Bioturbation in relation to the depth distribution of macrozoobenthos in the southwestern Baltic Sea

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ABSTRACT: Ongoing climate change is causing rapid changes in biodiversity and has ecological impacts on coastal marine systems. Predicting scenarios of how these pressures will affect bioturbation, a process vital to marine communities and human well-being, has become an important task. A first step is a better understanding of the interaction between macrofauna and the surrounding environment. Here, bioturbation (local and non-local sediment mixing) was surveyed using a high-resolution depth distribution of macrobenthos in the southwestern Baltic Sea, which is characterized by different sediment types and faunal communities. The distribution of local and non-local mixing with increasing non-local transports from west to east was explained by comparing vertical chlorophyll profiles and organisms' depth distributions. The main bioturbators were identified based on chlorophyll profiles and community bioturbation potential (BP_c) and by categorizing the main species into functional groups. *Diastylis rathkei* is most important for local sediment mixing, and bivalves, e.g. *Arctica islandica* and *Limecola balthica*, together with polychaetes, e.g. *Nephtys hombergii* and *Scoloplos armiger*, are most important for non-local transports. Significant correlations between modeled local and non-local mixing intensities and calculated BP_c ($105-1298$ m^{-2}) indicate that BP_c is a suitable bioturbation indicator; however, it does not provide information on the different modes of mixing. Some species categorized as biodiffusors in the literature were found to cause non-local mixing according to their feeding behavior (e.g. *L. balthica*), size (e.g. *Abra alba*) or biomass (e.g. *A. islandica*).

KEY WORDS: Bioturbation · Macrozoobenthos · Local and non-local transport · Bioturbation potential · Main bioturbator · Functional groups

INTRODUCTION

Benthic infaunal organisms affect the physical and chemical properties of the sediment they live in through burrowing, feeding, defecation and locomotion (Gray 1974, Rhoads 1974, Aller 1982, Rhoads & Boyer 1982, Gilbert et al. 1995, Lohrer et al. 2004). These bioturbation processes carried out by benthic organisms in marine sediments include both particle reworking and burrow ventilation (Kristensen et al. 2012).

Bioturbation depends on relationships between organisms and their surrounding environment. Therefore, determining and quantifying sediment mixing and its interaction with benthic infauna are necessary

steps in understanding, interpreting and predicting benthic ecosystem functioning (Williamson et al. 1999, Biles et al. 2002, Solan et al. 2004, Suding et al. 2008). Bioturbation influences sedimentary oxygen, pH and redox gradients (Stahl et al. 2006, Pischedda et al. 2008, Queirós et al. 2011), metal cycling (Teal et al. 2009), pollutant release or permanent burial (Gilbert et al. 1994, 1996, Ciarelli et al. 1999, Ciutat & Boudou 2003, Magnusson et al. 2003), bacterial activity and composition (Mermillod-Blondin & Rosenberg 2006, Gilbertson et al. 2012), and carbon (Kristensen 2001) as well as nitrogen cycling (Bertics et al. 2010). These regulating mechanisms are well recognized, as a result of which the evaluation of so-called ecosystem services has moved into focus in recent years

(Millennium Ecosystem Assessment 2005). Such services are often measured as proxies for ecosystem health and functioning to indicate environmental change (Widdicombe & Austen 1998, Lohrer et al. 2004, Webb & Eyre 2004, Thrush et al. 2006). Many of the processes mediated by bioturbation make important contributions to human well-being, such as the regulation of climate through burial of carbon in marine sediments. Thus, observing, understanding and explaining large-scale patterns of bioturbation are of relevance to policymakers and other stakeholders of the marine environment.

Particle reworking can be analyzed by the spatial and temporal distributions of certain tracers in the sediment (Meysman et al. 2003). Investigating their vertical profiles allows differentiation between 2 modes of sediment mixing: local and non-local. When using tracers that originate from the water column, local sediment mixing is indicated by an exponential decrease of the tracer with sediment depth, whereas non-local particle transport is defined by the occurrence of subsurface increase of the tracer due to e.g. discrete burrowing events or feeding behavior (Boudreau 1986).

Some macrozoobenthic species are major bioturbators in marine sediments (Boudreau 1998). It is important to expand our knowledge of bioturbation. This requires extensive studies on the most abundant and dominant species and their influence on sediment mixing, which, in turn, depends on their behavior and response to changing biotic and abiotic environmental factors (Gérino 1990, Biles et al. 2002, Ouellette et al. 2004). Effects of community structure on bioturbation and thus on ecosystem functioning are important due to ongoing global species loss and pressure on many habitats (Pimm et al. 1995, Watson et al. 1995). Even omnipresent macrobenthic species show some habitat preferences, as indicated by changes in abundance across environmental gradients (Ysebaert & Herman 2002, Thrush et al. 2003). Hence, changes in organism density and/or behavior may influence sediment mixing, affecting important processes such as nutrient cycling (Widdicombe & Austen 1998, Lohrer et al. 2004, Sandwell et al. 2009).

The southwestern Baltic Sea is characterized by shallow sandy areas as well as muddy basins with different patterns in the distribution and intensity of local and non-local sediment mixing (Morys et al. 2016). In a previous study, the percentage of non-local sediment mixing was found to

increase from west to east. Based on these findings, the present study attempts to explain the patterns found in the southwestern Baltic Sea by focusing on the interaction between sediment mixing and species' distribution. The depth distribution of macrozoobenthic organisms was determined as well as their community bioturbation potential (BP_c) within the sediment, and the species were categorized into functional groups following their biological traits, e.g. trophic guild, mobility, lifestyle mode (Bremner et al. 2006, Norling et al. 2007, Suding et al. 2008, Kristensen et al. 2012). Bioturbation intensities were estimated using vertical chl profiles at 6 stations. The same cores were used for determining macrofauna community structures. The aims of the present study were to: (1) explain observed bioturbation patterns based on the presence and depth distribution of macrofauna; (2) identify the main bioturbating species; and (3) categorize bioturbators into functional groups at each station.

MATERIALS AND METHODS

Study area

During a cruise onboard RV 'Alkor' (AL434) in April 2014, 6 stations in the southwestern Baltic Sea (Fig. 1, Table 1) were investigated, covering various sediment types with different macrozoobenthic communities (Tauber 2012, Schiele et al. 2015). Information on sediment properties was taken from the geological map of the southwestern Baltic Sea (Tauber 2012). In the west, 2 muddy stations (Lübeck Bay, LB; Mecklenburg Bay, MB) and one sandy station (Stoltera, ST) were analyzed. Arkona Basin (AB, mud), Oderbank (OB, sand) and Tromper Wiek (TW, silt) are located in the east. Salinity data were obtained from a CTD (Seabird
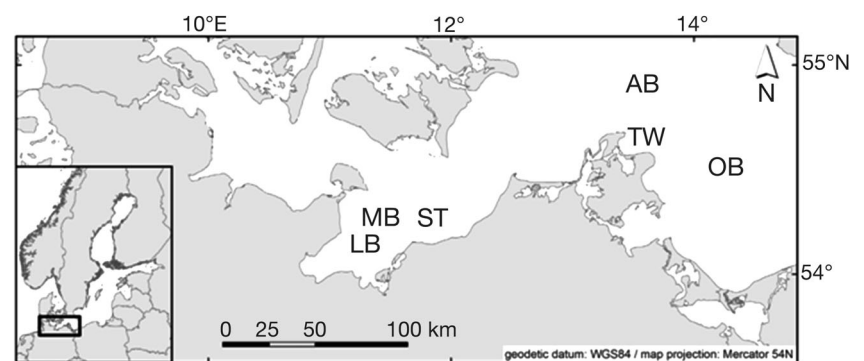

Fig. 1. Study area and distribution of the 6 stations investigated. LB: Lübeck Bay; MB: Mecklenburg Bay; ST: Stoltera; AB: Arkona Basin; TW: Tromper Wiek; OB: Oderbank (in Morys et al. 2016)

SBE9plus). The stations are within a salinity gradient from west (22 at LB) to east (8 at OB). All stations are located below the photic zone between 16 and 45 m water depth (Table 1). Each area differs in terms of dominant bioturbating organisms, which will be highlighted more precisely in the 'Discussion'. Further information characterizing each station is reported in Morys et al. (2016).

