Particle dynamics in sediments of the western Baltic Sea

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List of abbreviations

AB	Arkona Basin
AFDW	ash free dry weight
AL	RV Alkor
ANOSIM	analysis of similarities
BP_c	community bioturbation potential
BP_i	bioturbation potential index
chl	chlorophyll
CHNS-O	Analysis for determination of carbon, hydrogen, nitrogen, sulfur, oxygen
CTD	sensors for Conductivity, Temperature, Depth
d^{-1}	per day
DC	downward conveyor
dw	dry weight
E	extinction
EMB	RV Elisabeth Mann Borgese
GB	gallery-biodiffusor
HCl	muriatic acid
Hg	mercury
HPLC	high performance liquid chromatography
i	species
ind.	individuals
LB	Lübeck Bay
MB	Mecklenburg Bay
M	biological trait of mobility
MDS	multidimensional scaling
MUC	multicorer
n	number of data
n.a.	not available
OB	Oderbank
P	RV Poseidon
Pb	lead
PAH	Polyaromatic Hydrocarbon

R	biological trait of sediment reworking
rpm	rounds per minute
RV	research vessel
ST	Stoltera
t0	day 0
t1	after 5 days
t2	after 10 days
t3	after 15 days
t4	after 20 days
TC/TN	Total carbon to total nitrogen ratio
Th	thorium
TW	Tromper Wiek
UC	upward conveyor
vvG	van Veen grab
yr^{-1}	per year
Z	Zingst
z_m	mixing depth

List of formula symbols

A		abundance
B		biomass
C	($\mu g\ cm^{-3}$)	chlorophyll concentration
d	(cm)	length of the cuvette
df		degree of freedom
D_B	($cm^2 d^{-1}$)	sediment diffusive mixing coefficient
E663		extinction at wavelength 663 nm used for chlorophyll *a*
E750		turbidity value
Ev		evenness
F	($p < 0.05$)	F-significance-test
F0	($\mu g\ cm^{-3}$)	chlorophyll concentration without acidification
Fm	(Fm = 1.9174)	acidification coefficient
Fa	($\mu g\ cm^{-3}$)	chlorophyll concentration after acidification
H		Biodiversity (after Shannon-Wiener)
H_{max}		maximum possible value of H
J	($\mu g\ cm^{-2} d^{-1}$)	injection flux
k_D	(d^{-1})	degradation of chlorophyll
Kx	(Kx = 1.1883)	calibration factor for pure chl *a*,
L	(cm)	depth of injection or ingestion
p		abundance of a species on the total abundance
Qi		non-local exchange input to a certain layer (i)
r	(d^{-1})	first-order ingestion rate
S		number of species
Sp		production term (not relevant when using chlorophyll)
SSR		sum of the squared residuals
V	(cm^{-3})	volume for chlorophyll extraction, sediment

VE	(ml)	volume of extraction medium
x	($\mu g\ cm^{-3}$)	surface chlorophyll concentration
z	(cm)	depth in the sediment
ω	($cm\ yr^{-1}$)	sedimentation rate
λ	(d^{-1})	decay rate

Explanation

Large parts of the present thesis are already published (about one third) or submitted (about one third) in scientific journals cited below. In both these publications I am the first and corresponding author having done all the sampling, experiments, most of the laboratory analysis, all the data compilation, most of the discussion and writing of the draft for publications. The co-authors have supported the discussion and have proof-read the manuscripts.

Most of the concept of this PhD thesis was developed together with Gerhard Graf and Stefan Forster. I have performed sampling, experiments, chlorophyll analyses as well as the analysis and modeling of data independently. Data on macrozoobenthos were raised by the help of two Bachelor theses (Lena Engelmann and Paul Schulz), one Master thesis (Anna Zwicker) and Martin Powilleit. Additional data compilation, calculations and discussion only available in this PhD thesis were primarily my own work, however with the aid of Gerhard Graf, Stefan Forster and Martin Powilleit. This PhD thesis has been written and arranged without additional external assistance.

Some parts of the present thesis published as cited below were adopted and/or paraphrased while others (especially parts in the discussion) are partitioned for combining these findings with regard to the second manuscript and aspects that have not been published and/or submitted so far. The superscript 1 and 2 have been added to the heading of a paragraph in case the whole paragraph has been taken from these manuscripts or at the end of certain passages in case it has been combined with other findings.

Contents referring to the variability of bioturbation on different spatial scales are published in Marine Ecology Progress Series and are marked by the footnote 1:

Morys C, Forster S, Graf G (in press) Variability of bioturbation in various sediment types and on different spatial scales in the southwestern Baltic Sea. Mar Ecol Prog Ser. doi: 10.3354/meps11837

Contents referring to the explanation of the existing bioturbation patterns with regard to macrozoobenthos are submitted to Marine Ecology Progress Series, are currently under review and are marked by the footnote 2:

Morys C, Powilleit M, Forster S (submitted) Bioturbation in relation to the depth distribution of macrozoobenthos in the southwestern Baltic Sea.

Summary

Ongoing climate change causes rapid changes in biodiversity and ecological impacts on coastal marine systems. Predicting scenarios how these pressures will affect bioturbation, a process vital to marine communities and human benefit has become an important task. A first step is a better understanding in bioturbation patterns and in the interaction between macrofauna and the surrounding environment.[2]

In the present study bioturbation was surveyed at overall seven stations in the southwestern Baltic Sea with different sediment types, salinities and macrozoobenthic communities. Variability of bioturbation on different spatial scales was revealed by investigating 24 cores per station taken in distinct patterns. The cores were analyzed for vertical chlorophyll (chl) profiles which were modeled with both a local (tracer distribution indicating 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). Degradation of chl was determined experimentally by an incubation of fresh sediment under anoxic, dark conditions, was proved to follow first order kinetics and provided decay constants k_D of 0.01 d^{-1} for mud and 0.02 d^{-1} for sand. Bioturbation intensities indicate high variability between closely located sampling sites as well as across the southerwestern Baltic Sea. Stations display a difference in local mixing (D_B) by a factor of 20 and in non-local processes (J) by 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.[1]

The distribution of local and non-local mixing with an increase of non-local transports from west to east is explained by using high-resolution depth distribution of macrobenthos, determining main bioturbators based on vertical chl profiles, the community bioturbation potential (BP_c) and by categorizing main species into functional groups. Depth distribution of abundance (1959 – 112527 individuals m^{-2}) resembles chl profiles and indicated to be a more suitable tool for describing bioturbation than biomass (0.4 – 357 g dry weight m^{-2}). In the west, surficial biodiffusors (SB) inducing local mixing were generally most abundant as well as most organisms were found at the sediment surface and their numbers decreases exponentially with depth. In the east, depth distribution of chl and organisms indicate non-local transports to be dominant and gallery-biodiffusors (GB) become more important. *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* for non-local transports. Highly significant correlations between modeled bioturbation intensities and calculated bioturbation potential (BP_c = 105 – 1298 m^{-2}) indicate that the index is a general bioturbation indicator that may, however, not distinguish between local and non-local sediment mixing. Some species categorized as biodiffusors in the literature were found to affect non-local mixing according to their feeding behavior (e.g. *L. balthica*), size (e.g. *Abra alba*) or biomass (e.g. *A. islandica*) in the southwestern Baltic Sea.[2]

Seasonality in bioturbation was revealed by surveys covering all seasons between 2014 and 2015. No general seasonal bioturbation pattern was found. Intensities of local sediment mixing were found to depend on sediment's surface chl concentrations with increasing D_B when food supply is low. In turn, D_B decreases when food supply is high due to extended resting periods of organisms. Intensities of non-local sediment mixing rather depend on the abundance of GB. As GB become more abundant at the less saline stations more intense non-local sediment mixing can be expected in the context of global warming.

Zusammenfassung

Der fortwährende Klimawandel führt zu schnellen Veränderungen in der Biodiversität und wirkt sich auf die Ökologie mariner Küstensysteme aus. Die Vorhersage von Szenarien, wie sich diese Einflüsse auf die Bioturbation, einem unabdingbaren Prozess für marine Lebensgemeinschaften und für das menschliche Wohl auswirken, hat sich zu einer wichtigen Aufgabe entwickelt. Ein erster Schritt ist das bessere Verständnis über Bioturbationsmuster und die Interaktion zwischen Makrofauna und ihrer umgebenden Umwelt.

Die vorliegende Arbeit untersucht die Bioturbation an insgesamt sieben Stationen mit unterschiedlichen Sedimenttypen, Salzgehalten und Makrozoobenthosgemeinschaften in der südwestlichen Ostsee. Die Variabilität der Bioturbation auf verschiedenen räumlichen Skalen wurde durch die Untersuchung von 24 Kernen pro Station aufgezeigt, welche in bestimmten Mustern entnommen wurden. Vertikale Chlorophyll (chl) Profile wurden hinsichtlich der local (Tracerverteilung zeigt diffusiven Transport, D_B) und non-local (Auftreten von Maxima des Tracers unterhalb der Sedimentoberfläche, Injektionsflüsse J und Ingestionsraten r) Durchmischung nach Soetaert et al. (1996) modelliert. Die Inkubation von frischem Sediment unter anoxischen, dunklen Bedingungen wies nach, dass der Abbau von chl Kinetik erster Ordnung folgt und lieferte eine Abbaukonstante von k_D = 0,01 d^{-1} in Schlick und 0,02 d^{-1} in Sand. Bioturbationsintensitäten wiesen auf eine hohe Variabilität sowohl zwischen nah beieinander liegenden Beprobungsstandorten als auch größeren räumlichen Skalen entlang der südwestlichen Ostsee hin. Die Stationen zeigten einen Unterschied in local Sedimentdurchmischung (D_B) um einen Faktor von 20 und in non-local Prozessen (J) von 6. Non-local Transporte wurden in 33 bis 50% der untersuchten Fläche im Westen und 70 bis 100 % im Osten identifiziert. Die statistische Beschreibung der Ergebnisse unterstreicht die Notwendigkeit eines hohen Stichprobenumfangs bei der Verwendung von chl als Partikeltracer.

Die Verteilung von local und non-local Sedimentdurchmischung mit einer Zunahme der non-local Transporte von West nach Ost wurde mithilfe der hoch aufgelösten Tiefenverteilung des Makrobenthos, der Bestimmung von Hauptbioturbatoren basierend auf den vertikalen chl Profilen, des Bioturbationspotential der Gemeinschaften und der Kategorisierung der Hauptarten in funktionelle Gruppen erklärt. Die Tiefenverteilung der Abundanz (1959 – 112527 individuals m^{-2}) korreliert mit den chl Profilen und präsentiert sich als ein adäquateres Mittel für die Beschreibung der Bioturbation als Biomasse (0,4 - 357 g dry weight m^{-2}). Im Westen sind zum Einen die für die local Durchmischung

verantwortlichen Oberflächen-Biodiffusoren (SB) generell am abundantesten und zum Anderen wurden die meisten Organismen an der Sedimentoberfläche gefunden, deren Anzahl exponentiell mit der Tiefe abnimmt. Im Osten hingegen deuten die Tiefenverteilungen von chl und Organismen auf non-local Transporte hin und Gallery-Biodiffusoren (GB) gewinnen an Bedeutung. *Diastylis rathkei* ist die wichtigste Art für local Sedimentdurchmischung und einige Muscheln, z.B. *Arctica islandica* und *Limecola balthica* zusammen mit Polychaeten, z.B. *Nephtys hombergii* und *Scoloplos armiger* für non-local Transporte. Hoch signifikante Korrelationen zwischen modellierten Bioturbationsintensitäten und dem errechneten Bioturbationspotential (BP_c = 105 – 1298 m^{-2}) veranschaulichen, dass der Index einerseits generell ein guter Indikator für Bioturbation ist, andererseits nicht zwischen local und non-local Sedimentdurchmischung unterscheidet. Einige Arten, welche in der Literatur als Biodiffusoren kategorisiert sind, zeigen ihren Einfluss auf non-local Durchmischung aufgrund ihrer Nahrungsaufnahme (z.B. *L. balthica*), Größe (z.B. *Abra alba*) oder Biomasse (z.B. *A. islandica*) in der südwestlichen Ostsee.

Die Saisonalität der Bioturbation wurde zu allen Jahreszeiten zwischen 2014 und 2015 untersucht, wobei sich kein generelles saisonales Bioturbationsmuster zeigte. Vielmehr hängen die Intensitäten der local Sedimentdurchmischung vom Sedimentoberflächenchlorophyllgehalt ab, wobei sich D_B bei geringer Nahrungsverfügbarkeit vergrößert. Auf der anderen Seite verkleinert sich D_B bei steigendem Nahrungsangebot aufgrund von ausgedehnten Ruhephasen der Organismen. Intensitäten der non-local Sedimentdurchmischung hängen vielmehr von der Abundanz der GB ab. Da GB an den salzärmeren Stationen abundanter sind, kann im Zuge der Klimaerwärmung intensivere non-local Durchmischung erwartet werden.

1. Introduction [1,2]

Bioturbation defines transport processes in benthic habitats carried out by animals that describe 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) is of global importance as it occurs in most oxic sediments. (Kristensen et al. 2012). Animals living in the sediment induce particle movement due to building and maintaining burrows and foraging. Sediment mixing is not 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).[1]

Coastal areas, like the southwestern Baltic Sea, are productive and complex systems providing humans with many benefits. These regulating mechanisms are recognized and the so called ecosystem services have become more important during the past years (MEA 2005). Such services are often measured as proxies for ecosystem health and functioning indicating environmental change (Widdicombe & Austen 1998, Lohrer et al. 2004, Webb & Eyre 2004, Thrush et al. 2006). Thus, observing, understanding and explaining large-scale patterns of bioturbation are of relevance to policy-makers and other stake-holders of the marine environment. Information on bioturbation can generally be used for deriving such services: bioturbation, for example, affects the composition of the sediment and the condition of the overlying water, the distribution of organic matter in the sediments as well as of microbial substrates (Yingst & Rhoads 1980, Aller 1982, Blair et al. 1996). Bioturbation is a key component of benthic-pelagic coupling (Graf 1992). Organic matter and microorganisms are moved vertically and laterally within the sediment, significantly increasing the depth of the mixed layer and mediating ecosystem functioning in coastal habitats (Teal et al. 2008, 2013). 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 which are critical for 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). It 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, Gilbert et al. 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).[1,2]

Sediment mixing can be analyzed by the spatial and temporal distributions of certain tracers in the sediment (Meysman et al. 2003), such as inert particle tracers (e.g. luminophores) (Mahaut & Graf 1987, Maire et al. 2008) and reactive tracers (Gérino et al. 1998). The particle tracer chlorophyll *a* is often used to investigate sediment mixing because it indicates the input of particulate organic matter and is a representative for the food source for benthic organisms (Kanneworff & Christensen 1986, Boon et al. 1998). Investigating tracers' vertical profiles allows differentiating between two 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 while non-local particle transport is defined by the occurrence of subsurface maxima due to e.g. discrete burrowing events or feeding behavior (Boudreau 1986 a, b). 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 supposed to be mixed in the same way as sediment particles (Maire et al. 2008). Their vertical profile in the sediment can highlight two 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 the tracer with sediment depth. This process is analogue to diffusion and can be quantified by a bio-diffusion coefficient D_B, a measure of the intensity of local bio-mixing (Boudreau 1986 a, b, Boudreau & Imboden 1987, Meysman et al. 2010).[1] 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 the intensity of non-local bio-mixing and is defined by the occurrence of subsurface maxima due to e.g. discrete burrowing events (Boudreau 1986 b). Organisms with free movements through the sediment matrix, e.g. upward and downward conveyors may be responsible for non-local sediment mixing.[2] Chlorophyll was used in this 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).[1]

Increasing particle movements by faunal activity are well known (e.g. Graf & Rosenberg 1997). Benthic infaunal organisms affect the physical and chemical

properties of their surrounding sediment through their activity of burrowing, feeding, defecation and locomotion (Gray 1974, Rhoads 1974, Aller 1982, Rhoads & Boyer 1982, Gilbert et al. 1995, Lohrer et al. 2004). Bioturbation by benthic macrofauna depends on biomass, density, species composition and on the relationships between organisms and their surrounding environment (Welsh 2003). Bioturbating macrofauna determines the input and vertical depth distribution of organic material in the sediment (Shull 2009). Determination and quantification of sediment mixing as well as 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 b, Suding et al. 2008). Macrofauna represents major bioturbators in marine sediments (Boudreau 1998). It is important to extend our knowledge of bioturbation which requires an extensive study on most abundant and dominant species and their influence on sediment mixing depending on their behavior and response to changing biotic and abiotic environmental factors (Gérino 1990, Biles et al. 2002, Ouellette et al. 2004). The effects of community structure on bioturbation and thus on ecosystem functioning is important due to ongoing global species loss and pressure on many habitats (Pimm et al. 1995, Watson et al. 1995). Even omnipresent macrozoobenthic species show some habitat preferences indicated by changes in abundance across environmental gradients (Ysebaert & Herman 2002, Thrush et al. 2003). Hence, changes in organism density may influence sediment mixing affecting important processes such as nutrient cycling (Widdicombe & Austen 1998, Lohrer et al. 2004, Sandwell et al. 2009).[2]

Intensities of sediment mixing are influenced by a variety and partly contrasting factors. Relationships between the input of fresh organic matter (e.g. algal detritus, faecal pellets) and the metabolic reaction of the benthic community have often been observed in both coastal shelf seas, but also in the deep sea (Graf et al. 1982, Kanneworff & Christensen 1986, Pfannkuche 1992). Balzer (1996) and Schmidt et al (2002) report more intense sediment mixing when supply of food-rich particles to the seafloor is high. Additionally, a rapid reaction of benthic macrofauna to spring bloom sedimentation has often been found (Graf et al. 1982, Christensen & Kanneworff 1985, Boon et al. 1998, Gerino et al. 1998). While some authors could not find general correlations between food supply and bioturbation intensity (Sun et al. 1994, Boon & Duineveld 1998) others report 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). In contrast, Turnewitsch et al. (2000) state that in some areas in the Arabian Sea even negative

correlations were found. Additionally, some studies demonstrated that bioturbation depends on the quality of food (Taghon & Jumars 1984, Dauwe et al. 1998). Mugnai et al. (2003) and Maire et al. (2006) state that temperature controls sediment mixing.

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. However, this information is needed to better understand our ecosystems and as it increases the utility of large scale assessments of ecosystem processes and functioning influenced by bioturbation (e.g. regulating ecosystem services) (Queirós et al. 2013). Therefore, a field study was conducted in seven areas with different sediment types, salinities and contrasting macrozoobenthic communities in the German Exclusive Economic Zone (EEZ) of the Baltic Sea covering all seasons between 2013 and 2015. Each area is assumed to be homogenous in terms of sedimentological and faunistic properties. This leads to the assumption of a homogenous intensity of bioturbation within each station. The first aim of the present study was to determine bioturbation patterns and the extent of variability of sediment mixing between as well within the different areas in the southwestern Baltic Sea. Therefore, 24 cores sampled in distinct patterns at each station, were analyzed in spring 2014 using the naturally occurring tracer chlorophyll *a* which is thought to track the mixing of fresh organic matter.[1] Many studies focus on local sediment mixing because of the convenience of applying biodiffusive models rather than more complex non-local models. However, one should consider non-local transports that are particularly relevant for short time scale investigations and for the benthic fauna thus generating particular tracer profile shapes (Maire et al. 2008). For that reason the examination of the extent of local and non-local sediment mixing was emphasized in the present study. The question whether bioturbation patterns along the Baltic Sea can be explained by focusing on the interaction between sediment mixing and macrofauna is raised. The depth distribution of macrozoobenthic organisms was determined as well as their bioturbation potential (BP_c) introduced by Solan et al. (2004 a) within the sediment and compared to chl profiles. This investigation inquires whether the relationship between bioturbation and macrofauna can indeed be identified. Categorizing the species into functional groups following their biological traits, e.g. trophic guild, mobility, lifestyle mode is assumed to deliver a more generalized explanation of bioturbation patterns (Bremner et al. 2006, Norling et al. 2007, Suding et al. 2008, Kristensen et al. 2012).[2] Since bioturbation is the sum of all physical activities of macrofaunal organisms that were found to be affected by a variety of factors seasonal variability of bioturbation was investigated in order to derive main driving

factors influencing sediment mixing intensities. Extending our basic knowledge of bioturbation is assumed to improve our predictive capability.

2. Materials and Methods

2.1 Study area [1]

Seven stations in the southwestern Baltic Sea (fig. 1) with different sediment types and contrasting macrozoobenthic communities (Schiele et al. 2015) were investigated during different seasons between summer 2013 and autumn 2015 (tab. 1). The study area is mainly shaped by postglacial processes. A mosaic of rocks, till, gravel and coarser sands is found in shallow areas along the coast and on top of the offshore glacial elevations. Median grain size gets generally smaller with increasing water depth, thus, organic-rich muddy sediments is dominant in the basins (Darr et al. 2014).

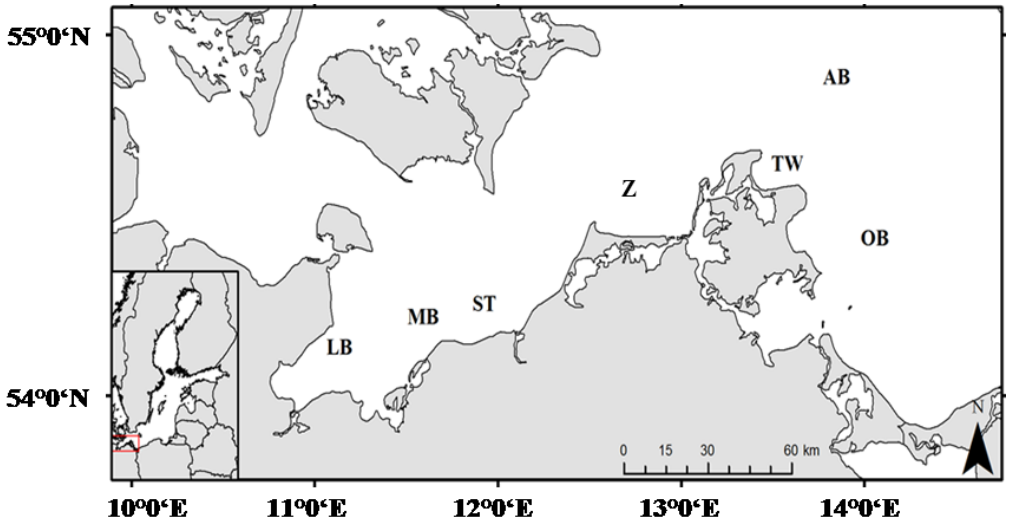


Fig. 1: Study area and distribution of the seven stations of investment: Lübeck Bay (LB), Mecklenburg Bay (MB), Stoltera (ST), Zingst (Z), Arkona Basin (AB), Tromper Wiek (TW), Oderbank (OB), in Morys et al. (in press).

Stations were selected because they represent major areas in the southwestern Baltic Sea of certain biotic and abiotic properties. Two muddy muddy (Lübeck Bay, LB; Mecklenburg Bay, MB) and two sandy (Stoltera, ST and Zingst, Z) stations in the west were investigated. In the east we analyzed one muddy (Arkona Basin, AB), sandy (Oderbank, OB) and silty (Tromper Wiek, TW) station. Information on sediment properties is taken from the geological map of the southwestern Baltic Sea (Tauber 2012). Based on the data supporting this map same granulometric properties are guaranteed for our stations as well as for closely located neighboring data points in each cardinal direction (1 – 2 nautical miles) exceeding our sampling stations.

The Baltic Sea is characterized by an outflow of Baltic water of low salinity (<15) through the Danish straits towards the Kattegat and inflow of more saline water from the Kattegat. This generalized current pattern is subject to variation, e.g. local weather conditions, windshear and atmospheric pressure variations over the northeast Atlantic, North Sea and Baltic (Dickson 1973). The water exchange between the western Baltic and the Baltic Proper is inhibited by the Darss and Drodgen Sills, causing highest temporal variability of salinity in the western part of the study area. The areas follow a salinity gradient from west to east with a difference in salinity of up to 15 (tab. 1). Salinity data were obtained from a CTD (Seabird SBE9plus). Pronounced differences in salinity between surface and near bottom waters (LB, MB, ST and AB up to 13, i.e. P475: MB) indicate the presence of a stable halocline (tab. 1). Bottom water salinities are higher during some sampling campaigns compared to modeled mean bottom salinities as shown in figure 2 (Dippner et al. 2005 as cited in Zettler et al. 2008). Particularly at AB salinities are higher in spring, autumn 2014 and winter 2015 during sampling (tab. 1) due to occasional and short term inflow events from the North Sea (Nausch et al. 2015). Due to the narrow connections between North and Baltic Sea the events of inflowing saline waters into the Baltic Sea are limited and occasionally with stagnation periods over weeks up to months (Zettler et al. 2007). In December 2013, for example, a major salt-water inflow into the Baltic Sea began due to a combination with the earlier effects of hurricane 'Xaver' and long phases of westerly winds oxygenating deep basins (Nausch et al. 2014).

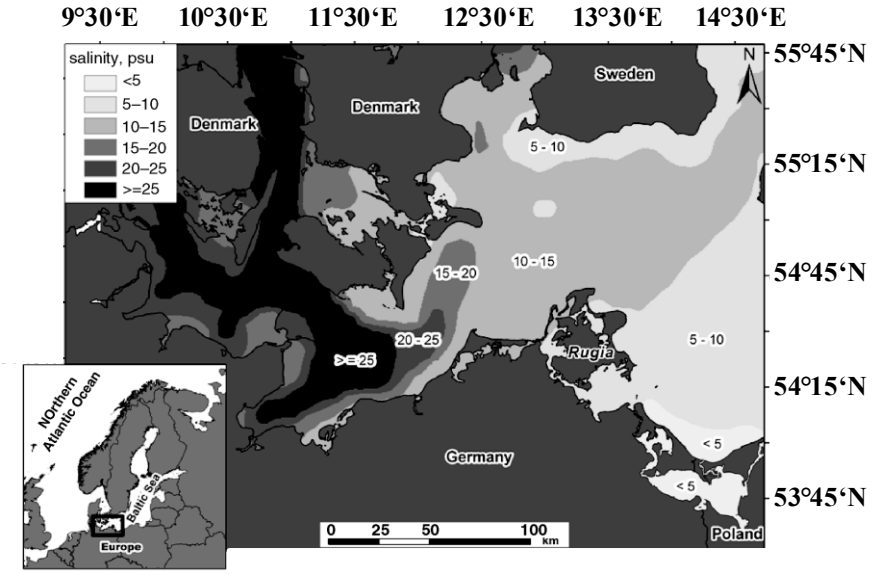


Fig. 2: Distribution of modeled mean bottom water salinity in the southern Baltic Sea on the basis of 1652 single data points during the period 1980-2000 (modified after Dippner et al. 2005 as cited in Zettler et al. 2008).

Tab. 1: Sediment type following Tauber 2012, median grain size (0 - 3 cm), water depth and total carbon to total nitrogen ratio TC/TN (*data provided by Bunke pers. comm.) at each station of investment. Number of cores, surface and bottom salinity, bottom water temperature, mean chl concentration in surface sediment (0 - 0.5 cm), chl inventory of bioturbated zone (sum of chl in 0-6 cm), number of cores taken at each station/cruise and area covered during sampling on AL 434 cruise in spring 2014.

