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Variability of bioturbation in various sediment types and on different spatial scales in the southwestern Baltic Sea

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ABSTRACT: Variability of bioturbation on different spatial scales was revealed through a survey at 6 stations in the southwestern Baltic Sea with different sediment types, salinities and macrozoobenthic communities. At each station, 6 sampling locations were investigated with 4 cores each (24 cores per station). The cores were analyzed for vertical chlorophyll (chl) profiles, which were modeled with both a local (tracer distribution decreasing exponentially with depth indicative of diffusive transport, D_B) and a non-local (presence of subsurface maximum of the tracer, injection flux J and ingestion rate r) mixing model developed by Soetaert et al. (1996; J Mar Res 54: 1207–1227). Degradation of chl was determined experimentally by an incubation of fresh sediment under anoxic, dark conditions and provided decay constants k_D of 0.01 d^{-1} for mud and 0.02 d^{-1} for sand. Mixing depths reach 7.1 ± 1.6 cm at stations in the west (except Lübeck Bay, LB), 2 cm deeper than at stations in the east, which reach 5.2 ± 1.7 cm (including LB), mainly depending on the macrozoobenthic community present. Bioturbation intensities indicate high variability between closely located sampling sites as well as across the southern Baltic Sea, and depend on the food supply from the water column. Stations indicate a difference in local mixing (D_B) of a factor of 20 and in non-local processes (J) of 6. Non-local transports account for 33 to 50% of the investigated area in the west and for 70 to 100% in the east. The statistical description of the results indicates the necessity of high sampling effort when using chl as a particle tracer.

KEY WORDS: Bioturbation · Local and non-local transport · Chlorophyll degradation · Mixing depth

INTRODUCTION

Bioturbation is a transport process in benthic habitats carried out by animals that describes their physical direct or indirect effects on the surrounding sediment and porewater (Meysman et al. 2006, Kristensen et al. 2012). This process includes the transport of particles (bio-mixing or sediment mixing) and the enhanced solute transport resulting from burrow ventilation (bio-irrigation) (Kristensen et al. 2012). Animals living in the sediment induce particle movement due to building and maintaining burrows as well as foraging. Sediment mixing is not always homogenous because mechanisms such as particle sorting during feeding, confined defecation sites and burrow constructions can affect the physical and chemical properties of the sediment, e.g. granularity, porosity and organic content (Kristensen et al. 2012).

Coastal areas, like the southern Baltic Sea, are productive and complex systems providing humans with many benefits. The description of ecosystem services has become an important task during the past few years (MA 2005). Information on bioturbation can generally be used for deriving such services; bioturbation, for example, affects the composition of the sediment, the condition of the overlying water, and the distribution of organic matter in the sediments and microbial substrates (Aller 1982, Blair et al. 1996,

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Yingst & Rhoads 1980). Organic matter and microorganisms are moved vertically and laterally within the sediment, significantly increasing the depth of the mixed layer (Teal et al. 2008). Sediment mixing can prolong the residence time of material within the surface sediments (Aller & Cochran 1976), where it is more easily resuspended or degraded. Bioturbation acts as a form of 'ecosystem engineering' by mediating biogeochemical processes that are critical to the marine ecosystem and by redistributing food resources in the upper centimeters of oceanic sediments (Meysman et al. 2006, Huhta 2007, Teal et al. 2008, Wilkinson et al. 2009). Furthermore, sediment mixing increases the recycling of nutrients, enhances benthopelagic coupling and can lead to the permanent burial or mobilization of contaminants and pollutants, depending on the circumstances (Graf 1992, Wheatcroft & Martin 1996, Kristensen et al. 2012).

For a quantitative understanding of biologically induced sediment mixing, a mathematical model is needed (Goldberg & Koide 1962). Such models describe spatial and temporal distributions of certain tracers in the sediment (Meysman et al. 2003). Particle tracers are assumed to be mixed in the same way as sediment particles (Maire et al. 2008). Their vertical profile in the sediment can highlight 2 different types of particle transport: local and non-local bio-mixing. The sum of many local and small events of sediment mixing results in an exponential decrease of a tracer originating from the surface with sediment depth, and subsurface peaks highlighting non-local transports. This process is analogous to diffusion and can be quantified by a bio-diffusion coefficient D_B, a measure of the intensity of local bio-mixing (Boudreau 1986a,b, Boudreau & Imboden 1987, Meysman et al. 2010). Organisms that move through the upper centimeters of the sediment and that belong to surface modifiers categorized by Queirós et al. (2013) are assumed to induce local sediment mixing. Non-local bio-mixing is characterized by an injection flux J or an ingestion rate r, which is a measure of its intensity and is defined by the occurrence of subsurface maxima due to e.g. discrete burrowing events (Boudreau 1986b). Organisms that freely move through the sediment matrix (e.g. gallery biodiffusors) or upward and downward conveyors may be responsible for non-local sediment mixing. Chlorophyll (chl) was used in the study as a particle tracer for bio-mixing, and its depth distribution was interpreted using a local and non-local model developed by Soetaert et al. (1996).

While much work has been done on the rates and mechanisms of bioturbation, there is still a gap in our understanding of general patterns of sediment mixing on different spatial scales. Therefore, a field study was conducted in 6 areas with different sediment types and contrasting macrozoobenthic communities in the German Exclusive Economic Zone (EEZ) of the Baltic Sea. Each area was assumed to be homogenous in terms of sedimentological and faunistic properties. This led to the assumption of a homogenous intensity of bioturbation within each station. At each station, 24 cores, sampled in distinct patterns, were analyzed using the naturally occurring tracer chl *a*, which is thought to track the mixing of fresh organic matter. The goal of this study was to determine the variability of sediment mixing in each area, as this information is needed to better understand our ecosystems and to enable large-scale assessments of ecosystem processes and functioning influenced by bioturbation (e.g. regulating ecosystem services) (Queirós et al. 2013). Our objectives were to (1) compare bioturbation intensity in different sediment types across the southern Baltic Sea; (2) determine the variability of bioturbation within 1 area of the same sediment type; and (3) examine the extent of local and non-local sediment mixing.

MATERIALS AND METHODS

Study area

Our approach represents a combination of field measurements and modeling. During the AL434 cruise in April 2014, 6 stations in the southwestern Baltic Sea (Fig. 1) with different sediment types and contrasting macrozoobenthic communities (Schiele et al. 2015) were investigated (Table 1).

Stations were selected to represent major areas of certain biotic and abiotic properties in the southern Baltic Sea. We investigated 2 muddy (Lübeck Bay, LB; Mecklenburg Bay, MB) and 1 sandy (Stoltera, ST) station in the west. In the east, we analyzed 1 muddy (Arkona Basin, AB), 1 sandy (Oderbank, OB) and 1 silty (Tromper Wiek, TW) station. Information on sediment properties was taken from the geological map of the southwestern Baltic Sea (Tauber 2012). Based on the data supporting this map, the same granulometric properties are guaranteed for our stations as well as for closely located neighboring data points in each cardinal direction (1 to 2 nautical miles) exceeding the sampling area covered at each station (Table 1). Salinity data were obtained from a CTD (Seabird SBE 9plus). The areas follow a salinity gradient from west (22 at MB) to east (8 at OB) (Table 1).

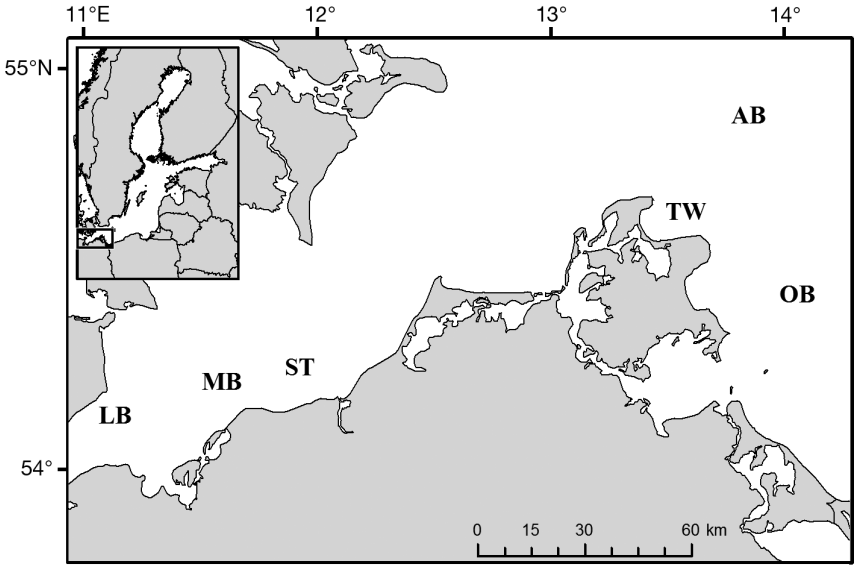

Fig. 1. Study area and distribution of the 6 investigated stations of Lübeck Bay (LB), Mecklenburg Bay (MB), Stoltera (ST), Arkona Basin (AB), Tromper Wiek (TW) and Oderbank (OB) (modified after Schiele et al. 2015)

Pronounced differences in salinity between surface and near bottom waters at some stations (5 to 6 units at LB, MB and 11 to 12 units at ST, AB) indicate the presence of a stable halocline. Usually, mean bottom water salinities are 3 to 9 units lower at ST and AB (Dippner et al. 2005, as cited in Zettler et al. 2008). The higher salinities observed during sampling (Table 1) can be explained by occasional and short-term inflow events from the North Sea (Nausch et al. 2015). Owing to the narrow connections between North and Baltic Sea, the events of inflowing saline waters into the Baltic Sea are limited and occasional, with stagnation periods over weeks to months (Zettler et al. 2007). In December 2013, a major saltwater inflow into the Baltic Sea began due to a combination of the earlier effects of hurricane Xaver and long phases of westerly winds, oxygenating deep basins and leading to increased bottom water salinities (Nausch et al. 2014).