Sampling and laboratory analyses

The sampling design used in this study consists of sampling stations and locations. Stations are the study areas LB, MB, ST, AB, TW and OB in the southwestern Baltic Sea. Locations define the sampling positions at each station where a multicorer (MUC, diameter = 10 cm) was deployed. At each station, 6 locations were investigated with 4 cores each, resulting in 24 cores in total (except at OB: 23 cores). The cores were sliced onboard immediately after retrieval at 0.5 cm intervals to 3 cm depth and at 1 cm intervals to 10 cm depth to analyze sediment mixing using vertical chlorophyll profiles. All sliced samples were deep-frozen (−18°C, including macrofauna) and stored until extraction (Sun et al. 1991). Chlorophyll was measured photometrically (663 and 750 nm), calculated based on HELCOM (1988) and is abbreviated below as 'chl' for simplification. The chosen method delivers a combination of chl a and its degradation products, which is regarded as organic matter in the present study. After chl analyses, residual sediment of each slice was sieved through a 500 µm screen to inspect the composition of macro-zoobenthos and the vertical depth distribution of abundance and biomass within the sediment at each station. A total of 24 cores were investigated at LB, MB and ST, 10 at AB and TW, and 6 at OB for the depth distribution of both chl and macrofauna. The animals were preserved with buffered 4% formaldehyde. A stereomicroscope with 10–40× magnification was used for sorting the organisms in the laboratory. Each organism was identified to the lowest taxonomic level possible and nomenclature was checked following the World Register of Marine Species (WoRMS Editorial Board 2017). At TW, species-specific polychaete abundance and biomass data are not available due to technical issues, impeding the calculation of BP_c. Therefore, we used 3 additional cores to determine species abundance of polychaetes only (see Table 2). Dry weight (60°C) was determined for biomass. Abundance and biomass were then used for calculating the bioturbation potential index for a single species, i, (BP_i) and community bioturbation potential index (BP_c), a metric first described by Solan et al. (2004), by the following equation:

$$BP_c = \sum_{i=1}^{n} \sqrt{B_i / A_i} \times A_i \times M_i \times R_i \quad (1)$$

BP_c combines species' abundance (A_i) and biomass (B_i, dry weight in the present study) with 2 biological traits describing sediment mixing: sediment reworking (R_i) and mobility (M_i). Categorical scales listed by Queirós et al. (2013) were used, who scored each taxon with increasing mobility from 1 (fixed tube) to 4 (free moving via burrows) and increasing sediment reworking from 1 (epifauna) to 5 (regenerators). Hence, BP_c is not a direct measure but rather estimates the potential of a macrobenthic community to mix the sediment (Queirós et al. 2013). Species that are not presented in the list were scored as follows: *Trochochaeta multisetosa* ($M_i = 2$; $R_i = 3$), *Halicryptus spinulosus* ($M_i = 2$; $R_i = 4$), *Bylgides sarsi* ($M_i = 3$; $R_i = 2$), *Dipolydora quadrilobata* ($M_i = 1$; $R_i = 3$), *Neoamphitrite figulus* ($M_i = 1$; $R_i = 3$) and *Parvicardium pinnulatum* ($M_i: = 2$; $R_i: = 2$). Individuals of *Sphaerodoropsis baltica* were too small for accurate determination of biomass, consequently their BP was zero. First, BP_i was calculated for each slice of all investigated cores at each station for a comparison with the depth distribution of abundance and biomass in this study. Second, BP_c was determined for each core

Table 1. Water depth, salinity (surface and near bottom), bottom water temperature, chl concentration in surface sediment (0–0.5 cm), chl inventory of bioturbated zone (0–5 cm), sediment type following Tauber (2012), median grain size (0–3 cm), and percentage of local, non-local and no sediment mixing (Morys et al. 2016) at each station during sampling. LB: Lübeck Bay; MB: Mecklenburg Bay; ST: Stoltera; AB: Arkona Basin; TW: Tromper Wiek; OB: Oderbank

			Station			
	LB	MB	ST	AB	TW	OB
Depth (m)	23	25	18	45	30	16
Salinity (surface)	17	17	11	8	8	8
Salinity (near bottom)	22	23	23	19	10	8
Temperature (bottom water) (°C)	5.5	5.9	5.8	5.5	4.5	5.6
Chl (surface) (µg cm^{-3})	17.2	7.1	5.9	10.8	8.4	21.1
Chl (0–5 cm) (µg 5 cm^{-3})	56.9	41.4	31	73.3	47.5	53.3
Sediment type	Mud	Mud	Sand	Mud	Silt	Sand
Median (µm)	19.4	17.4	148.8	22.9	27.3	181
Local mixing (%)	58	46	63	33	0	26
Non-local mixing (%)	29	29	37	67	100	70
No mixing (%)	13	25	0	0	0	4

separately, regardless of its faunal vertical distribution, for comparison with modeled mixing intensities (bioturbation coefficient [D_B], injection flux [J] and ingestion rate [R]) estimated by the bio-mixing model (see further Soetaert et al. 1996).

The most dominant species or their taxonomic groups in terms of abundance and/or biomass (see Table 2) were assigned to one of the 4 major categories of organisms' life traits reported by Kristensen et al. (2012) (as modified from François et al. 1997 and Solan & Wigham 2005): biodiffusors, upward conveyors, downward conveyors and regenerators.

Modeling bioturbation

For a quantitative description of bioturbation intensity, the vertical chl profiles were interpreted using the bio-mixing model developed by Soetaert et al. (1996). The model consists of 6 different models with increasing complexity. Continuous sedimentation without biological and hydrographical sediment mixing (model 1) or steady-state diffusive (local) mixing delivering a bioturbation coefficient D_B (cm^2 d^{-1}) (model 2) can be detected. Non-local sediment mixing is either quantified by the injection flux J (µg cm^{-2} d^{-1}) of particles to a certain depth (model 3) or into a layer (model 4a) or by ingestion rates R (µg d^{-1}) at a certain depth (model 4b) or in a layer (model 5). The visual fit between modeled and observed data is improved by introducing new parameters into the model, which increases the complexity. A 1-tailed F-test determines whether the more complex model significantly better explains the observed data (p < 0.05) (Sokal & Rohlf 1995):

$$F = \frac{(SSR1 - SSR2) /}{(df1 - df2) / (SSR2 / df2)} \quad (2)$$

with SSR2 and SSR1 being the sum of the squared residuals of observed and modeled values of the elaborate and simple model, respectively, and df1 and df2 being the degrees of freedom of the respective models. For a more detailed description of the bio-mixing model see Soetaert et al. (1996). Values of 0.01 d^{-1} for mud and 0.02 d^{-1} for sand were taken from experiments in a previous study (Morys et al. 2016) and were used as decay constants of chl as required in the model. Sedimentation rate ω was defined to be very low (0.00001 cm d^{-1}). Model results are presented in detail in a previous study (Morys et al. 2016), while here they are only reported for comparison with BP$_c$ and additional information obtained by the model, e.g. depth of J and R (= L).

Statistical analyses

Statistical analyses were carried out using the software package IBM SPSS Statistics 22. Depending on data distributions, either parametric (Pearson) or non-parametric (Spearman) bivariate correlations were performed to compare depth distributions of chl and abundance, biomass and BP using individual and averaged chl profiles. A significance level of p ≤ 0.05 was used throughout the data analyses. Abundance, biomass and BP were determined within each depth layer and core. First, chl profiles and depth distribution of organisms, biomass and BP were correlated for all individual cores investigated at each station to determine whether bioturbation patterns indicated by chl depth distribution actually depend on macrofauna abundance and/or biomass. Second, the same correlations were carried out using mean chl profiles and the depth distribution of the sum of organisms, biomass and BP using all cores taken at one station. The third step was to calculate BP$_c$ for each core covering all depth layers. The BP$_c$ of each core was correlated with modeled D_B, J and R of the same core, regardless of station, for an evaluation of both estimates of sediment mixing (BP$_c$ calculation vs. bio-mixing model based on tracer profiles). Cores indicating no sediment mixing (= model 1, D_B = 0) according to the bio-mixing model were excluded from all statistical analyses.

RESULTS

General characterization of the macrobenthos

Abundance

The composition of the macrozoobenthic communities at each station is presented in Table 2 and Fig. 2a. Macrobenthic species belong to several taxonomic groups, e.g. polychaeta, bivalvia, malacostraca, priapulida and gastropoda, depending on the station considered. LB, ST and AB were mainly populated by the class bivalvia. The communities at ST and AB showed a similar composition of macrobenthic taxa. Malacostraca dominated the fauna at MB, whereas polychaetes played a minor role at MB and OB. Polychaetes were the most dominant taxonomic group at TW. *Peringia* sp. became more dominant towards the east, where it was the most abundant species at OB. Priapulida were not present at OB.