	Station						
	LB	**MB**	**ST**	**Z**	**AB**	**TW**	**OB**
Sediment type	aphotic mud	aphotic mud	aphotic sand	aphotic sand	aphotic mud	silt	aphotic sand
Median (µm)	19.4	17.4	148.8	101.8	22.9	27.3	181
Water depth (m)	23	25	18		45	30	16
TC/TN *	8.1	8.4	8.9	8.2	8.3	8.4	8.6
AL 434, spring 2014							
Number of cores	24	24	24		24	24	23
Salinity (surface)	17	17	11		8	8	8
Salinity (bottom)	22	23	23		19	10	8
Bottom water temperature (°C)	5.5	5.9	5.8		5.5	4.5	5.6
Chl (0-0.5 cm) (µg 0.5 cm^{-3})							
Chl (0-6 cm) (µg 6 cm^{-3})							
Area covered per station	500m x 500m	250m x 250m	500m x 700m		750m x 700m	500m x 750m	500m x 500m
EMB 076, summer 2014							
Number of cores	6		24		9	9	9
Salinity (surface)	10.6		12		7.7	8.2	8.2
Salinity (bottom)	20.1		17.3		16.1	8.5	8.2
Bottom water temperature (°C)	8.6		14.4		11.1	16.9	15.9
Chl (0-0.5 cm) (µg 0.5 cm^{-3})	9.3		7.4		8.0	6.8	4.2
Chl (0-6 cm) (µg 6 cm^{-3})	48.4		51.9		50.6	54.1	28.0
P 475, autumn 2014							
Number of cores	6	6	6	6	6		6
Salinity (surface)	14.5	9.9	13	8.1	8.2		8
Salinity (bottom)	22.7	22.8	21.1	19.2	19		8.1
Bottom water temperature (°C)	14.3	14.3	14.7	15.1	15.1		16
Chl (0-0.5 cm) (µg 0.5 cm^{-3})	7.5	4.7	6.8	3.3	4.2		3.8
Chl (0-6 cm) (µg 6 cm^{-3})	47.1	46.7	46.7	23.1	38.4		30.6
EMB 093, winter 2015							
Number of cores			6	6	6		6
Salinity (surface)			20.1	9.8	9.7		9.2
Salinity (bottom)			21.4	15.2	24		9.3
Bottom water temperature (°C)			4.9	5.1	6.9		4.2
Chl (0-0.5 cm) (µg 0.5 cm^{-3})			6.2	4.3	5.7		3.5
Chl (0-6 cm) (µg 6 cm^{-3})			27.1	19.0	52.4		28.0
EMB 100, spring 2015							
Number of cores		6	6		6		6
Salinity (surface)		12.7	13.2		8.5		8.4
Salinity (bottom)		20.5	16.2		15		8.4
Bottom water temperature (°C)		4.3	5.1		4.8		5.8
Chl (0-0.5 cm) (µg 0.5 cm^{-3})		11.5	3.9		5.5		3.8
Chl (0-6 cm) (µg 6 cm^{-3})		62.6	21.9		31.8		31.4
EMB 111, autumn 2015							
Number of cores	6	6	6		6	6	6
Salinity (surface)	10.2	9.9	9.4		7.9	8	8
Salinity (bottom)	18.1	20.4	18.3		12.7	8.6	8
Bottom water temperature (°C)	13.3	12.6	13.5		8.5	16	18.3
Chl (0-0.5 cm) (µg 0.5 cm^{-3})	11.7	8.6	6.2		2.9	8.9	4.5
Chl (0-6 cm) (µg 6 cm^{-3})	51.2	44.7	26.0		31.7	87.9	26.6

According to Schiele et al. (2015), all stations are located underneath the photic zone. The authors modeled light penetration depth (averaged over the vegetation 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 are below 20-30 m water depth. The shallowest station is OB with 16 m; the deepest is AB with 45 m water depth.

The stations are characterized by different macrozoobenthic communities reported in Schiele et al. (2015). Oxygen depletion events have negative effects on the diversity and density of soft-bottom fauna (Arntz 1981). The larger rivers Trave, Warnow and Oder are an important food source. Schiele et al. (2015) analyzed macrozoobenthic data which are based on campaigns between 2004 and 2013 including 829 sampling stations in the southern Baltic Sea each consisting of 3-5 replicates (data sources: see Schiele et al. 2015). The most dominant species occurring at each station are listed in table 2.

Lübeck Bay (LB)

LB is part of MB and defined by aphotic muddy sediment dominated by infaunal bivalves (Schiele et al. 2015). In this area, anthropogenic pollution is remarkable as it was used as an industrial dumping site in the late 1950's until 1971. LB represents the highest heavy metal contamination and organic pollution along the coast of the German Baltic Sea (Leipe et al. 1998).

Mecklenburg Bay (MB)

MB is a basin with aphotic muddy sediment dominated by *Arctica islandica* (Schiele et al. 2015). It is part of the connection between North and Baltic Sea. At the bottom, saline waters coming from the North Sea flow into the Baltic Sea. At the surface, less saline waters from the Baltic is directed to Kattegat. This area is populated by marine-euryhaline species (Zettler et al. 2000). An annual stable thermocline causes critical reduction of oxygen leading to a loss of macrozoobenthos. Storms occurring in autumn and winter ventilate the bay enabling the organisms to recolonize (Gosselck et al. 1987).

Stoltera (ST)

ST is part of the Mecklenburg Bay located west from Rostock/Warnemünde. It is characterized by sandy sediments with shallow stone (or *Mytilus*-aggregates) and boulder grounds (Zettler 2001).

Zingst (Z)

The area north of the German peninsula of Darss is relatively shallow (<20 m). It is characterized by aphotic sand dominated by multiple infaunal bivalve species (Schiele et al. 2015). The Darss Sill separates the two basins MB to the southwest and AB to the northeast where fine-grained sediments accumulate (Winn et al. 1983, Lange 1984).

Oder River and the Arkona Basin (AB) system

The Oder River and AB system represent a typical coastal basin structure in the southern Baltic Sea. The river drains a highly industrialized and agriculturally used area and transports heavily polluted water before entering a lagoonal environment (Oder Haff), followed by a transition area (Pomeranian Bight). Due to the dynamic hydrological conditions, the deposited material can easily be resuspended (e.g. during storm events), and some of the initially deposited material is transported through the Swina, Dzwina, or Peenestrom into the Baltic Sea. Here, material is finally deposited in the deep basin (e.g. Witt et al. 2001).

Oder Basin (OB)

OB is a shallow station in the Pomeranian Bight. It is defined by aphotic sand dominated by multiple infaunal bivalve species including *Cerastoderma glaucum*, *Limecola balthica* and *Mya arenaria* (Schiele et al. 2015). The bottom is covered with fine sand and under calm conditions, a thin fluffy layer can be observed in valleys of sediment ripples due to previous storms (Witt et al. 2001).

Tromper Wiek (TW)

TW, a semi-enclosed bay that opens towards the northeast, is located in the fossil submarine Oder River Valley that runs parallel to the eastern coast of Rügen (Witt et al. 2001). According to the classification of Davis & Hayes (1984), TW is a wave-dominated environment (Kubicki et al. 2007). Westerly winds dominate in this area, but high waves are only generated by usually during spring occurring easterly winds due to the coastal configuration (Mohrholz 1998). In this area, gravel extraction by means of anchor hopper dredging has been performed for many years. Therefore, the sea bottom is covered with small craters which can have a negative impact on the marine environment (Klein 2003).

Arkona Basin (AB)

On time scales of decades to centuries, most of the material from land, transported by the River Oder, is deposited in the mud of the AB (Neumann et al. 1996). Material originating from TW which is located at the rim of the southern AB enters the basin only during strong wind events. AB is characterized by aphotic muddy sediment dominated by *L. balthica* (Schiele et al. 2015). Here, marine species reach their distribution boundary (Wasmund et al. 2004).

Tab. 2: Most dominant macrozoobenthic species at each station of investment: Lübeck Bay (LB), Mecklenburg Bay (MB), Stoltera (ST), Zingst (Z), Arkona Basin (AB), Tromper Wiek (TW), Oderbank (OB). Modified after Morys et al. (in press).

Station	Most dominant species	reference
LB	*Kurtiella bidentata* *Diastylis rathkei* *Capitella capitata* *Priapulus caudatus*	Schiele et al. (2015) Powilleit et al. (1994) Zwicker (2014) This study
MB	*Diastylis rathkei* *Arctica islandica* *Abra alba* *Priapulus caudatus* *Nepthtys hombergii*	Schiele et al. (2015) Powilleit et al. (1994) Zwicker (2014) This study
ST	*Limecola balthica* *Arctica islandica* *Scoloplos armiger*	Engelmann (2015) This study
Z	*Cerastoderma glaucum* *Mya arenaria* *Limecola balthica*	Schiele et al. (2015) This study
AB	*Limecola balthica* *Diastylis rathkei* *Scoloplos armiger*	Schiele et al. (2015) This study
TW	*Limecola balthica* *Scoloplos armiger*	This study
OB	*Peringia ulvae* *Cerastoderma glaucum* *Limecola balthica* *Mya arenaria* *Hediste diversicolor*	Schiele et al. (2015) Schulz (2015) This study

2.2 Sampling and laboratory analyses

2.2.1 Sampling and chlorophyll analyzes [1]

Cores for vertical tracer profiles using chlorophyll needed to quantify sediment mixing were taken by deploying a multicorer (MUC) at different stations and during different seasons. Number of cores and stations investigated during each season is given in table 1. 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. In order to obtain the bound pool of chlorophyll which is embedded in intact chloroplasts, the samples were deep frozen immediately and stored until extraction (Sun et al. 1991). After defrosting, they were homogenized and three subsamples of 1 cm^3 sediment were taken from each slice. After adding 9 ml of 96% ethanol the samples were stored in the dark for 24 hours and centrifuged at 4000 rpm for 5 minutes afterwards completing the procedure of chlorophyll extraction from the sediment sample. Each sample was extracted once; further extractions contained insignificantly low concentrations of the pigment. A simplified photometric method was employed (663 and 750 nm) using a Shimadzu UV 1202 (Holm-Hansen et al. 1965, Lorenzen 1967, Knap et al. 1994). Calculations are based on HELCOM (1988 a, b) using the following equation:

$$\text{mg chl cm}^{-3} = \frac{(\text{E663}-\text{E750}) \cdot \text{VE} \cdot 1000}{83 \cdot \text{V} \cdot \text{d}} \quad (1)$$

where E663 is the extinction at wavelength 663 nm used for chlorophyll *a,* E750 the turbidity value, VE the volume of extraction medium, V the volume of 1 cm^{-3} sediment used for chlorophyll extraction and d the length of the cuvette. E663 was chosen as errors due to different wavelengths for chlorophyll *a* were found to be insignificant (e.g. 663 nm SCOR-UNESCO), 664 nm (Jeffrey & Humphrey 1975) and 665 nm (Lorenzen & Jeffrey 1980). Turbidity may occur in the extract which can overestimate the chlorophyll values. As light is weakened by turbidity over a broad spectral range, a turbidity value can be measured at 750 nm where pigments usually do not absorb light anymore (Wasmund 1984). Chlorophyll is abbreviated below as “chl” for simplification. In fact, the chosen method delivers a combination of chlorophyll *a* and its degradation products which is regarded as fresh organic matter.

2.2.2 Evaluation of the photometric method

For evaluating the photometric method generally applied in this study, the photometric method (without acidification) was compared with fluorometric technique (with acidification). Therefore, 4 stations with 6 cores each were taken on cruise EMB 100 in spring 2015. Samples were treated as previously described and first measured photometrically. Immediately afterwards the same sample was measured fluorometrically and 100 µl of 1 N HCl was added to the sample that was then measured again after 30 seconds using a

Turner fluorometer. Chl concentration based on fluorometric measurements were calculated by the following equation (UNESCO 1994):

$$\text{mg chl cm}^{-3} = \text{Fm} \cdot \frac{1}{(\text{Fm}-1)} \cdot (\text{F0} - \text{Fa}) \cdot \text{Kx} \cdot \text{VE} \cdot \frac{1}{\text{V}} \quad (2)$$

where Fm is the acidification coefficient (F0/Fa) for pure chl *a* (Fm = 1.9174), F0 the chl concentration without acidification, Fa the chl concentration after acidification, Kx the calibration factor for pure chl *a* (Kx = 1.1883), VE the volume of extraction medium, V the volume of 1 cm^{-3} sediment used for chlorophyll extraction and d the length of the cuvette.

A second step was to perform photometric measurements by using one wavelength (663 nm) and by applying the trichromatic approach: 663 nm (chlorophyll *a*, SCOR-UNESCO), 647 nm (chlorophyll *b*, SCOR-UNESCO, Jeffrey-Humphrey 1975) and 630 nm (both without an acidification step). Therefore, samples from one core with 13 layers (and 3 replicates per layer) taken in summer 2013 (sandy sediment from Stoltera) were prepared as previously described. Chl concentrations were calculated by the following equation:

$$\text{mg chl cm}^{-3} = \frac{11.85 \cdot (E663-E750) - 1.54 \cdot (E647-E750) - 0.08 \cdot (E630-E750) \cdot VE}{\text{V} \cdot \text{d}} \quad (3)$$

where E663 is the extinction at wavelength 663 nm used for chlorophyll *a,* E750 the turbidity value, VE the volume of extraction medium, V the volume of 1 cm^{-3} sediment used for chlorophyll extraction and d the length of the cuvette.

2.2.3 Degradation of chlorophyll (k_D)

When applying the bio-mixing model by Soetaert et al. (1996), information on the decay of the tracer is needed which is chl in the present study. The first-order decay constant k_D for chl has a strong influence on modeling results.[1] Degradation experiments were carried out in different sediment types during three different seasons: mud and sand in winter 2015 (EMB 093), spring 2015 (EMB 100) and autumn 2015 (EMB 111). The first two centimeters of different types of fresh sediment (mud taken from Arkona Basin and sand from Stoltera or Oderbank) were taken from cores.[1] Additionally, in autumn samples from Tromper Wiek were taken for estimating decay of chl in silt and experiments using mud were carried out at three mud stations: Lübeck Bay, Mecklenburg Bay and Arkona Basin. After homogenization

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. The samples were incubated for 5, 10, 15 and 20 days and deep-frozen afterwards. Anaerobic incubations were emphasized 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 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.[1] 40 replicates were analyzed for each temperature and time in winter as well as 12 replicates in spring and summer.

2.2.4 Macrozoobenthic data [2]

After chl analyzes, residual sediment of each slice was sieved through a 500 µm screen for inspecting the composition of macrozoobenthos and the vertical depth distribution of abundance and biomass within the sediment at each station. 24 cores were investigated at LB, MB and ST, 10 at AB and TW and 6 at OB. 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 (Appeltans et al. 2011). Dry weight was determined for biomass.

Macrozoobenthic data at LB and MB were raised within the frame of a Master Thesis by Anna Zwicker, at ST by Lena Engelmann (Bachelor Thesis) and at OB by Paul Schulz (Bachelor Thesis). Taxonomic determination of organisms was checked by Martin Powilleit for all stations.

2.3 Modeling bioturbation [1]

For a quantitative characterization of bioturbation intensity, each 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 and the concentration of chl in some layer within the sediment being subjected to advection, mixing and first-order decay and can be described by (Berner 1980):

$$DB\ \frac{d^2C}{dz^2} - \omega\ \frac{dC}{dz} - \lambda\, C - rC + Qi + Sp = 0 \qquad (4)$$

where C is the chl concentration, z denotes depth into the sediment (cm, increasing downward), D_B is the sediment diffusive mixing coefficient (cm² 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}), Qi is the non-local exchange input to a certain layer (i) and Sp 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 how particles are mixed within the sediment. Sedimentation rate ω was defined to be very low (0.00001 cm yr^{-1}) (see Christiansen et al. 2002). Boundary conditions determine the integration constants and are adapted from Soetaert et al. (1996). There is a flux boundary at the sediment-water interface, continuity of concentration and continuity of flux between layers and the no-gradient boundary at depth. Model 1 is the simplest model that describes the situation of a continuous sedimentation without biological and hydrographical sediment mixing (D_B and Qi are set zero). The distribution of chl in the sediments is then influenced only by the flux at the sediment-water interface, sedimentation and decay. The least squares fit algorithm has to find the best value for this flux. Model 2 is applied in cases of steady-state diffusive mixing and delivers a biodiffusion coefficient D_B (cm² d^{-1}). The flux at the sediment-water interface and the biodiffusion coefficient D_B are the two 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). This model requires, in contrast to model 2, two 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 one additional parameter to fit, i.e. thickness of the deposition layer. Model 4b is similar to model 3 but the flux to a certain depth (L) has been derived by ingesting surficial sediment and is quantified by the ingestion rate 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 one-tailed F-test provides the information whether the more complex model significantly better explains the observed data ($p < 0.05$) (Sokal & Rohlf 1995):

$$F = (SSR1 - SSR2) / (df1 - df2) / (SSR2 / df2) \quad (5)$$

where SSR2 and SSR1 are the sum of the squared residuals of observed and modeled values of the elaborate and simple model, respectively, and df2 and df1 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 with the simpler model, is rejected when 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.

2.4 Variability of bioturbation

2.4.1 General patterns [1]

In spring 2014 during the AL434 cruise with RV 'Alkor' six of the overall seven stations in the southwestern Baltic Sea were investigated for a general estimate on how variable bioturbation is between and within the stations. During this sampling campaign the sampling design chosen consisted of stations and locations to cover various spatial scales. Stations represent the different study areas LB, MB, ST, AB, TW and OB in the Baltic Sea. Locations define the exact sampling positions within each station. Six locations were investigated at each station by deploying a multicorer (MUC) (fig. 3). 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). In fact, variability of bioturbation was defined on three different spatial scales: (i) between stations (on the basis of 24 cores/station and six different stations along the coast of the Baltic Sea), (ii) between locations (on the basis of 4 cores/location and 6 locations with a distance of a few hundred meters), (iii) within locations (on the basis of 4 cores/location, all cores from one MUC).

Determining the variability of bioturbation combines comparisons of chl depth profiles as well as bioturbation intensities D_B, J and r derived from the bio-mixing model (Soetaert et al. 1996). Statistical analyses were carried out using software packages SPSS and PRIMER.

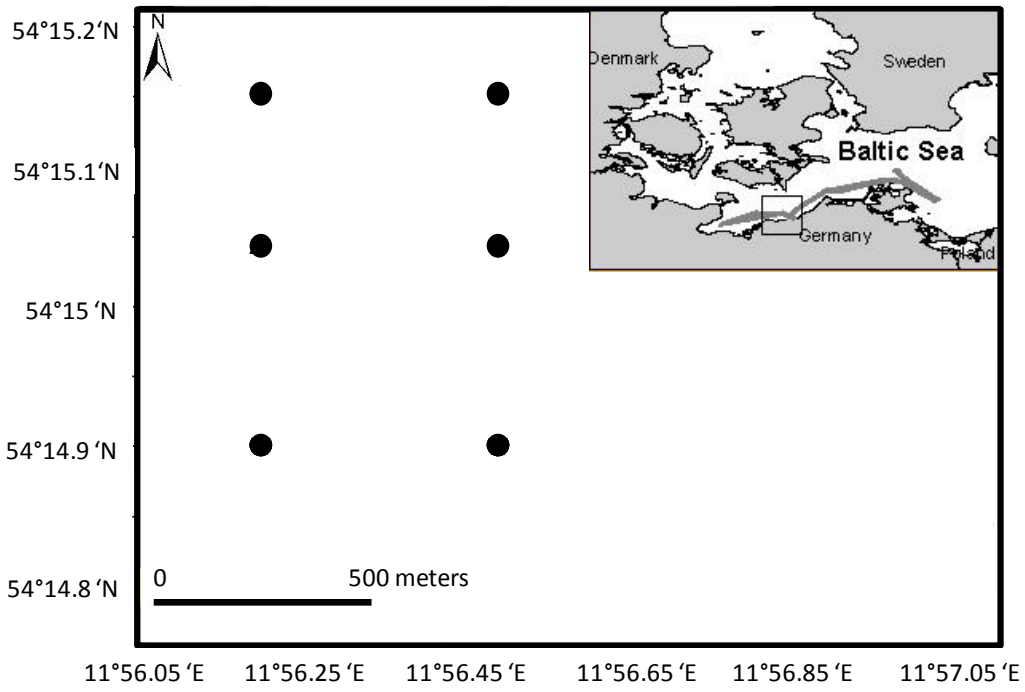


Fig. 3: Scheme of the sampling design within one station using the example of ST: 6 sampling locations (black dots) with 4 cores each (24 cores in total), in Morys et al. (in press).

Variability between stations [1]

As chl profiles within the sediment allows the differentiation between no, local and non-local sediment mixing, these tracer distributions were firstly compared to estimate similarities and dissimilarities between and within stations using MDS plot (transformation: square roots, resemblance: 2D Euclidean Distance). Chl concentration of each layer was normalized with the total chl concentration of each core. Based on the chl inventory of each core being equal 100%, the percentage of chl within each layer was then calculated. Secondly, these percentages were used for ANOSIM tests comparing the six stations (n = 24 cores per station) investigated. This comparison will answer the question whether chl profiles are significantly different between stations.

Variability between locations [1]

For a comparison of locations within one station a pair wise comparison of locations (n = 6 locations with n = 4 cores per location) was first carried out using ANOSIM test. This test gives information whether chl profiles of the 6 locations within one station tested are significantly different. A second step that is considered to be the most important criteria for defining similar locations was then to compare the numbers of no, local and non-local

sediment mixing within each location. Locations are defined to be similar as soon as 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 at one location) 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 were too low, the only alternative comparison was the differentiation between no, local or non-local sediment mixing. MDS plot and ANOSIM tests were carried out for all following analyses (i.e. seasonal changes in variability and seasonality in bioturbation). However, as these approaches deliver different results (as presented and discussed later) the differentiation between different modes of sediment mixing was considered to be a more powerful tool and was thefore used for all estimates of variability of bioturbation.

Variability within locations [1]

In order to compare single cores within one location, the distribution of the different modes of sediment mixing was used. Cores within one location (n = 4, taken from one MUC) were defined to be similar as soon as all 4 cores show one same mode of mixing.

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

Mixing depths were examined using measured chl profiles. The concentrations of chl never reached zero due to phaeopigments which were also detected by the method applied (Wasmund 1984). Changes in the tracer concentration with depth approaching zero indicate that a background value is reached. This was typically the case at chl concentrations around 1 - 2 µg cm^{-3} and when concentration change with depth declined to < 0.1 µg cm^{-3}. This depth is defined as the depth of the bioturbated zone. In order to find out whether mixing depths are significantly different between stations, Kruskal-Wallis test and its post-hoc test were carried out using estimated mixing depths of all cores per station (n = 24 cores per station, except OB: 23 cores, n = 6 stations).[1]

2.4.2 Seasonal changes in variability

The previously described approach of determining variability of bioturbation on different spatial scales within stations was performed during different seasons at ST and OB. At ST 24 cores taken in summer 2013 (Gadus), winter 2014 (Praunus), spring 2014 (AL434) and summer 2014 (EMB100) using the same sampling design with 4 cores taken at 6 locations as described above (fig. 3). This data set allows the determination of seasonal and inter-annual effects of the distribution of the different modes of sediment mixing. At OB, this sampling campaign was carried out twice: in spring (AL434) and summer (EMB100) 2014.

2.5 Bioturbation potential (BP) [2]

Abundance and biomass of macrobenthos obtained from AL434 cruise in spring 2014 were used for the bioturbation potential index (BP_i) calculating the community bioturbation potential BP_c, a metric first described by Solan et al. (2004 a), by the following equation:

$$BPc = \sum_{i=1}^{n} \sqrt{Bi / Ai} \times Ai \times Mi \times Ri \qquad (6)$$

BP_c combines species' abundance (A_i) and biomass (B_i, dry weight in the present study) with two biological traits describing sediment mixing: sediment reworking (R_i) and mobility (M_i). Categorical scales 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 macrozoobenthic community to mix the sediment (Queirós et al. 2013). The following species that are not presented in the list were scored as follows: *Trochochaeta multisetosa* (M: 2, R: 3), *Halicryptus spinulosus* (M: 2, R: 4), *Bylgides sarsi* (M: 3, R: 2) and *Dipolydora quadrilobata* (M: 1, R: 3), *Neoamphitrite figulus* (M: 1, R: 3), *Parvicardium pinnulatum* (M: 2, R: 2). Individuals of *Sphaerodoropsis baltica* were too small for accurate determination of biomass, consequently its BP_i was zero. Species and their corresponding scores used for calculating BP_c are given in appendix I. Firstly, 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. Secondly, BP_c was determined for each core separately, regardless of its faunal vertical

distribution, for a comparison to modeled mixing intensities (D_B, J and r) estimated by the bio-mixing model (Soetaert et al. 1996).

2.6 Categorization of macrozoobenthos [2]

The most dominant species or their taxonomic groups were assigned to one of the four 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. Biodiffusors are organisms that induce local sediment mixing over short distances. This category is divided into 3 subgroups: (1) epifaunal biodiffusors that live predominantly above the sediment−water interface generally mixing the sediment randomly along the surface (2) surficial biodiffusors that mix the sediment in the uppermost few centimeters and (3) gallery biodiffusors that conduct local sediment mixing due to burrowing activity. Upward conveyors are organisms that typically feed head-down at depth transporting particles to the surface. Particles are moved non-locally upwards when passing through the gut or when clearing the ingestion cavity and return during the refill of the voids with sediment from above. Some downward conveyors are organisms that feed head-up selecting and ingesting particles at the sediment surface and egesting them non-locally as faeces deeper in the sediment. They may also move particles upwards non-selectively when constructing and maintaining burrows. Holes at the bottom of their tubes created by sediment ingestion are refilled with surface sediment. The last category "regenerators" were not found in this study. Regenerators are excavators that dig and continuously maintain burrows transferring sediment from depth to the surface. The sediment is refilled with surface particles due to currents or collapse of burrow walls.

2.7 Biodiversity and eveness

One can assume that depth layers within the sediment of highest chl concentrations (= highest food supply) presents the areas with most individuals and/or species simultaneously. In order to investigate this hypothesis biodiversity was used as a tool. Biodiversity describes the number and variety of species, including the variability within and between species and ecosystems. Biodiversity H was calculated for each depth layer using Shannon-Wiener-index (Shannon 1948):

$$H = -\sum_i pi \cdot \ln pi \quad with \quad pi = \frac{Ai}{A} \tag{7}$$

with p_i presenting the abundance of a species (Ai) on the total abundance A.

Evenness Ev was used as a tool for describing whether the distribution of species is homogeneous or heterogeneous and was calculated using the following equation (Pielou 1975):

$$Ev = \frac{H}{Hmax} \quad with \quad Hmax = lnS \tag{8}$$

where H_{max} is the maximum possible value of H (if each species is equally likely) and S is the number of species.

2.8 Sediment mixing without fauna

For assessing sediment mixing without the presence of macrozoobenthos, three cores were taken at each of the following stations on EMB 100 cruise in April 2015 (fig. 4): (1) in the central Bornholm Basin (S 213, 89.8 m water depth), (2) Gotland Basin (S 256, 89.5 m water depth), (3) Farö Deep (S 286, 192.5 m water depth). The stations are located within the course of inflow waters from the major inflow event that started in December 2014. As shown in figure 4 b, c the inflowing water from the North Sea had already reached stations S 213 in Bornholm Basin and S 256 in Gotland Basin where oxygen concentrations are well above the 2 ml l^{-1} limit of oxygen deficiency (Diaz & Rosenberg 1995). The most northern station S 286 in Farö Deep remains oxygen-depleted with high H_2S concentrations because the inflow stream had not arrived at northern parts of Gotland Basin.

All stations are without macrofauna due to long stagnation periods of more than 10 years but differ at the time of sampling in terms of salinity, oxygen, and bottom current due to the inflow event of December 2014. *B. sarsi* was found at Bornholm Basin that had been flushed within the inflowing water (Gogina pers. comm., Naumann 2015).

Chl profiles were measured as described above for quantifying bioturbation intensities using the bio-mixing model (Soetaert et al. 1996) at different station without the presence of macrofauna during a major inflow event.

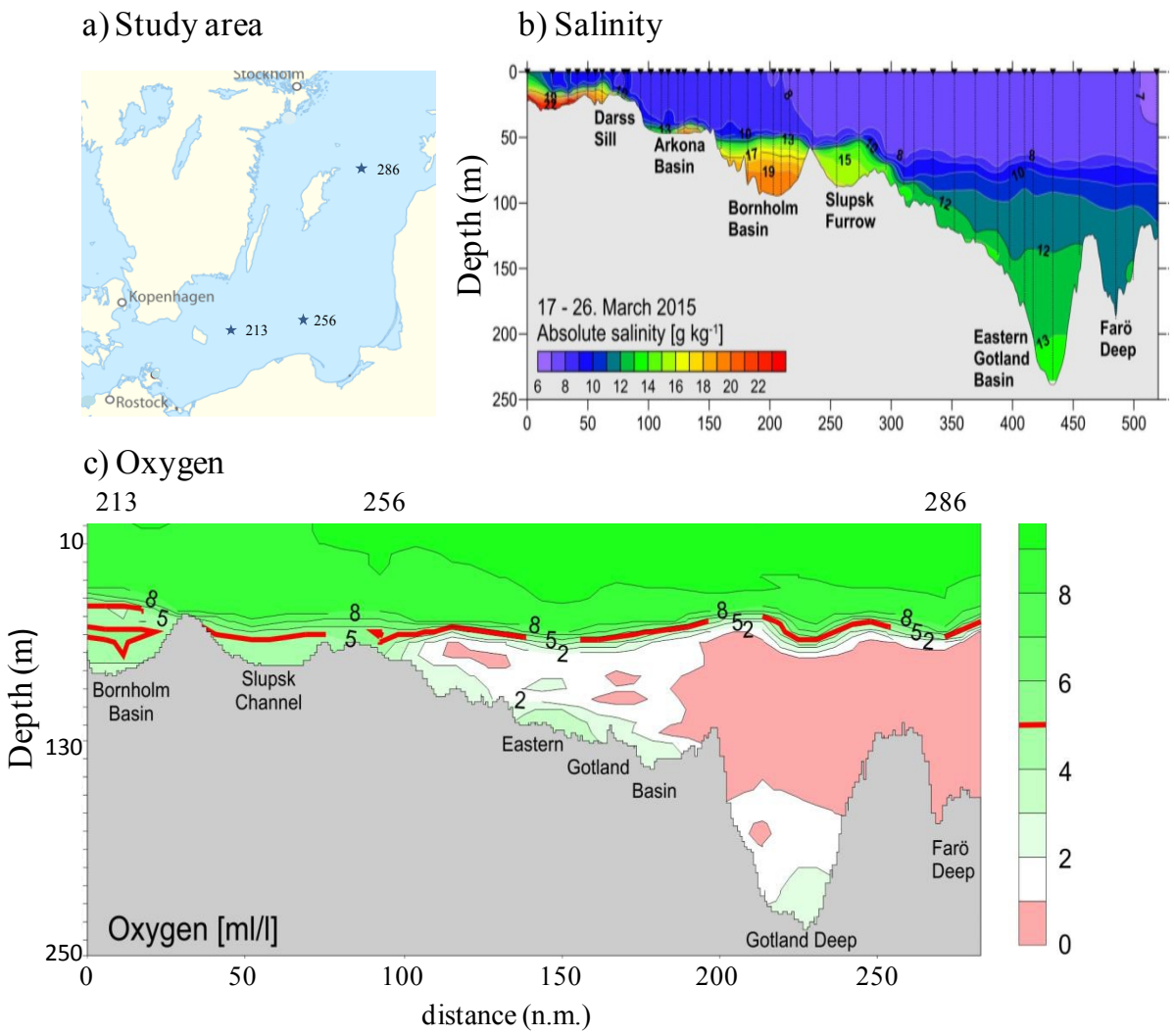


Fig. 4: (a) Study area and distribution of the stations of investment: (1) Bornholm Basin (S 213), (2) Gotland Basin (S 256), (3) Farö Deep (S 289). Situation: four months after the beginning of the major inflow event from December 2014. (b, c) Cross section: Bornholm Basin to northern parts of the Eastern Gotland Basin highlighting the course of the major inflow event from December 2014 by (b) salinity distribution and (c) oxygen distribution. Note that the inflowing water has reached stations investigated in this study in Bornholm (S 213) and Gotland Basin (S 256) indicated by high bottom salinity and oxygen. In turn, station at Farö Deep is still characterized by low salinity and remains oxygen-depleted. Figure (4b) is taken from Nausch et al. (2016) and (4c) from Naumann (2015).