According to Schiele et al. (2015), all stations were located underneath the photic zone. The authors modeled light penetration depth (averaged over the period from March until October) over the period from 2000 to 2010 using a regional adaptation of the ERGOM model (Friedland et al. 2012, Schernewski et al. 2015). Most stations were at depths of between 20 and 30 m. The shallowest station was OB at 16 m; the deepest was AB at 45 m water depth.

The stations were characterized by different macrozoobenthic communities (Table 2) reported in Schiele et al. (2015). These authors analyzed macrozoobenthic data based on surveys between 2004 and 2013, including 829 sampling stations in the southern Baltic Sea, each consisting of 3 to 5 replicates (see Schiele et al. 2015). The most dominant species occurring at each station are listed in Table 2. To give an overview on the way these organisms mix particles and to better understand the variability of bioturbation and the distribution of local and non-local sediment mixing at our stations, we used information on life traits provided by Queirós et al. (2013). These authors scored each taxon on categorical scales describing sediment mixing (reworking), increasing from 1 (epifauna that bioturbate at the sediment–water interface) to 5 (regenerators that excavate holes, transferring sediment at depth to the sediment surface), and mobility that reflects increasing mobility from 1 (organisms live in fixed tubes) to 4 (organisms move freely via burrow systems). These are 2 important traits regulating bio-mixing (Solan et al. 2004). Based on the life traits of each dominant species, we categorized it according to whether it induces rather local or non-local sediment mixing. We assumed surface modifiers and biodiffusors to be responsible for local bio-mixing, whereas free-moving upward or downward conveyors most likely induced non-local sediment mixing. Information is summarized in Table 2.

Sampling and laboratory analyses

To set up a sampling design, we differentiated between sampling station and location. Stations represent the different study areas LB, MB, ST, AB, TW, OB in the Baltic Sea. Locations define the exact sampling positions at each station. At each station, 6 locations were investigated by deploying a multicorer (MUC) (Fig. 2). At each location, 4 cores with a diameter of 10 cm were taken, resulting in 24 cores at each station in total (except at OB: 23 cores). The cores were sliced onboard immediately after retrieval at 0.5 cm intervals to 3 cm and at 1 cm intervals to 10 cm depth. To obtain the bound pool of chl that is embedded in intact chloroplasts, the samples were deep-frozen immediately and stored until extraction (Sun et al. 1991). After thawing, samples were homogenized and 3 subsamples of 1 cm^3 sediment were taken from each slice. After adding 9 ml of 96%

Table 1. Water depth; salinity (surface and near bottom); bottom water temperature (bwt); mean chl concentration in surface sediment (0 to 0.5 cm); integrated chl inventory of bioturbated zone (sum of chl in 0 to 6 cm) with n = 24 at LB, MB, ST, AB, TW and n = 23 at OB; total carbon to total nitrogen ratio (TC:TN); sediment type following Tauber (2012); median (0 to 3 cm); and remarks at each station during sampling. MZB: macrozoobenthos. *Data provided by D. Bunke (pers. comm.)

Stn	Depth (m)	Salinity Surface	Salinity Bottom	bwt (°C)	Chl (0–0.5 cm) (µg [0.5 cm]$^{-3}$)	Chl (0–6 cm) (µg [6 cm]$^{-3}$)	TC:TN ratio*	Sediment type	Median grain size (µm)	Area covered per station (m)	Remarks	Reference
LB	23	17	22	5.5	17.2	76.6	8.1	Aphotic mud	19.4	500 × 500	Industrial dumping site in late 1950s until 1971 High heavy metal contamination and organic pollution	Zettler et al. (2000) Leipe et al. (1998) Bunke (pers. comm.)
MB	25	17	23	5.9	7.1	54.3	8.4	Aphotic mud	17.4	250 × 250	Annual loss of MZB due to hypoxia below the stable thermocline Recolonization in winter	Gosselck et al. (1987) Zettler et al. (2000, 2008) Bunke (pers. comm.)
ST	18	11	23	5.8	5.8	36.2	8.9	Aphotic sand	148.8	500 × 700	Shallow stone and boulder grounds	Zettler (2001) Bunke (pers. comm.)
AB	45	8	19	5.5	10.8	81.6	8.3	Aphotic mud	22.9	750 × 700	Material from land transported by River Oder is deposited in the basin	Neumann et al. (1996) Wasmund et al. (2004) Zettler et al. (2008) Bunke (pers. comm.)
TW	30	8	10	4.5	8.4	53.4	8.4	Silt	27.3	500 × 750	Semi-enclosed bay Sea bottom covered with craters due to anchor hopper dredging for gravel extraction in the past	Davis & Hayes (1984) Mohrholz (1998) Klein (2003) Kubicki et al. (2007) Bunke (pers. comm.)
OB	16	8	8	5.6	24.5	62.2	8.6	Aphotic sand	181	500 × 500	Spring bloom reached the sediment during sampling High nutrient load by the River Oder Thin fluffy layer of sediment ripples in the valley Material resuspends easily	Witt et al. (2001) Zettler et al. (2008) Bunke (pers. comm.)

ethanol, the samples were stored in the dark for 24 h and centrifuged at 2772 × *g* for 5 min to complete chl extraction from the sediment sample. Each sample was extracted once; further extractions contained insignificant concentrations of the pigment. A simplified photometric method was employed (663 and 750 nm) using a Shimadzu UV 1202 spectrophotometer (Holm-Hansen et al. 1965, Lorenzen 1967, Knap et al. 1994). Calculations are based on HELCOM (1988a,b) and the chosen method delivers a combination of chl *a* and its degradation products, abbreviated below to chl for simplification, which we regard as fresh organic matter.

Degradation of chl (k_D)

When applying the bio-mixing model by Soetaert et al. (1996), information on the decay of the tracer is needed. The first-order decay constant k_D for chl has a strong influence on modeling results. On the EMB 100 cruise in April 2015, the first 2 cm of 2 different types of fresh sediment (mud from AB and sand from ST) were taken from cores and homogenized. Subsamples were put into sealable plastic bags and wrapped in aluminum foil as an additional gas barrier to keep them anoxic and to avoid light penetration. Afterwards, the samples were incubated for 5, 10, 15 and 20 d, and then deep-frozen. We emphasized anaerobic incubations because the major part of chl decay occurs within the anoxic layers of the sediments. Furthermore, samples were incubated at 5, 10, 15 and 20°C to find out whether degradation is temperature-dependent. Subsamples for the degradation at 5°C were kept in the refrigerator. For 10 and

Table 2. Abundance of organisms (ind. m^{-2}) and biomass (g dry wt m^{-2}), list of most dominant species occurring at each sampling station and their score on categorical scales after Queirós et al. (2013) reflecting mobility (2: limited movement; 3: slow, free movement through the sediment matrix; 4: free movement via burrow systems); sediment mixing (2: surficial modifier; 3: upward and downward conveyor; 4: biodiffusor) and our categorization of local or non-local bio-mixing. na: not applicable

Stn	Abundance (ind. m^2)	Biomass (g dry wt m^2)	Dominant species	Mobility	Sediment mixing	Local/ non-local	Reference
LB	1959	0.4	*Kurtiella bidentata*	2	2	Local	Schiele et al. (2015),
			Diastylis rathkei	3	2	Local	Zwicker (2014),
			Capitella capitata	2	3	Non-Local	Powilleit et al. (1994)
			Priapulus caudatus	2	4	Non-local	
MB	2840	104.7	*Diastylis rathkei*	3	2	Local	Schiele et al. (2015),
			Arctica islandica	2	2	Local	Zwicker (2014),
			Abra alba	2	2	Local	Powilleit et al. (1994)
			P. caudatus	3	3	Non-local	
			Nepthtys hombergii	3	4	Local	
ST	5085	356.7	*Limecola balthica*	2	2	Local	C. Morys, M. Powilleit,
			A. islandica	2	2	Local	S. Forster, unpubl. data
			Scoloplos armiger	3	4	Local	
AB	3503	48.7	*L. balthica*	2	2	Local	Schiele et al. (2015),
			D. rathkei	3	2	Local	C. Morys, M. Powilleit,
			S. armiger	3	4	Local	S. Forster, unpubl. data
TW	3618	1.2	*L. balthica*	2	2	Local	C. Morys, M. Powilleit,
			S. armiger	3	4	Local	S. Forster, unpubl. data
OB	112827	na	*Peringia ulvae*	2	2	Local	Schiele et al. (2015),
			Cerastoderma glaucum	2	2	Local	C. Morys, M. Powilleit,
			L. balthica	2	2	Local	S. Forster, unpubl. data
			Mya arenaria	2	2	Local	
			Hediste diversicolor	4	4	Local	