Table 2. Abundance, biomass, number of species, local sediment mixing (bioturbation coefficient, D_B, mean ± SD) (n as in Table 3), non-local sediment mixing (injection flux, J, mean ± SD) (n as in Table 3), bioturbation depth (L, mean ± SD) (n = all cores investigated per station), community bioturbation potential (BP_c), and species divided into the classes bivalvia, polychaeta, priapulida, malacostraca, gastropoda and asteroidea at each station. All species or classes include their percentages of total abundance/total biomass. The most dominant species with regard to abundance and/or biomass (>8% of total abundance/biomass) are in **bold**. See Table 1 for station abbreviations; na: not applicable

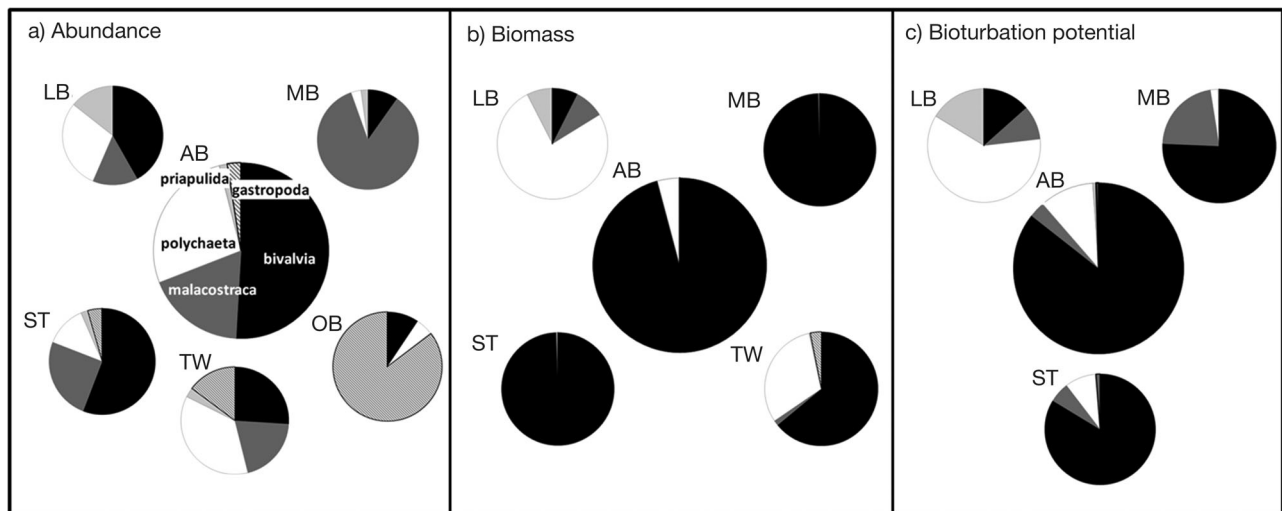|	LB	MB	ST	AB	TW	OB
Abundance (ind m^{-2})	1959	2840	5085	3503	3618	112527
Biomass: dry weight (g m^{-2})	0.4	104.7	356.7	48.7	1.2	na
Number of species	13	9	28	13	na	9
D_B (cm^2 d^{-1})	0.02 ± 0.03	0.4 ± 0.8	0.3 ± 0.3	0.2 ± 0.1	na	0.005 ± 0.003
J (µg cm^{-2} d^{-1})	0.09 ± 0.06	0.2 ± 0.1	0.3 ± 0.2	0.3 ± 0.1	0.3 ± 0.1	0.2 ± 0.09
L (cm)	2.6 ± 1.8	3.7 ± 2.0	3.4 ± 1.1	1.3 ± 0.4	1.8 ± 0.3	3.4 ± 1.0
BP_c (m^{-2})	104.9	500.8	1297.8	676	na	na
Bivalvia	**Kurtiella bidentata** (34.2%/5.3%) Other (7.8%/2.1%): A. alba Parvicardium pinnulatum Mytilus edulis juv.	**Arctica islandica** (3.9%/99%) Other (5.8%/0.6%): K. bidentata (juv.) Abra alba	**K. bidentata** (28.3%/0.1%) **A. alba** (16.7%/0.1%) **Limecola balthica** (6.4%/9.1%) A. islandica (1.7%/90.1%) Other (2.1%/0.02%): Corbula gibba M. edulis	**L. balthica** (48%/95.8%) Other (2.9%/0.03%): A. alba Cerastoderma sp.	**L. balthica** (20.4%/47.5%) Other (5.6%/16.6%): Mya arenaria M. edulis	9.4%/na Cerastoderma sp. L. balthica M. arenaria K. bidentata M. edulis
Polychaeta	**Capitella capitata** (24.6%/71.6%) Other (4.8%/4.6%): Bylgides sarsi Eteone longa Phyllodoce sp.	3.2%/0.03% B. sarsi E. longa Nephtys hombergii Paraonis fulgens	12.5%/0.4% Ampharete sp. Aricidea minuta B. sarsi Capitellidae E. longa Lagis koreni Neoamphitrite figulus N. hombergii Nephtys sp. Phyllodoce sp. Dipolydora quadrilobata Polydora sp. Scoloplos armiger Sphaerodoropsis baltica	26.9%/4.1% **S. armiger** Nephtys sp. Ampharete sp. Phyllodoce mucosa Trochochaeta multisetosa	36.3%/31% **S. armiger** Terebellides stroemi Pygospio elegans Ampharete sp.	5.1%/na
Priapulida	14%/7.5% **Halicryptus spinulosus** **Priapulus caudatus**	2.2% / 0.001% P. caudatus	2.1%/0.0009% H. spinulosus P. caudatus	1.5%/0.008% H. spinulosus P. caudatus	2.8%/0.3% H. spinulosus P. caudatus	
Malacostraca	**Diastylis rathkei** (14.3%/8.8%) Other (0.3%/na): Microdeutopus gryllotalpa	**D. rathkei** (84.9%/0.4%)	**D. rathkei** (24.9%/0.06%) Other (0.1%/na): Gammarus sp.	18.2%/0.04% D. rathkei Corophium sp. Amphipoda	20.1%/1.5% D. rathkei Pontoporeia femorata Gammarus sp.	0.2%/na Corophium volutator
Gastropoda	0.8%/0.0001% Retusa truncatula		5.1%/0.01% Peringia ulvae R. truncatula Retusa sp.	2.5%/0.007% Peringia sp.	14.8%/3.2% Peringia sp.	**P. ulvae** (85.3%/na)
Asteroidea			0.1%/0.03% Asterias rubens			

Fig. 2. Composition of the macrozoobenthic communities in terms of (a) relative abundance, (b) relative biomass and (c) relative bioturbation potential at each of the 6 stations. See Fig. 1 for station abbreviations. Biomass data are not available for OB

Biomass and bioturbation potential (BP)

The macrozoobenthic communities in the southwestern Baltic Sea were mainly dominated by bivalves in terms of biomass (Table 2, Fig. 2b). They constituted over 95% of the total biomass at MB, ST and AB. At TW, polychaetes accounted for about 40% of the total biomass. At LB, about 75% of the total biomass was constituted by polychaetes. The class bivalvia was important at all stations except LB, where it played a minor role. The BP_c composition showed a similar pattern to biomass (Fig. 2b,c). At MB, ST and AB, bivalves had the greatest potential to mix the sediment, contributing more than 75% of BP_c. According to BP_c, polychaetes were the main bioturbators at LB.

Depth distribution of macrobenthos and BP versus chl

To explain existing bioturbation patterns highlighted by chl profiles, these profiles were compared to the depth distribution of abundance, biomass and BP for each core investigated at all stations. The main objective was to determine whether the chl distribution within the sediment could be explained by the presence of macrofaunal organisms. If so, we expected most organisms to be living close to the sediment surface in cores for which the model detected local mixing. In contrast, abundance and/or biomass should increase below the sediment surface in cores for which non-local transport was found to a certain depth. However, we were not able to find significant correlations between chl profiles and depth distribution of organisms in each single core when looking at individual cores. The percentage of significant correlations between depth distribution of chl and abundance, biomass and BP per core are presented in Table 3. As the detailed analysis of single cores was not useful for explaining the different modes of sediment mixing at the stations, mean chl profiles were compared with depth distribution of the sum of organisms, biomass and BP found in each depth layer of all cores (Fig. 3). A list of all species occurring at each station is given in Table 2. The mean depth distributions of the animals' abundance and chl were highly correlated at all stations with correlation coefficient values (ρ) between 0.93 and 0.99 (Fig. 3a–f (i)). Depth distribution of biomass and BP_i showed similar patterns. Significant positive correlations between mean depth distributions of biomass and chl were found at LB, ST and TW with ρ values between 0.87 and 1.0 (Fig. 3a,c,e (ii)). At all other stations, biomass maxima were located far from chl peaks resulting in poor correlations (Fig. 3b (ii)). BP and chl were significantly correlated at LB and ST only with ρ values of 1.0 and 0.92, respectively.

