), 31 (T.p.), 21 (S.e.)	15 220	83 (T.p.), 10 (M.a.)
3	4F	60° 03.79' N, 29° 11.60' E	30	4	1.55	4.85	2.1	26.5	90 (Mar.), 10 (M.a.)	5140	80 (Mar.), 20 (M.a.)
4	2F	60° 05.01' N, 29° 29.94' E	21	3.2	3.97	2.75	1.2	42.6	94 (Mar.)	21 320	80 (Mar.)

(Sites 1–3: 571–714 ind. m^{-2}). Also, oligochaete biomass (presented only by the invasive *Tubificoides pseudogaster*) was much higher at Site 2 than the other sites (Fig. 4).

3.3. P_{flux} in cores

P fluxes were estimated from -0.52 to $+0.13$ $\text{mmol P m}^{-2} \text{d}^{-1}$ in cores from Site 3, and appeared strongly negative at Site 4 (-3.02 to -2.74 $\text{mmol P m}^{-2} \text{d}^{-1}$). Differences between the mean P_{flux} at Site 3 (-0.20) and Site 4 (-2.89) were significant (Kruskal-Wallis ANOVA, $p < 0.05$). P fluxes at Sites 1 and 2 were mostly positive (from the bottom sediment to underlying water), at $+0.74$ and $+1.18$ $\text{mmol P m}^{-2} \text{d}^{-1}$, respectively (Fig. 5). There was a significant difference in total P fluxes, with Site 2 being 2 times higher

than Site 1 (Kruskal-Wallis ANOVA, $p < 0.05$). Site 4 was distinguished from other sites by having a negative P flux (P uptake) and, in addition, by a high rate of excreted phosphates (3.46 $\text{mmol m}^{-2} \text{d}^{-1}$).

3.4. P excretion by benthic animals

The mass-specific P excretion rate (P_{exc}) was highest in the polychaete *M. arctica*; at least 4 times higher than the rates of the other species studied (Table 2, Fig. 3). For example, the 1 individual of *M. arctica* with DW of 9.1 mg could excrete 4 $\text{nmol P mg}^{-1} \text{DW h}^{-1}$. The P_{exc}/DW regression line of *M. arctica* differed significantly from the corresponding lines of the other species: *Limecola balthica*, *Saduria entomon* (F -test, $p < 0.001$) and *Monoporeia affinis* and *T. pseudogaster* ($t_{\text{intercept}} = 11.96$, $p < 0.001$; and $t_{\text{intercept}} = 10.29$, $p < 0.001$, respectively).

The P_{exc} rates of *L. balthica* and *M. affinis* were significantly higher than those of the other 2 species, *T. pseudogaster* and *M. affinis*, which were similar to each other (Fig. 3). An F -test did not reveal significant differences in the regression lines (and thus, level of P_{exc}) of *L. balthica* and *M. affinis* ($F = 0.003$, $t_{\text{intercept}} = 2.44$, $p > 0.05$) and *T. pseudogaster* and *M. affinis* ($F = 0.35$, $t_{\text{intercept}} = 2.10$, $p > 0.05$).

The whole benthic community excreted 0.72 $\text{mmol P m}^{-2} \text{d}^{-1}$ (Site 1) to 3.52 $\text{mmol P m}^{-2} \text{d}^{-1}$ (Site 4), averaging 1.59 ± 0.66 $\text{mmol m}^{-2} \text{d}^{-1}$ (Fig. 4). No significant differences in P_{exc} were found between Sites 1 and 3, where it averaged 0.32 – 0.46 $\text{mmol m}^{-2} \text{d}^{-1}$. The polychaete *M. arctica* contributed 79–98% to the total P excretion. The input of the oligochaete *T. pseudogaster* was important only at Site 2 (11.5%). P_{exc} com-