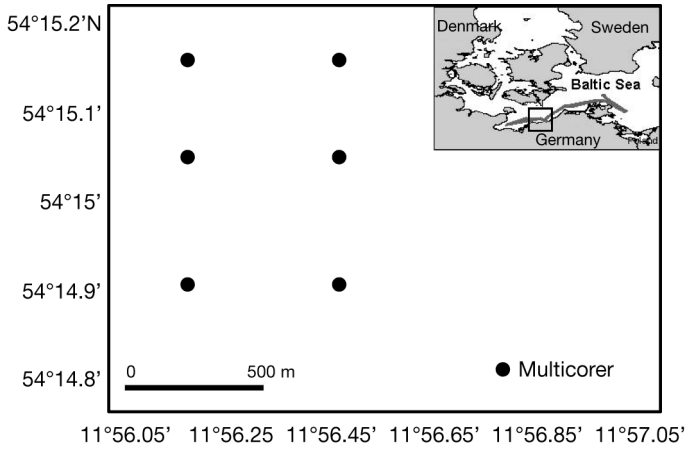

Fig. 2. Scheme of the sampling design within 1 station using the example of ST: 6 sampling locations (●) with 4 cores each (24 cores in total)

15°C, samples were put into temperature-controlled water baths. The remaining samples were kept at room temperature. Temperature was checked every hour until stabilization and afterwards twice a day. For the initial chl content, samples of each sediment type were deep-frozen immediately after retrieval. The samples were measured as described previously. A total of 12 replicates were analyzed for each temperature and time.

Modeling bioturbation

For a quantitative characterization of bioturbation intensity, vertical chl profiles were interpreted using the bio-mixing model by Soetaert et al. (1996). This model presumes steady-state conditions with a constant supply of chl, with the concentration of chl in some layers within the sediment being subjected to advection, mixing and first-order decay, as described by (Berner 1980):

$$D_B \frac{d^2C}{dx^2} - \omega \frac{dC}{dx} - \lambda C - rC + Qi + S_p = 0 \quad (1)$$

where C is chl concentration, x denotes depth into the sediment (cm, increasing downward), D_B is the sediment diffusive mixing coefficient ($cm^2\ d^{-1}$), ω is the sedimentation rate ($cm\ yr^{-1}$), λ is the decay rate (d^{-1}), r is a first-order ingestion rate (d^{-1}), Q_i is the nonlocal exchange input to a certain layer (i) and S_p the production term that is not relevant when using chl as a tracer.

Soetaert et al. (1996) developed fitting routines to model the depth distribution of ^{210}Pb in ocean sediments. They described models for steady-state diffusive (local) mixing and non-local mixing, differentiating between 6 ways in which particles are mixed within the sediment (Fig. 3). The diagenetic equations of the various models that were used in this study are presented in Fig. 3. ω was defined as very low (0.00001 cm yr^{-1}) because of the time span of 35 to 69 d (half-life of chl) considered. Boundary conditions determine the integration constants and are adapted from Soetaert et al. (1996) (Fig. 3, present study). There is a flux boundary at the sediment–water interface (B0, B1), continuity of concentration (B2) and continuity of flux (B3, B4) between layers and the no-gradient boundary (B5) at depth. Model 1 is the simplest model and describes the situation of continuous sedimentation without biological and hydrographical sediment mixing (D_B and Q_i are set to 0). The distribution of chl in the sediments is then influenced only by the flux at the sediment–water interface (Flux 1), sedimentation and decay. The least-squares fit algorithm has to find the best value of Flux 1. Model 2 is applied in cases of steady-state diffusive mixing and delivers a biodiffusion coefficient D_B (cm^2 d^{-1}). Flux 1 and D_B are the 2 parameters that need to be estimated by least-squares fit. Model 3 is used for the description of non-local sediment mixing by additional injection fluxes J (µg cm^{-2} d^{-1}) of particulate matter from the sediment surface into the sediment down to a certain depth (L). In contrast to Model 2, Model 3 requires 2 extra fitting parameters: injection flux J of chl that is injected into the sediment and the depth at which this injection occurs (L). Contrary to Model 3, the flux in Model 4a is injected into a layer and there is 1 additional parameter to fit, i.e. thickness of the deposition layer. Model 4b is similar to Model 3 but the flux to depth L has been derived from ingesting surficial sediment and is quantified by r (d^{-1}). Model 5 is the same as Model 4b but the ingestion of the tracer is injected into a layer. Introducing new parameters into the model with increasing complexity improves the visual fit between modeled and observed data. A 1-tailed F-test provides the information on whether the more complex model significantly better explains the observed data ($p < 0.05$) (Sokal & Rohlf 1995):

$$F = (SSR_1 - SSR_2)/(df_1 - df_2)/(SSR_2/df_2) \quad (2)$$

where SSR_2 and SSR_1 are the sum of the squared residuals of observed and modeled values of the elaborate and simple model, respectively, and df_2 and df_1 are the degrees of freedom (number of observations − number of parameters − 1) of the respective models. The null hypothesis, stating that the residual variance between modeled and observed data in the more complex model is identical to the simpler model, is rejected when the calculated F-value exceeds the critical value. In this case, the alternative hypothesis notifies that the complex model has significantly reduced this variance. The 'best model' is chosen when reducing its number of parameters results in an increase in the sum of squared residuals.

Determination of mixing depth (z_m)

An average bioturbation depth was examined using our measured chl profiles. The concentrations of chl never reached 0 due to phaeopigments, which we also detected by the method applied (Wasmund 1984). Changes in the tracer concentration with depth approaching 0 indicate that a background value is reached. This was typically the case at chl concentrations of around 1 to 2 µg cm^{-3} when concentration change with depth declined to <0.1 µg cm^{-3}. This depth is defined as the depth of the bioturbated zone.

Statistics

Determining the variability of bioturbation along the coast of the southwestern Baltic Sea combines comparisons of chl depth profiles as well as their corresponding modeled bioturbation intensities D_B, J and r using the bio-mixing model (Soetaert et al. 1996).

Tracer distribution within the sediment

Statistics analyzing variability of bioturbation between and within stations as well as within locations were carried out using the software packages SPSS and PRIMER.

Variability between stations. As chl profiles within the sediment allows differentiation between local, non-local and an absence of sediment mixing, these tracer distributions were firstly compared to estimate similarities and dissimilarities between and within stations using an MDS plot (transformation: square roots; resemblance: 2D Euclidean distance). Chl concentration of each layer was normal-

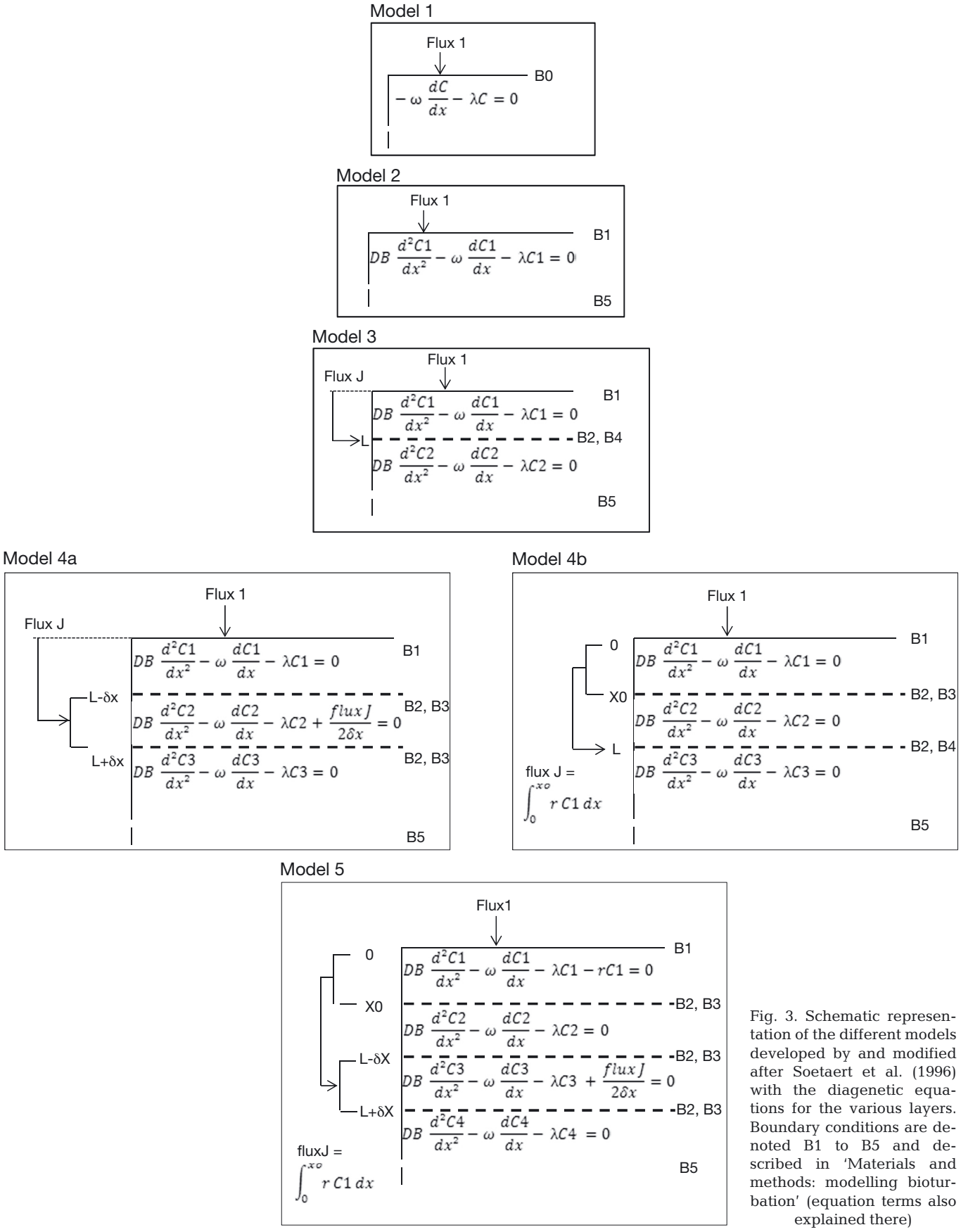

Fig. 3. Schematic representation of the different models developed by and modified after Soetaert et al. (1996) with the diagenetic equations for the various layers. Boundary conditions are denoted B1 to B5 and described in 'Materials and methods: modelling bioturbation' (equation terms also explained there)