As reported in Morys et al. (2016), stations in the western part of the southwestern Baltic Sea (LB, MB, ST) are mainly characterized by local sediment mixing, whereas sediments in the east are dominated by subsurface maxima in chl due to non-local processes. The distributions of macrozoobenthos confirmed these patterns. Abundances at LB, MB and ST decreased exponentially with depth (Fig. 3a–c (i)). LB was the station with lowest abundance, biomass and BP,

Table 3. Total number (n) of cores investigated for macro-fauna analyses and number of cores indicating no, local or non-local sediment mixing at each station. (Note that at LB and MB, 24 cores were investigated in total but 1 core at LB and 2 cores at MB were without any organisms; thus, a correlation was not possible.) The percentage of all investigated cores that show a significant correlation (p < 0.05) between depth distribution of abundance, biomass and bioturbation potential of organisms and chl are in **bold**. Additional numbers of cores that show a significant correlation between local, non-local and no sediment mixing (indicated by chl depth distribution) and depth distribution of abundance, biomass and bioturbation potential of organisms are given below. These analyses include both parametric and non-parametric correlations (see 'Materials and methods'). See Table 1 for station abbreviations; na: not applicable

	LB	MB	ST	AB	TW	OB
Investigated cores (n)	23	22	24	10	10	6
Local mixing (n)	14	10	15	2	0	1
Non-local mixing (n)	6	7	9	8	10	4
No mixing (n)	3	5	0	0	0	1
Abundance						
Significant correlation (%)	**69.6**	**50**	**83.3**	**80**	**80**	**83.3**
Local mixing	10	7	14	1	na	1
Non-local mixing	4	2	6	7	8	4
No mixing	2	2	na	na	na	0
Biomass						
Significant correlation (%)	**65.2**	**40.9**	**70.8**	**20**	**80**	**na**
Local mixing	10	6	11	0	na	na
Non-local mixing	4	1	6	2	8	na
No mixing	1	2	na	na	na	na
Bioturbation potential						
Significant correlation (%)	**65.2**	**40.9**	**62.5**	**20**	**na**	**na**
Local mixing	10	6	11	0	na	na
Non-local mixing	4	1	4	2	na	na
No mixing	1	2	na	na	na	na

which all showed an exponential decrease with sediment depth (Table 2, Fig. 3a (i–iii)). Thirteen species, with *Kurtiella bidentata* (<3 mm), *Capitella capitata*, *Diastylis rathkei* and *Priapulus caudatus* occurring most frequently, were found in the cores up to a maximum depth of 4 cm (Table 2, Fig. 3a (i)). *C. capitata* constitutes the largest part of biomass and BP (Fig. 3a (i,iii)). MB was also characterized by comparably low abundance as well as the lowest number of species, with *D. rathkei* being most abundant. Most organisms occurred up to 4 cm depth, but some, e.g. *Abra alba*, *Arctica islandica* and *Nephtys hombergii*, reached a maximum depth of 9 cm (Table 2, Fig. 3b (i)). Biomass (*A. islandica* constituting 99%) and BP indicated their maxima between 2 to 5 cm and 6 to 7 cm (Fig. 3b (ii,iii)). According to BP, *D. rathkei* was the most important bioturbator within the upper 1.5 cm and was superseded by *A. islandica* in deeper horizons (Fig. 3b (iii)). ST was the station with highest biomass, BP_c and

number of species. Organisms were mainly located within the upper 4 cm, but reached a depth of 9 cm. The most abundant species were *K. bidentata*, *D. rathkei* and *A. alba* (juvenile stages with maximum size of 6 mm) (Fig. 3c (i)). *A. islandica* constituted the main part of the biomass, whereas BP indicated a variety of organisms in the first centimeter (Fig. 3c (ii,iii)). However, *A. islandica* and *Limecola balthica* became more important deeper in the sediment.

Stations in the east (AB, TW and OB) were characterized by subsurface peaks in mean chl profiles (Fig. 3d–f) and 70–100% of the area is mixed non-locally (Morys et al. 2016, Table 1). At AB, the chl maximum was close to the sediment surface (injection depth = 0.9 cm according to the model by Soetaert et al. 1996) and was inhabited by most organisms (*L. balthica* being most abundant) (Fig. 3d (i)). The second most abundant organisms belonged to the class polychaeta (especially *Scoloplos armiger*), with most individuals between 1 and 3 cm. Depth distribution of biomass and BP indicated 2 maxima: within the top 2 cm and between 4 and 8 cm (Fig. 3d (ii)). *L. balthica* reaching a depth of 9 cm accounted for 96% of the total biomass and constituted the major part of BP (Fig. 3d (iii)). Depth distribution of chl, abundance and biomass at TW was characterized by a subsurface maximum between 1 and 3 cm (Fig. 3e (i)). The most abundant organisms belonged to the class polychaeta (*S. armiger* was most abundant) (Fig. 3e (i)). Most individuals were located between 1 and 4 cm, but a few organisms were also found up to 7 cm depth. *L. balthica* and polychaetes constituted the main part of the biomass (Fig. 3e (ii)). Evidence for non-local sediment mixing was not as distinct at OB, with a comparatively small increase in chl between 2 and 3.5 cm (Fig. 3f (i)). In the same layer, a slight increase in abundance was apparent. OB was the station with the highest abundance, with *Peringia ulvae* being most abundant. *Hediste diversicolor* was also one of the most important organisms and was mainly located between 2 and 4 cm but reached a depth of up to 6 cm (Fig. 3f (ii)).
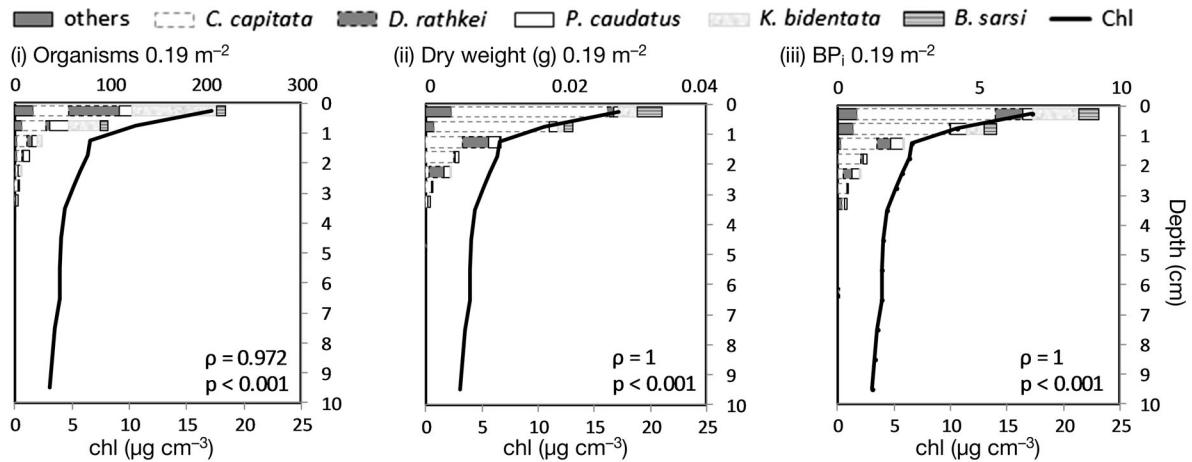
DISCUSSION
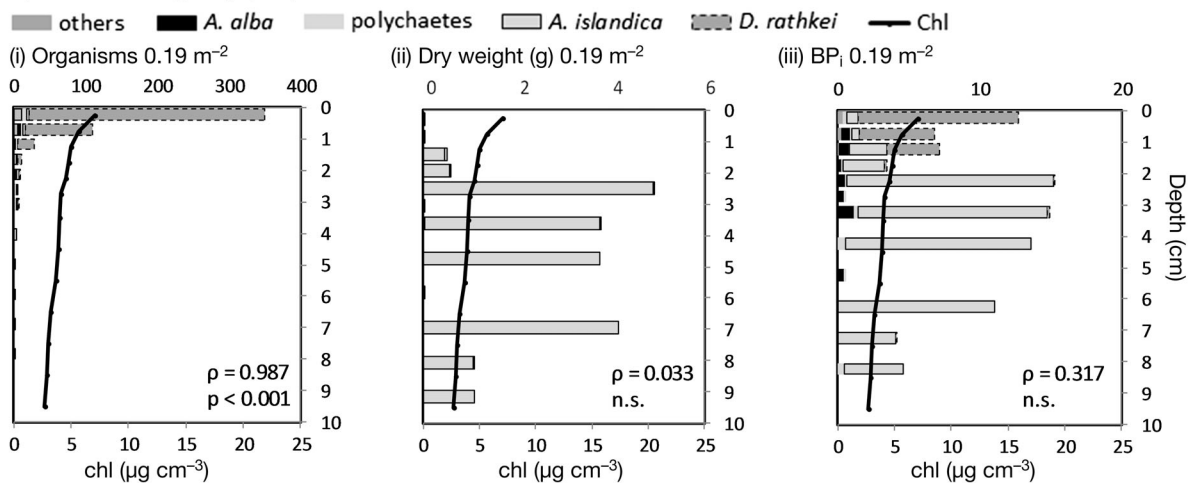
General distribution patterns