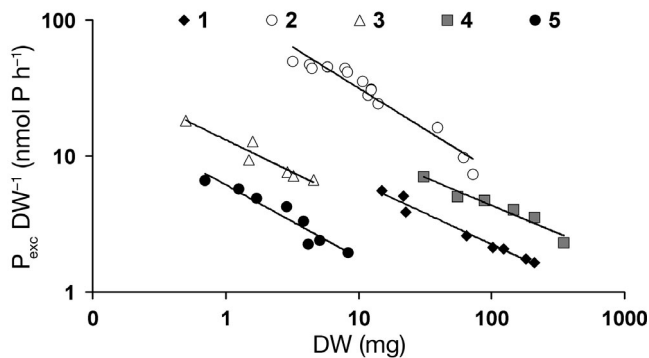


Fig. 3. Intensity of soluble reactive phosphorus excretion rates (relative value per unit dry mass $P_{\text{exc}} \text{DW}^{-1}$) versus the body dry mass (DW) and regression lines of diverse taxa collected at the study sites. 1: *Limecola balthica*; 2: *Marenzelleria arctica*; 3: *Monoporeia affinis*; 4: *Saduria entomon*; 5: *Tubificoides pseudogaster*

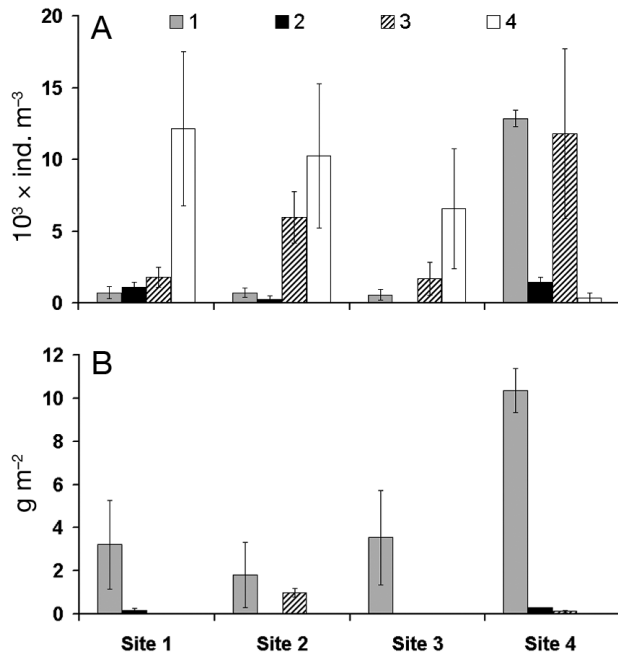


Fig. 4. (A) Abundance and (B) biomass of benthic animals found in sediment cores. 1: *Marenzelleria arctia*; 2: *Monoporeia affinis*; 3: *Oligochaeta*; 4: *Nematoda*

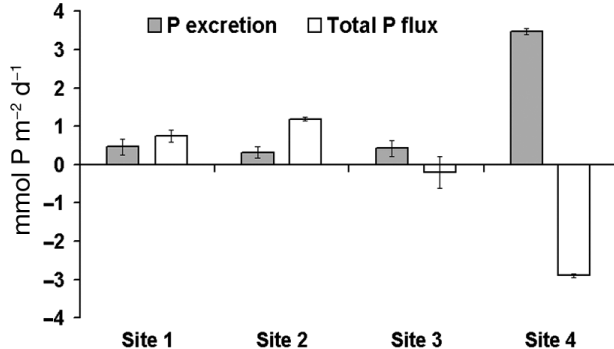


Fig. 5. Total phosphorus flux (P_{flux} ; $\text{mmol m}^{-2} \text{d}^{-1}$) and P excreted by whole benthic community (P_{exc} ; $\text{mmol m}^{-2} \text{d}^{-1}$), estimated in sediment cores at the study sites

Table 2. Mean (\pm SE) mass-specific excretion rates (P_{exc}) of soluble reactive phosphorus ($\text{nmol P}_{\text{exc}} \text{mg}^{-1} \text{h}^{-1}$) obtained experimentally for different taxa with dry mass (DW) at water temperature 15°C , and power functions of P_{exc}/DW regressions ($P_{1\text{exc}}-P_{5\text{exc}}$). n: number of experimental series; R^2 : coefficient of determination