ized with the total chl concentration of each core. Based on the chl inventory of each core being equal to 100%, the percentage of chl within each layer was then calculated. Secondly, these percentages were used for ANOSIM tests comparing the 6 stations (n = 24 cores per station) investigated. This comparison was used to answer the question of whether chl profiles are significantly different between stations.

Variability within stations (= *between locations*). For a comparison of locations within 1 station, a pair-wise comparison of locations (n = 6 locations with n = 4 cores per location) was first carried out using ANOSIM. This test gives information on whether chl profiles of the 6 locations within 1 station tested are significantly different. A second step, which we considered to be the most important criteria for defining similar locations, was then to compare the numbers of local, non-local and no sediment mixing within each location. Locations are defined as similar when they indicate the same distribution of the modes of sediment mixing. In cases of a sufficient number of cores indicating the same mode of sediment mixing within previously defined similar locations (n = minimum of 2 cores indicating the same mode of sediment mixing at 1 location, n = minimum of 2 locations), these cores were then tested (Kruskal-Wallis test) for significant differences in terms of intensity. If the number of cores with the same mode of sediment mixing within similar locations was too low, the only alternative comparison was the differentiation between no, local or non-local sediment mixing.

Variability within locations. To compare single cores within 1 location, the distribution of the different modes of sediment mixing was used. Cores within 1 location (n = 4, taken from 1 MUC) were defined as similar as soon as all 4 cores showed 1 same mode of mixing.

Modeled D_B and J

To compare mixing intensities between stations, all modeled values of local (D_B) and non-local (J) sediment mixing estimated at 1 station were used for a non-parametric Kruskal-Wallis test and its post hoc test. No sediment mixing (D_B = 0) was excluded from all statistical analyses. Ingestion rates (r) occurred too rarely for an appropriate statistical test. To test differences between locations within 1 station, D_B and J of similar locations were used as long as they were represented in sufficient number.

Mixing depth z_m

To find out whether mixing depths were significantly different between stations, Kruskal-Wallis tests and post hoc tests were carried out using estimated mixing depths of all cores per station (n = 24 cores per station, except OB: 23 cores, n = 6 stations).

RESULTS

Degradation of chl

During the anoxic incubation experiment with muddy sediments from AB, chl increased initially at all temperatures, before decreasing after 5 d (Fig. 4a). This phenomenon occurred several times. During the first 5 d of incubation, the sediment changed from partially oxic to completely anoxic conditions. Samples for the initial chl value (t_0) were not incubated but rather frozen immediately after retrieval and therefore treated differently to all the other samples. This seems to result in different extraction conditions due to e.g. physiological modifications of phototrophic cells during incubation. For that reason, the

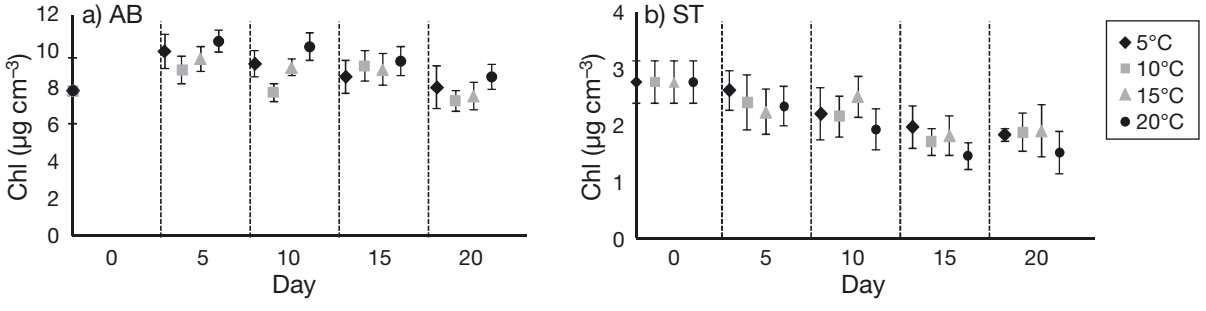

Fig. 4. Time courses of chl concentration (n = 12) in incubated fresh surface sediments including 0, 5, 10, 15 and 20 d. Anoxic incubation was performed at 5, 10, 15 and 20°C. (a) Arkona Basin (AB) (mud); (b) Stoltera (ST) (sand). Data were treated as an exponential function. Note the lower initial value in AB

initial values were ignored because we assume these values to be higher than measured. The data were then fitted starting with t_1 (after 5 d) to estimate k_D. In general, the degradation of chl depends on the source concentration following first-order kinetics (Sun et al. 1991). There was little difference in the chl concentration over time between the 4 temperatures (Fig. 4a). As we did not find a temperature dependency of chl degradation, we obtained k_D of 0.01 in muddy sediments from AB, which we used for the other mud stations (LB, MB) as well.

The chl concentration in sandy sediments from ST decreased constantly over time (Fig. 4b). As we also assume the initial value to be higher in reality and in order to treat our data in the same way, we ignored the initial value from the curve. k_D values obtained for 5, 10, 15°C were 0.02 d^{-1}, being lower than for 20°C at 0.03 d^{-1}. As temperatures of bottom waters in the Baltic Sea are usually not higher than 15°C (Leppäranta & Myrberg 2009), we used k_D = 0.02 d^{-1} for all sand stations (ST and OB as well as TW) in our study.

Variability of bioturbation between stations

Mean tracer distribution and bioturbation intensity

For a general overview of sediment mixing at our sampling stations, chl concentrations of each depth layer (13 layers per core) of all 24 cores at each station were averaged (Fig. 5) to detect whether local or non-local sediment mixing is dominant at each station. The mean chl profiles were modeled using the bio-mixing model by Soetaert et al. (1996) (Fig. 5). Chl profiles obtained at the western stations in the southern Baltic Sea (LB, MB, ST) show an exponential decrease with depth, indicating local mixing to be dominant. Sediments at ST are most intensively mixed, with a D_B of 0.4 cm^2 d^{-1} being 67 times higher than at LB (D_B = 0.006 cm^2 d^{-1}) and 8 times higher than at MB (D_B = 0.05 cm^2 d^{-1}). Stations in the east are characterized by subsurface maxima in chl due to non-local processes. At OB, evidence for non-local mixing is not as distinct as at AB and TW, due to the chosen scale. However, according to the bio-mixing