Differences in macrobenthos community along the southwestern Baltic Sea coast

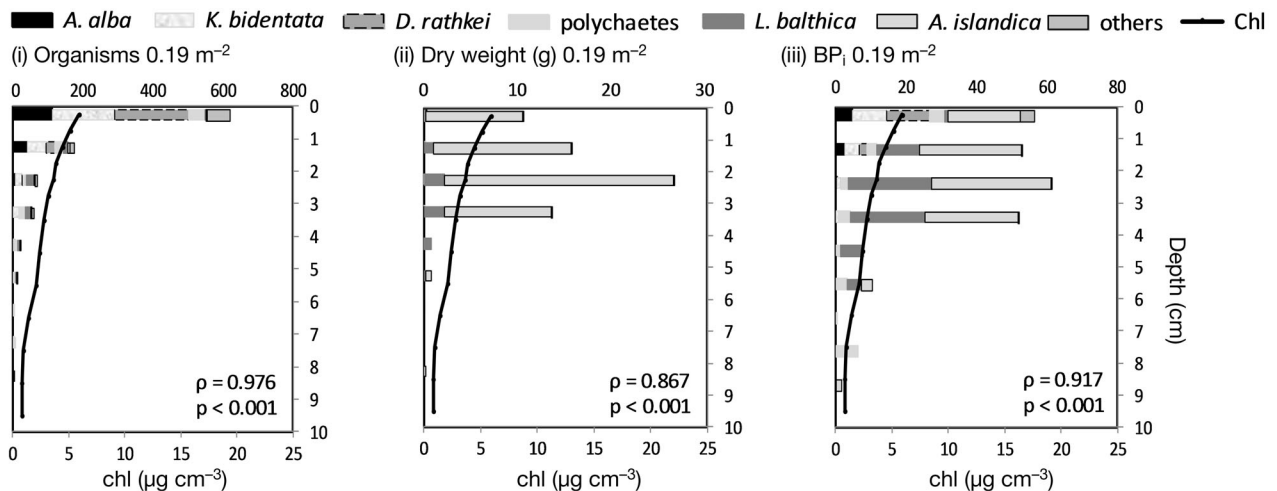The composition of the macrozoobenthic community differs between the stations investigated in this

Fig. 3. Mean chlorophyll depth profiles (lines) (LB, MB, ST: n = 24 cores; AB, TW: n = 10 cores; OB: n = 6 cores) and depth distribution of macrozoobenthos at (a) LB (b) MB (c) ST (d) AB (e) TW and (f) OB (see Fig. 1 for station abbreviations). (i) Depth distribution of the sum of macrobenthic species found in all cores investigated. Note, abundances found on different spatial scales due to different number of samples investigated. Different scales were deliberately chosen for exact comparison with chl within the area analyzed. (ii) Depth distribution of the sum of biomass given as dry weight (g) of each species found in each layer investigated. Biomass data are not available for OB. Note, Fig. 3f (ii) presents the depth distribution of the number of *Hediste diversicolor* to highlight its occurrence within the layer of subsurface maxima of chl. (iii) Depth distribution of bioturbation potential index (BP_i) of each species within each depth layer. Results of bivariate correlations between depth distributions of chl, abundances, biomasses and BP_c are given as Spearman correlation coefficients (ρ) and p-values; n.s.: not significant (ρ is significant at p < 0.05)

d) Arkona Basin (AB)

Legend: others | polychaetes | *L. balthica* | —— Chl

(i) Organisms 0.08 m^{-2}

$\rho = 0.926$
$p < 0.001$

(ii) Dry weight (g) 0.08 m^{-2}

$\rho = -0.259$
n.s.

(iii) BP$_i$ 0.08 m^{-2}

$\rho = -0.239$
n.s.

chl (µg cm^{-3})

e) Tromper Wiek (TW)

Legend: others | polychaetes | *L. balthica* | —— Chl

(i) Organisms 0.08 m^{-2}

$\rho = 0.944$
$p < 0.001$

(ii) Dry weight (g) 0.08 m^{-2}

$\rho = 0.929$
$p < 0.001$

chl (µg cm^{-3})

f) Oderbank (OB)

Legend: *Peringia sp.* | *M. arenaria* | polychaetes | *L. balthica* | others | —— Chl

(i) Organisms 0.05 m^{-2}

$\rho = 0.942$
$p < 0.001$

(ii) *H. diversicolor* 0.05 m^{-2}
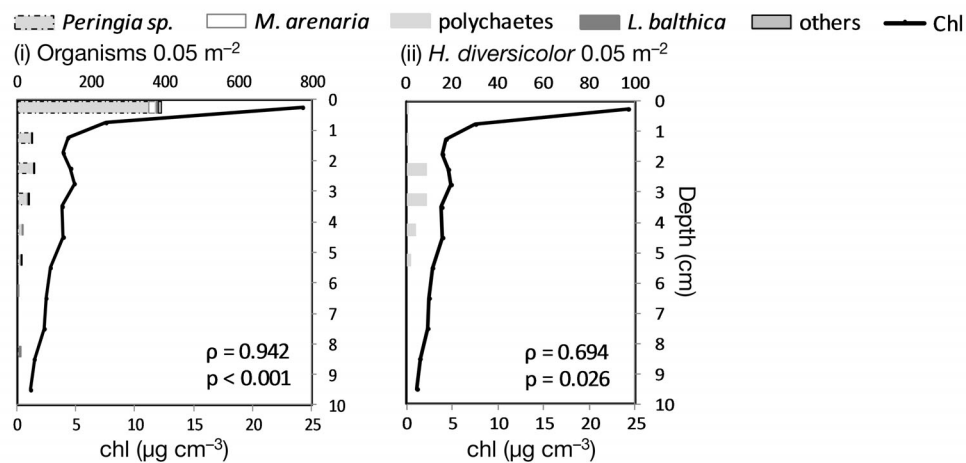
$\rho = 0.694$
$p = 0.026$

chl (µg cm^{-3})
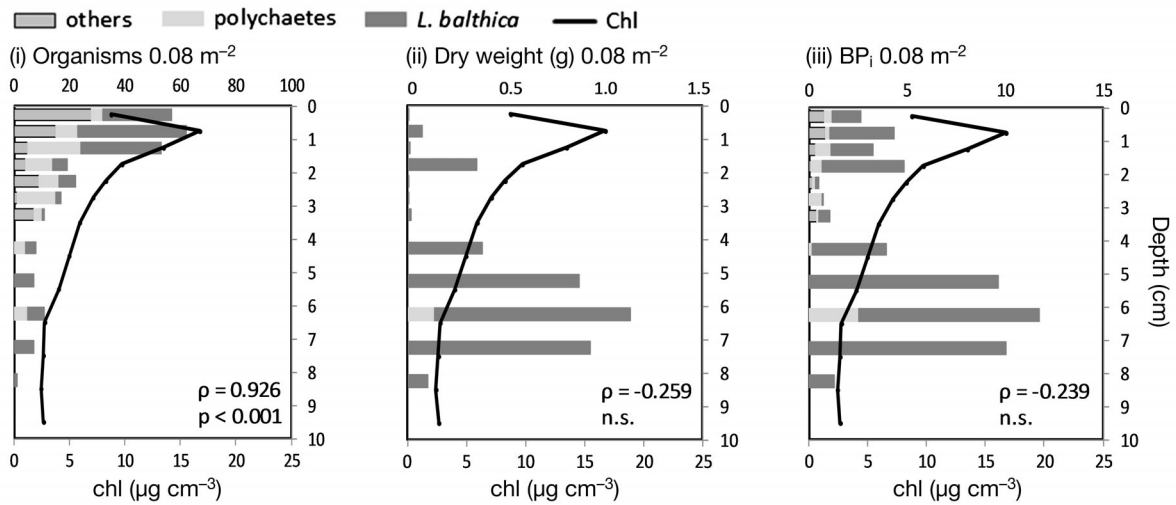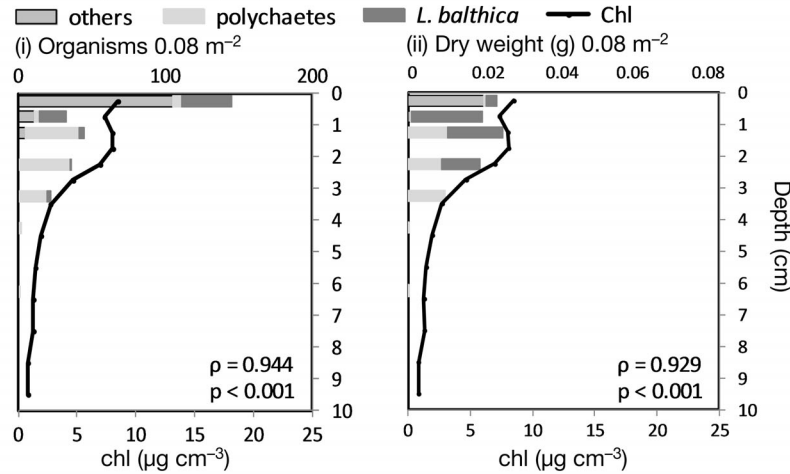
Fig. 3 (continued)