2.9 Anthropogenic effect

In order to determine anthropogenic effects on both abundance of macrozoobenthic organisms and bioturbation intensities, three stations of different levels of mercury contaminations according to Leipe et al. (2013) within the Lübeck Bay were investigated (fig. 5). Mercury (Hg) is a key element for assessing marine pollution and in most of its compounds it has a high toxicity to organisms (Leipe et al. 2013). During the late 1950s and early 1960s, industrial waste that was highly enriched in various contaminants (heavy metals, PAHs) was dumped in LB from a metal hut located in the city of Lübeck. Due to transport of

surface sediments material is spread over the whole inner part of MB (Leipe et al. 1998). In 2008, more than forty years after dumping has stopped the hot spot of Hg is still obvious (fig. 5, Leipe et al. 2013).

In autumn 2014 on P475 cruise, three cores were taken at three stations within LB that are characterized by different levels of Hg-concentrations at the sediment surface (fig. 5): (i) low: Hg = 209 µg kg^{-1} (Bunke, pers. comm.), (ii) intermediate: Hg ~ 256 µg kg^{-1} (Leipe, pers. comm.), (iii) high: Hg ~ 283 µg kg^{-1} (Leipe, pers. comm.). Chl profiles were measured for quantifying bioturbation intensities using the bio-mixing model (Soetaert et al. 1996) and the residual sediment was sieved in order to obtain macrofauna. Macrofauna data were raised by Zwicker (2014).

Mixing depths, modeled bioturbation intensities and abundance of macrofauna were tested for significant differences using Kruskal-Wallis tests.

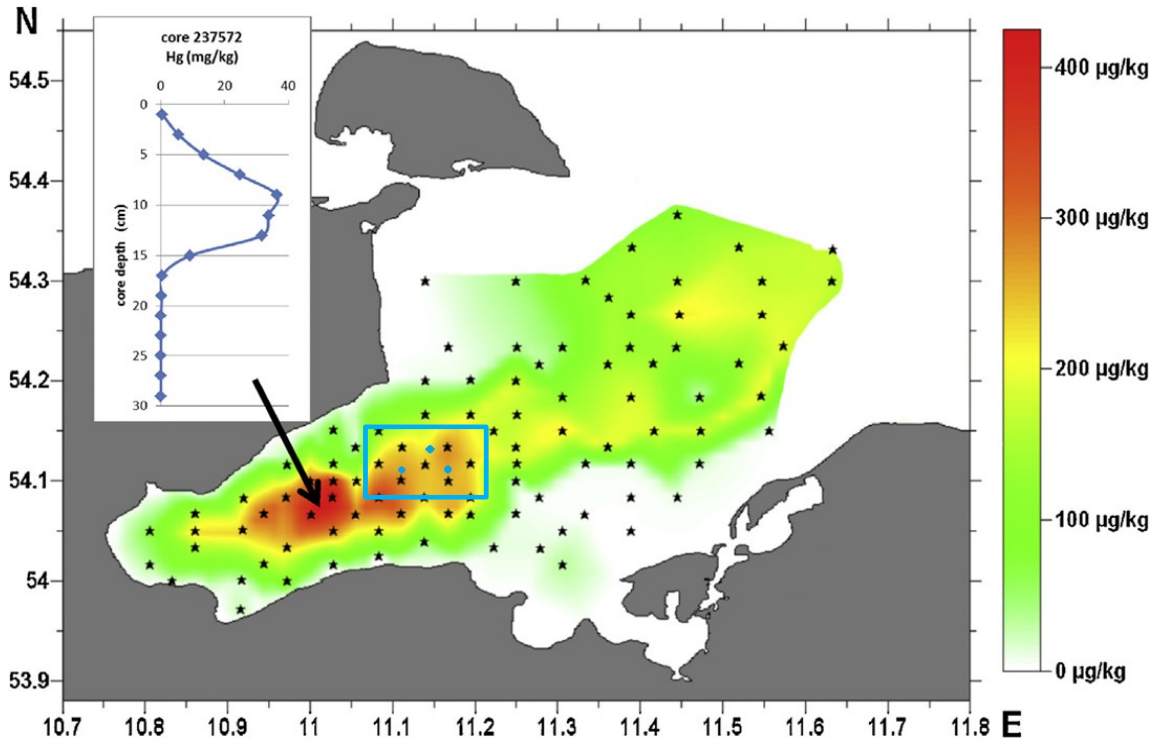


Fig. 5: Map taken from Leipe et al. (2013) displaying the distribution of mercury (Hg) in recent surface sediments in the Mecklenburg Bay. Depth profile of a core from the "hot spot" of the dumping site from the 1960's (maximum Hg concentrations in the core profile are 100 times higher than in the recent surface). Stations of investment of the present study that are characterized by low, intermediate and high Hg contamination are presented by blue dots in the blue box.

2.10 Seasonality of bioturbation

In order to determine seasonality of bioturbation along the coast of the southwestern Baltic Sea, cores were taken during different seasons at the stations of investigation. Number of cores and an overview which station was investigated during each season is given in table 1. ST, AB and OB were studied during all seasons: spring, summer and autumn in 2014 as well as winter, spring, summer and autumn in 2015. In general, on the basis of the results of AL434 cruise in spring 2014 determining 'variability of bioturbation within stations' using 24 cores per station on different spatial scales, the number of cores within one location was reduced. In fact, one core was taken at 6 locations that are about 300 to 500 meters apart from each other resulting in 6 cores per station. Samples were treated and chl was determined as described above.

Firstly, the percentages of local and non-local sediment mixing within and between stations during different seasons were compared in order to determine seasonality in the extent of both modes of sediment mixing.

Secondly, modeled values of local (D_B) and non-local (J) sediment mixing derived by the bio-mixing model (Soetaert et al. 1996) were compared using non-parametric Kruskal-Wallis test and its post-hoc tests. Numbers of cores indicating each mode of sediment mixing and thus used for each test are given in table 10 (p. 60). No sediment mixing ($D_B = 0$) was excluded from all statistical analyzes. Ingestion rates (r) occurred too rarely for an appropriate statistical test. The aim of these comparisons is the determination of seasonal differences in bioturbation intensities within and between stations.

Thirdly, Kruskal-Wallis test and its post-hoc tests were carried out using estimated mixing depths (n = all cores taken per station/season, tab. 1; exact number of data used is given in table 10, p. 60).

3. Results

3.1 Evaluation of the photometric method

In spring 2015 on EMB 100 cruise, chl profiles derived from the monochromatric method were compared with the fluorometric approach (with acidification) using the same extracts (fig. 6). Six cores were analyzed at four stations (two muddy sediments: Mecklenburg Bay and Arkona Basin; two sandy sediments: Stoltera and Oderbank) and the results of mean chl profiles (n = 6 cores per station) derived from the two methods are presented in figure 6. At all stations chl depth distributions indicate similar courses of chl with lower concentrations estimated by the fluorometric method. Both profiles display the same mode of sediment mixing and correlate significantly with correlation coefficients r between 0.58 and 0.995. Bioturbation rates from the bio-mixing model are up generally higher using photometric determined chl concentrations. Consequently, bioturbation patterns remain the same but intensities cannot be directly compared to the literature.

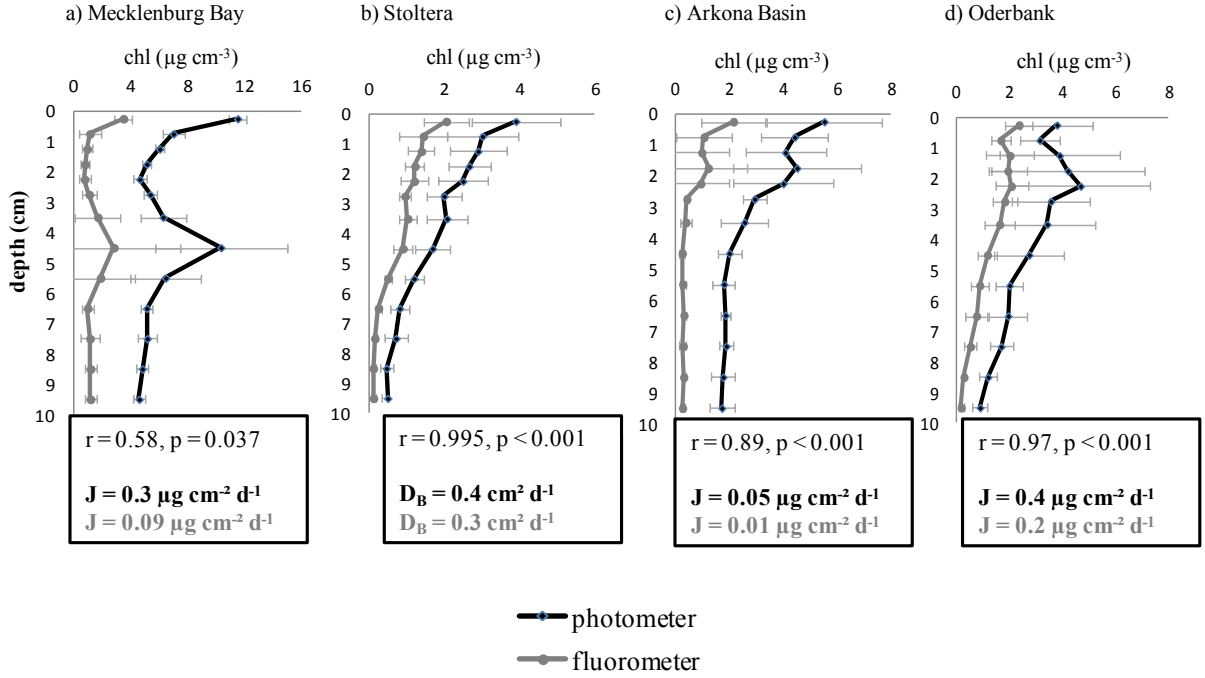


Fig. 6: Mean chl depth profiles with standard deviation derived from 6 cores taken at (a) Mecklenburg Bay, (b) Stoltera, (c) Arkona Basin and (d) Oderbank on EMB 100 cruise in spring 2015 comparing two different methods of chl measurement: photometric (663 nm, without acidification) and fluorometric (with acidification). Spearman- (MB, AB) or Pearson- (ST, OB) correlations with coefficients r and p or ρ-values were performed comparing chl depth distribution of both methods applied. Modeled bioturbation intensities are given with D_B (cm² d^{-1}) for local and J (µg cm^{-2} d^{-1}) for non-local sediment mixing using mean chl profiles. Note that bioturbation patterns estimated by both methods are the same but intensities are higher using the photometric approach.

The trichromatic measurements of chl were compared with the monochromatric method (one wavelength: 663 nm) generally applied in this study. Chl concentrations and thus depth profiles of chl estimated by the two methods are very similar with a highly significant Pearson-correlation ($r = 1$, $p < 0.001$).

3.2 Degradation of chlorophyll (k_D) [1]

In the anoxic incubation experiments during different seasons with muddy sediments from Arkona Basin (EMB 093, winter and EMB 100, spring) chl increased initially at all temperatures before decreasing after 5 days (fig. 7 a, c). This phenomenon occurred several times. During the first 5 days of incubation, the sediment changed from partially oxic to completely anoxic conditions. Samples for the initial chl value (t0) were not incubated but rather frozen immediately after retrieval and therefore treated differently than 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 initial values were ignored because these values are aussumed to be higher than measured. The data were then fitted starting with t1 (after 5 days) to estimate k_D. In general, the degradation of chl depends on the source concentration following first-order-kinetics (Sun et al. 1991). In winter and spring 2015 there were only little differences between chl concentrations over time between the four temperatures and a decay constant of $k_D = 0.01\ d^{-1}$ was obtained (fig. 7 a, c). The time course of chl in muddy sediments (all mud stations) in autumn fluctuated remarkably without explainable reasons and was therefore not considered further. As no dependency of chlorophyll degradation on both incubation temperatures and surrounding bottom water temperature during sampling (seasonal effect) was found, a decay constant of $k_D = 0.01\ d^{-1}$ was used for all mud stations (LB, MB and AB) and seasons.[1]

The chl concentration in sandy sediments from Stoltera decreased constantly over time during both spring and autumn (fig. 7 d, e). In winter, the same phenomenon as found in mud with chl increasing initially at all temperatures before decreasing after 5 days, was discovered as well in sand taken from Oderbank (fig. 7 b). However, as the initial value is generally assumed to be higher in reality and in order to treat the data in the same way, the initial value of the curve was ignored. Chl concentrations over time differed only slightly between the four temperatures and three seasons and a general k_D of $0.02\ d^{-1}$ was estimated. In spring 2015, however, a decay value obtained for 20°C with $0.03\ d^{-1}$ is higher than for 5, 10, 15°C. As temperatures of bottom waters in the Baltic Sea are usually not higher than 15°C

(Leppäranta & Myrberg 2009), k_D = 0.02 d^{-1} was used for all sand stations (ST and OB) and all seasons.[1] Temperature difference between winter/spring and autumn 2015 of the surrounding bottom water is remarkably high at Stoltera with an increase of more than 8°C. This fact leads to a confident assumption of a constant decay rate during different seasons without any dependency of chl degradation on temperature.

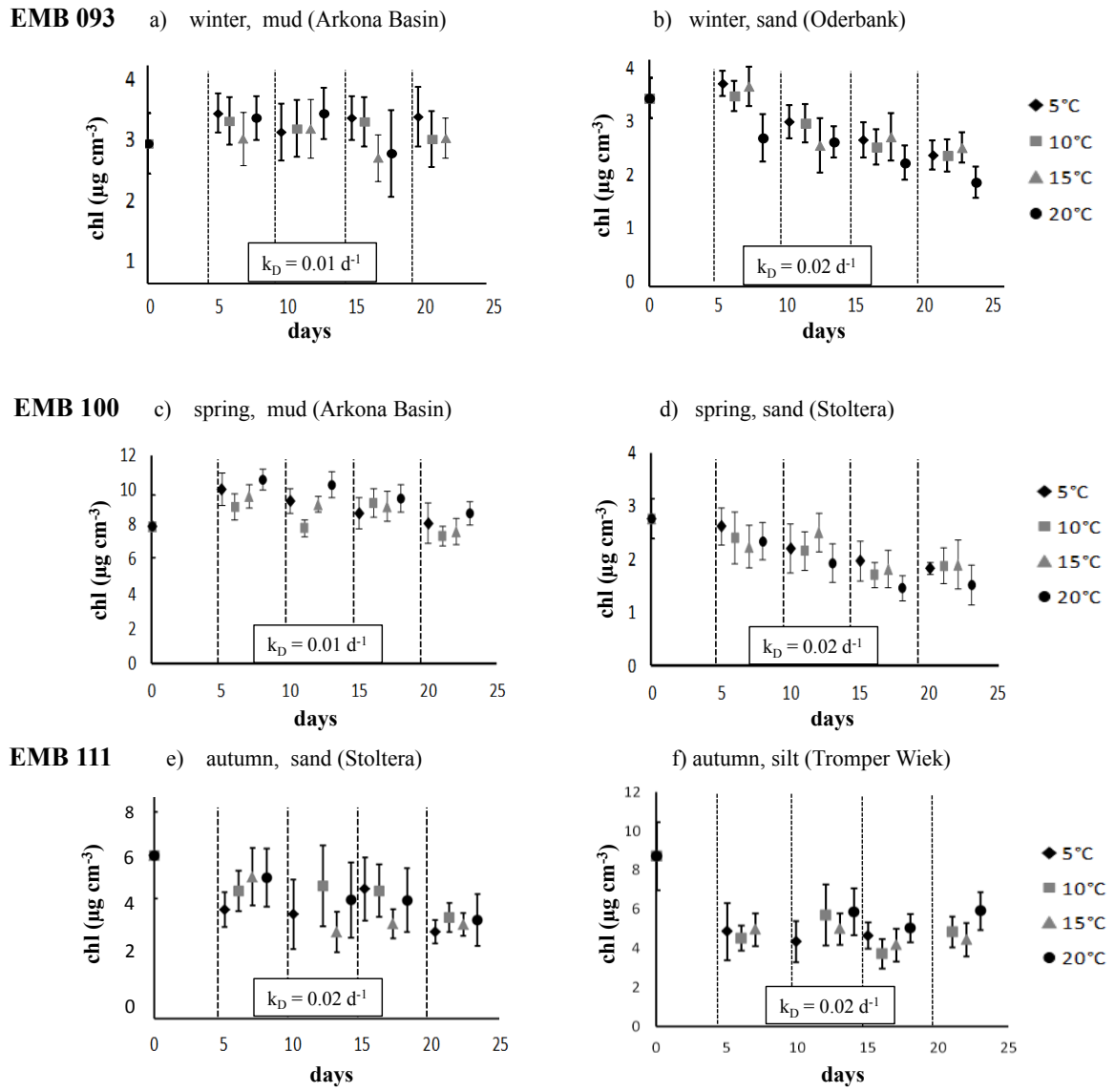


Fig. 7: Degradation of chl: Time courses of chl concentration in incubated fresh surface sediments including 0, 5, 10, 15 and 20 days. Data were treated as an exponential function and are shifted in the plot for a better illustration of the standard deviations. Anoxic incubation was performed at 5, 10, 15 and 20°C during different cruises/seasons using different types of sediment: winter 2015 with n = 40 per sediment type, temperature and incubation length: (a) mud (Arkona Basin), (b) sand (Oderbank); spring 2015 with n = 12: (c) mud (Arkona Basin), (d) sand (Soltera); autumn 2015 with n = 12: (e) sand (Stoltera), (f) silt (Tromper Wiek). Note the lower initial value in mud (all seasons) and sand (winter). Values of chl decay constant k_D (d^{-1}) derived from the exponential function (excluding initial chl concentration (day 0) except at Tromper Wiek) for each season and sediment type are given in the corresponding diagram. Figures (7 c, 7 d) are modified after Morys et al. (in press).

During the incubation experiment using silt from Tromper Wiek in autumn 2015 chl concentration decreased constantly over time with a bisection of chl within the first 5 days. For that reason the initial value (t0) was included into the data fit (fig. 7 f) and a decay constant of $k_D = 0.02\ d^{-1}$ was obtained which was used for Tromper Wiek during each season investigated.

3.3 Variability of bioturbation [1]

3.3.1 General patterns [1]

Variability of bioturbation between stations [1]

For a general overview of sediment mixing at the sampling stations chl concentrations of each depth layer (13 layers per core) of all 24 cores at each station were averaged (fig. 8) and mean profiles were modeled to detect whether local or non-local sediment mixing is dominant at each station. Chl profiles obtained at the western stations (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 the station 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, an injection flux ($J = 0.05\ \mu g\ cm^{-2}\ d^{-1}$) in 2.1 cm depth was detected by the bio-mixing model at OB. At AB a distinct subsurface maximum in chl (increase of 6 $\mu g\ cm^{-3}$) close to the sediment surface and an ingestion rate of 3.9 d^{-1} was determined. TW indicates an injection flux of 0.3 $\mu g\ cm^{-2}\ d^{-1}$.

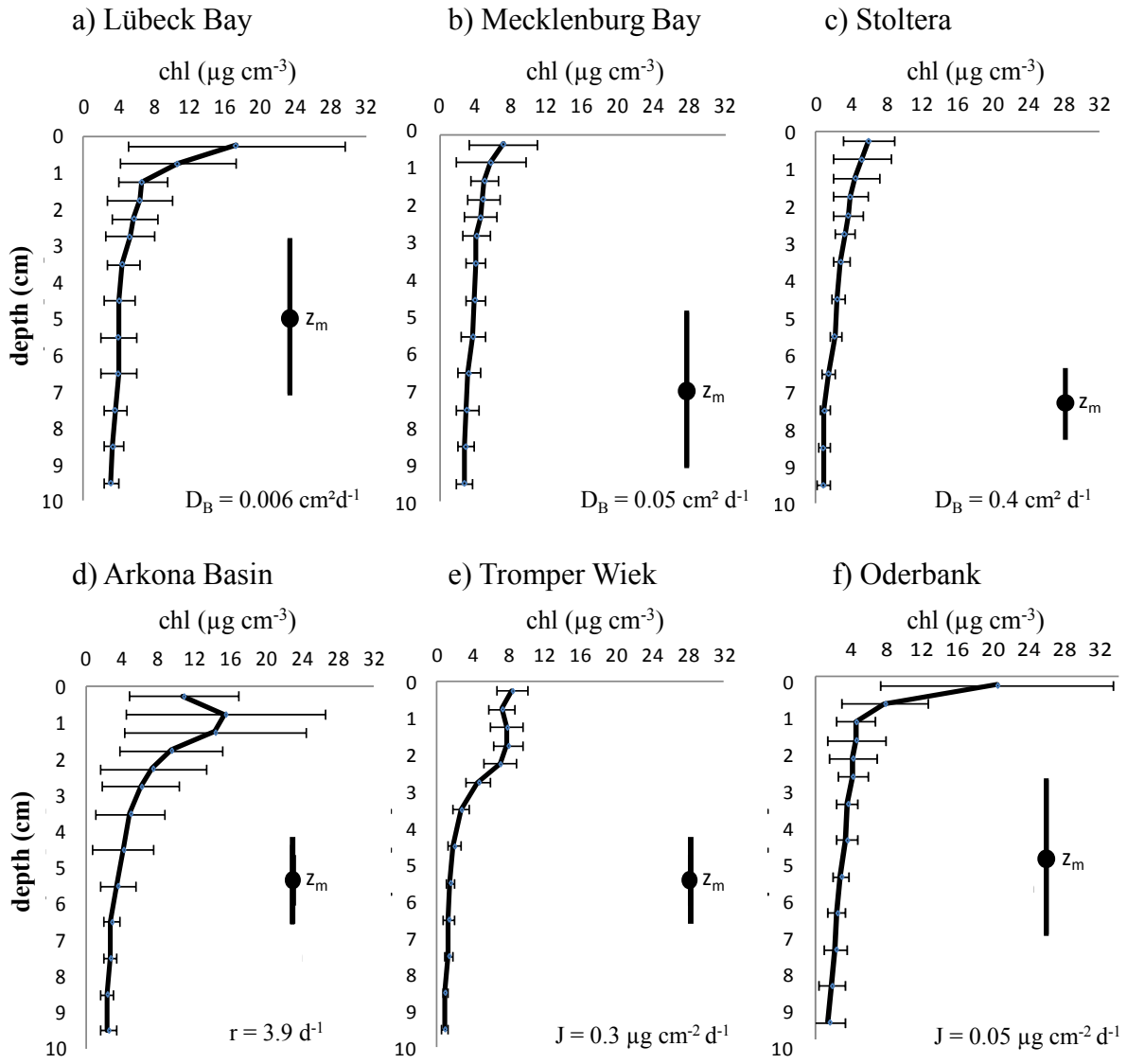


Fig. 8: Mean chl depth profiles with standard deviation for each sampling station (a) LB, (b) MB, (c) ST, (d) AB, (e) TW, (f) OB (n = 24, except OB: n = 23). Black dots indicate mean mixing depths (z_m) with standard deviation (vertical bars). Biodiffusion coefficient (D_B), injection flux (J) and ingestion rate (r) at each station provided by the bio-mixing model by Soetaert et al. (1996) using mean chl profiles, in Morys et al. (in press).

Firstly, all MDS results using normalized chl profiles were plotted to illustrate differences in the chl depth distribution between sampling stations (fig. 9) (n = 6 stations with 4 cores each resulting in 24 cores per station, except OB: 23 cores). At stations LB and MB approximately two third 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 results present a binary division with half of the cores matching LB, MB and ST. The remaining cores show great distance to other stations in the plot. TW is a homogenous station with all 24 cores embedded closely to each other and it shows only occasional matches with other stations. At OB there is a broad

distribution of the data in the plot indicating a heterogeneous station. Hence, there is a tendency towards increasing dissimilarities when stations are further apart from each other in the Baltic Sea except LB and OB. ANOSIM test 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.

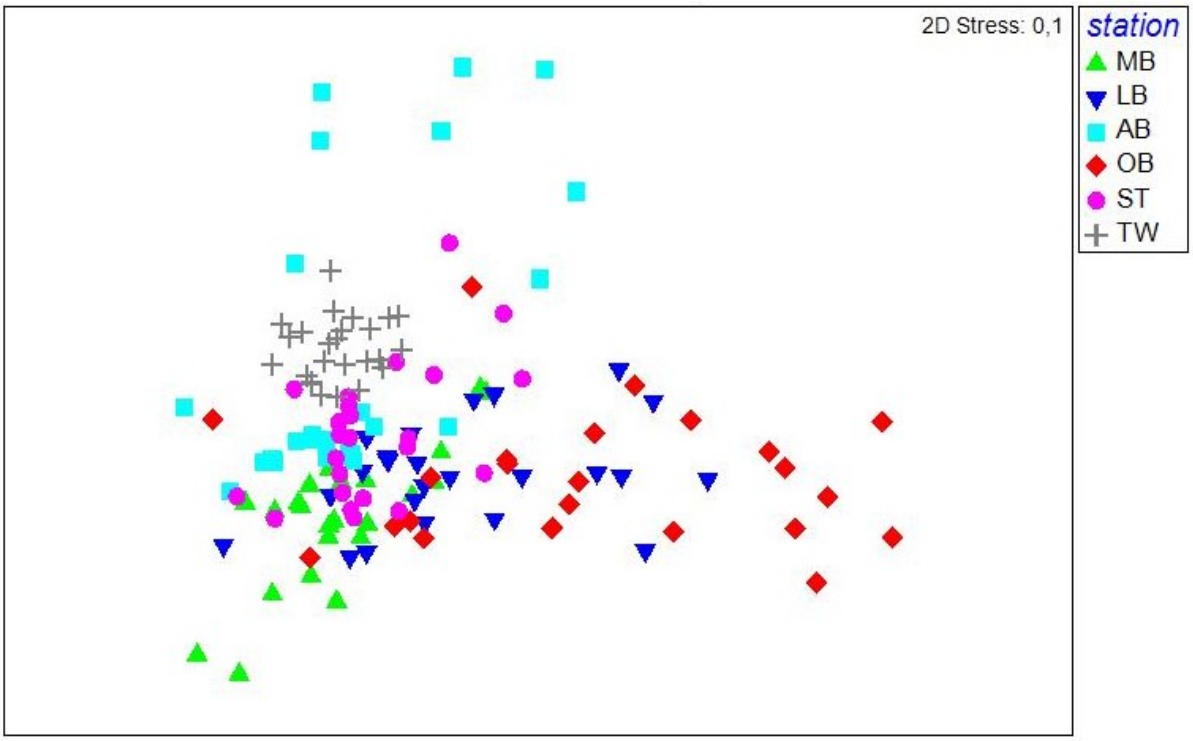


Fig. 9: MDS plot of all stations on the basis of normalized chl concentrations of each depth layer and core. ANOSIM test showed that stations represented by 24 cores (OB: 23) are highly significant different, in Morys et al. (in press).

The extent of local, non-local and no sediment mixing at each station indicates differences between stations (fig. 10). In the west (LB and MB) non-local sediment mixing covers approximately 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. 8). All in all, the extent of non-local sediment mixing increases from west to east.