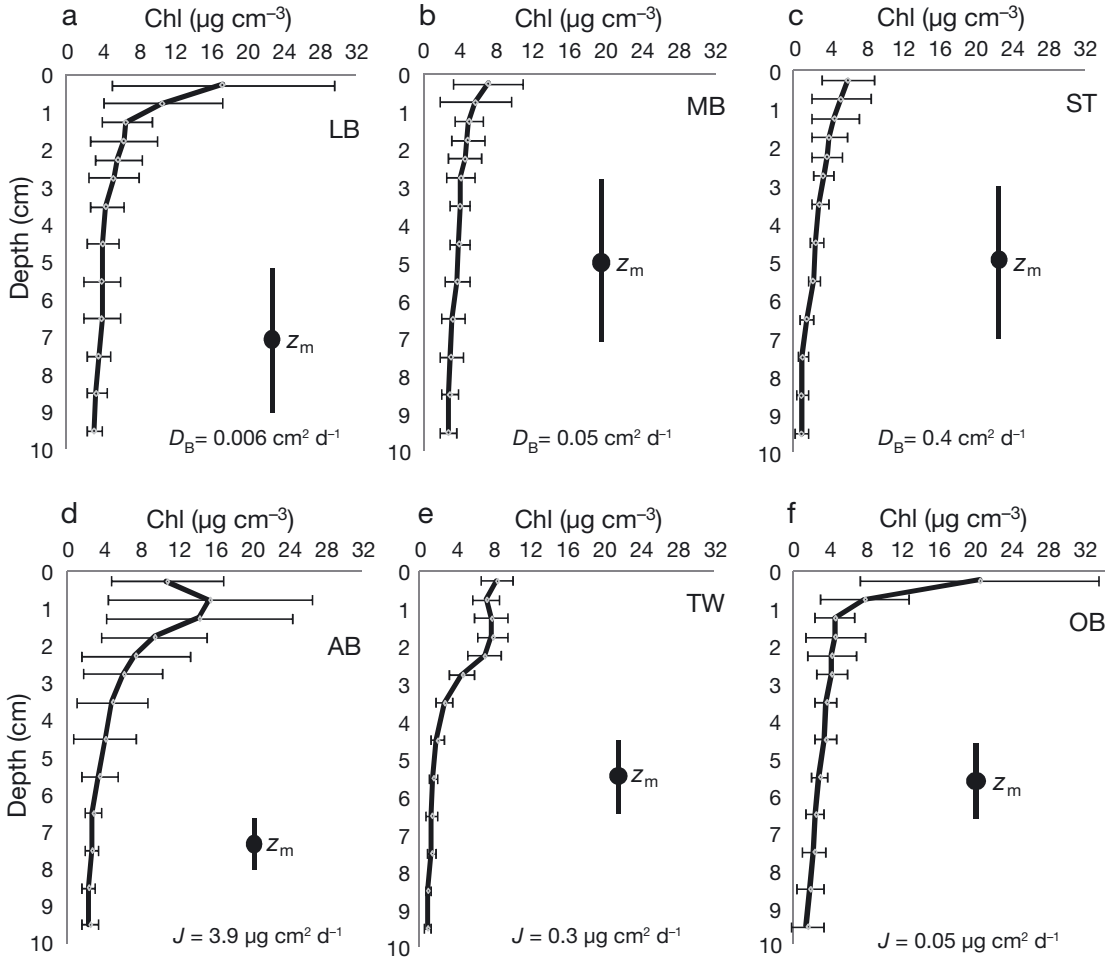

Fig. 5. Chl depth profiles with SD for each sampling station. (a) Lübeck Bay (LB; n = 24); (b) Mecklenburg Bay (MB; n = 24); (c) Stoltera (ST; n = 24); (d) Arkona Basin (AB; n = 24); (e) Tromper Wiek (TW; n = 24); (f) Oderbank (OB; n = 23). (●) Mean mixing depths (z_m; ± SD) estimated from all cores investigated. Biodiffusion coefficient (D_B), injection flux (J) and ingestion rate (r) at each station provided by the bio-mixing model by Soetaert et al. (1996) using mean chl profiles

model applied, OB is characterized by non-local bio-mixing, with an injection flux (J = 0.05 µg cm^{-2} d^{-1}) to 2.1 cm depth. AB shows a distinct subsurface maximum in chl (increase of 6 µg cm^{-3}) close to the sediment surface and is characterized by an ingestion rate of 3.9 d^{-1}. TW indicates an injection flux of 0.3 µg cm^{-2} d^{-1}. Mean mixing depths are also presented in Fig. 5. Kruskal-Wallis results indicate that our estimated mixing depths in the southern Baltic Sea are highly significantly different, with 2 subsets of stations with similar mixing depths: MB and ST as well as LB, AB, TW and OB. Mixing depth at MB and ST is 7.1 ± 1.6 cm, with chl penetrating the sediment 2 cm deeper than at the other stations LB, AB, OB and TW (5.2 ± 1.7 cm).

All MDS results using normalized chl profiles were first plotted to illustrate differences in the chl depth distribution between sampling stations (Fig. 6) (n = 6 stations with 4 cores each, resulting in 24 cores per station, except OB: 23 cores). At LB and MB, about two-thirds of the cores are similar to each other, whereas the rest show great differences. ST is a heterogeneous station with the cores widely spread in the plot. About one-third of the cores show similarities to LB and MB. At AB, the results present a binary division, with half of the cores matching LB, MB and ST. The remaining cores show great distance from other stations in the plot. TW is a homogenous station with all 24 cores embedded closely to each other and shows only occasional matches with other stations. At OB, there is a broad distribution of the data in the plot, indicating a heterogeneous station. All in all, there is a tendency towards increasing dissimilarities when stations are further apart from each other in the Baltic Sea, except LB and OB. ANOSIM testing using normalized chl showed a global R of 0.408 with a significance level of 0.1%, indicating highly significant differences between all sampling stations. A pair-wise comparison presents all stations being significantly different from each other.

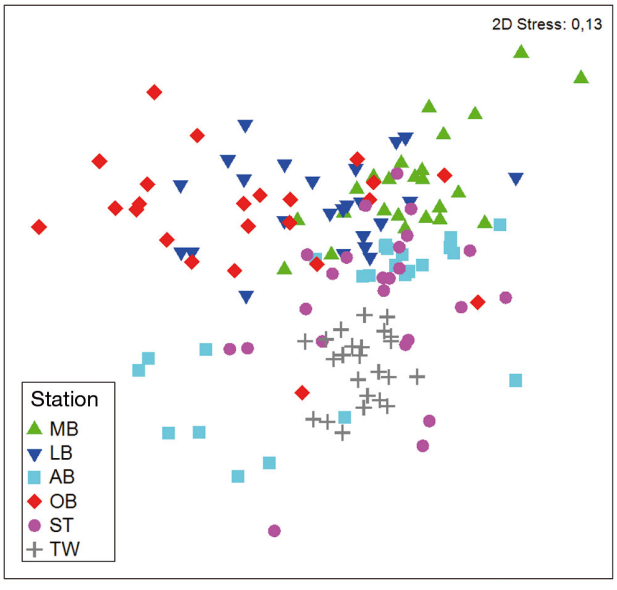

Fig. 6. MDS plot of all stations on the basis of normalized chl concentrations of each depth layer and core. ANOSIM test showed that stations represented by 24 cores (OB: 23) are highly significantly different

Local and non-local sediment mixing

A comparison of the extent of local, non-local and no sediment mixing by the benthic fauna assemblages at each station indicates differences between stations (Fig. 7). In the west (LB and MB), non-local sediment mixing covers about 30% of the investigated area. The bio-mixing model identified no sediment transport in 13% of the samples at LB and in 17% at MB. At ST, non-local sediment mixing occurred in 48% of the cores. Towards the east, stations present mainly non-local sediment mixing (70%) at AB and OB. AB is the station with most ingestion rates (25%) compared to all other stations. At TW, non-local processes were detected in all 24 cores. These findings match the dominant particle transport (local or non-local) estimated by the mean chl profiles described above (Fig. 5). All in all, the percentages of non-local sediment mixing increase from west to east.

Modeled sediment mixing (D_B and J)

The Kruskal-Wallis test comparing D_B and J between stations (numbers of cores indicating local [D_B] or non-local [J, r] sediment mixing that were used for the statistical test are given in Table 3) indicates that intensities of both local and non-local sediment mixing are highly significantly different between stations. No sediment mixing (D_B = 0) was excluded from all statistical analyses. Ingestion rates r could not be compared statistically because of their infrequent occurrence (Table 3). Comparing D_B between stations using the Kruskal-Wallis post hoc test, 2 similar subsets are indicated: LB and OB as well as MB, ST and AB. TW was not considered as all 24 cores showed non-local sediment mixing. LB (D_B = 0.02 ± 0.03 cm^2 d^{-1}, n = 14) and OB (D_B = 0.005 ± 0.003 cm^2 d^{-1}, n = 6) are the least intense locally mixed stations. Sediments at MB (D_B = 0.4 ± 0.8 cm^2 d^{-1}, n = 11), ST