Species	n	R^2	DW (mg)	P_{exc}	Formula for calculation
<i>Limecola balthica</i>	8	0.98	93 ± 26	0.31 ± 0.05	$P_{1\text{exc}} = 1.84 \text{ DW}^{-0.46}$
<i>Marenzelleria arctia</i>	16	0.71	9 ± 1	4.29 ± 0.27	$P_{2\text{exc}} = 12.4 \text{ DW}^{-0.51}$
<i>Monoporeia affinis</i>	9	0.84	2.4 ± 0.4	0.99 ± 0.12	$P_{3\text{exc}} = 1.33 \text{ DW}^{-0.47}$
<i>Saduria entomon</i>	7	0.94	129 ± 34	0.42 ± 0.06	$P_{4\text{exc}} = 4.8 \text{ DW}^{-0.54}$
<i>Tubificoides pseudogaster</i>	8	0.91	3.5 ± 0.9	0.39 ± 0.06	$P_{5\text{exc}} = 0.62 \text{ DW}^{-0.54}$

prised 27–61% of total P fluxes at Sites 1 and 2, where the P fluxes were positive.

3.5. Correlations

P excreted by zoobenthos (P_{exc}) and the total phosphate flux (P_{flux}) varied between cores. Spearman's rank correlation found a significant ($p < 0.05$) relationship between the biomass/abundance of zoobenthos (and dominating species) and P_{exc} and P_{flux} (Table 3). The biomass of zoobenthos, *M. arctia* and *M. affinis* correlated positively with P_{exc} and negatively with P_{flux} (Table 3). The total abundance of zoobenthos and P_{flux} correlated negatively. At the same time, a significant positive correlation was found between the biomass of oligochaetes and P flux, but no correlation was found for variables of this taxa and the total P_{exc} . The highest negative correlation ($p < 0.01$) was found between P_{flux} and the abundance of *Marenzelleria* (-0.52 ; $p < 0.05$) while the high positive correlations were found between P_{exc} and its abundance and biomass ($+0.92$ and $+0.96$; $p < 0.01$).

4. DISCUSSION

The P fluxes derived from incubation measurement at our study sites (i.e. the total P flux) ranged from -2890 to $+1180 \mu\text{mol P m}^{-2} \text{d}^{-1}$. P fluxes directed from the overlying water into the sediment were extremely large at Site 4 ($-2890 \mu\text{mol m}^{-2} \text{d}^{-1}$). At the other sites, P fluxes ranged from -520 to $+1180 \mu\text{mol m}^{-2} \text{d}^{-1}$, which is in the range of values obtained at other time periods from the Gulf of Finland and other regions (Table 4). In the case of artificially created anoxia in sediments from the Gulf of Finland, P fluxes from the sediment to the overlying water were 1100 – $1300 \mu\text{mol m}^{-2} \text{d}^{-1}$ (Thouvenot-Korppoo et al. 2012).

Some studies have concluded that P fluxes appear to be related primarily to oxygen conditions, and that oxygenated sediments are essentially uninfluenced by bioturbation due to specific community composition (e.g. larger species present; Gray & Elliott 2009, Ekeroth et al. 2012). Another study (Łukawska-Matuszewska & Burska 2011) showed an apparent effect of benthic bioturbation on sedi-

Table 3. Spearman rank correlation between abundance (N) and biomass (B) of different benthic taxa and the total flux (P_{flux}) and benthic excretion (P_{exc}) of phosphates in all cores. **Bold** represents significance at $**p < 0.01$ and $*p < 0.05$. -: not applicable

Variables	P_{flux}	P_{exc}
P_{exc}	-0.46*	-
Total abundance	-0.57*	0.27
N <i>Marenzelleria</i>	-0.52*	0.92**
N <i>Monoporeia</i>	-0.39*	0.60*
N Oligochaeta	0.08	0.38
Total biomass	-0.44*	0.98**
B <i>Marenzelleria</i>	-0.48*	0.96**
B <i>Monoporeia</i>	-0.48*	0.62*
B Oligochaeta	0.48*	0.05

ment P fluxes ($-912 \pm 648 \mu\text{mol m}^{-2} \text{d}^{-1}$) in the Gulf of Gdansk. We found clear and strong relationships between the amounts of different benthic taxa and the P flux rate as well as its direction through the sediment–water interface in our study area, showing that macrofauna notably affect P fluxes in oxygenated sediment.