study along the southwestern Baltic Sea, and is in agreement with the community structures reported in Prena et al. (1997), Zettler et al. (2000), Gogina et al. (2010) and Schiele et al. (2015). Both abundance and biomass increase with increasing grain size and decrease with increasing water depth. Sandy stations show highest abundances (OB, even when the high abundance of *Peringia* sp. is excluded) and biomasses (ST, Table 2; OB: 95.4 ± 34.7 g ash-free dry weight m^{-2} according to Powilleit & Kube 1999).

Differences in depth distribution of macrobenthos along the southwestern Baltic Sea coast

Depth distribution of abundance and biomass were also different between stations. Similarities in the depth distribution of abundance were found at stations characterized by the highest chl concentrations at the sediment surface (LB, MB, ST and OB) where most organisms inhabit the top centimeter (Fig. 3). There are few organisms (with high biomass) in deeper horizons, e.g. *Arctica islandica*, *Abra alba*, *Limecola balthica*, *Nephtys hombergii* (Fig. 3a–c,f). These adult organisms are specialized to live deeper in the sediment, being still able to feed on food resources in upper horizons due to their free mobility within the matrix and/or long siphons. Hence, they benefit from, for example, avoiding competition for food and space and refuge from predators. Different patterns indicating a subsurface increase in abundance were found at AB due to almost exclusively juvenile *L. balthica* and at TW due to polychaetes that only feed occasionally at the surface and usually take refuge from predators within the sediment.

Depth distribution of macrobenthos vs. chl

On average, depth distributions of chl and abundance correlated well at all stations but correlations between chl and biomass profiles were not significant at MB and AB (Fig. 3). These 2 stations differ from the other stations in their low abundance and high biomass of bivalves below 4 cm depth (e.g. 8 individuals of *A. islandica* found in the 24 cores at MB contributed 51% of total biomass). As a result, there are only a few subsurface peaks in chl, i.e. non-local transports created by these organisms that are eliminated when averaging chl profiles. The patterns determined by mean profiles were not found in each single core (Table 3). However, using mean profiles seems to be a more suitable measure for the description of bioturbation because it takes patchiness into account. For that reason, the identification of the main bioturbators is based on mean profiles.

Main bioturbators

Chl as a particle tracer

The input of food supply for benthic macrofauna occurs primarily via sedimentation of phytoplankton, which can be measured by using chl as a tracer (Kanneworff & Christensen 1986, Jeffrey & Mantoura 1997, Boon & Duineveld 1998). The distribution of chl within the sediment depends on its sedimentation, degradation and sediment mixing (Soetaert et al. 1996, Maire et al. 2008). The minor temperature dependency of chl degradation (Morys et al. 2016) supports its use as the first-order decay constant (k_D) required in the bio-mixing model by Soetaert et al. (1996) and implies that the velocity of decomposition only depends on the available chl in the organic matter.

One limitation of using chl as a particle tracer is that sediment mixing can be biased due to positive selection of chl-rich particles by benthic organisms (Taghon 1982, Lopez & Levington 1987, Mahon & Dauer 2005). The highly significant correlations between depth distribution of chl and macrofauna indicated, regardless of the fact that some organisms indeed select particles, how organisms mix particles within the sediment and explained the different bioturbation patterns. Furthermore, Maire et al. (2008) have pointed out that the chl concentration is affected when passing through animals' guts (Abele-Oeschger & Theede 1991), which complicates its use in the case of non-local transport associated with feeding. Chl is rapidly turned into pheophytin and pheophorbide (Abele-Oeschger & Theede 1991) which are, when egested, also detected by the photometric method. In addition, some suspension-feeding species, e.g. *L. balthica* (Olafsson 1989) and *A. alba* (Bernard et al. 2016) may take chl directly from the water column and release it within the sediment, potentially affecting chl profiles and resulting in an overestimation of mixing rates. Furthermore, as mentioned in our previous study (Morys et al. 2016), D_B decreases with increasing surface chl concentration due to long resting periods (Jumars & Wheatcroft 1989, Wheatcroft et al. 1990). The fact that organisms react rapidly to changing environmental conditions (i.e. food supply) explained the low intensities of local sediment mixing at OB due to the previously sedimented spring bloom.

However, measured chl profiles reflect a certain status at the time of sampling, potentially covering a time span of up to 3 mo due to the half-life periods of 69 d (mud) and 34 d (sand) (Morys et al. 2016). Meysman et al. (2003) stated that non-local events merge with increasing half-life periods of the tracer. Downcore profiles derived from short-lived tracers such as chl apparently violate the assumptions of the biodiffusion model (Fickian analogy), whereas radiotracers, e.g. ^{210}Pb, often do fit an exponential depth distribution. On this basis, we found more complex patterns (local and non-local sediment mixing) that represent the current status of early spring, including all environmental, biological and physical conditions, and that may conceivably change during different times of the year.

Consequently, when using chl as a tracer, we have to keep in mind that some organisms, as they are free in their movements, may have left the place of intense sediment mixing that is highlighted in our cores. In individual cores, various organisms responsible for a present chl profile may not be found any more at the sampling time. This leads to a more complicated identification of responsible bioturbators as, for example, in 40% of the cores indicating non-local mixing at ST, *L. balthica* (considered as a non-local bioturbator in this study) was found together with other organisms within the horizon of the subsurface peak. A small area from an individual core is difficult to interpret. In contrast, an overview of mean depth distribution gained from many cores allows an insight into typical patterns.

Identification of main bioturbators

In this study, defining main bioturbators is based on a quantitative description of the species' depth distribution. The main aim was to explain the bioturbation patterns in the southwestern Baltic Sea with an increase of non-local processes from west (30–50% of the cores) to east (70–100%) as found in Morys et al. (2016). Both the depth distribution of chl and macrofauna (especially abundance) indicated the dominant mode of sediment mixing (local or non-local) at each station. On this basis, detecting the most abundant organisms in the horizon of highest chl concentration allowed the identification of the main bioturbators for the dominant mode of mixing. However, at most stations (except TW), both local and non-local sediment mixing was detected. Thus, it was also necessary to differentiate between both transports and to consider information on the species'

life traits (e.g. feeding, mobility) to identify main bioturbators. Main bioturbators for local sediment mixing were identified in cases where (1) they were most abundant at the sediment surface, (2) their abundance decreased exponentially with depth and (3) they induced local mixing according to their biological life traits. *Diastylis rathkei* is the main bioturbator for local transports at most stations (except OB) plus *Kurtiella bidentata* at LB and ST. At OB, *Peringia ulvae* plays the most important role. According to François et al. (2002), polychaetes belonging to gallery biodiffusors may also transport particles locally in upper horizons of the sediment. Furthermore, filter-feeding bivalves are often described as surficial modifying organisms in the literature (e.g. Queirós et al. 2013). These organisms may clearly affect local sediment mixing at our stations. However, the identification of the main bioturbators in this study is based on most abundant organisms; first, because the depth distribution of abundance was found to be a suitable tool for explaining the mean chl profiles and second, because abundance is one of the most important parameters influencing bioturbation (e.g. Solan et al. 2004).