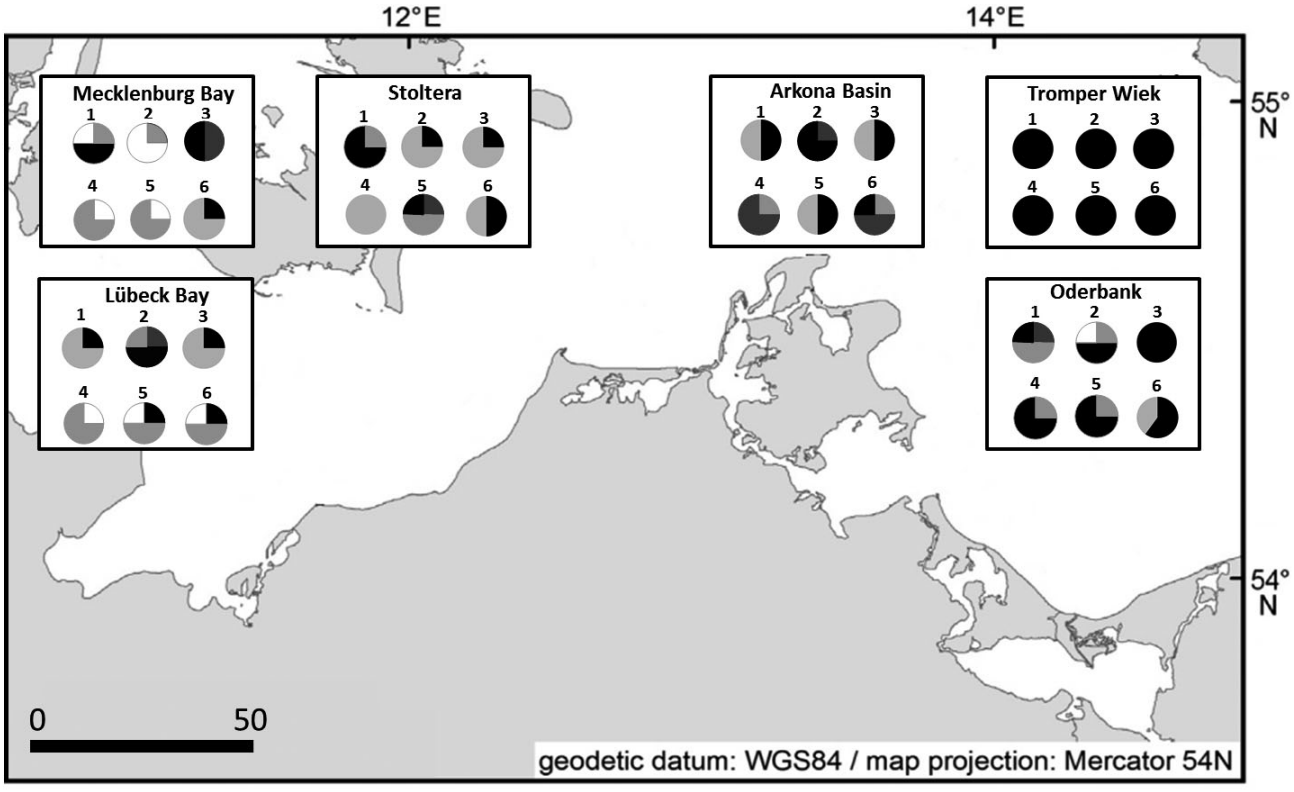

Fig. 7. Schematic overview of the modes of sediment reworking at all sampling locations (numbers) at the investigated stations. Pie charts show the percentage of local sediment mixing (light grey), non-local injection flux (black), non-local ingestion rate (dark grey) and no sediment mixing (white) at each location. Note the increase of non-local sediment mixing from west to east

(0.3 ± 0.3 cm^2 d^{-1}, n = 15) and AB (0.2 ± 0.1 cm^2 d^{-1}, n = 8) are 40 to 80 times more intensely locally mixed. Results are presented in Table 3.

Injection fluxes J indicated 3 subsets among stations according to the Kruskal-Wallis post hoc test: LB, MB, OB and MB, ST, AB, OB, as well as ST, AB, TW. LB shows lowest injection fluxes with 0.09 ± 0.06 µg cm^{-2} d^{-1} and TW highest with 0.3 ± 0.1 µg cm^{-2} d^{-1}. MB and OB are not significantly different to LB, but also indicate a homogenous subset with ST and AB. We consider LB as a low, MB, ST, AB and OB as intermediate, and TW as a high non-locally mixed station. Results are presented in Table 3.

Table 3. Mean modeled values (± SD) derived from the local and non-local bio-mixing model (Soetaert et al. 1996) for local (D_B) and non-local (J, injection flux and r, ingestion rate) at each station, and the number of cores (n) indicating each type of sediment mixing

Stn	D_B (cm^2 d^{-1})	J (µg cm^2 d^{-1})	r (d^{-1})	No sediment mixing (n)
LB	0.02 ± 0.03 (14)	0.09 ± 0.06 (6)	2 (1)	(3)
MB	0.4 ± 0.8 (11)	0.2 ± 0.1 (5)	0.06 ± 0.06 (2)	(6)
ST	0.3 ± 0.3 (15)	0.3 ± 0.2 (8)	0.3 (1)	–
AB	0.2 ± 0.1 (8)	0.3 ± 0.1 (10)	1670 ± 4080 (6)	–
TW	–	0.3 ± 0.1 (24)	–	–
OB	0.005 ± 0.003 (6)	0.2 ± 0.09 (15)	8 (1)	(1)

Variability of bioturbation within stations

Tracer distribution

Statistical analyses using ANOSIM tests (normalized chl profiles) were carried out for each station separately to highlight differences between locations (n = 6 locations and n = 4 cores per location). ANOSIM results showed that locations at stations LB, MB, ST and AB are highly significantly different. There were no significant differences found between locations at TW and OB. At station MB, the global R of 0.23 with a significance level of 0.2% indicates that the locations are significantly different. However, ANOSIM pair-wise comparisons do not show any dissimilarity. ANOSIM results of the comparison of sta-

Table 4. ANOSIM comparing all locations within each station using normalized chl concentrations of each depth layer and core presenting global R and its significance level in order to find significant differences. Number of homogenous subsets derived from the distribution of local, non-local and no sediment mixing within each location and the composition of locations belonging to each subset derived from Fig. 7

Stn	Global R	Significance level (%)	Subsets (n)	Subset 1	2	3	4	5
LB	0.183	3	4	1, 3	2	4	5, 6	
MB	0.23	0.2	5	1	2	3	4,5	6
ST	0.146	4.1	5	1	2,3	4	5	6
AB	0.478	0.1	4	1,3,5	2	4	6	
TW	0.07	17.1	1	1,2,3,4,5,6				
OB	0.016	37	4	1	2	3	4,5,6	

tions and locations are presented in Table 4. However, defining similar locations within 1 station and their composition as presented in Table 4 is not based on ANOSIM pair-wise comparison but rather on the distribution of no, local and non-local sediment mixing (derived from Fig. 7) because of different results gained by the 2 approaches. We defined the differentiation between the modes of sediment mixing according to the bio-mixing model as the most important criteria for similarities and dissimilarities between and within locations.

Local and non-local sediment mixing

The extent of local, non-local (both injection flux and ingestion rate) and no sediment mixing of cores within 1 location were used to describe the variability within 1 station (derived from Fig. 7). In cases of different patterns, locations are considered to be different. Locations with the same distribution of the different types of sediment mixing are considered as subsets. Results are presented in Table 4. Station AB indicates 3 subsets of homogenous locations. LB is more heterogeneous, with 4 subsets respectively. Stations MB, ST and OB show only 2 locations to be similar, resulting in 5 subsets. TW shows a homogenous distribution with all 24 cores, indicating non-local sediment mixing (Table 4).

Modeled sediment mixing (D_B and J)

Some previously described homogenous subsets estimated by the distribution of local and non-local sediment mixing at each location indicated 2 or more cores with the same mode of sediment mixing. In these cases, their corresponding bioturbation intensities derived from the bio-mixing model were compared performing Kruskal-Wallis tests. This test allowed highlighting of differences in mixing intensities between similar locations. At LB, for example, D_B of the 3 cores indicating local sediment mixing at locations 1 and 3 (Fig. 7), were compared using a Kruskal-Wallis test and were found to be significantly different between the 2 locations (1 and 3). This indicates only 2 locations to be similar (5 and 6) with an injection flux J being 1.5 times higher at location 6. As there is a factor of 20 between lowest injection flux (J = 0.04 µg cm^{-2} d^{-1}) and highest (J = 0.8 µg cm^{-2} d^{-1}) estimated by all 24 cores at LB, locations 5 and 6 seem to be very similar. At MB, 2 locations (4 and 5) are similar, presenting the same distribution of the different modes of sediment mixing: 1 core with no mixing and 3 cores with local mixing. D_B values of the 3 cores of each location (4 and 5) were statistically compared and found to be without significant differences. There are 2 similar locations (2 and 3) at ST, with 3 cores indicating local and 1 indicating non-local sediment mixing. Local sediment mixing is not significantly different and J was found to be 1.8 times higher at location 3. As both locations show highest injection fluxes estimated at ST, they do not seem to be different in terms of non-local sediment mixing. AB presents a subset of 3 locations with the same distribution of local and non-local sediment mixing without significant differences in D_B and J (1, 3, 5). Locations 4 and 6 show significantly different J. TW is homogenous without significant differences in J. OB shows 2 similar locations (4 and 5) without significantly different J, but with a 3 times higher D_B at location 5. As there is a factor of 5 between lowest (0.002 cm^2 d^{-1}) and highest D_B (0.01 cm^2 d^{-1}) at OB, local sediment mixing seems to be different at both locations. These results, the number of previously defined homogenous locations and their composition (which locations are similar to one another), are given in Table 4.

Variability of bioturbation within locations

We determined similarity within locations by looking at the distribution of local and non-local sediment mixing of the 4 cores (1 MUC) at each location. All 4 cores showing the same type of sediment mixing indicates similar locations (derived from Fig. 7). LB, MB and AB do not present any location with similar cores. ST and OB each show 1 location with similar cores, whereas all locations are similar at TW.

Comparison of tracer distribution and modeled values

Mean chl profiles match findings of the model-derived dominant type of sediment mixing and indicate local mixing in the west and non-local in the east. Modeled values of D_B and J using mean chl profiles (Fig. 5) present different results from considering the cores separately (Table 3). At MB, for example, estimated D_B is up to 44 times higher than the mean value of 0.05 $cm^2\ d^{-1}$. At AB, mean chl profile is characterized by an ingestion rate. Although AB is the station with most ingestion rates in our study, the majority of the cores indicated injection fluxes.

ANSOSIM tests determining differences between stations using normalized chl profiles indicate all stations to be significantly different. Kruskal-Wallis tests using modeled values, in contrast, present subsets of more and less intense mixed stations (both local and non-local). The MDS plot indicated a tendency towards increasing dissimilarity with increasing distance between stations, except for LB and OB. These findings match homogenous subsets regarding injection fluxes. There is a tendency towards increasing intensity of non-local sediment mixing from west to east.