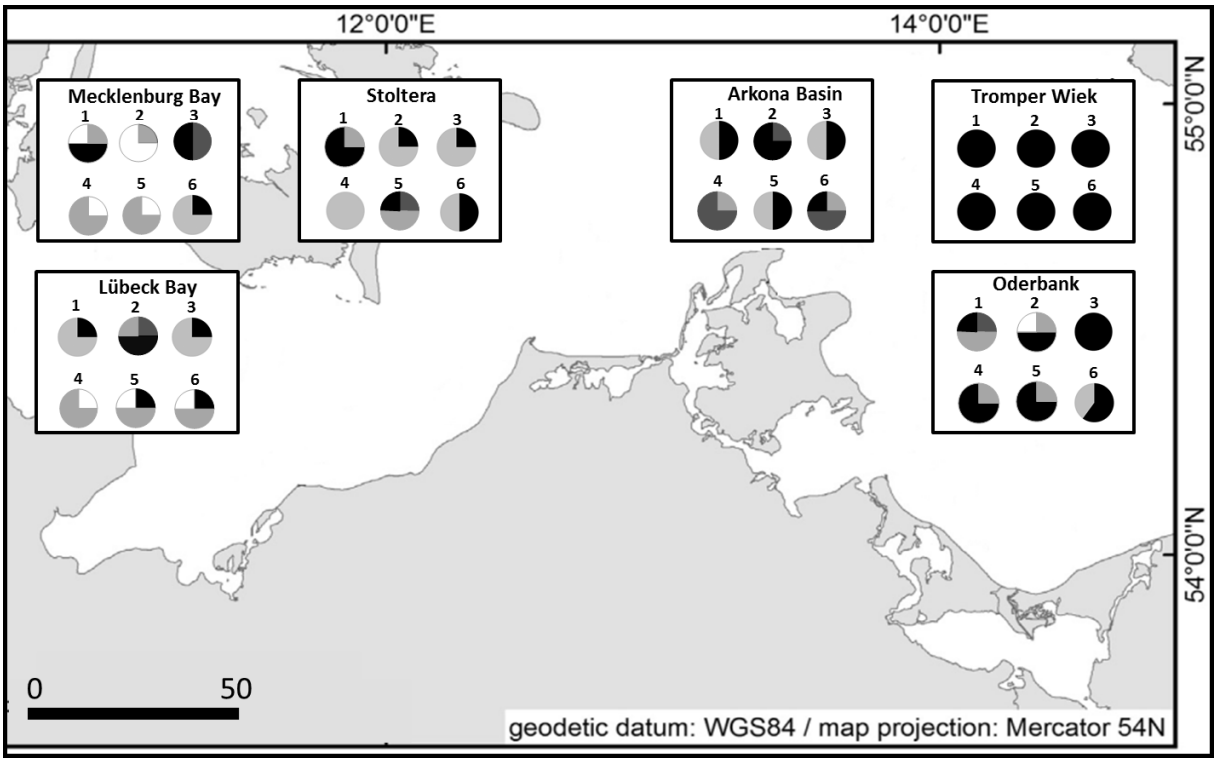


Fig. 10: Map with a schematic overview of the modes of sediment reworking at all sampling locations (numbers) at the investigated stations. Circle diagrams show the percentage of local sediment mixing (grey), non-local injection flux (black), non-local ingestion rate (dark grey) and no (white) sediment mixing at each location, in Morys et al. (in press).

Kruskal-Wallis test comparing D_B and J between stations (numbers of cores indicating local (D_B) or non-local (J) sediment mixing that were used for the statistical test are given in table 10, p. 60) presents 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 analyzes. Ingestion rates (r) were not compared statistically because of their infrequent occurrence (tab. 10). By comparing D_B between stations using Kruskal-Wallis post-hoc test, two 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 ($D_B = 0.02 \pm 0.03$ cm² d^{-1}, n = 14) and OB (0.005 ± 0.003 cm² d^{-1}, n = 6) are the least intense locally mixed stations. Sediments at MB ($D_B = 0.4 \pm 0.8$ cm² d^{-1}, n = 11), ST ($D_B = 0.3 \pm 0.3$ cm² d^{-1}, n= 15) and AB ($D_B = 0.2 \pm 0.1$ cm² d^{-1}, n = 8) are 40 to 80 times more intense locally mixed. Results are presented in table 10 (p. 60).

Injection fluxes J indicated three subsets among stations according to 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. LB is considered as a low, MB, ST, AB and OB as intermediate and TW as a high non-locally mixed station. Results are presented in table 10 (p. 60).

Kruskal-Wallis test results (n = 24 per station, except OB: n = 23) indicate that the estimated mixing depths in the southwestern Baltic Sea are highly significantly different with two subsets of stations with similar mixing depths: MB and ST as well as LB, AB, TW and OB. Mixing depth at stations MB and ST is 7.1 ± 1.6 cm with chl penetrating the sediment approximately 2 cm deeper than at the other four stations (5.2 ± 1.7 cm). Mean mixing depths are presented in figure 8.

Variability of bioturbation within stations [1]

Statistical analyzes 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 comparing stations and locations are presented in table 3. However, defining similar locations within one station and their composition as presented in table 3 is not based on ANOSIM pair wise comparison but rather on the distribution of no, local and non-local sediment mixing that will be described later (derived from figure 10) because of different results gained by the two approaches. The differentiation between the modes of sediment mixing according to the bio-mixing model is definded as the most important criterion for similarities and dissimilarities between and within locations.

Tab. 3: ANOSIM results comparing the six locations within each station using normalized chl depth profiles (n = 24, OB: n = 23). Global R and its significance level are given highlighting significant differences between locations. Number of homogenous subsets is derived from the distribution of no, local and non-local sediment mixing within each location as presented in figure 10. The composition of locations belonging to each subset is given (derived from figure 10), in Morys et al. (in press).

Station	Global R	Significance level (%)	Subsets (n)	Subset 1	2	3	4	5
LB	0.183	3.0	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	37.0	4	1	2	3	4,5,6	

Percentages of no, local and non-local (both injection flux and ingestion rate) sediment mixing of cores within one location were used to describe the variability within one station (derived from figure 10). 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 3. Stations LB and AB indicate 4 subsets of homogenous locations. Stations MB, ST and OB show only two locations to be similar resulting in 5 subsets. TW shows a homogenous distribution with all 24 cores indicating non-local sediment mixing (tab. 10).

Some previously described homogenous subsets estimated by the distribution of local and non-local sediment mixing at each location indicated two or more cores of 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. These tests allowed highlighting differences in mixing intensities between similar locations. At LB, for example, D_B of the three cores at locations 1 and 3 (fig. 10), were compared using Kruskal-Wallis test and were found to be significantly different between the two locations (1 and 3). This indicates only two 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 cm² 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 two locations (4 and 5) are similar presenting the same distribution of the different modes of sediment mixing: one core with no mixing and three cores with local mixing. D_B of the three cores of each location (4 and 5) were found to be without significant differences. There are two similar locations (2 and 3) at ST with three cores indicating local and one non-local sediment mixing. Local sediment mixing is not significantly different and injection flux 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 three 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 injection fluxes J. TW is homogenous without significant differences in J. OB shows two 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 location is similar to one another), are given in table 3.

Variability of bioturbation within locations [1]

Similarity within locations was determined by looking at the distribution of local and non-local sediment mixing of the four cores (taken from one MUC) at each location. All four cores showing the same type of sediment mixing indicate similar locations (derived from figure 10). LB, MB and AB do not present any locations with similar cores. Both ST and OB show one location each with similar cores whereas all locations are similar at TW.

All in all, mean chl profiles match the findings of the model-derived dominant type of sediment mixing and indicate local mixing in the west and non-local mixing in the east. Modeled values of D_B and J using mean chl profiles (fig. 8) present different results than considering the cores separately (tab. 10). At MB, for example, mean D_B of 0.4 ± 0.8 $cm^2\ d^{-1}$ is up to 44 times higher than the mean D_B of 0.05 $cm^2\ d^{-1}$ estimated using the mean chl profile. At AB, mean chl profile is characterized by an ingestion rate. Even though AB is the station with most ingestion rates in the present study, the majority of the cores indicate injection fluxes.

ANOSIM 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). MDS plot highlighted a tendency towards increasing dissimilarity with increasing distance between stations except for LB and OB. These findings match homogenous subsets with regard to 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 no, local and non-local sediment mixing within one 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. The most important criterion to describe variability of bioturbation in this study is the differentiation between local and non-local sediment mixing. These findings were considered to be more important. Therefore, OB is characterized as a heterogeneous station. Additionally, all following determinations of variability of bioturbation are now based on the distribution of the different modes of particle transport.

Consequentially, 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 only occur occasionally (except at AB where this type of transport covers 25% of the investigated area) (tab. 10). In summary, LB is defined 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 southerwestern Baltic Sea. Results gained at TW present this station to be homogenous with similar chl profiles and no significant differences in injection fluxes. At AB 3 locations were found 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 whether closely located cores (within one location) are more similar than cores on a broader spatial scale.

3.3.2 Seasonal changes in variability

For a general overview of seasonal and inter-annual variability of sediment mixing mean chl profiles of 24 cores taken at ST in summer 2013 as well as in winter, spring and summer 2014 are presented in figure 11. Mean chl profiles and modeled intensities show different patterns between seasons. In summer 2013 and spring 2014 sediment mixing at ST is characterized by local mixing that was confirmed by the bio-mixing model. D_B of 0.4 $cm^2\ d^{-1}$ is 4 times higher in spring 2014 (fig. 11 a, c). In winter and summer 2014 injection fluxes J are predominant with J = 0.6 $\mu g\ cm^{-2}\ d^{-1}$ being twice as high in summer than in winter 2014 (fig. 11 b, d).

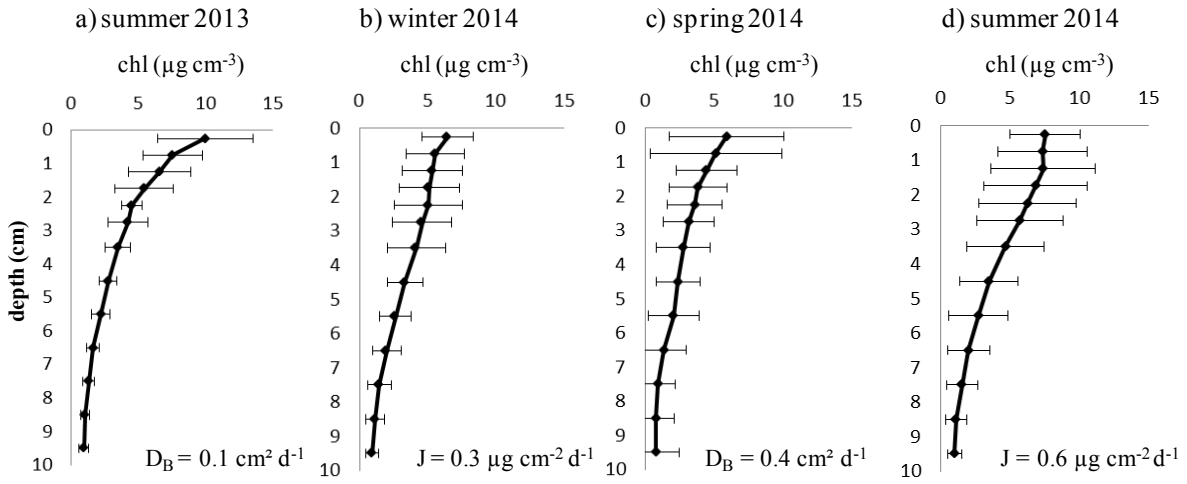


Fig. 11: Mean chl depth profiles with standard deviation for different seasons at ST, n = 24 cores per season: (a) summer 2013 (b) winter 2014 (c) spring 2014 (d) summer 2014. Biodiffusion coefficient (D_B) and injection flux (J) for each season provided by the bio-mixing model by Soetaert et al. (1996) using mean chl profiles.

A comparison of the percentages of local and non-local sediment mixing at ST during different seasons on the basis of 24 cores per season indicates slight differences (fig. 12). The percentage of local sediment mixing is highest in summer 2013 with 87.5% and lowest in winter 2014 with 58.3%. Spring and summer 2014 show the same distribution of both modes of sediment mixing. Inter-annual differences (summer 2013 and 2014) were found with cores indicating 20% more local sediment mixing in 2013. All in all, local sediment mixing is dominant during all seasons and years.

Percentages of local and non-local (both injection flux and ingestion rate) sediment mixing of cores within one location (derived from figure 12) were used to describe the variability within the station ST during different seasons (n = 6 locations with 4 cores each, resulting in 24 cores per season). In summer 2013 all four cores at three locations (2, 4, 5) indicate local sediment mixing with D_B not significantly different according to Kruskal-Wallis test. For that reason, these three locations are defined to present a homogenous subset (tab. 4). Locations 1 and 3 show the same distribution of the different modes of sediment mixing with similar D_B (Kruskal-Wallis) but differences in injection fluxes by a factor of 11 and are therefore considered to be different from each other. In winter 2014 locations 1 – 3 show the same patterns in the distribution of the different modes of sediment mixing. Results using Kruskal-Wallis test present D_B not to be significantly different, however, injection flux J of 1.1 µg cm^{-2} d^{-1} at location 2 is remarkably higher than the mean injection flux J = 0.5 ± 0.3 µg cm^{-2} d^{-1} during winter at ST. For that reason, location 2 is excluded from the homogenous subset of location 1 and 3. Five subsets were determined in spring 2014 and

three in summer 2014 indicating homogeneous locations in terms of mode of sediment mixing and bioturbation intensity.

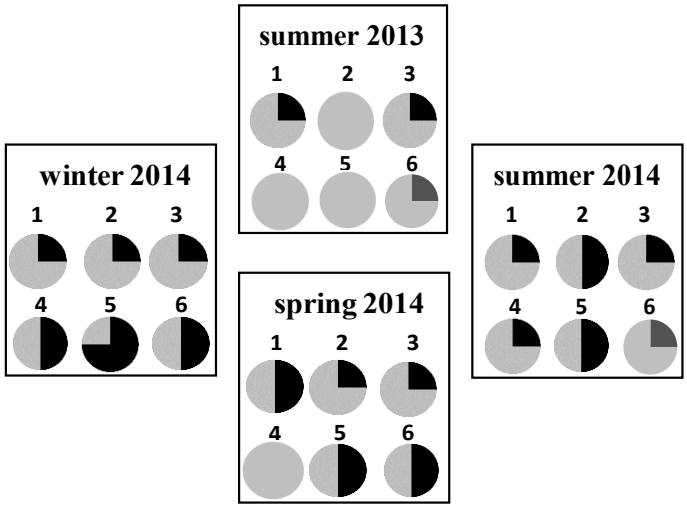


Fig. 12: Schematic overview of the modes of sediment mixing at all sampling locations (numbers) at ST during the different seasons and years investigated (n = 24 cores per season). Circle diagrams show the percentage of local sediment mixing (grey), non-local injection flux (black) and non-local ingestion rate (dark grey) at each location.

Overall, variability of bioturbation within the station ST during different seasons indicates slightly different patterns. Bioturbation patterns were found to be more homogeneous in summer 2014 with 3 of 6 locations being similar while in spring 2014 only 2 locations indicated similar distributions of mixing modes (tab. 4). Summer 2013 was the only season with three locations indicating similar cores in terms of mixing mode (fig. 12).

Tab. 4: Number of homogenous subsets at ST during four seasons derived from the distribution of local and non-local (both injection fluxes and ingestion rates) sediment mixing within each location and the composition of locations belonging to each subset derived from figure 12.

Season	Subsets (n)	Subset 1	2	3	4	5
Summer 2013	4	1	3	2, 4, 5	6	
Winter 2014	4	1,3	2	4, 6	5	
Spring 2014	5	1	2, 3	4	5	6
Summer 2014	3	1, 3, 4	2, 5	6		

At OB, mean chl profiles of 24 cores taken in spring and summer 2014 were plotted and modeled (fig. 13 a, b) for an overview of seasonal variability of sediment mixing at a second sandy station. In spring 2014 surface chl concentration is much higher due to the previously sedimented spring bloom. Subsurface maxima of chl are not distinct during both seasons (injection depth L = 3.3 cm in spring and L = 4.7 cm in summer according to the model). However, non-local injection fluxes J were detected by the bio-mixing model for both

profiles with J of 0.2 µg cm^{-2} d^{-1} being 4 times higher in summer (fig. 13 a, b). These results indicate more intense sediment mixing in summer than in spring.

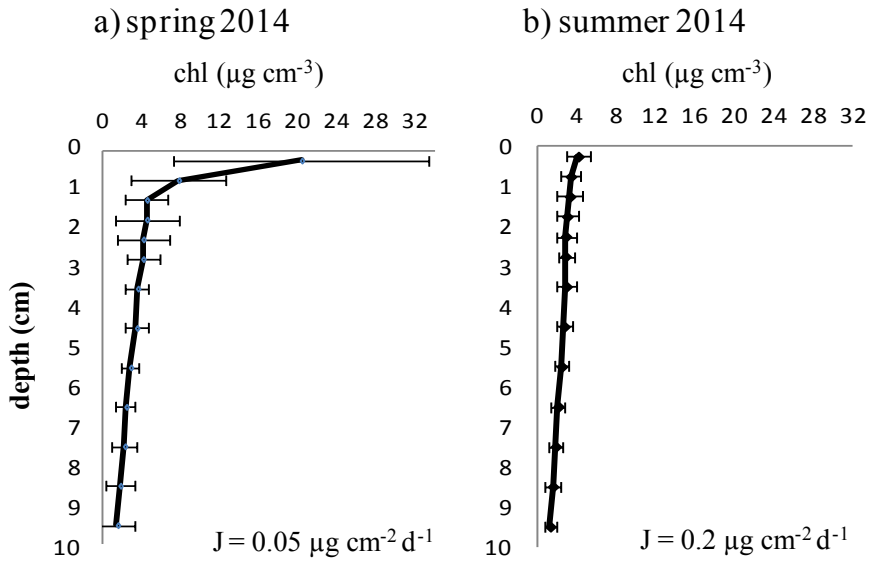


Fig. 13: Mean chl depth profiles with standard deviation for different seasons at OB: (a) spring 2014 (n = 24), (b) summer 2014 (n = 24). Injection flux (J) for each season provided by the bio-mixing model by Soetaert et al. (1996) using mean chl profiles.

Comparing the percentages of no, local and non-local sediment mixing at OB between spring and summer 2014 on the basis of 24 cores per season similar patterns can be seen (fig. 14). Sediments at OB are mainly mixed non-locally during both seasons with 70% of the cores in spring and 58% in summer indicating non-local transports. Only one core shows no mixing whereas in the remaining 30% (spring) and 40% (summer) of the cores local sediment mixing was detected.

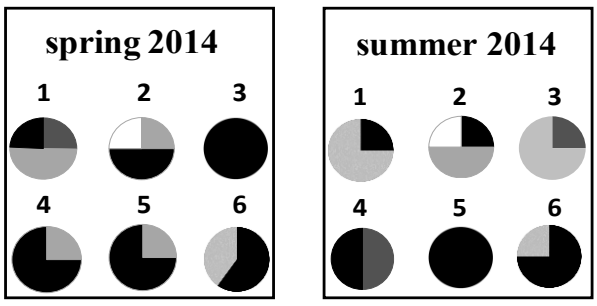


Fig. 14: Schematic overview of the modes of sediment mixing at all sampling locations (numbers) at OB during spring and summer 2014 (n = 24 cores per season). Circle diagrams show the percentage of local (grey) and no (white) sediment mixing, non-local injection flux (black) and non-local ingestion rate (dark grey) at each location.

OB was defined to be one of the most heterogeneous stations in terms of the distribution of different sediment mixing modes in spring compared to the other stations of investigation (AL434 cruise, see tab. 3). These findings were confirmed by determining

variability of bioturbation in summer 2014 when all 6 locations are different from each other (fig. 14, tab. 5). During both seasons one location presented all cores with the same mode of sediment mixing (location 3 in spring and 5 in summer, derived from figure 14). Results of variability of bioturbation within the station OB during two different seasons are given in table 5.

Tab. 5: Number of homogenous subsets at OB derived from the distribution of no, local and non-local (both injection fluxes and ingestion rates) sediment mixing within each location and the composition of locations belonging to each subset derived from figure 14.

	Season	
	Spring 2014	**Summer 2014**
n (subsets)	**4**	**6**
Subset 1	1	1
Subset 2	2	2
Subset 3	3	3
Subset 4	4,5,6	4
Subset 5		5
Subset 6		6

3.4 Bioturbation depending on macrozoobenthos

3.4.1 General characterization of the macrozoobenthos [2]

The composition of the macrozoobenthic communities at each station is presented in figure 15 a. Macrozoobenthic abundances consist of several taxonomic groups: polychaeta, bivalvia, malacostraca, priapulida and gastropoda, depending on the station considered. LB, ST and AB are mainly populated by the class bivalvia. The communities show a similar composition of macrozoobenthic taxa at ST and AB. Malacostraca dominate the fauna at MB whereas polychaetes play a minor role at MB and OB. *Peringia* sp. becomes more dominant towards the east where it is the most abundant species at OB. Priapulida are not present at OB.

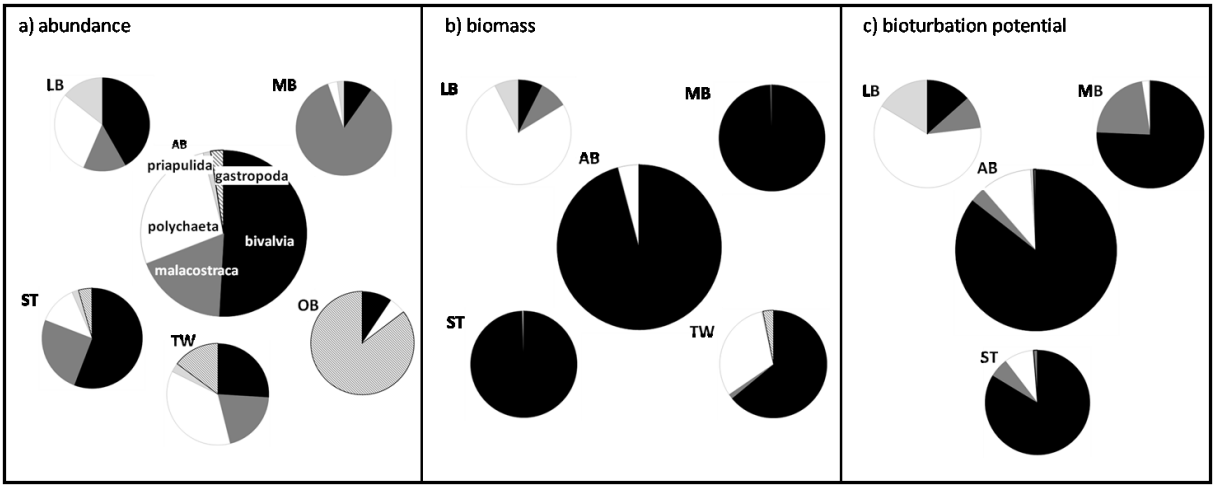


Fig. 15: Composition of the macrozoobenthic communities with (a) the relative abundance at higher taxonomic levels at the stations of investment: Arkona Basin (AB, large pie diagram), Lübeck Bay (LB), Mecklenburg Bay (MB), Stoltera (ST), Tromper Wiek (TW) and Oderbank (OB), with (b) the relative biomass and with (c) the relative bioturbation potential. Data on biomass are not available for OB. BP_c was not calculated for TW because of the difficult identification of deep-frozen polychaetes, in Morys et al. (in press).

The macrozoobenthic communities in the southwestern Baltic Sea are mainly dominated by bivalves with regard to biomass (fig. 15 b). They constitute more than 95% of total biomass at MB, ST and AB. At TW, polychaetes account for about 40% of total biomass. BP_c was not calculated for TW because of difficulties identificatying deep-frozen polychaetes. At LB, about 75% of total biomass is constituted by polychaetes. The important class bivalvia at all other stations plays a minor role at LB. The composition of bioturbation potential shows patterns similar to biomass (fig. 15 c). At MB, ST and AB bivalvia have greatest potential to mix the sediment (> 75%). According to BP_c, polychaetes are the main bioturbators at LB.

3.4.2 Depth distribution of abundance, biomass, BP [2]

A general overview of the depth distribution of most abundant organisms found in the cores versus the mean chl profiles at each station is presented in figure 16. A list of all species occurring at each station is given in table 7. The sum of organisms (fig. 16 (i)), biomass (fig. 16 (ii)) and bioturbation potential BP_i (fig. 16 (iii)) separated into main species found in all layers are plotted and compared with the mean depth distribution of chl of the same investigated cores. BP_i was calculated and evaluated by comparing it to the method applied in this study for identifying main bioturbators. This will be discussed later. The mean depth distributions of the animals' abundance and chl correlate highly significant at each

station with values of Spearman correlation coefficient r between 0.93 and 0.98 (fig. 16 a - f (i)).

Biomass and bioturbation potential BP_i indicate similar patterns. Significant correlations between mean depth distributions of biomass and chl were found at LB, ST and TW with r between 0.82 and 0.97 (fig. 16 a, c and e (ii)). At all other stations, maxima in biomass are located apart from the chl peak (fig. 16 b and d (ii)). Bioturbation potential was not calculated for TW because of difficulties identifying deep-frozen polychaetes and for OB for which data on biomass are not available. BP_i and chl only correlated significantly at LB and ST with r of 1 and 0.88, respectively. However, when considering each core separately, correlations were found between chl and the tested parameters even in cases of no overall correlation using mean profiles and the other way around. The percentage of significant correlations between depth distribution of chl and abundance/biomass/BP_i per core are presented in table 6.[2]

Tab. 6: Total number (n) of cores investigated for macrofauna 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 one core at LB and two cores at MB were without any organisms, thus, a correlation was not possible.) Bold characters present percentage of all investigated cores that show a significant correlation between depth distribution of abundance/biomass/BP_i of organisms and chl. Additionally numbers of cores that show a significant correlation between no, local or non-local sediment mixing (indicated by chl depth distribution) and depth distribution of abundance/biomass/BP_i of organisms are given below, in Morys et al. (submitted).