The P fluxes were directed from the overlying water into the sediment (sedimentary uptake) and estimated as being very large ($-2890 \mu\text{mol m}^{-2} \text{d}^{-1}$) at Site 4, which also had a very high abundance and biomass of the polychaete *M. arctia* (17 000 ind. m^{-2} and 40 g m^{-2} ; A. A. Maximov unpubl. data). No clear effect of *M. arctia* bioturbation on P flux was found at lower abundances (1000 ind. m^{-2} ; Sites 1 and 2). *Marenzelleria* spp. stimulate P retention by oxygenating the sediment because of their high abundance (Renz & Forster 2014). Recent experiments by

Table 4. Total phosphorus flux (P_{flux}) estimated in different parts of the Baltic Sea

Area	P_{flux} ($\mu\text{mol m}^{-2} \text{d}^{-1}$)	Reference
Gulf of Finland	38 to 684	Conley et al. (1997)
	-6 to 1000	Pitkänen et al. (2001)
	-245 to 1774	Lukkari (2008)
	3 to 2795	Norkko et al. (2015)
Eastern Gulf of Finland	-2580 to 1180	This study
Gulf of Gdansk	-926 to 679	Łukawska-Matuszewska & Burska (2011)
Gotland Deeps	69 to 137	Graca et al. (2006)
Eastern Gotland Basin	-263 to 457	Norkko et al. (2015)
Southern Baltic Proper	-32 to 734	Norkko et al. 2(015)
Northern Baltic Proper	41 to 888	Koop et al. (1990)
Gulf of Bothnia	-21 to 174	Norkko et al. (2015)

Quintana et al. (2018) revealed that due to the oxidizing effect of bioirrigation in low salinity muddy sediments by *M. arctia* the PO_4^{3-} adsorption capacity increased two-fold relative to defaunated sediments, suggesting that *M. arctia*'s presence in sediments can result in increased P retention.

The polychaete *M. arctia* is distinguished as a 'gallery-diffuser', able to dig systems of galleries, tubes or burrows in sediment and therefore to enhance bioirrigation. Bioirrigation as a result of burrowing worms can stimulate the exchange of solutes between sediment particles and bottom water by increasing the area of the contact zone at the sediment–water interface and transporting newly settled particles to the deeper sediment layers via their burrows. In addition, polychaetes are able to increase the particle surface area for microbial colonization, altering the size of particles and pore spaces (Josefson et al. 2012). Thus, activities of gallery-diffusers lead to the transport of matter from the surface to the deep part of the tubes due to fecal egestion and urine excretion, and to solute diffusion through the burrow walls. At the same time, high concentrations of phosphates were found in the bottom water ($3.97 \mu\text{mol l}^{-1}$) at Site 4, almost triple of that of other sites ($1.45\text{--}1.55 \mu\text{mol l}^{-1}$), along with some depletion in the bottom water oxygen (2.75 ml l^{-1} or 3.93 mg l^{-1}). An uptake of phosphates at Site 4 may be the result of combined effects, including external nutrient loading (from Neva River runoff), physical processes and P dynamics in the pore water, that require further study.

Tubificids (oligochaetes) are upward-conveyors that burrow into the sediment vertically and ingest sediment there before defecating on the sediment surface.

Fisher et al. (1980) found that oligochaetes feed and mix sediment within the top 5 cm, transporting particulate material through the gut; they can release soluble P with urine and deposit the particulate material in feces on the sediment surface. This explains the positive relationship between oligochaete biomass and the P flux rate found in this study. In contrast to the polychaete *M. arctia*, oligochaetes constructed no visually oxygenated galleries in the sediment and, in accordance with the findings of Zhang et al. (2010), did not significantly alter P in the pore water.