To identify the main bioturbators for non-local sediment mixing, mean injection depths were taken into account (Table 2). Dominant organisms (in terms of both abundance and biomass) within these depth layers were identified as being responsible for non-local mixing. This mode of mixing is carried out by a variety of organisms along the Southwestern Baltic Sea. In the west, *Capitella capitata* (LB) and *Priapulus caudatus* (LB, MB) were defined to be the main bioturbators. Furthermore, *N. hombergii* and *A. islandica* were responsible for non-local sediment mixing at MB and ST. Towards the east (including ST), *L. balthica* (ST, AB, TW, OB) and *Scoloplos armiger* became the most important bioturbators (ST, AB, TW). ST indicates more complex patterns as there is a variety of species playing an important role in particle transport. At OB, *Hediste diversicolor* belongs to the main bioturbators in the upper horizon of the sediment. *Mya arenaria* is responsible for non-local sediment mixing in deeper horizons of the sediment as adults may occur down to 8 cm depth. Some organisms, as shown in Table 4, were identified as having a superior role in sediment mixing due to their dominant abundance within the macrobenthos community. Other organisms that were not captured by the MUC, presumably due to their rare occurrence, e.g. *A. islandica* at LB (Zwicker 2014), or habitation of very deep horizons of the sediment, e.g. *Arenicola marina* at ST (M. Gogina pers. comm.), may also affect

Table 4. The main bioturbators of local and non-local sediment mixing at each station determined in this study and their assignment to the 4 major categories of organism life traits according to Kristensen et al. (2012). Species with a superior role in sediment mixing due to their dominance in abundance are in **bold**. *Scoloplos armiger*, categorized as biodiffusor (Queirós et al. 2013), was assigned to gallery biodiffusors in this study because this species was indicated to induce non-local sediment mixing. See Table 1 for station abbreviations; na: not applicable

Station	Local	Life trait	Reference	Main bioturbators Non-local	Life trait	Reference
LB	*Diastylis rathkei* *Kurtiella bidentata*	Surficial biodiffusors Surficial biodiffusors	Queirós et al. (2013)	*Capitella capitata* *Priapulus caudatus*	Upward conveyor Gallery biodiffusor	D'Andrea et al. (1996) Powilleit et al. (1994)
MB	*D. rathkei*	Surficial biodiffusors	Queirós et al. (2013)	Upper sediment (0–4 cm): **P. caudatus** *Abra alba* Deep sediment: *Arctica islandica* *Nephtys hombergii*	Gallery biodiffusor Surficial biodiffusor Surficial biodiffusor, gallery biodiffusor	Powilleit et al. (1994) Queirós et al. (2013) Queirós et al. (2013) Hartmann-Schröder (1996)
ST	*K. bidentata* *D. rathkei* *A. alba*	Surficial biodiffusors Surficial biodiffusors Surficial biodiffusors	Queirós et al. (2013)	*Limecola balthica* *N. hombergii* *S. armiger* *A. islandica*	Surficial biodiffusor, gallery biodiffusor (Gallery) biodiffusor Surficial biodiffusor	Queirós et al. (2013) Hartmann-Schröder (1996) Queirós et al. (2013) Queirós et al. (2013)
AB	*D. rathkei*	Surficial biodiffusor	Queirós et al. (2013)	**L. balthica** Polychaetes **S. armiger**	Surficial biodiffusor (Gallery) biodiffusor	Queirós et al. (2013) Queirós et al. (2013)
TW	na			Polychaetes **S. armiger** *L. balthica*	(Gallery) biodiffusor Surficial biodiffusor	Queirós et al. (2013) Queirós et al. (2013)
OB	*Peringia ulvae*	Surficial biodiffusor	Queirós et al. (2013)	Upper sediment (2–4 cm, max. 6 cm): **Hediste diversicolor** *L. balthica* Deep sediment: *Mya arenaria*	Gallery biodiffusor Surficial biodiffusor Downward conveyor	François (1999), Duport et al. (2006) Queirós et al. (2013) Muus (1967)

the typical chl profiles determined at each station and potentially be main bioturbators as well. This consideration indicates that bioturbation may be even more intense at our stations, to an extent that we are not able to assess. However, these organisms would not be considered main bioturbators due to their low abundance. The main bioturbators identified in the present study were confirmed by Gogina et al. (2017), who calculated BP_c based on van Veen grab data taken at the same stations during the same cruise.

Categorization of macrobenthos and derived life traits

The main bioturbators of local and non-local sediment mixing at each station determined in this study were assigned to 4 major categories of organisms' life traits (Kristensen et al. 2012) (Table 4). The differentiation between surficial and gallery biodiffusors was found to be important in identifying which functional group induces the different modes of sediment mixing. While local sediment mixing is carried out by surficial biodiffusors at each station, non-local mixing was found to potentially be induced by gallery biodiffusors. These findings are in agreement with François et al. (2002), Mermillod-Blondin et al. (2004) and Duport et al. (2006). Sediments at LB are mixed non-locally by (gallery) biodiffusors and upward conveyors. At MB, ST, AB and TW only biodiffusors are responsible for both local (surficial) and non-local (gallery) sediment mixing. Bioturbating organisms at OB belong to biodiffusors and downward conveyors (Table 4).

Based on the present study, we point out that the assignment of organisms to the functional groups as listed in Queirós et al. (2013) needs to be improved. We found, for example, that *L. balthica*, which is generally defined as a surficial biodiffusor in the literature, is responsible for non-local sediment mixing in the southwestern Baltic Sea. This deposit feeder retains a connection to the sediment surface via its siphons (Brafield & Newell 1961, Mortimer et al. 1999, Karlson et al. 2005). The inhalant siphon draws in particles from the surface while the exhalant siphon ejects both faeces and pseudofaeces (Hulscher 1973, Mortimer et al. 1999). We argue that *L. balthica* also belongs to the functional group of conveyors. Furthermore, some species seem to switch between certain life traits due to their size and/or life stage. *A. alba*, for example, was found to induce local mixing during juvenile stages (ST) despite the fact

that the effect on non-local sediment mixing in surface sediments might not be visible due to the limited spatial resolution of 0.5 cm. Adult organisms that inhabit deeper parts of the sediment were identified as being responsible for non-local transports (MB). In addition, as the number of species in deeper horizons of the sediment is reduced, only a few species may be responsible for the subsurface peaks in these depth layers. Due to the high biomass of *A. islandica* and the habitation of deep horizons, we argue that this species belongs to conveyors rather than surficial biodiffusors as stated in the literature.

West–east gradient

The different macrobenthic communities along the coast of the southwestern Baltic Sea indicate an increase in the number of polychaetes from west to east with decreasing salinity (Tables 1 & 2). At the more saline stations (LB, MB, ST), we found between 91 (MB) and 636 (ST) polychaetes m^{-2}, while their abundance increased eastwards up to 942 (AB), 1313 (TW) and 5739 (OB) polychaetes m^{-2}. Most species of this taxonomic group at TW and OB belong to the functional group of gallery biodiffusors (M. Gogina pers. comm., Appendix). According to Yamada et al. (2007), the different dominant functional groups at stations of various salinities may be explained by the adaptation of species to low salinities. *S. armiger* and *H. diversicolor* are the most abundant gallery biodiffusors at the less-saline stations TW and OB and are characterized by a wide range of salinity tolerance (Hartmann-Schröder 1996, Hesselberg 2003), whereas many marine species (e.g. *A. islandica*, *N. hombergii*) reach their distribution limit at AB. As *S. armiger* and *H. diversicolor* were found within the depth layers of mean injection depths (Table 2), they seem to transport particles non-locally and are responsible for the remarkable subsurface chl peaks. All in all, the increasing extent of non-local transports from west to east may be explained by increasing abundance of gallery biodiffusors.

D_B, J and R vs. BP

Depth distributions of BP and biomass show similar patterns (Fig. 3a–d (iii)). This indicates the strong impact of biomass rather than abundance used in the index. However, at ST, *L. balthica* (9%) accounts for much less of the total biomass than *A. islandica* (90%). The fact that BP, which by including abun-

dance accentuates the effect of *L. balthica* relative to *A. islandica* (Fig. 3c (iii)), provides a better correlation with chl depth distribution than biomass indicates that including abundance in the BP is particularly important for this species. Generally, BP highlights well the layers of intense mixing (both local and non-local) that are indicated by our chl depth distributions (Fig. 3a–d (iii)). Non-local transports are indicated by an increase in BP within horizons that match the modeled injection depths derived by the bio-mixing model. However, MB and AB are examples of poor fit of BP versus chl, indicating that here the index combining abundance and biomass cannot mirror the tracer distribution as closely as abundance alone.