	LB	**MB**	**ST**	**AB**	**TW**	**OB**
n = investigated cores	**23**	**22**	**24**	**10**	**10**	**6**
n = no mixing	3	5	0	0	0	1
n = local mixing	14	10	15	2	0	1
n = non-local mixing	6	7	9	8	10	4
Abundance						
significant correlation (%)	**69.6**	**50**	**83.3**	**60**	**80**	**83.3**
no mixing	2	2	n.a.	n.a.	n.a.	0
local mixing	10	7	14	1	n.a.	1
non-local mixing	4	2	6	7	8	4
Biomass						
significant correlation (%)	**65.2**	**40.9**	**70.8**	**20**	**80**	**n.a.**
no mixing	1	2	n.a.	n.a.	n.a.	
local mixing	10	6	11	0	n.a.	
non-local mixing	4	1	6	2	8	
bioturbation potential (BP_i)						
significant correlation (%)	**65.2**	**40.9**	**62.5**	**2**	**n.a.**	**n.a.**
no mixing	1	2	n.a.	n.a.		
local mixing	10	6	11	0		
non-local mixing	4	1	4	2		

As already mentioned, 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 confirm these patterns. Abundances at LB, MB and ST decrease exponentially with depth (fig. 16 a – c (i)).[2]

LB is the station with lowest abundance, biomass and BP_i, all indicating an exponential decrease with sediment depth (tab. 7, fig. 16 a (i – iii)). 13 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 (tab. 7, fig. 16 a (i)). *C. capitata* constitutes the largest part of biomass and BP_i (fig. 16 a (i, iii)). [2]

MB is also characterized by comparably low abundance but indicates lowest number of species with *D. rathkei* being most abundant. Most organisms occur up to 4 cm but some, e.g. *Abra alba*, *A. islandica* and *Nephtys hombergii* can reach a maximum depth of 9 cm (tab. 7, fig. 16 b (i)). Biomass (*A. islandica* constituting 99%) and BP_i indicate their maxima between 2 to 5 cm and 6 to 7 cm (fig. 16 b (ii, iii)). According to BP_i, *D. rathkei* is the most important bioturbator within the upper 1.5 cm and is superseded by *A. islandica* in deeper horizons.[2]

ST presents the station with highest abundance, biomass, BP_i and number of species (tab. 7). Organisms are mainly located within the upper 4 cm but may reach a depth of 9 cm. The most abundant species are *K. bidentata*, *D. rathkei* and *A. alba* (juvenile stages with maximum size of 6 mm) (fig. 16 c (i)). Biomass is mainly constituted by *A. islandica* whereas BP_i indicates a variety of organisms in the first centimeter (fig. 16 c (ii, iii)). However, *A. islandica* and *L. balthica* become more important deeper in the sediment. [2]

Stations in the east AB, TW and OB are characterized by subsurface peaks in mean chl profiles (fig. 16 d – f) and 70 - 100% of the area is mixed non-locally (fig. 10, tab. 10). At AB, maximum of chl is close to the sediment surface (0.9 cm depth) where most animals were found simultenously (*L. balthica* being most abundant) (fig. 16 d (i)). The second most abundant organisms belong to the class polychaeta (esp. *Scoloplos armiger*) with most individuals between 1 and 3 cm. Depth distribution of biomass and BP_i indicate two maxima: within the top 2 cm and between 4 and 8 cm (fig. 16 d (ii)). *L. balthica* reaching a depth of 9 cm accounts for 96% of total biomass and constitutes the major part of BP_i (fig. 16 d (iii)).[2]

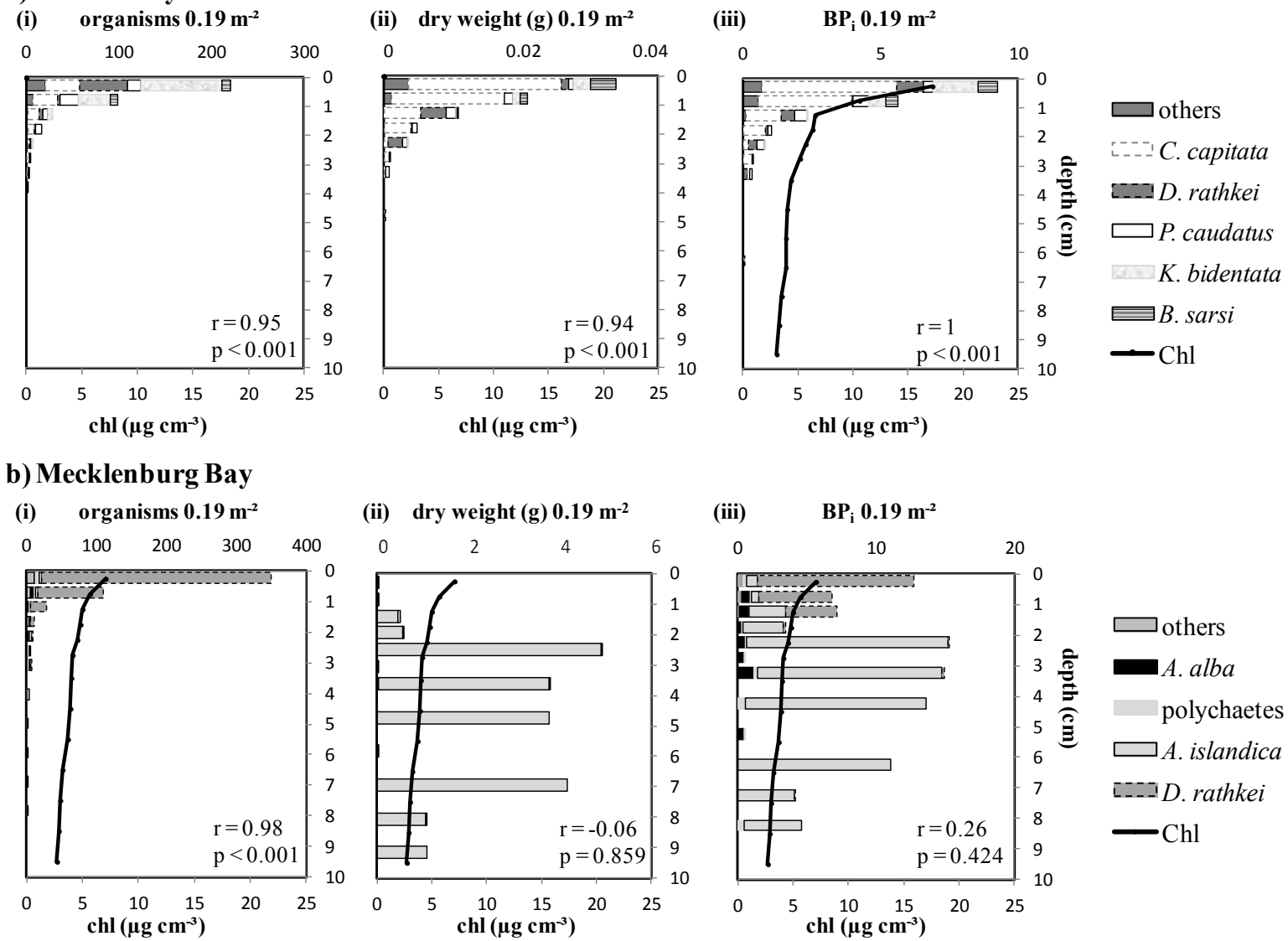
Depth distribution of chl, abundance and biomass at TW is characterized by a subsurface maximum between 1 and 3 cm (fig. 16 e (i)). The most abundant organisms belong to the class polychaeta (*S. armiger* most abundant) (fig. 16 e (i)). Exact taxonomic determination of the polychaetes was difficult because of the poor quality due to the deep-freezing technique. Most individuals are located between 1 and 4 cm, but a few organisms were also found up to 7 cm depth. Biomass is mainly constituted by *L. balthica* and polychaetes (fig. 16 e (ii)).[2]

Evidence for non-local sediment mixing is less distinct at OB with a comparably small increase in chl between 2 and 3.5 cm (fig. 16 f (i)). In the same layer, a slight increase in abundance is apparent. OB is the station with remarkably highest abundance and *Peringia ulvae* being most abundant. *Hediste diversicolor* is also one of the most important organisms and is mainly located between 2 and 4 cm but can reach a depth of up to 6 cm (fig. 16 f (ii)).[2]

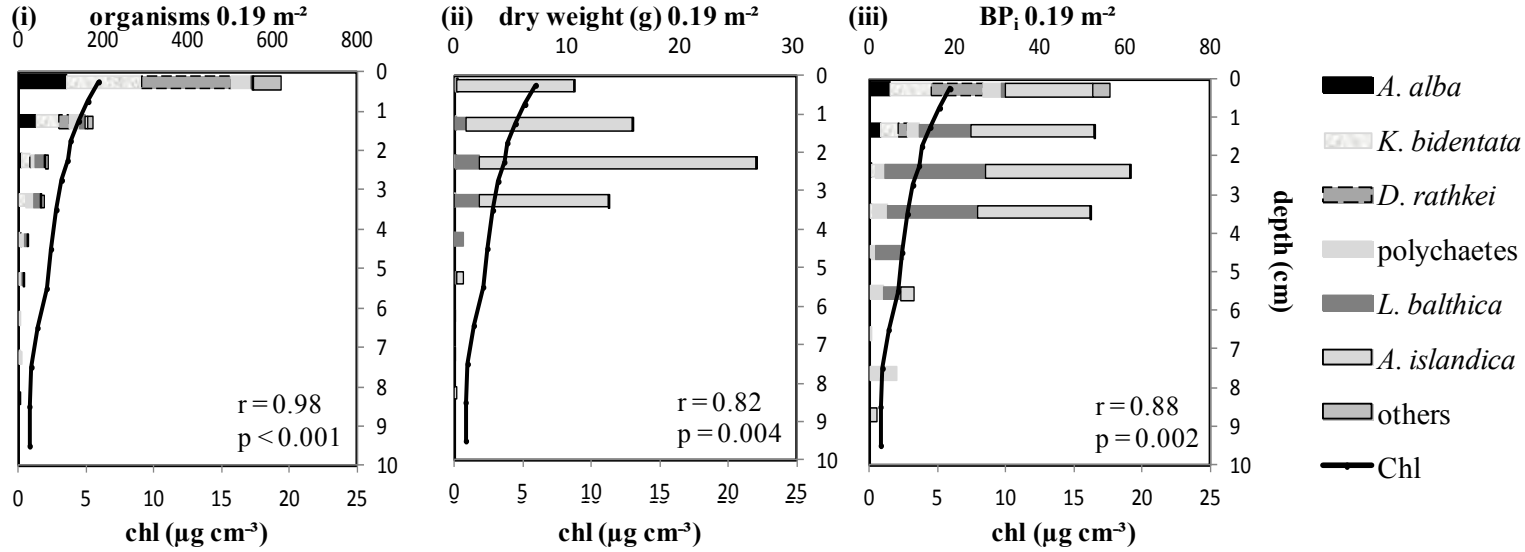
The differences in depth distribution of abundances were confirmed by the ANOSIM test using normalized abundances found in each core. A global R of 0.439 (abundance) and 0.165 (biomass: dry weight) with a significance level of 0.1% indicated highly significant differences between stations. Depth distribution of BP_i was determined at LB, MB, ST and AB and shows similar patterns like biomass' depth distribution (fig. 16 a – d (iii)). However, at MB and AB, BP_i also shows a maximum close to the sediment surface where many small organisms are located. ANOSIM test displays a global R of 0.262 with a significance level of 0.2% highlighting highly significant differences between stations with respect to BP_i, thus confirming the findings based on tracer and fauna depth distribution. [2]

3.4.3 Modeled bioturbation in relation to macrozoobenthos [2]

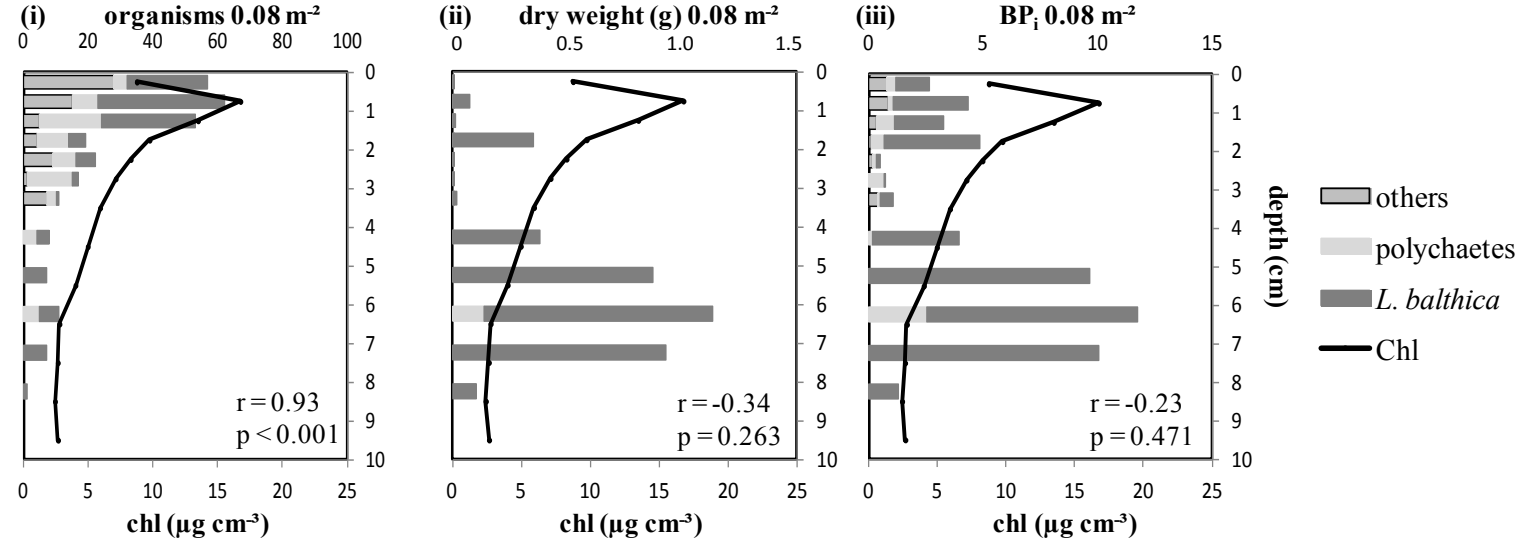
In order to analyze the relationship between modeled intensities of sediment mixing (D_B, J and r) and macrobenthos (abundance/biomass) linear regressions were performed (fig. 17). Highly significant regressions with low R^2 were found between injection fluxes J and abundance ($p = 0.014$, $R^2 = 0.19$) and biomass ($p = 0.017$, $R^2 = 0.18$) (fig. 17 a, b). There is no significant relationship between abundance/biomass and D_B ($p = 0.518$ / $p = 0.459$) nor abundance/biomass and ingestion rates r ($p = 0.692$ / $p = 0.860$). The effect of a stimulated diffusive distribution of particulate matter within the sediment by local sediment mixing is not visible neither by increasing abundance nor by increasing biomass. In contrast, non-local mixing (injections fluxes J) increases with increasing numbers and biomass of animals.[2]


a) Lübeck Bay
(i) organisms 0.19 m-2
(ii) dry weight (g) 0.19 m-2
(iii) BPi 0.19 m-2
r = 0.95
p < 0.001
r = 0.94
p < 0.001
r = 1
p < 0.001
chl (µg cm-3)
depth (cm)
others
C. capitata
D. rathkei
P. caudatus
K. bidentata
B. sarsi
Chl
b) Mecklenburg Bay
(i) organisms 0.19 m-2
(ii) dry weight (g) 0.19 m-2
(iii) BPi 0.19 m-2
r = 0.98
p < 0.001
r = -0.06
p = 0.859
r = 0.26
p = 0.424
chl (µg cm-3)
depth (cm)
others
A. alba
polychaetes
A. islandica
D. rathkei
Chl

c) Stoltera



d) Arkona Basin



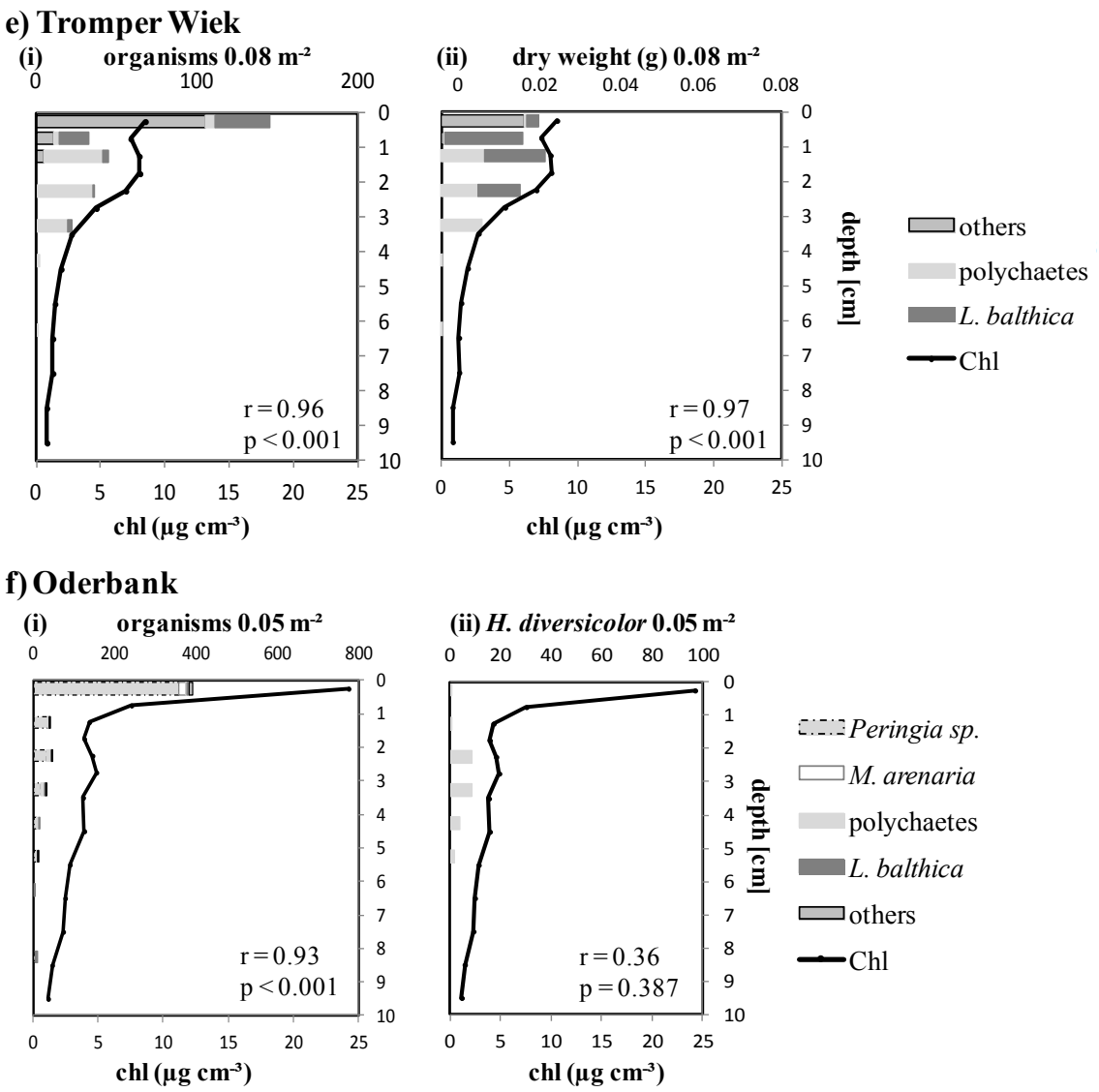


Fig. 16: Chlorophyll depth profiles (lines, LB, MB, ST: n = 24, AB, TW: n = 10, OB: n = 6) and depth distribution of macrozoobenthos at (a) LB, (b) MB, (c) ST, (d) AB, (e) TW, (f) OB. (i) Depth distribution of the sum of macrozoobenthic species found in all cores investigated. (Note abundances found on different spatial scales due to different number of samples investigated: LB, MB, ST: 24 cores; AB and TW: 10 cores; OB: 6 cores. 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. Figure 16 f (ii) presents the depth distribution of the number of *H. diversicolor* to highlight its occurrence within the layer of subsurface maxima of chl. (iii) Depth distribution of bioturbation potential (BP_i) of each species within each depth layer. Results of bivariate correlation between depth distribution of chl and abundance, biomass as well as BP_c are presented with Pearson- or Spearman- correlation coefficients r and p or ρ-values, in Morys et al. (submitted).

Tab. 7: Abundance (ind. m^{-2}), biomass (g m^{-2}), number of species, local sediment mixing D_B, non-local sediment mixing (injection flux J), community bioturbation potential (BP_c) per m^2, most abundant species and the remaining species divided into the following classes: bivalvia, polychaeta, malacostraca, priapulida, gastropoda and asteroidea at each station. All species or classes include their percentages of total abundance/total biomass. Species in bold characters predominate abundance within a taxonomic class, in Morys et al. (submitted).

	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	n.a.
Number of species	13	9	28	13	13	9
D_B (cm^2 d^{-1})	0.02 ± 0.03	0.4 ± 0.8	0.3 ± 0.3	0.2 ± 0.1	n.a.	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
BP_c m^{-2}	104.9	500.8	1297.8	676	n.a.	n.a.
most abundant species	- *K. bidentata* (34.2%/5.3%) - *C. capitata* (24.6%/71.6%) - *D. rathkei* (14.3%/8.8%) - priapulida (14%/7.5%) (*H. spinulosus, P. caudatus*)	- *D. rathkei* (84.9%/0.4%) - *A. islandica* (3.9%/99 %) - *A. alba* (2.6%/0.6 %)	- *K. bidentata* (28.3%/0.1%) - *D. rathkei* (24.9%/0.06%) - *A. alba* (16.7%/0.1%) - *L. balthica* (6.4%/9.1%) - *A. islandica* (1.7%/90.1%)	- *L. balthica* (48%/95.8%) - polychaetes (26.9%/4.1%) - *S. armiger* - *Nephtys* sp. - *Ampharete* sp. - *Phyllodoce mucosa* - *T. multisetosa*	- polychaeta (36.3%/31%) - ***S. armiger*** - *Terebellides stroemi* - *P. elegans* - *Ampharete* sp. - *L. balthica* (20.4%/47.5%)	- *P. ulvae* (85.3%/n.a.)
bivalvia	7.8 % / 2.1 % - *A. alba* - *P. pinnulatum* - *Mytilus edulis* juv.	3.2 % / 0.01 % - *K. bidentata* (juv.)	2.1 % / 0.02 % - *Corbula gibba* - *M. edulis*	2.9 % / 0.03 % - *A. alba* - *Cerastoderma* sp.	5.6 % / 16.6 % - *M. arenaria* - *M. edulis*	9.4% / n.a. - *Cerastoderma* sp. - *L. balthica* - *M. arenaria* - *K. bidentata* - *M. edulis*
polychaeta	4.8 % / 4.6 % - *B. sarsi* - *Eteone longa* - *Phyllodoce* sp.	3.2 % / 0.03 % - *B. sarsi* - *E. longa* - *N. homgergii* - *Paraonis fulgens*	12.5 % / 0.4 % - *Ampharete* sp. - *Aricidea minuta* - *B. sarsi* - Capitellidae - *E. longa* - *Lagis koreni* - *N. figulus* - *N. homgergii* - *Nephtys* sp. - *Phyllodoce* sp. - *D. quadrilobata* - *Polydora* sp. - *S. armiger* - *S. baltica*			5.1% / n.a. - ***H. diversicolor*** - *Marenzelleria neglecta*
priapulida		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	0.3 % / na % - *Microdeutopus gryllotalpa*		0.1 % / n.a. - *Gammarus* sp.	18.2 % / 0.04 % - *D. rathkei* - *Corophium sp.* - amphipoda	20.1 % / 1.5 % - *D. rathkei* - *Pontoporeia femorata* - *Gammarus* sp.	0.2 % / n.a. - *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.	
asteroidea			-0.1 % / 0.03 % - *Asterias rubens*			

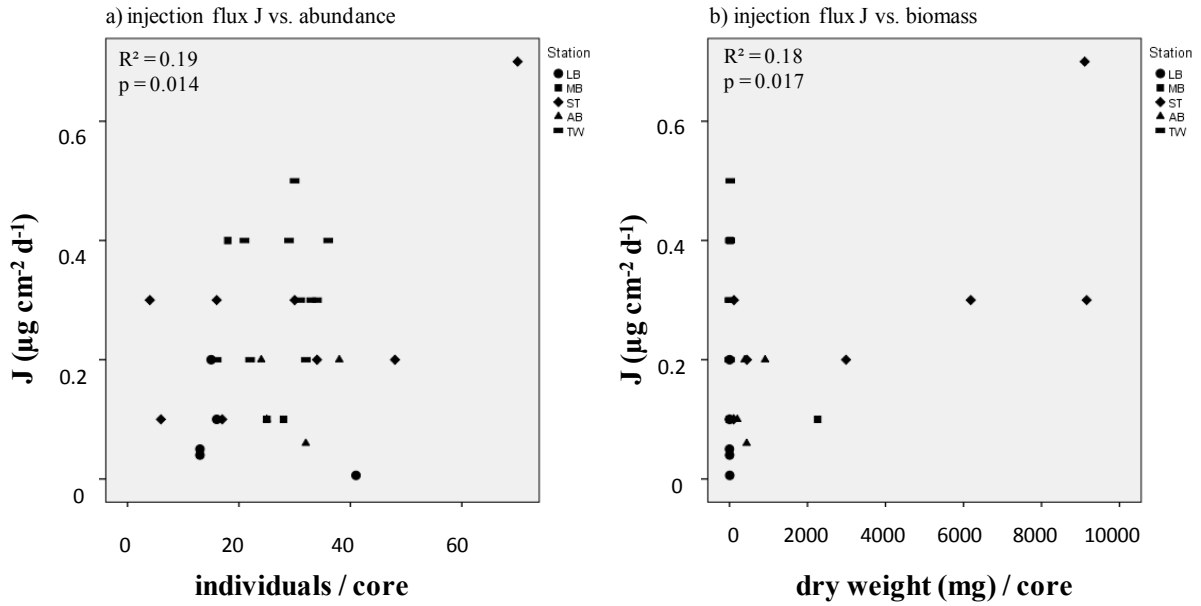


Fig. 17: (a) Linear regression between abundance of macrozoobenthic organisms found per core and non-local sediment mixing (injection flux J (µg cm^{-2} d^{-1})) of the same core at each station. (b) Linear regression between biomass (dry weight (mg)) of macrozoobenthic organisms per core and non-local sediment mixing (injection flux J (µg cm^{2} d^{-1})) of the same core at each station. P-values and values of regression R^2 are given in the upper left hand corner. OB was not considered due to different environmental conditions during sampling (i.e. sedimenting spring bloom). Injection fluxes J are highly dependent on abundance (p = 0.014) and biomass (p = 0.017). No dependency between neither local sediment mixing (p = 0.518 and p = 0.459) nor ingestion rates (p = 0.692 and p = 0.860) and abundance and biomass, respectively, in Morys et al. (submitted).

3.4.4 Depth distribution of functional groups

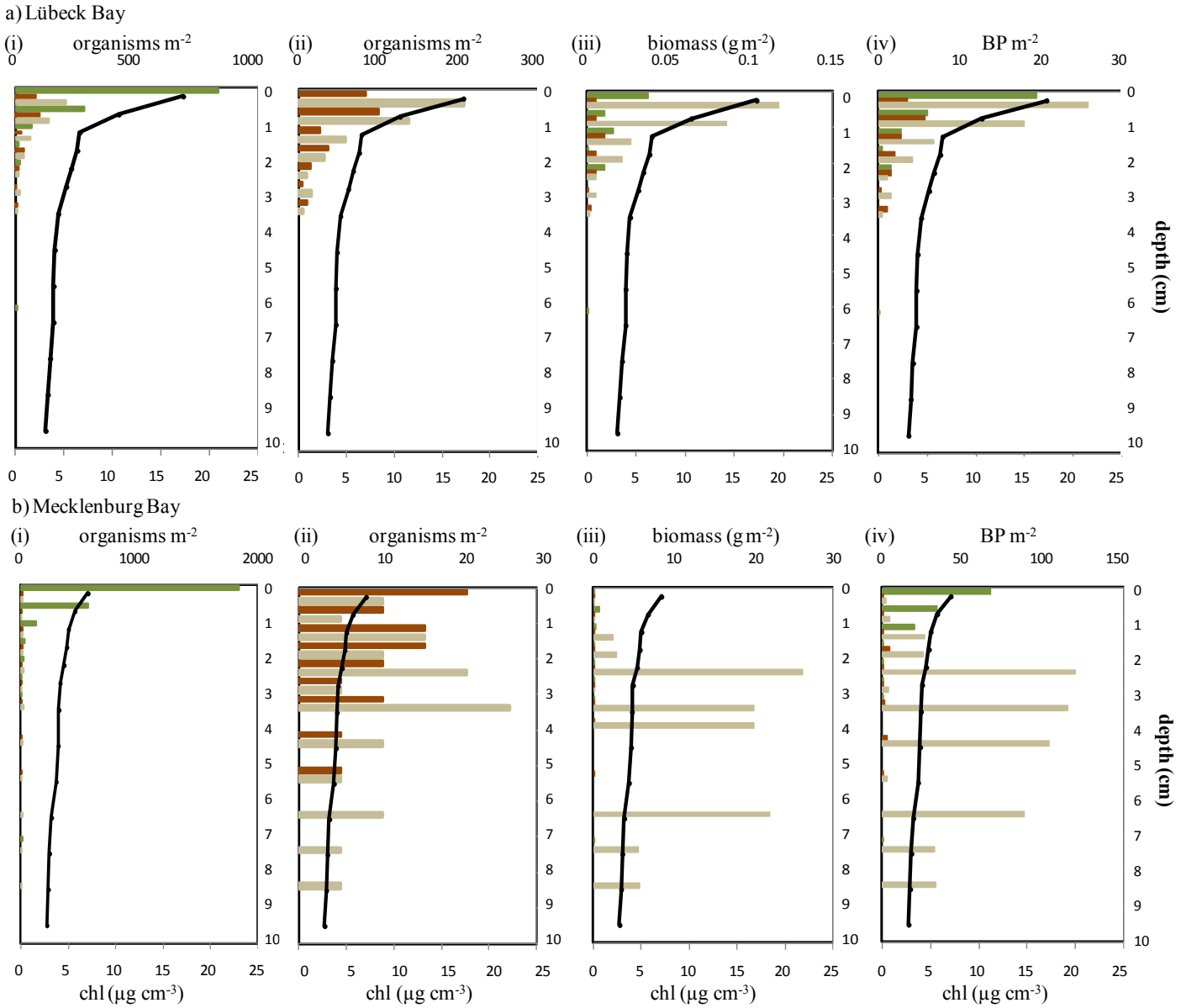
After assigning each species to one of the four categories with regard to its biological life trait (Kristensen et al. 2012) depth distribution of the macrofaunal categories was illustrated (fig. 18). Surfical biodiffusors (SB) are most abundant in the top centimeter of the sediment at all stations and their number decreases exponentially with depth and only a few individuals were found up to a maximum depth of 4 cm. At OB, SB (*Periniga* sp.) were found at 8 cm depth, however, presumably due to uncertainties during slicing of the cores.