The significant relationships we found in this study between abundance/biomass of the amphipod *M. affinis* and P fluxes confirm the important influence of high abundances of this taxon on P release from the sediment to the underlying water. Direct relationships between P

excreted by some amphipods and activity of extracellular phosphatase in water were recorded experimentally (Berezina et al. 2017), which confirms the high bioavailability of excreted compounds, facilitating further cyanobacteria and algae growth and blooms. Amphipods are regenerators and gallery-digging species, feeding in the sediment to a depth of 6 cm and transferring sediment to the surface. They, and the mobile isopod *S. entomon*, are able to re-suspend surface sediment, providing additional P release. The re-suspension by the 2 crustaceans *M. affinis* and *M. mixta* resulted in a notable P release to the water in the central Baltic Sea (Ekeröth et al. 2012). A negative but minor effect of *M. affinis* on P release was revealed previously (Tuominen et al. 1999, Karlson 2007).

At the same time, benthic uptake rates in sediments inhabited by *M. affinis* were shown to be higher than those containing the bivalve mollusk *L. balthica* (Ekeröth et al. 2012). There was no significant P uptake from the sediment bioturbated (and re-suspended) by *L. balthica* recorded from coastal oxygenated sediments in the Gulf of Finland (Lethoranta & Heiskanen 2003). The burrowing bivalve *L. balthica* has been recorded elsewhere as stimulating P release to the water column (Karlson et al. 2005, Viitasalo-Frösén et al. 2009). *L. balthica* is therefore a biodiffuser that can move sediment in a random manner over a short distance, resulting in diffusive sediment transport and having a low effect on P uptake.

The positive relationship between the rate of P liberation from sediment cores and the biomass of benthic fauna, confirming importance of the excreted P release, was observed in previous studies (Holdren & Armstrong 1980). At study sites in the Baltic Sea, characterized mainly by oxygenated sediment surface, benthic animals contributed notably (up to 61%) to the total P flux from the sediment to the water directly via excretion. Another example (Oosterschelde Estuary, the Netherlands) based on a comparison of *in situ* measurements and individual nutrient excretion rates showed that excretion by the blue mussel *Mytilus edulis* contributed 31–85% to the total phosphate flux from the mussel bed (Prins & Smaal 1994). At the same time, notable differences were revealed for the mass-specific SPR excretion rates between the benthic taxa. For example, the invasive polychaete *M. arctia* generally showed higher P excretion rates than the native species *L. balthica*, *M. affinis* and *S. entomon*.

This study has shown that the activity of benthic animals is among the primary factors influencing nutrient cycling and eutrophication of the Baltic Sea,

and potentially other marine systems, especially in well-mixed coastal or estuarine areas. Animal excretory products may be not only in inorganic form (i.e. dissolved inorganic phosphorus, DIP), but also organic (dissolved organic phosphorus, DOP), and even particulate P fractions; and they may be highly bioavailable (Nausch & Nausch 2007). Benthic animals can recycle P if they convert it (either directly via excretion or indirectly via microbial-mediated processes) from organic to inorganic form. They can also influence nutrient regeneration if they only redistribute P (without changing its chemical form) from the sediment to the water, or vice-versa. Therefore, P cycling in the seafloor can be affected by benthic animal-mediated recycling and regeneration.

The obtained results showed that the activity of recently established *M. arctia* in the sediment may notably influence the direction of phosphate flux (P release or uptake), but this effect is dependent on its abundance. P immobilization would be greatly increased at abundances >3500 ind. m⁻². Mobile swimming organisms (amphipods and isopods) can transfer phosphates between benthic and pelagic habitats, i.e. they may facilitate increasing pelagic algal production of phytoplankton through enhanced P mobilization from the sediment to the water.

The conclusion of our study is that benthic animal-controlled P flux is a steady-state phenomenon in oxic bioturbated marine sediments, but it is species- and context-specific. Further detailed studies are still needed in each type of marine environment to assess possible consequences at the ecosystem level.

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