Spearman correlations between BP_c and our modeled D_B ($\rho = 0.46$ and p = 0.011) as well as J ($\rho = 0.52$ and p = 0.007) were highly significant (Fig. 4a,b), whereas there was no significant correlation with R ($\rho = 0.21$ and p = 0.61). These findings are in agreement with Gogina et al. (2017). Keeping in mind that the bio-mixing model (Soetaert et al. 1996) and BP_c are 2 vastly different approaches for quantifying sediment mixing, data in the present study indicate that BP_c seems to be a suitable metric for both local and non-local sediment mixing. However, the index may not distinguish between local and non-local sediment mixing, resulting in loss of important information that was obtained in this study. Queirós et al. (2015) state that BP_c is a good predictor of bioturbation distance (the average distance transport of a particle in a bioturbation random-walk model (Schiffers et al. 2011), but not for more detailed aspects, e.g. mixing depth, activity and D_B, thus confirming our findings. Gogina et al. (2017) also report a certain mismatch between BP_c and modeled sediment mixing rates using chl

profiles. The authors state that BP_c presents the possible bioturbation activity of a present community excluding intra- and interspecific interactions, individual fitness and behavior, and, therefore, does not cover all aspects of a species' biology, such as life history, feeding behavior, size and depth distribution (Braeckman et al. 2014, Queirós et al. 2015, Gogina et al. 2017).

CONCLUSIONS

The high-resolution depth distribution of macrofauna determined in this study was necessary for a precise description of the relationship between bioturbation and the corresponding organisms. Chl was found to be a suitable particle tracer as it indicates the rapid reaction of macrofauna to changing environmental conditions (i.e. spring bloom at OB) and as most organisms were found in horizons of highest chl concentrations. Vertical profiles of chl, abundance, biomass and BP allowed the identification of the main bioturbators along the southwestern Baltic Sea coast. Correlations between biomass depth distribution and chl were not significant at most stations but gave additional hints on important bioturbators at depth (e.g. *Arctica islandica*). BP_c and modeled intensities of local (D_B) and non-local sediment mixing (J) were positively correlated, but in this study, the index BP_c does not seem to provide any additional insight or interpretation of the bioturbation process. Categorizing the main bioturbators into functional groups according to their biological life traits and the comparison with their depth distribution within the sediment resulted in some deviation from life traits definitions. Gallery biodiffusors seemed to be responsible for
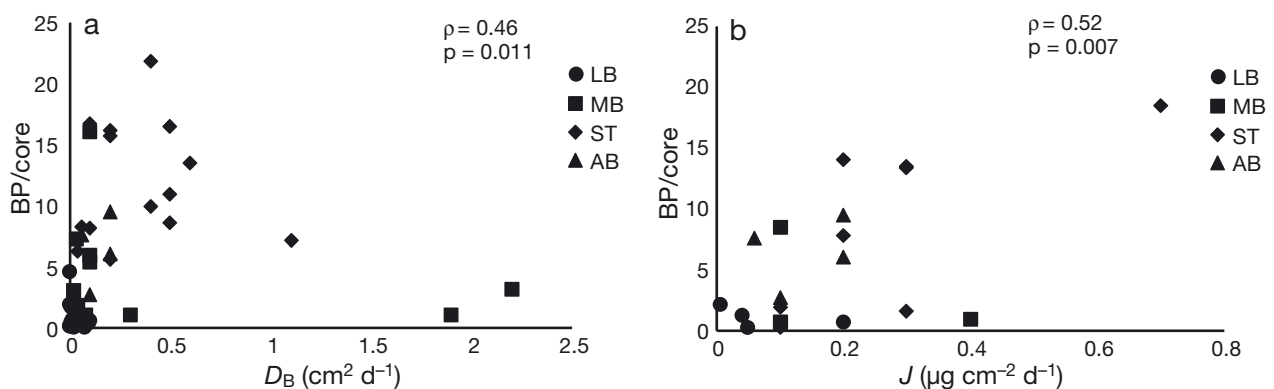

Fig. 4. (a) Correlation between local sediment mixing (bioturbation coefficient, D_B [cm^2 d^{-1}]) and community bioturbation potential (BP_c; calculated for a single core of 0.078 m^2). (b) Correlation between non-local sediment mixing (injection flux, J [µg cm^{-2} d^{-1}]) and BP_c. Correlations are given as Spearman correlation coefficients (ρ) and p-values (ρ is significant at p < 0.05). Note that no sediment mixing ($D_B = 0$) was excluded from all statistical analyses. See Fig. 1 for station abbreviations

non-local sediment mixing rather than for the diffusive distribution of particles within the sediment. Other species were also found to induce non-local sediment mixing due to their feeding behavior (e.g. *Limecola balthica*), size (e.g. *Abra alba*) or biomass (e.g. *A. islandica*, *L. balthica*).

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Appendix.

Bioturbation potential (BP) allocations for all macrozoobenthic species found in the present study for calculating the BP index (BP$_i$) after Solan et al. (2004). M_i and R_i are the reworking and mobility traits, respectively, mainly taken from Queirós et al. (2013). M_i scores: 1 = organisms in fixed tubes; 2 = limited movement; 3 = slow/free movement through the sediment matrix; 4 = free movement via burrow system. R_i scores: 1 = epifauna; 2 = surficial modifiers; 3 = upward and downward conveyors; 4 = biodiffusors; 5 = regenerators. Assignment to functional groups after Kristensen et al. (2012). OB: Oderbank

Species	M_i	R_i	Functional group	Reference
Abra alba (juvenile)	2	2	Surficial biodiffusor	Queirós et al. (2013)
Abra alba (adult)	2	3	Downward conveyor	Present study
Ampharete sp.	2	3	Upward/downward conveyor	Queirós et al. (2013)
Arctica islandica	2	3	Downward conveyor	Present study
Amphipoda	2	2	Surficial biodiffusor	Queirós et al. (2013)
Aricidea minuta	3	2	Surficial biodiffusor	Queirós et al. (2013)
Asterias rubens				Excluded (abundance <1%)
Bylgides sarsi	3	2	Surficial biodiffusor	Hartmann-Schröder (1996)
Capitella capitata	2	3	Upward conveyor	D'Andrea et al. (1996), Queirós et al. (2013)
Cerastoderma sp.	2	2	Surficial biodiffusor	Queirós et al. (2013)
Corbula gibba	2	2	Surficial biodiffusor	Queirós et al. (2013)
Corophium sp.	2	2	Surficial biodiffusor	Queirós et al. (2013)
Diastylis rathkei	3	2	Surficial biodiffusor	Queirós et al. (2013)
Dipolydora quadrilobata	1	3	Upward/downward conveyor	Queirós et al. (2013)
Eteone longa	3	4	Gallery biodiffusor	Mermillod-Blondin et al. (2003)
Gammarus sp.			Surficial biodiffusor	Excluded (abundance <1%)
Halicryptus spinulosus	2	4	Gallery biodiffusor	Powilleit et al. (1994), Queirós et al. (2013)
Hediste diversicolor	4	4	Gallery biodiffusor	François (1999), Duport et al. (2006)
Kurtiella bidentata	2	2	Surficial biodiffusor	Queirós et al. (2013)
Lagis koreni	1	3	Upward conveyor	Queirós et al. (2013)
Limecola balthica	2	3	Downward conveyor	Present study
Marenzelleria neglecta			Gallery biodiffusor	Only found at OB, no BP calculated
Microdeutopus gryllotalpa			Surficial biodiffusor	Queirós et al. (2013), excluded (abundance <1%)
Mya arenaria	2	3	Downward conveyor	Muus (1967)
Mytilus edulis	1	1	Epifaunal biodiffusor	Queirós et al. (2013)
Neoamphitrite figulus	1	3	Downward conveyor	Queirós et al. (2013)
Nephtys hombergii	3	4	Gallery biodiffusor	Hartmann-Schröder (1996), present study
Paraonis fulgens	3	2	Surficial biodiffusor	Queirós et al. (2013)
Parvicardium pinnulatum	2	2	Surficial biodiffusor	Queirós et al. (2013)
Peringia ulvae	3	2	Surficial biodiffusor	Queirós et al. (2013)
Phyllodoce sp.	3	4	Gallery biodiffusor	Janson et al. (2012)
Polydora sp.	1	3	Upward/downward conveyor	Queirós et al. (2013)
Pontoporeia femorata	2	2	Surficial biodiffusor	Present study
Priapulus caudatus	2	4	Gallery biodiffusor	Powilleit et al. (1994)
Pygospio elegans	1	3	Upward/downward conveyor	Queirós et al. (2013)
Retusa truncatula	2	2	Surficial biodiffusor	Queirós et al. (2013)
Scoloplos armiger	3	4	Gallery biodiffusor	Present study
Sphaerodoropsis baltica				Excluded (abundance <1%)
Terebellides stroemii	1	3	Downward conveyor	Queirós et al. (2013)
Trochochaeta multisetosa	2	3	Upward/downward conveyor	M. L. Zettler, M. Gogina (pers. comm.)