The depth distribution of gallery-biodiffusors (GB) and upward/downward conveyors (UC/DC) indicate different patterns across the southwestern Baltic Sea (fig. 18). At LB, abundance of both GB and UC/DC is highest in the top centimeter and decreases exponentially with depth (fig. 18 a (i, ii)). There is no vertical zoning of both macrozoobenthic categories visible. At MB, GB and UC/DC coexist within the first 5 cm of the sediment (fig. 18 b (i, ii)). However, maximum of GB is located within the top 2 cm and of UC/DC directly below between 2 and 4 cm. GB reach their distribution limit at 5 cm and only DC (i.e. *A. islandica*) occur below with a second peak between 6 and 7 cm. GB at ST are mainly located within the first 2 cm but occur parallel to UC/DC down to 7 cm

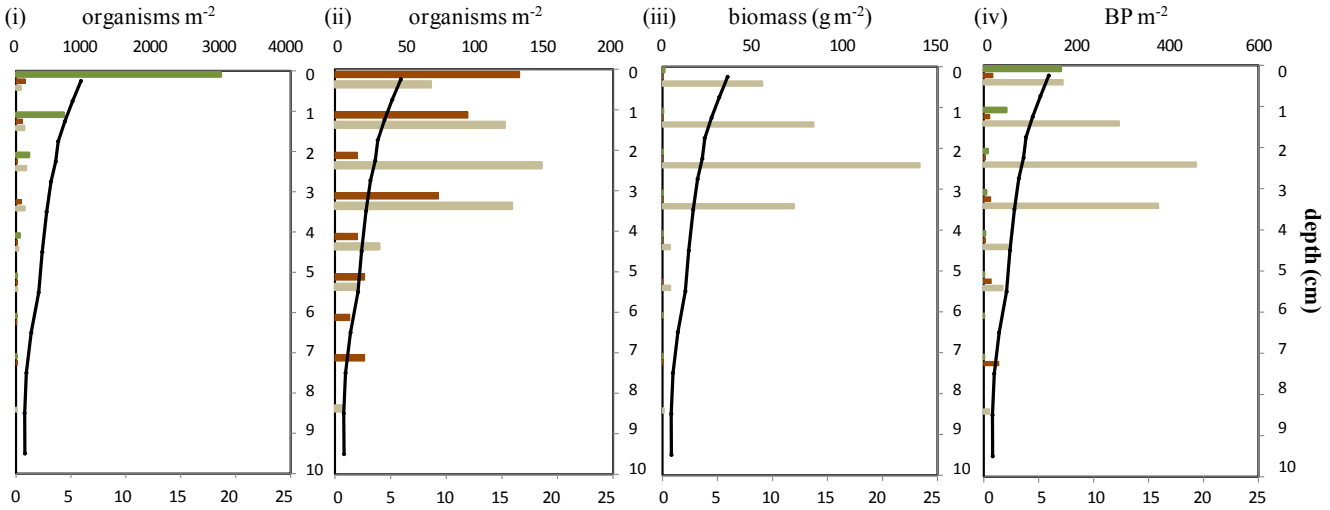
(fig. 18 c (i, ii)). Maximum of UC/DC is between 1 and 4 cm with highest abundance in the depth layer of 2 - 3 cm in which the number of GB decreases rapidly. A second peak of GB was found between 3 and 4 cm depth indicating a coexistence of both macrozoobenthic categories. At AB, maximum of GB is within the same depth layer of 0.5 – 1 cm where mainly juvenile DC (i.e. *L. balthica*) are located (fig. 18 d (i, ii)). GB reach a maximum depth of 4 cm. Adult UC/DC inhabit the sediment between 4 and 8 cm. The less saline stations TW and OB display similar patterns in the depth distribution of GB and DC/UC (fig. 18 e, f (i, ii)). Maximum in UC/DC is found within the top centimeter where mainly juvenile *L. balthica* are located. UC/DC reach their depth distribution limit at 4 cm at TW whereas at OB they were found up to 9 cm (i.e. *L. balthica*). GB inhabit the sediment below the juvenile UC/DC between 1 and 4 cm at TW and 1 and 6 cm (maximum between 2 and 3 cm) at OB. At OB, a small peak in adult UC/DC (i.e. *L. balthica*) can be seen between 3 and 4 cm being directly located below the maximum of GB (fig. 18 f (i, ii)). There is no evidence of vertical zoning of the macrozoobenthic categories at TW (fig. 18 e (i, ii)).

Biomass of the different categories was determined at LB, MB, ST and AB and is mainly constituted by UC/DC at all stations (fig. 18 a – f (iii)). Maxima in biomass are generally confirmed by peaks in abundance of UC/DC. However, at AB maximum of juvenile UC/DC is not visible in the depth distribution of biomass (fig. 18 d (iii)). The depth distribution of BP_i, combining data on abundance and biomass, indicates UC/DC constituting the major part on sediment mixing within the previously described depth horizons (fig. 18 a - d (iii)). Additionally, SB play an important role in particle transport within the top centimeter of the sediment at LB, MB and ST according to BP (fig. 18 a – c (iii)).

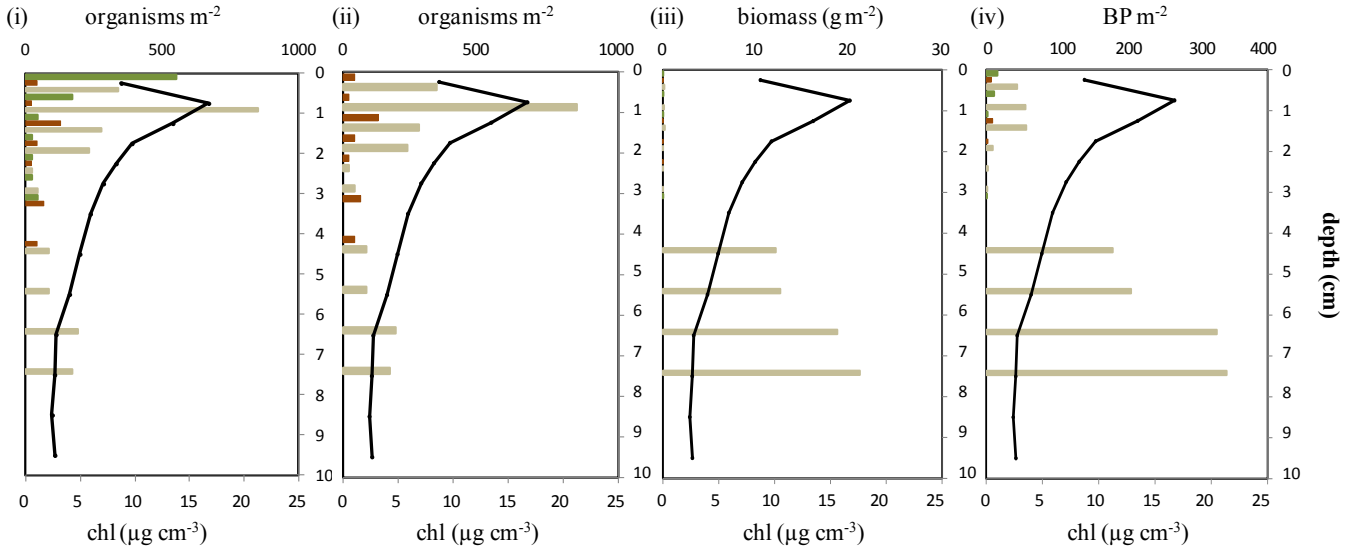
All in all, vertical zoning of the functional groups exist at most stations. At the muddy stations (LB, MB, AB) there are hints of UC/DC inhabiting the sediment 2 – 4 cm deeper than at sandy stations.


a) Lübeck Bay
(i) organisms m-2
(ii) organisms m-2
(iii) biomass (g m-2)
(iv) BP m-2
depth (cm)
b) Mecklenburg Bay
(i) organisms m-2
(ii) organisms m-2
(iii) biomass (g m-2)
(iv) BP m-2
depth (cm)
chl (µg cm-3)
chl (µg cm-3)
chl (µg cm-3)
chl (µg cm-3)

c) Stoltera



d) Arkona Basin



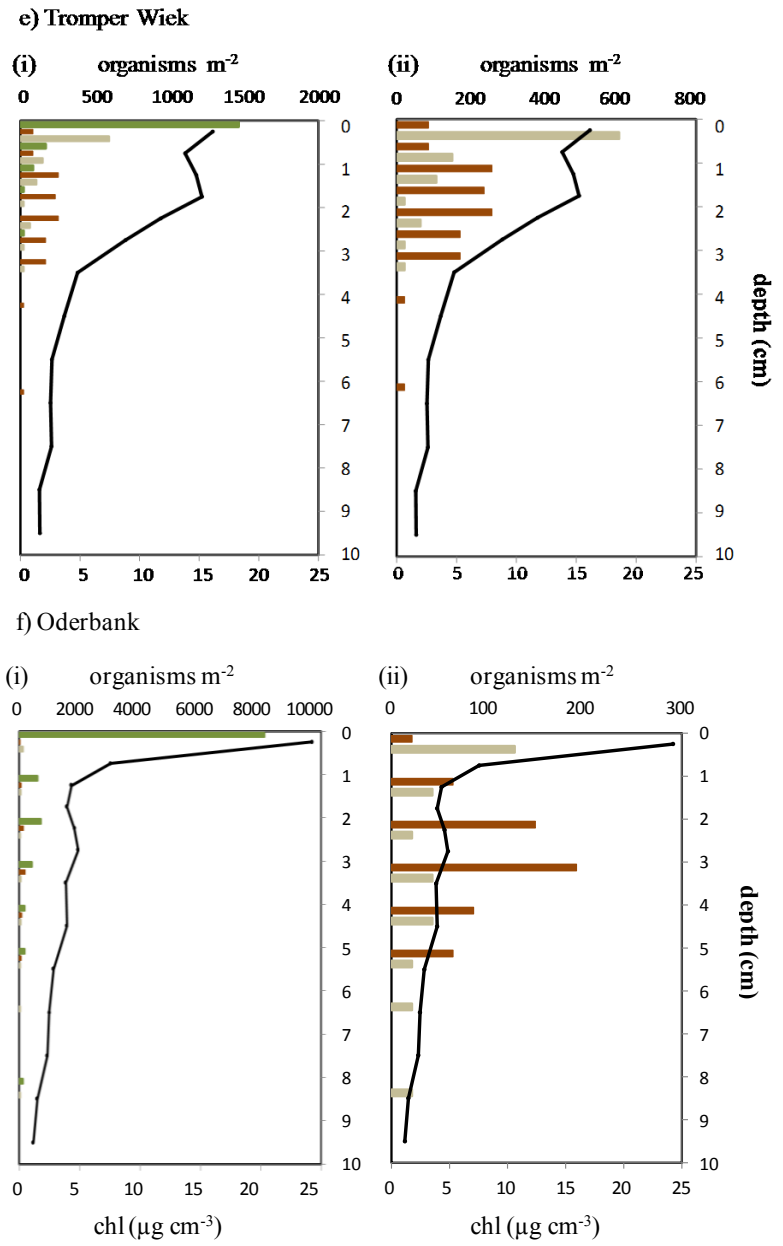


Fig. 18: Chl depth profiles (lines, LB, MB, ST: n = 24; AB, TW: n = 10, OB: n = 6) and depth distribution of macrozoobenthic categories after Kristensen et al. (2012) at (a) LB (n = 24), (b) MB (n = 24), (c) ST (n = 24), (d) AB (n = 6), (e) TW (n = 4), (f) OB (n = 6). (i) Depth distribution species belonging to either surficial biodiffusors, gallery-biodiffusors or upward/downward conveyors per m². (ii) Depth distribution of gallery-biodiffusors and upward/downward conveyors. (iii) Depth distribution of biomass of each macrozoobenthic category given as dry weight (g) of in each layer investigated. Biomass data are not available for TW and OB. (iv) Depth distribution of bioturbation potential (BP_i) of each macrofaunal category within each depth layer.

3.4.5 Biodiversity and eveness

Depth distribution of biodiversity and evenness is presented in figure 19. TW was not considered due to the difficult taxonomic determination of polychaetes. No significant Pearson-correlations was found comparing depth distribution of biodiversity and chl (n = 5 stations; LB, MB, ST: n = 24 cores; AB and OB: n = 6). In contrast, highly significant negative correlations between depth distribution of evenness and chl were found (n = 5 stations; LB, MB, ST: n = 24 cores; AB and OB: n = 6). Evenness increases with decreasing chl concentration, thus, indicating a more homogenous distribution of the organisms with depth or more specifically in areas of low food supply.

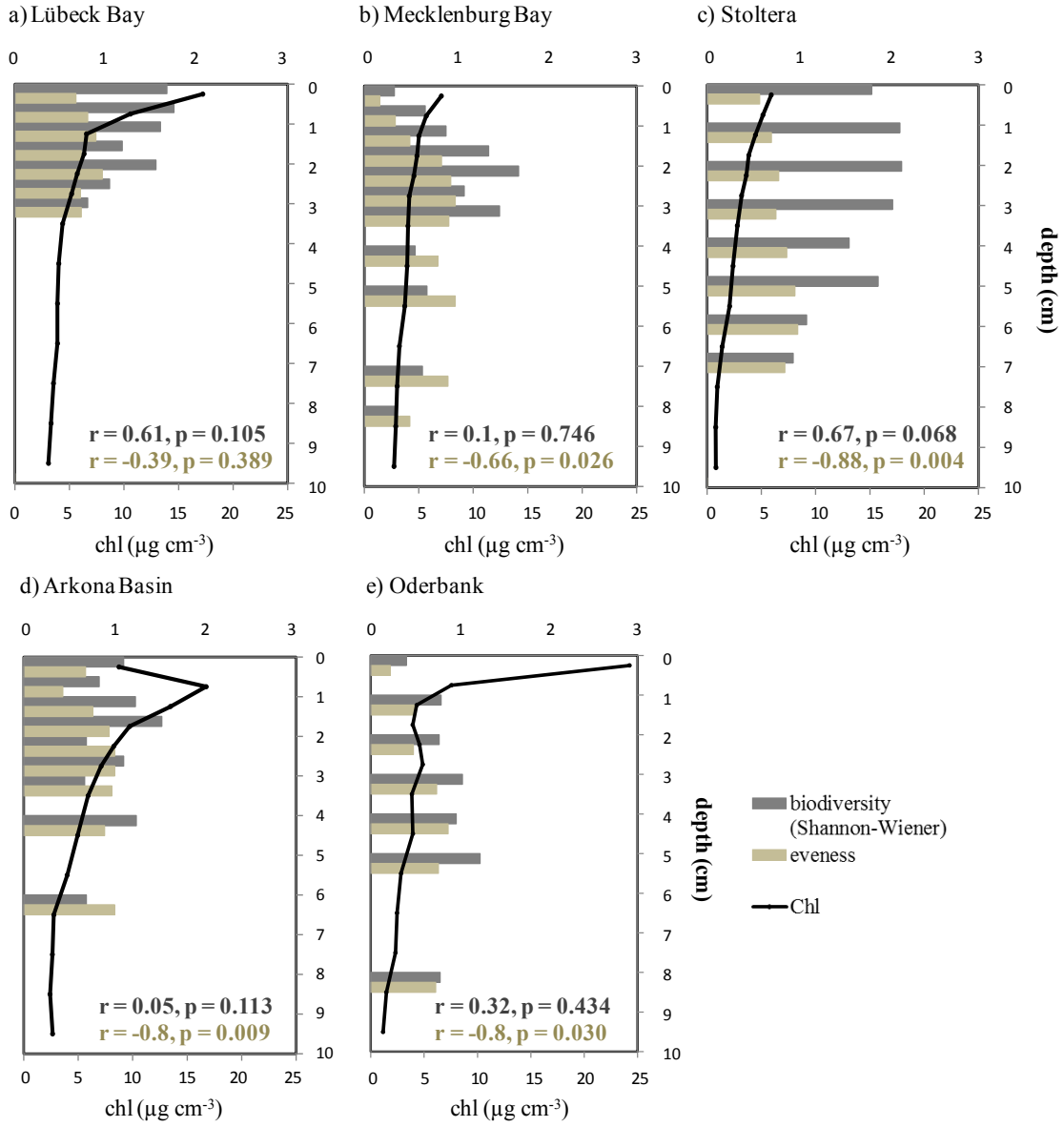


Fig. 19: Depth distribution of biodiversity (grey) and evenness (gold) at: (a) Lübeck Bay, (b) Mecklenburg Bay, (c) Stoltera, (d) Akrona Basin and (e) Oderbank. LB, MB, ST: n = 24 cores; AB and OB: n = 6. Pearson-correlation coefficients r and p-values comparing depth distribution of biodiversity and chl as well as evenness and chl.

3.4.6 Sediment mixing without fauna

Local sediment mixing was detected at S 213 in Bornholm Basin as well as at S 286 in Farö Deep using mean chl profiles of the three cores taken at each station (fig. 20). D_B at Farö Deep was remarkably high with D_B = 9.3 cm² d^{-1} (fig. 20 c) whereas the modeled value at Bornholm Basin was D_B = 0.7 cm² d^{-1} (fig. 20 a). At S 256 in Gotland Basin a subsurface peak in chl and thus non-local sediment mixing (ingestion, r = 17.7 d^{-1}) was indentified (fig. 20 b). Various modes of sediment mixing were found when considering each of the three cores separately. At Bornholm Basin (S 213), two cores indicated local sediment mixing and one displayed an injection flux. At S 256 in Gotland Basin cores indicated local sediment mixing, injection fluxes as well as ingestion rates. Chl profiles at the most northern station (S 286) no mixing was found in two cores and the third one highlighted local mixing.

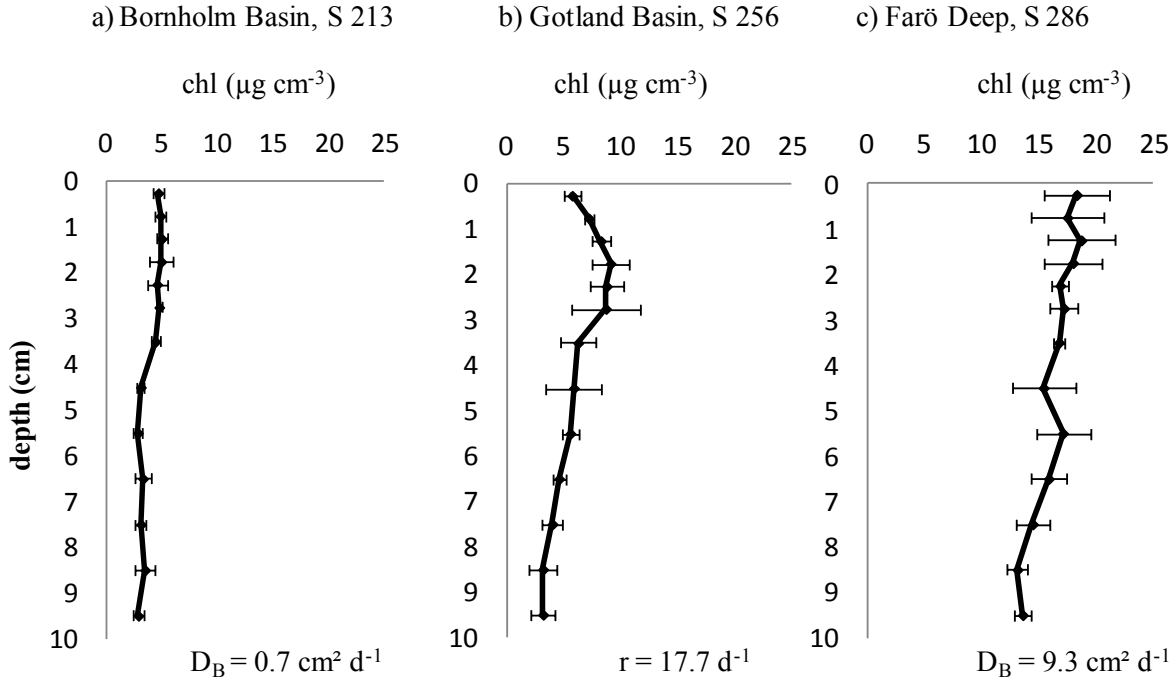


Fig. 20: Mean chl profiles with standard deviation at (a) Bornholm Basin (S 213), (b) Gotland Basin (S 256) and (c) Farö Deep (S 286) (n = 3 cores per station). Biodiffusion coefficient (D_B) and ingestion rate (r) provided by the bio-mixing model by Soetaert et al. (1996) using mean chl profiles.

3.4.7 Anthropogenic effect

All mean chl profiles (n = 3) at the sampling stations of different levels of Hg contamination (n = 3: low, intermediate, high) indicate an exponential decrease with depth

(fig. 21). Local sediment mixing was confirmed by the bio-mixing model by Soetaert et al. (1996). Lowest D_B was determined at the highest contaminated site (D_B = 0.02 cm² d^{-1}) with a factor of 3.5 lower than at the intermediate contaminated station where most intense local sediment mixing (D_B = 0.07 cm² d^{-1}) was found (fig. 21).

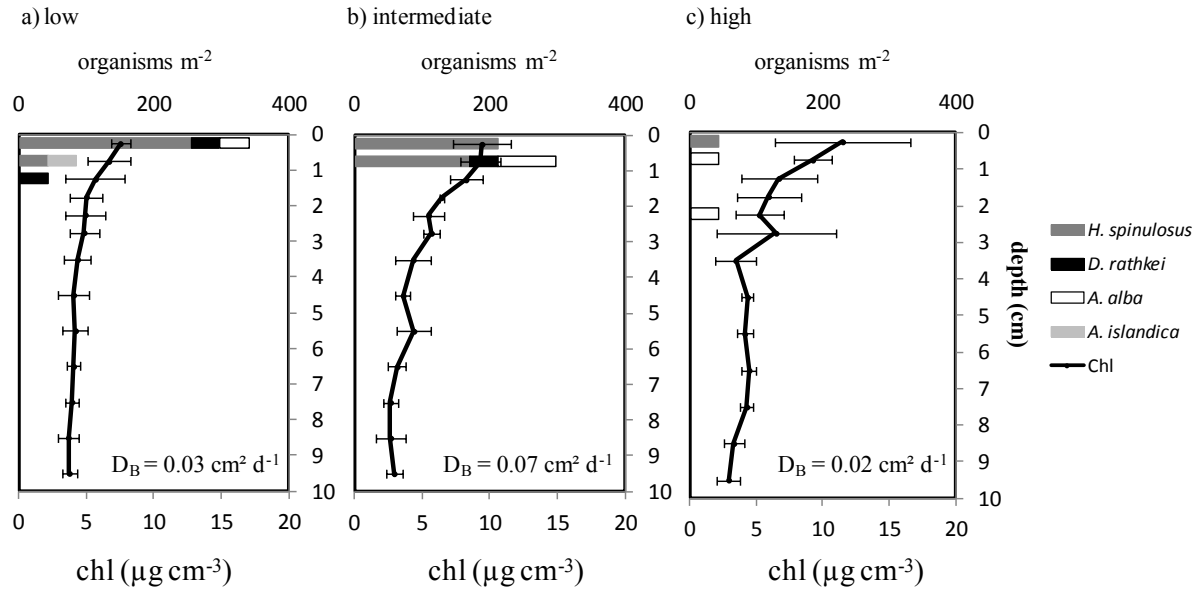


Fig. 21: Mean chl profiles with standard deviation and depth distribution of the sum of macrozoobenthic species found in all cores investigated at each sampling station at LB (a) low (b) intermediate and (c) high contamination (n = 6 cores per station). Biodiffusion coefficient (D_B) provided by the bio-mixing model by Soetaert et al. (1996) using mean chl profiles.

Abundance at the three stations of different levels of contamination (low, intermediate, high) at LB was compared using Kruskal-Wallis test. Results (p = 0.109) indicate no significant differences in abundance between the stations. However, lowest abundance (170 individuals per m²) was found at the highest contaminated site. No difference was found between intermediate (510 individuals per m²) and low contaminated (467 individuals per m²) station. Number of species decreased with increasing level of contamination (low: 4, intermediate: 3, high: 2 species).

The sum of organisms separated into species found in all layers is plotted and results are presented in figure 21 (n = 3 cores per station). At the low contaminated station highest abundance was found in the top half centimeter and the number of organisms decreases exponentially with depth (fig. 21 a). No organisms were found deeper than 1.5 cm. At the intermediate contaminated site organisms were only found within the top centimeter with greater abundance between 0.5 and 1 cm (fig. 21 b). At the high contaminated station one

organism was found in each of the first two half centimeter as well as at 2.5 cm depth (fig. 21 c).

Highest mean bioturbation intensities of local sediment mixing (n is given in table 8) was found at the high contaminated station (mean D_B = 0.2 ± 0.2 cm² d^{-1}) with a factor of 7 higher than at the low contaminated site (mean D_B = 0.03 ± 0.03 cm² d^{-1}) (tab. 8). However, Kruskal-Wallis test presents all stations not to be significantly different from each other with regard to intensity of local sediment mixing. Non-local sediment mixing was only found at the intermediate contaminated site with J = 0.1 µg cm^{-2} d^{-1}.

Tab. 8: Total number of cores investigated, of these: number of cores indicating local and non-local (injection fluxes J) sediment mixing, mean bioturbation intensities of local (D_B) and non-local (J) sediment mixing at the three stations of different levels of Hg contamination in the surface sediment.

	total n	D_B (cm² d^{-1})	n D_B	J (µg cm^{-2} d^{-1})	n J
Low (Hg = 209 µg kg^{-1})	3	0.03 ± 0.03	3		0
Intermediate (Hg ~ 256 µg kg^{-1})	3	0.1 ± 0.1	2	0.1	1
High (Hg ~ 283 µg kg^{-1})	3	0.2 ± 0.2	3		0

Mixing depths are not significantly different between the stations of different levels of Hg contamination according to Kruskal-Wallis test (p = 0.102). However, material was found to not be transported deeper than 3.5 cm at the high contaminated site whereas at the others sediments were mixed up to 7 cm.

3.5 Seasonality of bioturbation

Seasonality within stations

For a general overview of seasonal differences in sediment mixing at the sampling stations chl concentrations of each depth layer (number of cores used per station/season is given in table 1) of the cores taken at each station/season were averaged and bioturbation intensity was determined using the bio-mixing model (Soetaert et al. 1996). Mean modeled results are presented in table 10. Mean tracer profiles indicate different modes of sediment mixing between seasons at all stations and their modeled bioturbation intensities are given in table 9. At LB, sediments are mixed locally in spring, summer and autumn 2014 with increasing intensity (tab. 9). LB is the least mixed station during all seasons compared to the others. In autumn 2015 ingestion rates were found to predominate. At MB, inter-annual differences were determined in spring and autumn 2014 / 2015 indicating both local sediment mixing and injection fluxes to be dominant during the same season. Bioturbation intensities

are also comparably low (tab. 9, 10). Sediments at ST are mainly mixed locally but in winter and summer 2014 the bio-mixing model displays injection fluxes to predominate. Highest local mixing intensities were found in spring 2014 and 2015 ($D_B = 0.4$ cm² d^{-1}) and lowest in autumn 2015 ($D_B = 0.08$ cm² d^{-1}). One of the overall highest injection fluxes was found at ST ($J = 0.6$ µg cm^{-2} d^{-1}) in summer 2014 compared to the other stations and seasons. At Z only two seasons were investigated, however, particles are transported by different modes of mixing during both seasons of comparably intermediate intensities. Non-local sediment mixing is mainly found at AB with highest intensity in winter 2014. In summer and autumn 2014 local transports are dominant displaying intermediate intensities. Seasonal differences at TW show that in spring 2014 and autumn 2015 non-local sediment mixing is dominant while in summer 2014 particles are mainly distributed locally within the sediment. At this station, highest values of local mixing ($D_B = 0.9$ cm² d^{-1}) and ingestion rate ($r = 21.4$ µg d^{-1}) were found. At OB non-local sediment mixing was found to predominate during all seasons with highest intensities in winter 2015 ($J = 0.6$ µg cm^{-2} d^{-1}, highest overall values together with summer 2014 at ST) and lowest in spring 2014 ($J = 0.05$ µg cm^{-2} d^{-1}).

All in all, dominant modes of sediment mixing and bioturbation intensities estimated by mean chl profiles vary between seasons. There is no pattern apparent whether one mode of sediment mixing predominated or whether bioturbation intensities are highest during a certain season.

Tab. 9: Bioturbation intensities: biodiffusion coefficient (D_B = cm² d^{-1}), injection flux (J = µg cm^{-2} d^{-1}) and ingestion rate (r = d^{-1}) provided by the bio-mixing model by Soetaert et al. (1996) using mean chl profiles at each station during each season investigated. Number of cores used for mean chl profiles is given in table 1.

	LB	**MB**	**ST**	**Z**	**AB**	**TW**	**OB**
Summer 2013			$D_B = 0.1$				
Winter 2014			$J = 0.3$				
Spring 2014	$D_B = 0.006$	$D_B = 0.05$	$D_B = 0.4$		$r = 3.9$	$J = 0.3$	$J = 0.05$
Summer 2014	$D_B = 0.009$		$J = 0.6$		$D_B = 0.07$	$D_B = 0.9$	$J = 0.2$
Autumn 2014	$D_B = 0.03$	$J = 0.5$	$D_B = 0.3$	$r = 0.1$	$D_B = 0.2$		$r = 0.2$
Winter 2015			$D_B = 0.2$	$D_B = 0.1$	$J = 0.5$		$J = 0.6$
Spring 2015		$J = 0.09$	$D_B = 0.4$		$J = 0.05$		$J = 0.4$
Autumn 2015	$r = 0.3$	$D_B = 0.03$	$D_B = 0.08$		$r = 1.7$	$r = 21.4$	$J = 0.2$

A comparison of the extent of local and non-local sediment mixing at each station during different seasons indicates some slight seasonal differences (fig. 22). In general, each

station is dominated by the same mode of sediment mixing throughout the sampling campaign: sediments at LB, MB and ST are mainly mixed locally while at AB, TW and OB non-local sediment mixing predominates. The major discrepancy was detected considering TW. This station was found to be the most homogenous area during AL434 cruise with all 24 cores displaying non-local sediment mixing. In summer 2014, however, 100% of the cores taken in the same area indicated local sediment mixing. Furthermore, local sediment mixing was detected in all cores investigated at OB that is usually dominated by non-local sediment mixing. Similarly, MB where local particle transport predominates was found to be mainly mixed non-locally in autumn 2014. However, as no consistent pattern was obvious and due to the reduction of sample size after the first cruise (AL434), there seems to be no significant differences in the extent of local and non-local sediment mixing.