ANOSIM tests comparing normalized chl profiles within stations mostly confirm findings estimated by the distribution of local, non-local and no sediment mixing within 1 location. Results at OB present various distributions of both types of sediment mixing, but this station is characterized by homogenous locations according to ANOSIM. ANOSIM comparisons of normalized chl profiles and modeled quantities of sediment mixing may present different results. As the most important criterion to describe variability of bioturbation in this study is the differentiation between local and non-local sediment mixing, we consider these findings to be more important and therefore OB as a heterogeneous station.

Consequently, when combining all findings, LB and OB are stations of low local sediment mixing, whereas MB, ST and AB present significantly higher D_B. Non-local sediment mixing is mainly characterized by injection fluxes J, and ingestion rates r occur only occasionally (except at AB, where this type of transport covers 25% of the investigated area) (Table 3). We summarize LB as a low, MB, ST, AB and OB as intermediate, and TW as a high non-locally mixed station. A comparison within stations indicates differences across the southern Baltic Sea. Results gained at TW present this station to be homogenous, with similar chl profiles and no significant differences in injection fluxes. AB shows 3 locations without any significant differences. Stations in the east (LB, MB and ST) indicate only 2 similar locations. OB is the only station without any similar locations. There is no general pattern apparent for whether closely located cores (within 1 location) are more similar than cores on a broader spatial scale.

DISCUSSION

Chl as a tracer

The minor temperature dependency of chl degradation in our experiments supports its use as a first-order decay tracer in the bio-mixing model by Soetaert et al. (1996), which was developed for radioactive tracers. In a biological context, these decay kinetics imply that the velocity of decomposition is only dependent on the available chl in the organic matter stored in the sediment. Chl is, in turn, an indicator for the presence and quality of food and, therefore, a limiting factor of bioturbation activities associated with foraging.

We cannot explain the initial increase of chl during incubation in muddy sediments. We speculate that the initial values should be higher than measured. Sun et al. (1991) defined 2 pools of chl *a*: 'free' outside of chloroplasts and 'bound' within the intact chloroplasts. The authors hypothesize that the initial degradation during the first 5 d consists of 2 steps: first, chl is released from a bound state; second, the released chl degrades, with the rate of release being initially larger than the degradation rate. When deep-freezing the samples, the complete chl inventory is immediately released from the bound pool. This would imply that the chl concentration after 5 d of incubation is at least equal to the immediately deep-frozen initial value. Sun et al. (1991) also found an initial increase of chl in muddy sediments of Long Island Sound when treating the samples without deep-freezing. In contrast, we found highest values after 5 d despite deep-freezing fresh sediment after retrieval. For that reason, there seems to be an additional biological process releasing chl when the sediment becomes anoxic, e.g. carried out by microorganisms that are able to destroy chloroplasts. Reasons for the incomplete initial extraction of chl may be found in a different composition of the sedimented phytoplankton bloom. Macrophyte debris likely occurs in the sedimentary organic matter, reducing k_D in our sediments (see Bianchi & Findlay 1991).

Some others, in contrast, report a dependency between degradation rate and temperature. Sun et al. (1994) estimated k_D ranging from 0.021 d^{-1} (4°C) to 0.06 d^{-1} (18°C). Green et al. (2002) calculated k_D using the equation by Sun et al. (1993) with k_D of 0.017 d^{-1} at 2°C in February and 0.079 d^{-1} at 22°C in August. The values obtained in winter fit quite well with our estimated constants for sand (0.02 d^{-1}) at water temperatures between 4.5 and 5.9°C. It seems that degradation of chl may depend on the present temperature of the surrounding water (season) rather than on temperature during incubation.

Various studies have estimated a value of 0.03 d^{-1} for chl degradation rates (Bianchi & Findlay 1991, Sun et al. 1991, 1993). The constants obtained in this study (0.01 d^{-1} for mud and 0.02 d^{-1} for sand) are lower. The authors used HPLC, which is a more exact measurement of chl *a* because it distinguishes between different chl species or derivatives (Meyns et al. 1994). In our study, the applied photometric method overestimates 'true' chl values, as chl degradation products from senescent phytoplankton and detritus absorb at the same wavelength spectrum as chl *a* (Wasmund 1984). However, as we chose this method for the basis of our study, it was necessary to use the same analysis for estimating k_D.

Variability of bioturbation between stations

Macrozoobenthos community

As bioturbation is the sum of all physical activities of such organisms, mixing intensity should depend on the properties of the present benthic community, e.g. abundance, depth distribution and activity (Wheatcroft et al. 1990, Wheatcroft & Martin 1996). Data on abundance and biomass at each station are given in Table 2 (C. Morys, M. Powilleit, S. Forster unpubl.). LB, the station with lowest intensities for both local and non-local sediment mixing, represents lowest abundance and biomass. However, ST, the station with second highest abundance and biomass, displayed intermediate mixing intensities. It seems that there is a combination of different factors beyond abundance and biomass influencing mixing intensities. Some of them will be discussed below.

Although it is well known that faunal activity increases particle movement (e.g. Graf & Rosenberg 1997), we still have a generally poor understanding of bioturbation and little predictive capability (Wheatcroft et al. 1990, Boudreau 1998). The difference in benthic communities found at our stations (Table 2) imply variability between stations reported in this study.

LB and MB are closely located, with similar abiotic properties (Table 1), and are dominated by local sediment mixing. However, LB shows lower intensities of local sediment mixing. Zwicker (2014) compared the macrobenthic community present during our study at LB and MB. Both stations are dominated by surface-modifying organisms (Table 2). However, the composition of the benthic community is different. Occasional hypoxia events in the lower part of the water column in both areas can cause a loss of macrobenthic organisms, with a reduction in the long-lived *Arctica islandica* that is replaced by short-lived polychaetes (Spionidae, Capetellidae) (Schulz 1968, Gosselck & Georgi 1984, Gosselck et al. 1987, Gosselck 1992). At LB, *A. islandica* was not detected but *Capitella capitata* showed great abundance. These findings can be associated with the hypoxia event in September 2013 at LB (Petenati 2013). *C. capitata* was not found at MB. Another species indicating hypoxia events is *Diastylis rathkei*. This mobile species is able to avoid hypoxia by migrating to neighboring areas (Jarre 1989). *D. rathkei* was found at MB in remarkably greater abundance than at LB. Furthermore, organisms are smaller at LB than at MB (Zwicker 2014). Another indicator for a recolonization at LB is *Kurtiella bidentata*, which is sensitive to hypoxia (Borja et al. 2000). This species only occurred in juvenile stages at LB (Zwicker 2014). Differences in size and abundance of *A. islandica, D. rathkei*, *K. bidentata* and *Nephtys hombergii* explain different intensities of local sediment mixing at both stations. Non-local sediment mixing at LB may be induced by the upward conveyor *C. capitata*.

ST, mainly characterized by local sediment mixing, is dominated by the surface-modifying species *Limecola balthica, D. rathkei* and *A. alba* (C. Morys, M. Powilleit, S. Forster unpubl. data). *A. alba*, sensitive to changes in temperature and salinity, was exclusively found in juvenile stages, indicating recolonization of the area (Zettler et al. 2000). According to Zettler (2001), the distribution of small-sized *A. islandica* (<30 mm) in the area around ST indicates a successful recruitment in the 1980s and 1990s after a long period of hypoxia (Gosselck et al. 1987, Prena et al. 1997). *A. islandica* found during our sampling are mainly larger than 30 mm, indicating the ongoing recruitment reported by Zettler (2001). Local sediment mixing is significantly different from LB but not MB. The different compositions of the macrobenthic community at LB, MB and ST do not result in significant differences in non-local sediment mixing.

AB, TW and OB show different patterns in sediment mixing than stations in the west. All 3 stations indicate only surface-modifying organisms or biodiffusors to be most abundant. Biodiffusors include organisms with activities that result in local sediment mixing over short distances (Kristensen et al. 2012). There is no indication of organisms possibly responsible for non-local sediment mixing. *L. balthica* occurs frequently at all stations and is supposed to be a surficial modifier according to Queirós et al. (2013). Brafield & Newell (1961) observed this species to be a deposit feeder. Sometimes the end of the tube containing the exhalent siphon as a second small hole can be noticed (Hulscher 1973). This feeding track allows localization of the buried bivalve situated centrally beneath the star-figure generated by the siphon's foraging activity. We assume that the tube is refilled with surface particles when the bivalve retracts its siphon, creating sub-surface peaks of chl. More work has to be invested to find out whether *L. balthica* actually belongs to surficial modifiers.

All in all, according to the life traits and abundance of organisms found at our stations, many bivalves and *D. rathkei* can be associated with local sediment mixing. We were not able to find organisms possibly responsible for non-local sediment mixing, according to their life traits by Queirós et al. (2013). For that reason, more effort needs to be directed into understanding the traits of macrobenthic organisms. Furthermore, it seems that the composition of benthic communities and abundance are not the only factors influencing sediment mixing (see Food supply and quality).