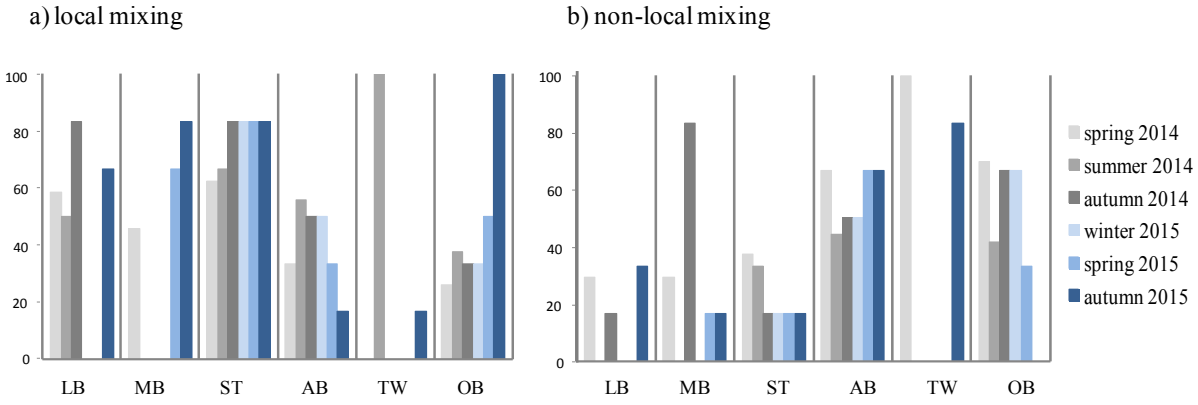


Fig. 22: Bar graph presenting the percentage of (a) local and (b) non-local sediment mixing (both injection flux and ingestion rate) at each station during the different seasons investigated. Number of cores taken at each station/season is given in table 1. Note the almost consistent pattern of decreasing extent of local and increasing extent of non-local sediment mixing from west to east during all seasons.

D_B and J derived from the bio-mixing model (Soetaert et al. 1996) at each station during different seasons were compared for determining seasonality in bioturbation intensities within stations. In figure 23 modeled results are presented with standard deviations for each station and season investigated. Table 10 gives an overview of all mean bioturbation intensities (D_B, J and r) as well as the number of cores displaying no, local and non-local (both injection fluxes and ingestion rates) sediment mixing. Kruskal-Wallis and its post-hoc tests were carried out for determining significant seasonal differences in mixing intensities as well as surface chl concentrations at each station (number of data used for each statistical test is summarized in table 10). No sediment mixing (D_B = 0) was excluded from all statistical

analyzes. Ingestion rates (r) were not considered because of their infrequent occurrence (tab. 10).

At LB, local sediment mixing ($p = 0.565$) and injection fluxes ($p = 0.795$) are not significantly different between seasons (fig. 23 a). However, as shown in figure 23 a highest D_B-values were found in autumn 2014 with lowest mean surface chl concentrations at the same time despite that fact of no significant differences in surface chl concentration ($p = 0.066$). At MB, Kruskal-Wallis tests presents no seasonality in local ($p = 0.211$), non-local ($p = 0.247$) sediment mixing and surface chl concentration ($p = 0.078$). Despite this finding, highest D_B-values were again found with simultaneously lowest mean surface chl concentration (spring 2014) (fig. 23 b). Local sediment mixing is significantly different between seasons at ST ($p = 0.001$) and Kruskal-Wallis post hoc test indicates summer 2013 to be different. In summer 2013, ST is characterized by comparably high surface chl concentration (fig. 23 c) that is confirmed by a separate subset according to Kruskal-Walli post hoc test ($p < 0.001$). In fact, lowest local mixing intensities were also found at ST with highest surface chl concentration. Injection fluxes are not significantly different between seasons ($p = 0.730$). At AB, significant differences in D_B were found between summer and winter ($p = 0.040$). Lowest local mixing intensities were found in spring and summer 2014 in which surface chl concentration was highest (confirmed by Kruskal-Wallis post hoc test, $p < 0.001$) (fig. 23 d). Kruskal-Wallis post hoc test displays injection fluxes to be different from the other seasons in spring 2014 ($p = 0.021$). Local sediment mixing and surface chl concentrations are not significantly different between seasons at TW ($p = 0.727$ and 0.223, respectively) but injection fluxes differ between spring 2014 and autumn 2015 ($p = 0.001$) (fig. 23 e). No seasonality was found at OB, however, local mixing was found to be different in spring 2014 ($p = 0.002$). As shown in figure 23 f, surface chl concentration is remarkably high compared to the other seasons in spring 2014. This finding was confirmed by Kruskal-Wallis post hoc test comparing surface chl concentrations during the different seasons ($p = 0.014$). Here again, lowest D_B was found during seasons with highest surface chl concentrations. Injection fluxes are not significantly different between seasons ($p = 0.574$).

All in all, no general pattern of seasonality in bioturbation intensities of both local and non-local sediment mixing was found. However, local mixing intensities (D_B) seem to depend on surface chl concentrations.

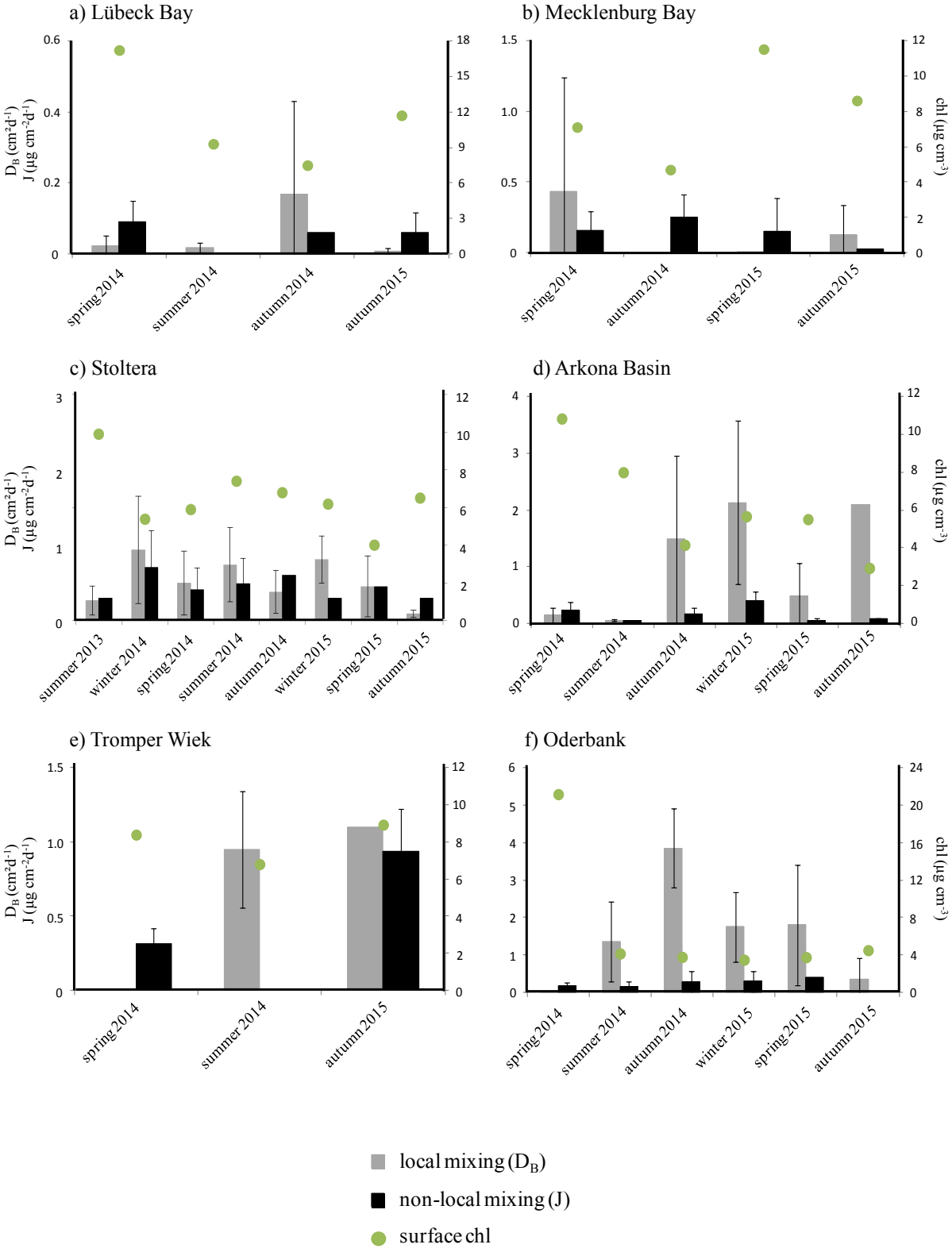


Fig. 23: Bar diagram presenting bioturbation intensities of local (grey) and non-local (black) sediment mixing (injection fluxes J) with standard deviation during the different seasons investigated at (a) Lübeck Bay, (b) Mecklenburg Bay, (c) Stoltera, (d) Arkona Basin, (e) Tromper Wiek and (f) Oderbank. Mean surface chl concentrations are displayed by the green dots. Numbers of data are given in table 10.

Tab. 10: Total number of cores investigated, of these: number of cores indicating no, local and non-local (both injection fluxes and ingestion rates) sediment mixing, mean bioturbation intensities of local (D_B) and non-local (J, r) sediment mixing at each station of investment during the different seasons investigated, data estimated in spring 2014 can be found in Morys et al. (submitted).

Season	Stat.	n total	D_B ($cm^2\ d^{-1}$)	n D_B	J ($\mu g\ cm^{-2}\ d^{-1}$)	n J	r (d^{-1})	n r	n no sediment mixing
Summer 2013	ST	24	0.2 ± 0.1	21	0.2	2	1.2	1	0
Winter 2014	ST	24	0.6 ± 0.5	14	0.5 ± 0.3	10		0	0
Spring 2014	LB	24	0.02 ± 0.03	14	0.09 ± 0.06	6	2	1	3
	MB	24	0.4 ± 0.8	11	0.2 ± 0.1	5	0.06 ± 0.06	2	6
	ST	24	0.3 ± 0.3	15	0.3 ± 0.2	8	0.3	1	0
	AB	24	0.2 ± 0.1	8	0.3 ± 0.1	10	1670 ± 4080	6	0
	TW	24		0	0.3 ± 0.1	24		0	0
	OB	23	0.005 ± 0.003	6	0.2 ± 0.09	15	8	1	1
Summer 2014	LB	6	0.02 ± 0.01	3		0		0	3
	ST	24	0.5 ± 0.3	16	0.3 ± 0.2	7	52.3	1	0
	AB	9	0.06 ± 0.02	5	0.05	1	8.5 ± 13.3	3	0
	OB	24	1.4 ± 1.1	9	0.2 ± 0.1	11	4.1 ± 6.3	3	1
	TW	9	0.9 ± 0.4	9		0		0	0
Autumn 2014	LB	6	0.2 ± 0.3	5	0.06	1		0	0
	MB	6		0	0.3 ± 0.2	5		0	1
	ST	6	0.3 ± 0.2	5	0.4	1		0	0
	Z	6	0.3 ± 0.2	4	0.2	1	0.5	1	0
	AB	6	1.5 ± 1.5	3	0.2 ± 0.1	3		0	0
	OB	6	3.9 ± 1.1	2	0.3 ± 0.3	3	0.2	1	0
Winter 2015	ST	6	0.5 ± 0.2	5	0.2	1		0	0
	Z	6	0.3 ± 0.4	3	0.2 ± 0.1	3		0	0
	AB	6	2.1 ± 1.4	3	0.4 ± 0.2	3		0	0
	OB	6	1.8 ± 0.9	2	0.3 ± 0.3	2	1 ± 0.6	2	0
Spring 2015	MB	6	0.001	1	0.2 ± 0.2	4		0	1
	ST	6	0.3 ± 0.3	5	0.3	1		0	0
	AB	6	0.5 ± 0.6	2	0.06 ± 0.04	4		0	0
	OB	6	1.8 ± 1.6	3	0.4	1	0.8	1	1
Autumn 2015	LB	6	0.01 ± 0.008	4	0.06 ± 0.06	2		0	0
	MB	6	0.1 ± 0.2	5	0.03	1		0	0
	ST	6	0.06 ± 0.03	5	0.2	1		0	0
	AB	6	2.1	1	0.1 ± 0.01	2	1.2 ± 2.2	2	1
	OB	6	0.4 ± 0.6	6		0		0	0
	TW	6	1.1	1	0.9 ± 0.3	3	19.8 ± 0.8	2	0

Kruskal-Wallis and its post hoc test were carried out to determine seasonal differences in mixing depths at each station. Number of cores used for each statistical test is given

in table 1. Results indicate no significantly differences between seasons at LB ($p = 0.062$, $z_m = 4.6 \pm 2.1$ cm) and MB ($p = 0.286$, $z_m = 6.5 \pm 2.3$ cm). Significant seasonal differences in mixing depths were found at ST ($p = 0.014$) with lowest mixing depths in both summers 2013 and 2014 ($z_m = 6.6 \pm 1.0$ cm) and particulate material being transported deepest in spring 2014 ($z_m = 7.4 \pm 0.6$ cm). Mixing depths during the remaining seasons are not significantly different with $z_m = 7.0 \pm 0.8$ cm. Kruskal-Wallis and its post hoc test presented significant differences at AB between spring 2014/autumn2015 (= homogenous subset according to Kruskal-Wallis post hoc test) and winter 2015 ($p = 0.034$). Lowest mixing depths were estimated in spring 2014 and autumn 2015 with $z_m = 5.5 \pm 1.1$ cm while highest mixing depths were reached in winter 2015 with $z_m = 6.6 \pm 0.6$ cm. During the remaining seasons sediments are mixed down to 6.3 ± 0.6 cm. At OB mixing depths were found to be different in spring 2014 ($p = 0.001$, $z_m = 4.9 \pm 2.0$ cm) while material is transported 2 cm deeper during the remaining seasons with $z_m = 6.7 \pm 1.5$ cm. Mixing depths are significantly different between all seasons investigated ($p < 0.000$) and vary between $z_m = 5.5 \pm 1.2$ cm (spring 2014) and $z_m = 7.2 \pm 0.7$ cm (summer 2014).

All in all, no general patterns of seasonal variability of mixing depths were found at the stations of investment. Mean mixing depths vary up to 2 cm between seasons (except at LB and MB where no significant differences were found).

Seasonality between stations

Non-local sediment mixing increases from west to east almost throughout the sampling campaign (fig. 22). A few discrepancies at some stations have already been described. In general, these findings confirm the patterns derived from 24 cores at each station during spring 2014 describing variability of bioturbation along the coast of the southwestern Baltic Sea.

Kruskal-Wallis and its post hoc tests comparing D_B and J between stations during different seasons (numbers of cores used for the statistical test are given in table 10) present intensities of both local and non-local sediment mixing being different between stations during different seasons (tab. 11). No sediment mixing ($D_B = 0$) was excluded from all statistical analyzes. Ingestion rates r were not considered because of their infrequent occurrence (tab. 10). The findings of seasonal differences between stations with regard to mixing intensities during spring 2014 (AL434) presenting LB and OB as low and MB, ST and AB as intermediate locally mixed stations as well as LB as low; MB, ST, AB and OB as intermediate and TW as high non-locally mixed stations were partly confirmed during the

following seasons. Results of modeled values of D_B and J are given in table 10 and have previously been described. Table 11 presents the assignment of stations to low, intermediate and high intensities of local (D_B) and non-local sediment mixing (with regard to injection fluxes J). This assignment is primarily based on Kruskal-Wallis results. However, in cases of no significant differences considering single bioturbation intensitie some cores at TW and OB were often found with noticeable high bioturbation intensities despite no statistical differences compared to the other stations which were then assigned to stations of high intensities.

Comparing D_B, LB was found to be the station with lowest mixing intensities throughout all seasons. However, Kruskal-Wallis test indicated no significant differences between stations during some seasons (i.e. autumn 2014, winter and spring 2015, tab. 11). Sediments at MB were found to be mixed of intermediate intensity while ST, AB and OB indicate various intensities of local sediment mixing between seasons. All in all, no general pattern of significant differences in bioturbation intensity was found throughout the sampling campaign.

Non-local sediment mixing is not significantly different between stations during most seasons (except spring and summer 2014, tab. 11). However, in autumn 2014 and 2015 remarkably high injection fluxes were derived from the bio-mixing model at OB and TW, respectively. For that reason, non-local sediment mixing at OB is considered to be highly intensively in autumn 2014 and at TW in autumn 2015. These findings result in more intense non-local sediment mixing at stations in the east.

Tab. 11: Results of Kruskal-Wallis and its post-hoc (p-values) test comparing intensities of local (D_B) and non local (injection flux) sediment mixing between seasons at the stations of investment. Stations are assigned to low, intermediate and high intensities of local as well as non-local sediment mixing on the basis of D_B and J-values as well as results of Kruskal-Wallis. *Assignment of stations despite no statistical differences compared to the other stations on the basis of some cores indicating remarkably high bioturbation intensities.

season	**p-value**		**low**		**inter-mediate**		**high**	
	local	non-local	local	non-local	local	non-local	local	non-local
spring 2014	< 0.001	< 0.001	LB OB	LB	MB ST AB	MB ST AB OB		TW
summer 2014	< 0.001	0.046	LB AB	AB OB	ST	ST	OB TW	
autumn 2014	0.083	0.650					OB	OB*
winter 2015	0.118	0.486					OB*	
spring 2015	0.377	0.463					OB*	
autumn 2015	0.011	0.146	LB		MB		ST AB OB	TW*

Kruskal-Wallis tests were carried out to determine seasonal differences in mixing depths between stations (number of data used for each test are given in table 1). The findings of AL434 cruise in spring 2014 with ST and MB displaying higher mixing depths were not confirmed during the following seasons. However, mixing depths are significantly different between stations during most seasons. In summer 2014 ($p = 0.001$) and autumn 2014 ($p = 0.022$) lowest mixing depths were found at LB with z_m of 2.6 ± 1.7 cm indicating transport of particulate matter 4 cm deeper than at the remaining stations (z_m = 6.7 ± 1.1 cm) and with z_m of 4.3 ± 1.4 cm being 2 cm deeper (z_m = 6.7 ± 0.8 cm). In winter 2015 ($p = 0.119$) no significant differences were found between ST, AB and OB as well as in spring 2015 ($p = 0.261$) between MB, ST, AB and OB. In autumn 2015 Kruskal-Wallis results ($p = 0.009$) present sediments at ST and TW with z_m of 6.9 ± 0.9 cm to be mixed deeper than at the remaining stations (z_m = 5.5 ± 1.0 cm).

All in all, no general pattern is visible at which station along the coast of the southwestern Baltic Sea sediments are mixed deepest.

4. Discussion

4.1 Evaluation of the chosen methods

4.1.1 Chlorophyll as a tracer [1]

Chl is the main photosynthetic pigment of plants in both terrestrial and marine environments. It has been recognized as a suitable indicator of phytoplankton's biomass (Jeffrey & Mantoura 1997). Phytoplankton is the basis of all animal production in the open sea being fundamental for the world's fishery. Growth of zooplankton and food webs in general are supported by phytoplankton. Chl is deposited at the sea floor in senescent or dead phytoplankton where it serves as food resources for macrozoobenthic organisms (Lasker 1975). Here, chl becomes a suitable indicator for the presence and quality of food patricles and, therefore, is a limiting factor of bioturbation activities associated with foraging.

Methods for measuring chl have a long history and various techniques have been developed. Based on the Mackinney (1941) values, Arnon in 1949 and Richards & Thompson in 1952 published first equations for the spectroscopic determinations of chl *a* and *b*. These are classic methods in marine science up to the present day, notwithstanding the technical developments and important advantages. In 1965, Holm-Hansen et al. determined chl *a* fluorometrically which was fifty times more sensitive than previous methods. Knowing that chl degradation products from senescent phytoplankton and detritus, which absorb at the same wavelength spectrum as chl *a*, overestimate "true" chl values (Wasmund 1984), lead to the introduction of an acidification step to both the spectroscopic (Lorenzen 1967, Marker 1972) and fluorometric (Holm-Hansen et al. 1965) methods. In an acidic medium, the chl molecule loses its central magnesium atom decreasing the height of its absorption maximum (Wasmund 1984). Degradation products are phaeophytin and phaeophorbid, both belonging to the term "phaeopigments" as they do not differ in spectrophotometric analyses. Another degradation product is chlorophyllid which is also similar spectrophotometrically to chl (Wasmund 1984). Thin-layer chromatography allowed the separation and quantification of phytoplankton chlorophylls, carotenoids and their breakdown products (Jeffrey 1968, 1974, 1976) as well as the determination of phytoplankton taxa (Jeffrey 1974, Hallegraeff 1981, Jeffrey & Hellegraeff 1987). The application of automated performance liquid chromatography methods also allowed the separation of chlorophylls and their breakdown products (Gieskes & Kraay 1983, 1986,

Mantoura & Llewellyn 1983, Wright & Shearer 1984, Roy 1987, Zapata et al. 1987). The International Council for Science SCOR (Scientific Committee on Oceanic Research) evaluated the spectrophotometric and fluorometric methods in 1978 in Sydney. It was found that the last two mentioned methods are appropriate for a precise knowledge of pigment composition.

Chl in sediments could be analyzed by an acidification technique, since degradation products from senescent cells, detritus and faecal pellets can be expected (Lorenzen & Jeffrey 1980). However, environmental studies often require large amounts of measurements. As long as biomass estimations are the ultimate aim, analytical error may be outweighed by other uncertainties (Lehman 1981). Photometric/fluorometric methods are simple, faster and more convenient as they offer suitable results for the purpose of the present study: the determination of vertical chl profiles in sediments without the need of information of exact quantities of the pigments. Therefore, the photometric and fluorometric methods were the only ones considered.

Results of comparing photometric and fluorometric methods displayed both similar depth distributions of chl in the sediment and a significant Spearman-correlation of chl concentrations using the same sample and applying both techniques was obtained. Therefore, the photometric method was confidently chosen as the basis of chl measurements in this study. However, chl concentrations estimated by the fluorometric method are lower resulting in lower modeled bioturbation intensities. As the main aim of this study is the evaluation and determination of variability of bioturbation at 7 stations along the coast of the southwestern Baltic Sea a high number of replicates were analyzed as well as a fast and simple method was needed. The photometric approach was found to be most convenient and was applied for all samples. The differences in modeled bioturbation intensities have to be kept in mind when comparing them with other coastal areas.

The comparison of monochromatic and trichromatic photometric method indicated remarkably similar results leading to a confident rejection of chl measurements using three wavelengths.

Degradation of chl [1]

The minor temperature dependency of chl degradation in the experiments of the present study supports its use as a first order decay constant (k_D) in the bio-mixing model by Soetaert et al. (1996) which was developed for tracers with radioactive decay. In a biological

context, this decay kinetics implies that the velocity of decomposition is only dependent on the available chl in the organic matter stored in the sediment.[1]

The initial increase of chl during incubation in muddy sediments (all seasons investigated) and sand (winter) cannot be explained. Speculatively, the initial values should be higher than measured. Sun et al. (1991) defined two 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 days consists of two steps: chl *a* is firstly released from a bound state, and secondly the released chl *a* 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, also in the present study, the chl concentration after 5 days of incubation is at least equal to the immediately deep-frozen initial value. Sun et al. (1991) also found an initial increase of chl *a* in muddy sediments of Long Island Sound when treating the samples without deep-freezing. In contrast highest values in the present study were found after 5 days besides deep-freezing fresh sediment after retrieval. For that reason, there seems to be an additional biological process releasing chl when the sediment becomes anoxic. 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 the sediments investigated in this study (see Bianchi & Findlay 1991).[1]

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) and 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 assumption that degradation of chl may depend on the present temperature of the surrounding water (season) rather than on temperature during incubation was rejected in this study. Degradation of chl in sediments along the coast of the southwestern Baltic Sea is independent from the temperature during the decay process as well as from seasonal variability of water temperature. It was proved that chl decays following first order kinetics.[1]

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 (k_D = 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 allows to distinguish between different chl species or derivatives (Meyns et al. 1994). In this 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 this method was chosen for the basis of this study, it was necessary to use the same analysis for estimating k_D.[1]

4.1.2 MUC as a sampling device [2]

The multicorer (MUC) was deliberately chosen in this study to obtain high-resolution depth distributions of macrobenthos and their comparison with chl profiles. Zwicker (2014) compared macrofaunal communities at LB and MB estimated by the 24 cores used in the present study and by three van Veen grabs on the same cruise/stations. Macrobentic communities estimated by the two methods were slightly different due to various differences during sampling. Firstly, abundances of certain species differ because MUC samples were sieved through a 500 µm mesh and grab samples through 1 mm. As a result small species (e.g. *P. caudatus*) or juvenile stages (i.e. *K. bidentata*) were retained. Secondly, abundances of some polychaetes are higher in the grabs due to the 13 times greater area covered capturing patches. Thirdly, infrequently occurring bivalves, e.g. *A. islandica* and *L. balthica* were not captured in the cores at LB. Additionally, MUC samples presented higher abundances of *D. rathkei* because this device captures the cumacea as soon as it hits the sediment surface whereas this mobile species may escape when the grabs are veered causing bow waves. Despite the differences obtained by a MUC in contrast to grabs generally used in monitoring programs, data in such a detail derived in this study were necessary for the determination of main bioturbators. High-resolution depth profiles would not be given by a grab due to destruction of the sediment’s vertical zoning. These findings are helpful for understanding different patterns in sediment mixing (i.e. distribution of local/non-local transports, seasonal effects) in various sediment types in the southwestern Baltic Sea.

4.1.3 Bio-mixing model

The major result of the present study is the successful explanation of the various bioturbation patterns along the coast of the southwestern Baltic Sea by the macrofaunal compositions and more important by their depth distribution. On the basis of the evidence for highly significant relationships between sediment mixing and macrofauna it can be assumed that no sediment mixing will be found in areas without macrofauna. However, cores at two of the overall three stations in Bornholm and Gotland Basin investigated for determining

bioturbation without macrofauna indicated subsurface maxima in chl displaying non-local sediment mixing. Only the northernmost station was characterized by mainly no sediment mixing. This station, in turn, was the only one where the water from the major inflow event had not arrived. During this event 320 km^3 of water entered the Baltic Sea transporting 3.98 Gt salt in total (Naumann et al. submitted). The current reached a velocity of up to 20 cm s^{-1} (Naumann per. comm.). Such currents most likely explain the presence of mixed sediments within areas of no macrofauna as they lead to resuspension of particles (Sanford 2008). Resuspension events erode and mix surface sediments which is then redeposited and buried. As resuspension events are faster than sedimentation rates particles are likely to be resuspended and redeposited many times before they are finally buried (Sanford 1992).

It becomes apparent that modeled sediment mixing may in some cases present a combination of particle transport induced by macrofauna and by hydrodynamic conditions eroding, depositing and burying particulate matter. However, the highly significant correlations between the particle tracer chl and macrofauna depth profiles derived in the present study indicate a very strong dependency between both estimates. On the basis of these findings it can be suggested that macrofaunal organisms actively move to horizons of high food supply rather than being responsible for the depth distribution of food itself. However, using the example of Mecklenburg Bay, about 70% of the cores displayed highest chl concentrations at the sediment surface with an exponential decrease of the tracer. These characteristics were found despite the fact of resuspension taking place at bottom current velocities greater than 40 mm s^{-1} which frequently occur in the area as a result of the density-driven horizontal component of advective water transport along the bottom (Springer as cited in Kersten et al. 1998). One would assume more subsurface peaks (i.e. non-local transports) at Mecklenburg Bay if currents were the driving factor of sediment mixing.

All in all, hydrodynamic-driven resuspension clearly influences modeled results on sediment mixing and its extent remains uncertain. However, the present study gives evidence for macrofauna playing the major part on existing bioturbation patterns in the German part of the southwestern Baltic Sea.