Food supply and quality

Benthic communities depend on food supply from the water column. It can be assumed that ingestion rates increase with increasing quality and quantity of food (Taghon & Jumars 1984). As a result, more intense sediment mixing would take place when more chl is present. Sun et al. (1994) and Boon & Duineveld (1998) could not find positive correlations between chl and bioturbation intensity at any of their study sites. Additionally, Christensen & Kanneworff (1985) as well as Boon et al. (1998) reported a rapid reaction of benthic macrofauna to spring bloom sedimentation. However, OB is the only station where the spring bloom had reached the floor, but does not indicate high mixing rates compared to the other stations.

Turnewitsch et al. (2000) could not find a single functional relation between food supply and sediment mixing valid for all areas of the Arabian Sea. The authors state that in some areas even negative correlations were found. Their results, however, contrast with positive relationships in the northeast Atlantic (Legeleux et al. 1994, Shimmield et al. 1995) and in the equatorial Pacific (Pope et al. 1996, Smith et al. 1997). We performed Spearman correlations between D_B, J and r (number of data used is given in Table 3) and the corresponding surface and inventory chl (sum of chl of first 6 cm) concentration. We found highly significant negative correlations between D_B and surface chl concentration ($r = -0.83$, $p < 0.001$) and chl inventory ($r = -0.48$, $p < 0.001$). Stations with highest chl concentrations (mean surface chl at LB: 18.7 µg cm^{-3}, n = 14; mean surface chl at OB: 26.4 µg cm^{-3}, n = 6) indicate lowest intensities of local sediment mixing. Although the photometric method only gives a hint of the quality of the material, the remarkably green extract gave evidence of fresh food supply, especially at OB owing to the recently sedimented spring bloom. This, in turn, means that local sediment mixing is highest when food supply is low. Movements while foraging is the most expensive energetic means of locomotion (Jumars & Wheatcroft 1989). If food supply is high, necessary foraging activity and the amount of ingested sediment may be reduced, resulting in extended resting periods (Jumars & Wheatcroft 1989, Wheatcroft et al. 1990). We were not able to find a correlation between injection fluxes J and surface chl ($r = -0.15$, $p = 0.212$) nor between J and chl inventory ($r = 0.07$, $p = 0.580$). Ingestion rates r are also independent from surface chl ($r = -0.14$, $p = 0.915$) and chl inventory ($r = 0.11$, $p = 0.750$).

Furthermore, Dauwe et al. (1998) compared bioturbation potential of macrofauna with contrasting food supply. They reported a maximum in sediment mixing when the arriving material is of intermediate quality, whereas the depth of the bioturbated zone is not as high with low quality organic matter. The total carbon to total nitrogen ratio (TC:TN) at our study sites is not significantly different (D. Bunke pers. comm.). We were not able to find a general positive correlation between nutritional quality of organic matter in the sediment and bioturbation intensity at our study sites.

Mixing depth

Our estimated bioturbation depths reach from 5.2 ± 1.7 to 7.1 ± 1.6 cm. Stations in the west (MB, ST, except LB) indicate chl penetrating 2 cm deeper into the sediment. MB and ST are the only stations where

A. islandica was found in the cores at MB and ST, but not at LB (Zwicker 2014, C. Morys, M. Powilleit, S. Forster unpubl.). This species was found deepest (down to 9 cm) within the sediment, enabling the bivalve to transport material to deep horizons. Organisms at LB reach their depth distribution limit at 3.5 cm and at TW at 4.5 cm (Zwicker 2014), preventing chl from penetrating as deep. At AB and OB, *L. balthica* was the only species found in deeper horizons of the sediment. However, this bivalve does not seem to be able to transport particles as deeply.

Our estimated mixing depths are within the range of the worldwide mean of 9.8 ± 4.5 cm reported by Boudreau (1994). Teal et al. (2008) have assembled a global database and examined a mixed layer depth of 5.75 ± 5.67 cm (n = 791), which fits quite well with our estimated mixing depths. Mixing depths in coastal areas can reach from 7 to 16 cm. Nittrouer et al. (1984) reported mixing depths of 7 cm offshore from the mouth of the Columbia River. Gilbert et al. (1998) worked in Mediterranean coastal sediments (Gulf of Fos) and found mixing depths of up to 10 cm, whereas Gerino (1990), who also worked on Mediterranean coastal sediments found polychaetes down to 16 ± 2 cm. Wheatcroft & Martin (1996) analyzed bioturbation along an organic-carbon gradient off the Palos Verdes peninsula, and report mixing depths between 7 and 11 cm. Particles at our sampling stations are not mixed as deep as in other coastal areas because organisms do not occur deeper than 9 cm, whereas Gerino (1990) found polychaetes down to 16 ± 2 cm.

Variability of bioturbation within stations

Results showed that bioturbation intensity is variable within most stations. As no general pattern exists for whether closely located cores (taken from 1 MUC) are more similar than cores on a broader spatial scale (locations), a high sampling effort is necessary when exploring a new or unknown area. After investigating 24 cores at TW, however, there were no significant differences between locations. For that reason we are able to confidently reduce the number of samples (number of locations as well number of cores within locations) in the future at TW without loss of important information. LB, MB, ST, AB and OB are, in contrast, heterogeneous areas in term of bioturbation intensity, with many different modes of sediment mixing. A reduction in the number of samples might lead to different results.

Modeled bioturbation

Boon & Duineveld (1998) investigated sediment mixing at 3 different stations in the North Sea using chl and applying the model by Soetaert et al. (1996). Of their stations, 2 present similar sediment types (mixture of fine sand and silt). During the same season as our studies (March), one of these stations was characterized by diffusive mixing with D_B = 0.015 cm^2 d^{-1}, while the other one was described by non-local mixing and D_B = 0.022 cm^2 d^{-1}. The contrasting modes of dominant sediment mixing at 2 stations with similar sedimentological properties match our results quite well. As the authors did not present data on injection fluxes, we are not able to compare the non-local transport intensities with each other. Boon & Duineveld (1998) estimated D_B values that are as low as at our least mixed station (LB: D_B = 0.02 ± 0.03 cm^2 d^{-1}). Firstly, this fact can be explained by the different k_D values used. As a linear correlation exists between k_D and D_B, D_B increases with increasing k_D values. Boon & Duineveld (1998) used a k_D of 0.03 d^{-1}, which is higher than the k_D of 0.01 (mud) and 0.02 d^{-1} (sand) in the present study. Secondly, the authors used RP-HPLC for chl measurements, which results in lower concentrations than using the photometric method. Our D_B of 0.3 ± 0.5 cm^2 d^{-1} (except least mixed stations LB and OB) is up to 40 times higher. Using ^{234}Th, Wheatcroft & Martin (1996) reported 0.03 cm^2 d^{-1} near the outfall off the Palos Verdes peninsula and 0.1 cm^2 d^{-1} at unimpacted sites. Gerino (1990) found D_B of 0.05 cm^2 d^{-1} using luminophores. Both studies, carried out in coastal areas, indicated lower mixing intensities compared to our study. Nittrouer et al. (1984), using ^{234}Th, found mixing intensities of 0.38 cm^2 d^{-1} offshore from the mouth Columbia River, which matches our findings.

Non-local transports and ecosystem services

The spatial distribution of local and non-local transports shows remarkably different patterns in the southern Baltic Sea, with an increase of non-diffusive processes towards the east. Therefore, we should describe bioturbation not only by using D_B, but rather by additional values for the non-diffusive part, including the percentages of both types of sediment mixing. The modeled D_B and injection fluxes gained from our investigated locations indicate strong differences, with factors varying from 3 (both sandy stations) to 30 (Mecklenburg Bight) within 1 station. This fact again illustrates the importance of investi-

gating sufficiently large numbers of samples when describing bioturbation within a certain area.

When comparing all stations, high variability of the quantitative description of sediment mixing is visible. Local bio-mixing differs by a factor of 20, injection fluxes by 6 and bioturbation depths by 1.4 between stations. There are first hints that the variability of D_B, injection fluxes and amount of local versus non-local transports depend on the different compositions of the macrofauna population, the patchy distribution of the benthic organisms, and their adaptation to different salinities, as well as on food supply. As a consequence, we cannot assign one general value for bioturbation, as assumed, but rather have to investigate each station separately. Our findings are important, as information on bioturbation can generally illustrate ecosystem services. Bioturbation increases the recycling of nutrients, enhances bentho–pelagic coupling and may release or permanently bury contaminants (Graf 1992, Wheatcroft & Martin 1996, Kristensen et al. 2012), and the information is used in biogeochemical models. For that reason, we have to take the regional and geographical variability of bioturbation into account in order to precisely derive ecosystem services.

CONCLUSIONS

In this study, a high number of parallel cores taken on different spatial scales in the southwestern Baltic Sea allowed a precise description of and novel insights into bioturbation patterns. Comparing the 6 stations investigated, we found an increase in the percentage of non-local sediment mixing from west to east. On smaller spatial scales, within stations no general patterns were apparent, indicating similarities between closely located cores (within 1 location and taken from 1 MUC), and dissimilarities between cores on a broader spatial scale (between locations, a few hundred meters apart from each other). The extent of variability depends on the area considered. Bioturbation intensities of local sediment mixing correlate negatively with chl surface concentrations and inventories, indicating that organisms' activity is low when food supply is high.

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