4.1.4 Modeled bioturbation vs. bioturbation potential [2]

Depth distribution of BP_i within the sediment showed similar patterns as biomass' depth distribution (fig. 16 a – d (iii)). This indicates the strong impact of biomass rather than abundance in the index used. At ST, for example, *L. balthica* (9%) accounts much less than

A. islandica (90%) of total biomass. The fact that BP_i, which by including abundance accentuates the effect of *L. balthica* relative to *A. islandica* (fig. 16 c (iii)) provides a better correlation than biomass indicates that for this species including abundance into BP is particularly important. Additionally, BP_i highlights well layers of intense mixing confirming the chl depth distributions (fig. 16 a – d (iii)). However, MB and AB are examples of poor fit of BP versus chl indicating that here the index combining abundance and biomass cannot mirror tracer distribution as closely as abundance alone. Significant correlations between depth distribution of chl and BP_i were only found at two stations (LB, ST, fig. 16 a, c (iii)). However, the metric BP_i indicated non-local transports by subsurface maxima that match the modeled injection depths.[2]

Spearman-correlations between BP_c per core and the modeled injection fluxes J as well as D_B were significant (fig. 24 a, b) whereas there was no correlation with ingestion rates r. Keeping in mind that the bio-mixing model (Soeatert et al. 1996) and BP_c are two vastly different approaches for quantifying sediment mixing, data in the present study indicate that BP_c is a suitable metric for both local and non-local sediment mixing, but conversely, the index may not distinguish between local and non-local sediment mixing resulting in the loss of important information that were obtained in this study.[2]

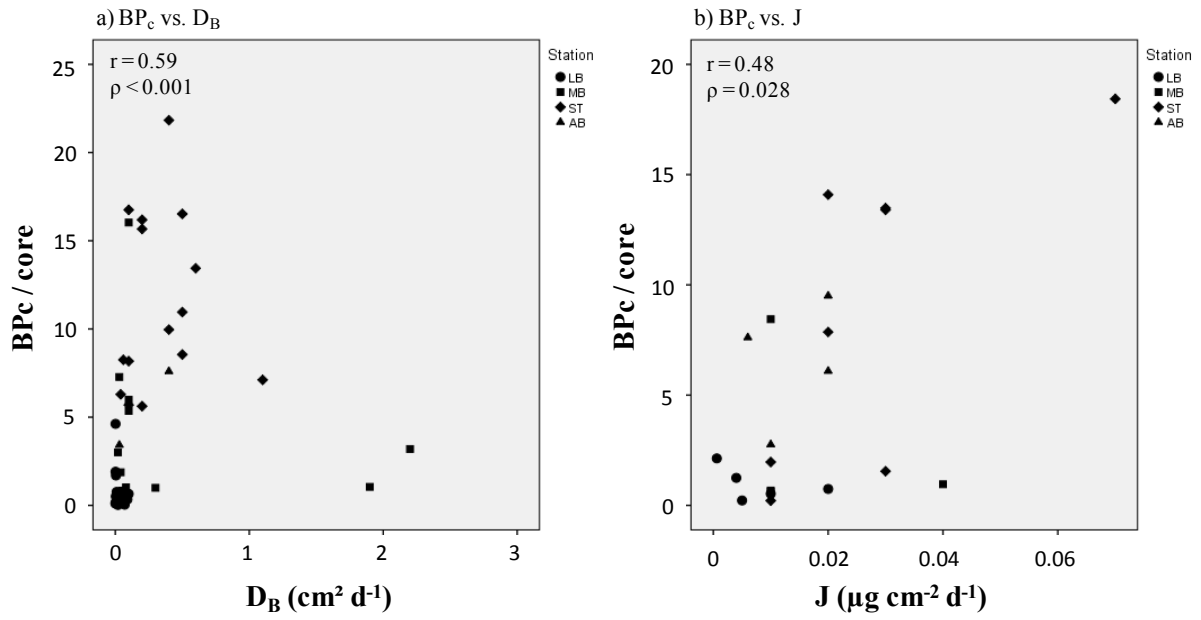


Fig. 24: (a) Spearman correlation (with r and ρ-values) between D_B and BP_c estimated from the same cores (b) Spearman correlation (with r and ρ-values) between J and BP_c. Note that no sediment mixing (D_B = 0) was excluded from all statistical analyses. No significant correlation between ingestion rate r and BP_c (r = -0.21 and ρ = 0.610), in Morys et al. (submitted).

Gogina et al. (submitted) correlated BP_c derived from the same stations/seasons with modeled bioturbation intensities of the present study. Highly significant correlations were found between BP_c and D_B, J but not between BP_c and r. Correlation-coefficients were, however, at best moderate and indicate that in about 50 % of cases the BP_c does not match with modeled values of this study. Gogina et al. (submitted) report higher BP_c at sandy stations (i.e. OB) and lowest at LB and therefore confirm modeled results. Queirós et al. (2015) suggest that BP_c is a good predictor of bioturbation distance (the average distance travelled by particle in a bioturbation random walk model (Schiffers et al. 2011), but not for bioturbation characteristics such as bioturbation depth, activity and D_B.

Braeckman et al. (2014) calculated BP_c on sandy and muddy sediments along the Belgian North Sea coast using wet weight. The authors report BP_c for sandy sediments an order of magnitude higher than in mud. In this study the calculated BP_c in sands exceeds that of muds by a factor of 2 – 3. Braekman et al. (2014) present a BP_c for sand of 3952 ± 2813 m^{-2} that is 2 times higher than BP_c in the southwestern Baltic Sea with $BP_c = 1887$ m^{-2} (using wet weight for comparison) presumably due to higher abundance, biomass and size of organisms in the North Sea.[2]

4.2 Variability of bioturbation

4.2.1 Variability of bioturbation patterns [1]

Variability of bioturbation on different spatial scales was revealed at overall seven stations of various sediment types, salinities and macrozoobenthic communities. Chl profiles allowed the differentiation between no, local and non-local sediment mixing and delivered important information on bioturbation patterns. Mean chl depth profiles were found to be a suitable tool for highlighting distinctive bioturbation patterns in a certain marine area. In contrast, a more detailed insight in bioturbation (i.e. single cores) complicates its interpretation and estimate of general patterns. In general, the extent of non-local sediment mixing increases from west to east. Some stations were found to be more heterogeneous (i.e. OB) than others (i.e. TW). No general pattern exists whether closely located cores (taken from one MUC) are more similar than cores on a broader spatial scale. These findings underline the necessity of a high sampling effort in order to estimate the range of variability when exploring a new or unknown area. The differences between stations in the Baltic Sea will be discussed in the following section.[1]

Since bioturbation is the sum of all physical activities of macrofaunal organisms, sediment mixing should somehow depend on the properties of the present benthic community, e.g. abundance, depth distribution and activity (Wheatcroft et al. 1990, Wheatcroft & Martin 1996). In the present study the relationship between bioturbation and macrofauna was clearly evident.[2]

Macrofaunal composition [1,2]

A first indication of the different bioturbation patterns is given by the various compositions of benthic communities (tab. 7, fig. 15). The distribution of macrozoobenthic communities along the southwestern Baltic Sea determined in this study mainly confirms the findings by Prena et al. (1997), Zettler et al. (2000), Gogina et al. (2010), Schiele et al. (2015) and species' abundance correlate highly significant with sediment's grain size ($r = 0.52$, $\rho < 0.001$), water depth ($r = -0.27$, $\rho = 0.009$) but not with near bottom salinity ($r = 0.08$, $\rho = 0.450$). Biomass correlates with sediment's grain size ($r = 0.39$, $\rho < 0.001$), with water depth ($r = -0.22$, $\rho = 0.038$) and near bottom salinity ($r = 0.42$, $\rho < 0.001$). Both abundance and biomass increase with increasing grain size and decreases with increasing water depth. Sandy stations show greatest abundances (OB) and biomasses (ST, tab. 7; OB: 95.4 ± 34.7 g AFDW according to Powilleit & Kube 1999). There is no significant correlation between abundance and salinity and correlation between biomass and salinity are not convincing as data on biomass are not available for OB (station with lowest salinity).[2]

LB and MB are closely located with similar abiotic properties (tab. 1) and are dominated by local sediment mixing presumably due to the abundance of *K. bidentata* (LB) and *D. rathkei* (LB, MB). Nevertheless, the composition of the benthic community is different at both stations (tab. 7, fig. 15, 16) due to a variety of reasons. Firstly, occasional hypoxia events can cause a loss of macrozoobenthic organisms with a reduction of the long-lived *A. islandica* that is replaced by short-lived polychaetes (spionida, capetellida) (Schulz 1968, Gosselck & Georgi 1984, Gosselck et al. 1987, Gosselck 1992). At LB *A. islandica* was not detected but *C. capitata* showed great abundance. These findings can be associated with the hypoxia event in September 2013 at LB (Diaz & Rosenberg 1995, Petenati 2013). *C. capitata* was not found at MB. *N. hombergii* that is adapted to hypoxia to some extent may switch to anaerobic metabolism (Arndt & Schiedek 1997). This species was not found at MB but not at LB indicating the limit of being capable of surviving anoxia at LB. Another species indicating hypoxia events is *D. rathkei*. This mobile species is able to avoid hypoxia migrating to

neighboring areas (Jarre 1989). *D. rathkei* was occured at MB with remarkably greater abundance than at LB. Furthermore, organisms are smaller at LB than at MB. Another indicator for a recolonization at LB is *K. bidentata* that is sensitive to hypoxia (Borja et al. 2000). This species was only found in juvenile stages at LB.[1]

Secondly, the Hg-concentrations in surface sediments at LB influences macrofaunal abundances. Due to resuspension the heavy metal contamination is spread within the Mecklenburg Bay (see fig. 5). Liehr (1998) studied the effect of heavy metals on *A. islandica* at LB with a reference station in the uncontaminated Mecklenburg Bay (MB). The author found higher densities of individuals at MB. Furthermore, there were remarkable differences in the composition of shell chemistry between both study sites. Life expectancy seems to be reduced at LB with the oldest recorded exemplar being 14 years old, whereas at MB they may reach an age of 35. In this study, *A. islandica* was only found at the low contaminated station presumably indicating decreasing abundance with increasing level of contamination. Leipe et al. (2005) showed a reduced activity of bacteria as a consequence of the anthropogenic pollution in this area. Schinko (2005) also records decreasing numbers of foraminifera in high contaminated sediments of the LB, especially of foraminifera with a calcareous shell. The author found deformed shells at high PAH-concentrations that can cause cancer and mutation (e.g. Fent 2003). The differences in abundance as well as in number and composition of species found at the different sites seem to go along with the various levels of Hg-contamination, thus, being one of the reasons for different macrofaunal compositions at LB and MB. No significant differences in sediment mixing intensities were found indicating no significant effect of heavy metal concentration on bioturbation at LB. On the other hand, data obtained by three replicates per study site are not sufficient for confident statements. There is some evidence of Hg-contamination influencing bioturbation (i.e. decrease of abundance, number of species) at LB; however, this contamination does not seem to be the driving factor for the differences in sediment mixing between LB and MB.

ST is dominated by the *D. rathkei, K. bidentata* and *A. alba* that seem to be the driving organisms for local sediment mixing. *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 et al. (2000) the distribution of small sized *A. islandica* (<30 mm) in the area around ST indicates a successful recruitment in the 1980/90's after a long period of hypoxia (Gosselck et al. 1987, Prena et al. 1997). *A. islandica* found during this study are mainly larger than 30 mm indicating the ongoing growth of the population reported by Zettler et al. (2000).[1]

Towards the east, the extent of non-local sediment mixing increases due to changing composition of macrozoobenthic communities. Stations in the east are dominated by polychaetes and *L. balthica*. *L. balthica* 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 localizing the buried bivalve situated centrally beneath the star-figure generated by the siphon's foraging activity. On the basis of this study, the tube seems to be refilled with surface particles while the bivalve retracts its siphon creating sub-surface peaks of chl. *S. armiger* occurs frequently at AB and TW and *H. diversicolor* at OB.[1]

Depth distribution of macrofauna [2]

The high resolution depth distribution of macrobenthos (abundance and biomass) and chl was then a step having a closer insight in existing biotubration patterns. At stations in the west (LB, MB, ST), dominated by local mixing, most organisms inhabit the top centimeter where highest chl concentrations were found. These organisms feed on food resources from the water column whereas there are only a few specialists that are mainly indicated by high biomass in deeper horizons of the sediment, e.g. *A. islandica*, *A. alba*, *L. balthica*, *N. hombergii*. On the other hand, at stations in the east (AB, TW, OB), dominated by non-local mixing, the distribution of animals indicated subsurface maxima in the same depth layers as chl. At AB, juvenile *L. balthica* was most abundant within the subsurface maxima of chl close to the sediment surface. At TW and OB these chl peaks are generated by polychaetes that only feed occasionally at the surface and usually hide from predators within the sediment.[2]

In fact, mean depth distribution of abundance and chl correlated well (fig. 16). Conversely, correlations between depth distribution of biomass and chl were not significant at MB and AB. The relative abundance and biomass of the taxonomic groups at each station show different patterns (fig. 15). Biomass at MB and AB is almost exclusively constituted by bivalves whereas at LB and TW polychaetes also make a remarkable contribution. Bivalves composing the major part of biomass at MB and AB are adults and occur infrequently. As a result there are only a few subsurface peaks in chl, i.e. non-local transports created by these organisms. While in many cores at these stations the peaks could not be associated with an organism, averaging chl profiles consolidates the very few chl subsurface maxima. The

patterns determined by mean profiles, however, were not found in each single core (tab. 6) underlining again the necessity of parallel sampling.[2]

Main bioturbators [2]

As there is some evidence that the existing bioturbation patterns in the Baltic Sea depend on the depth distribution of macrofauna and because chl profiles are the basis for estimating bioturbation patterns, the definition of main bioturbators was performed based on a quantitative description of the species' depth distribution. One important aspect that has to be kept in mind is that despite the fact of one mode of sediment mixing being dominant at each station both local and non-local mixing was detected considering single cores. Therefore, when determining main bioturbators it is necessary to differentiate between local and non-local transports as both modes take place at most stations (except TW).[2]

In most cores indicating non-local mixing, no bioturbating organism could be associated with the subsurface peak in chl. In contrast, general patterns of sediment mixing derived by mean chl profiles and depth distributions of abundance/biomass was again a useful step towards indentifying main bioturbators. Most abundant species that occur most frequently at the sediment surface and that show an exponential decrease with depth are defined to be responsible for local sediment mixing. Secondly, for non-local sediment mixing depth distribution of most abundant organisms was compared to subsurface peaks in chl. In some cores, subsurface maxima could directly be associated with animals. Therefore, additional hints were given by the comparison of mean chl profiles and the depth distribution of the sum of organisms and biomass (fig. 16). Furthermore, mean injection depths presented by the bio-mixing model and the locations of organisms within these layers were used for the determination of main bioturbators responsible for non-local sediment mixing. The determination of main bioturbators will we presented in more detail below. [2]

Measured chl profiles present a certain status at the time of sampling. As most animals are free in their movements they may have left the place of intense bioturbation highlighted in the cores. The experimentally examined degradation of chl of 0.01 d^{-1} for mud and 0.02 d^{-1} for sand imply half-life periods of 69 and 34 days, respectively. For that reason, activities that have taken place up to three months before sampling may be observed. This, in turn, also means that a present chl profile may be the sum of different events carried out by various animals which may not be found in the cores anymore. In cases of an agreement between subsurface peak and a likely bioturbator, there is still no evidence that this animal has indeed

achieved non-local transport at this exact position in the sediment. *L. balthica*, for example, considered as a non-local bioturbator in our study, was found in 23 of 24 cores investigated at ST. However, 67% of the cores show local sediment mixing and in only 40% of the subsurface maxima this bivalve was found together with other species. A detailed reflection of a small area given by one core complicates its interpretation. In contrast, an overview of mean depth distribution gained by many cores, allows an insight in typical patterns. As reported in Meysman et al. (2003) many commonly encountered sediment mixing modes apparently violate the assumptions of the biodiffusion model (Fickian analogy), particularly for short-lived tracers. In contrast down-core profiles of radiotracers, e.g. ^{210}Pb, often do fit an exponential depth distribution. The authors state that non-local events merge with increasing half-life periods of the tracer. In this study more complex patterns were obtained covering various modes of sediment mixing over a time span of up to three months. However, Fornes et al. (2003) proved very rapid sediment mixing by in situ measurements using the ^{234}Th method with particles transported down to 12 cm depth after 1.5 days. Therefore, bioturbation analyzed in this study using chl presents a current status that is related to all environmental, biological and physical conditions during sampling. Sediment mixing may conceivably change during different times of the year. [2]

Local sediment mixing is carried out by organisms that show highest abundances at the sediment surface. Their exponential decrease with depth indicates that these organisms stimulate the diffusive distribution of chl within the sediment by moving particles through the upper centimeters of the sediment. *D. rathkei* is the main bioturbator for local transports at most stations (except OB) plus *K. bidentata* at LB and ST. At OB *P. ulvae* plays the most important role.[2]

Non-local sediment mixing is carried out by a variety of organisms along the southwestern Baltic Sea. In the west, *C. capitata* (LB) and *P. caudatus* (LB, MB) were defined to be the main bioturbators. Gerino et al. (2007) confirm these findings of non-local transports being driven by *C. capitata*. Furthermore, *N. hombergii* and *A. islandica* were found to be responsible for non-local sediment mixing at MB and ST. Towards the east (including ST), *L. balthica* (ST, AB, TW, OB) and *S. armiger* become 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, *H. diversicolor* belongs to the main bioturbators in the upper horizon of the sediment. Gogina et al. (submitted) also strongly underlines this species potentially dominating bioturbation at the same stations during the

same sampling campaigns. Mugnai et al. (2003) found *H. diversicolor* probably to be the major responsible of non local mixing associated with deep tracer peaks in the Venice Lagoon. Nogaro et al. (2008) confirms the findings of this polychaete inducing non-local transport. *M. arenaria* is responsible for non-local sediment mixing in deeper horizons of the sediment as adults may occur down to 8 cm depth at OB. Main bioturbating organisms defined in the present study along the coast of the southwestern Baltic Sea are summarized in table 12. [2]

Functional groups [2]

Main bioturbators of local and non-local sediment mixing at each station determined in this study were assigned to the 4 major categories of organisms' life traits (Kristensen et al. 2012) (tab. 12). Local sediment mixing is carried out by surficial biodiffusors at each station. At all stations biodiffusors could also be associated with non-local sediment mixing. Sediments at LB are mixed non-locally by biodiffusors and upward conveyors. At MB, ST, AB and TW only biodiffusors are responsible for both local and non-local sediment mixing. Bioturbating organisms at OB belong to biodiffusors and downward conveyors (tab. 12).[2]

Biodiffusors are supposed to induce local sediment mixing over short distances and can be divided into epifaunal, surfical and gallery-biodiffusors (Kristensen et al. 2012). In the present study, however, gallery-biodiffusors were often identified in horizons of subsurface peaks or mean injection depths implying their association with non-local sediment mixing rather than exclusively redistributing particles with analogy to diffusive processes. Mermillod-Blondin et al. (2004) and Duport et al. (2006) confirm these findings as the authors found the gallery-biodiffusor *H. diversicolor* to be responsible for non-local transports. This species rakes the sediment surface causing particles to fall down to the tube bottom (Goerke 1971, Lambert & Retière 1987, Esnault et al. 1990). According to François et al. (2002) gallery-biodiffusors induce local sediment mixing in layers with very dense gallery systems by transporting particles non-locally at the end of the burrows. Reasons why certain biodiffusors may be responsible for non-local sediment mixing are diverse and given in the following section. [2]

Feeding behavior

The gallery-biodiffusors *P. caudatus*, *N. hombergii* (MB), *S. armiger* (AB, TW) and *H. diversicolor* (OB) could be associated with non-local transports in this study. Polychaetes

may move particles non-locally due to their free movements through the sediment matrix while foraging. *L. balthica* is generally defined as a surficial biodiffusor but was found to be one of the most important species responsible for non-local sediment mixing in the southwestern Baltic Sea. It has often been reported that *L. balthica* is a deposit-feeder retaining a connection to the sediment surface via their siphons (Brafield & Newell 1961, Mortimer et al. 1999, Karlson et al. 2005). The inhalant siphon draws in particles from the surface creating a star-figure with a central hole while the exhalant siphon ejects both faeces and pseudofaeces that can be seen as a second small hole (Hulscher 1973, Mortimer et al. 1999). The tube around the siphons seems to be refilled with surficial particles during retraction of the siphons resulting in an accumulation of fresh material around the bivalve. In the present study *L. balthica* seems to belong to downward conveyors rather than surficial biodiffusors. [2]

Size

Some species seem to switch between certain life traits due to their size and/or life stage. *A. alba*, for example, was defined to be responsible for local sediment mixing at ST but also for non-local transports at MB. At ST this bivalve was almost exclusively found in juvenile stages focusing on the top centimeter whereas at MB individuals were mainly adults inhabiting the sediment down to 6 cm depth. Thus, the effect on non-local sediment mixing in surface sediments at ST might not be visible due to the limited spatial resolution of 0.5 cm. [2]

Biomass and depth distribution

Depth distribution of organisms may indicate their role restricted to different horizons of the sediment. At MB, *A. islandica, A. alba* and *N. hombergii* were the only species found below 4 cm depth demonstrating their responsibility for the transport of particulate matter up to depth. Additionally, *A. islandica* contributes the major part of biomass demonstrating its superior role in sediment mixing (fig. 16 b (ii)).[2]

Mixing depth [2]

The estimated bioturbation depths in this study reach from 5.2 ± 1.7 cm to 7.1 ± 1.6 cm. These mixing depths are estimated based on AL434 cruise because no patterns in seasonal variability were found. As macrofaunal depth distribution was analyzed on the same line, this information was used for explaining differences. 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 detected in the cores. This species was found deepest (down to 9 cm depth) 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 preventing chl to penetrate 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 deep. The estimated mixing depths of the present study are within the range of the world-wide 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 the mixing depths estimated in this study. Mixing depths in coastal areas can reach from 7 to 16 cm. Nittrouer et al. (1984) report 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 worked in the same area report mixing depths of 14 ± 2 cm. Wheatcroft & Martin (1996) analyzed bioturbation along an organic-carbon gradient off the Palos Verdes peninsula with highest mixing depths (9 – 11 cm) near the outfall and lower values nearby unimpacted sites (7 – 9 cm). Particles at sampling stations of this study 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. Smith et al. (2000) report a mean mixed layer depth of 4.6 cm in the oxygen minimum zone on the Oman margin and 11.1 cm along well-oxygenated Atlantic and Pacific slopes in the northwest Arabian Sea. Black et al. (2012) estimated mixing depths with a range of 3.5 ± 1.3 to 7.0 ± 0.5 cm derived from chl profiles in the Gulf of Eilat. Nickell et al. (2003) derived mixing depths between 7 and 18 cm at Loch Creran on the west coast of Scotland. [2]

Comparing injection depths L between stations using Kruskal-Wallis and its post-hoc test considering all seasons indicated significant differences between stations ($p < 0.001$) and three subsets of various depths: low with L = 1.9 ± 1.1 cm estimated at LB, AB and TW (n = 72), intermediate with L = 3.1 ± 1.5 cm at LB, ST and OB (n = 84) as well as high at MB with L = 4.6 ± 2.2 cm (n = 18). The injections depths determined in this study go along well with other study sites. Smith et al. (1986) report L = 2 – 6 cm in the NE Atlantic. Soetaert et al. (1996) found injection depths ranging between 1.6 and 5.8 cm at the ocean margin in NE Atlantic. Injection depth of L = 3 cm was estimated at one study site in Loch Creran, Scotland by Schmidt et al. (2007). Fornes et al. (2003) found subsurface peaks between 2 and 3 cm.

Local and non-local mixing

The findings of either local or non-local sediment mixing dominating the particle transport in a certain marine area were confirmed by various other studies (e.g. Duport et al. 2007, Gerino et al. 2007, McClintic et al. 2008). The spatial distribution non-local sediment mixing increasing from west to east in the southwestern Baltic Sea was determined with only a very few discrepancies throughout the sampling campaign. These discrepancies may be explained by the reduction of sampling size with an unvaried randomness of cores displaying certain modes of sediment mixing. In turn, higher sampling size might have resulted in a consistent pattern throughout the seasons. Mugnai et al. (2003) measured bioturbation activities and mixing rates in autumn and spring in the Venice Lagoon and found biodiffusion to be dominant in autumn and bioadvection in spring (active transport of sediment trough the gut of head-down conveyor-belt feeder; belongs to non-local mixing in this study; Fisher et al. (1980), Rice (1986) and Gerino et al. (1994)). Gerino et al. (2007) did not find seasonal variability in the extent of local and non-local sediment mixing during autumn 1998 and spring 1999 at four selected sites in the Venice Lagoon. On the basis of the findings of this study indicating various patterns of dominant modes of sediment mixing at different areas studied in the southwestern Baltic Sea, 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 (Morys et al. in press).

Tab. 12: 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 organisms' life traits by Kristensen et al. (2012). Species in bold characters indicate a superior role in sediment mixing. *S. armiger* categorized as a biodiffusor (Queirós et al. 2013) was assigned to gallery-biodiffusors in this study because this species was indicated to induce non-local sediment mixing, in Morys et al. (submitted).

	Main bioturbators					
Station	**local**	**Life trait ***	**Reference**	**non-local**	**Life trait ***	**Reference**
LB	*D. rathkei* *K. bidentata*	surficial biodiffusors surficial biodiffusors	Queirós et al. (2013)	*C. capitata* *P. 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*** *A. alba* *deep sediment: *A. islandica* *N. hombergii*	 gallery-biodiffusor surficial biodiffusor surficial biodiffusor gallery-biodiffusor	 Powilleit et al. (1994) Queirós et al. (2013) Maire et al. (2006) Hartmann-Schröder (1996)
ST	*K. bidentata* *D. rathkei* *A. alba*	surficial biodiffusors surficial biodiffusors surficial biodiffusors	Queirós et al. (2013)	*L. 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) Maire et al. (2006), 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	n.a.			polychaetes ***S. armiger*** *L. balthica*	 (gallery)-biodiffusor surficial biodiffusor	 Queirós et al. (2013) Queirós et al. (2013)
OB	*P. ulvae*	surficial biodiffusor	Queirós et al. (2013)	*upper sediment (2-4 cm, max. 6 cm): ***H. diversicolor*** *L. balthica* *deep sediment: *M. arenaria*	 gallery-biodiffusor surficial biodiffusor downward conveyor	 Francois (1999), Duport et al. (2006) Queirós et al. (2013) Muus (1967)

4.2.2 Variability of bioturbation intensity [1]

Although increasing particle movements by faunal activity are well known (e.g. Graf & Rosenberg 1997), we still have a generally poor understanding of bioturbation and little predictive capability (Wheatcroft et al. 1990, Boudreau 1998). Combining the findings of the present study, especially bioturbation intensities were found to be highly variable within and also between stations.[1] No general seasonal pattern was found but a tendency towards sediment mixing of different intensities between stations. D_B-values estimated at LB were significantly different almost throughout the sampling campaign whereas no general differences were found between the other stations. For that reason, LB is considered a station of low sediment mixing and is surmounted by MB, ST, AB, TW and OB. Gogina et al. (submitted) calculated bioturbation potential at the same stations during the same sampling campaigns. Accordingly, the authors confirm the findings of the present study presenting high fluctuations of the seasonal cycle from year to year without an obvious common pattern. Generally, differences between stations are more pronounced than between seasons within stations both derived by the digenetic model (present study) and calculation of BP (Gogina et al. submitted). The authors also confirm that OB is the highest potentially mixed station and LB the lowest one.

The findings of no seasonal patterns in bioturbation intensities of local sediment mixing within and between were confirmed by other studies in coastal areas (e.g. Schmidt et al. 2002, Wheatcroft 2006, Gerino et al. 2007, McClintic et al. 2008). Schmidt et al. (2002) recognized seasonal trends in bioturbation intensity derived from ^{234}Th activities associated with high particle input to the seafloor at northwestern Iberian Margin. The authors found bioturbation rates to be highest in spring whereas sediments are less dynamic in winter and summer when sedimentation is lower. However, Schmidt et al. (2002) assumed bioturbation to be higher in summer than winter due to higher ^{234}Th surface activities indicating higher particle flux. Wheatcroft (2006) investigated sediment mixing at four 70-m stations on the continental shelf offshore from the Eel River (northern California) in four-month intervals between February 1995 and March 1998, and in August 1999. The author reports no statistically significant seasonal pattern despite a hint of higher mixing intensities in fall when carbon flux to the seafloor is highest. McClinitic et al. (2008) evaluated temporal variations in bioturbation intensity on the West Antarctic continental shelf. The authors state that D_B derived from ^{234}Th showed no distinct seasonality and did not correlate with organic carbon flux into the sediment traps or ^{234}Th within the sediment.

Gerino et al. (2007) investigated four sites at the Venice Lagoon in autumn 1998 and spring 1999 and state biodiffusion not to be significantly different between seasons. D'Andrea et al. (2004) report estimates for D_B running tracer input experiments for 131 - 162 days being similar throughout the period between July 1997 to November in the intertidal Debidue flat (South Carolina) with some depression of biodiffusion in the winter, most likely related to lower temperatures.

In contrast, Balzer (1996) and Gerino et al. (1998) report seasonal effects on bioturbation. Balzer (1996) analyzed sediments Norwegian Sea (Voering Plateau) five times between May 1986 and February 1987 with respect to seasonal variation in sediment mixing rates. The author found that a seasonally varying mixing coefficient with higher values during summer when supply of food-rich particles is high fitting better the measured profiles ^{234}Th profiles than a constant coefficient over time. Gerino et al. (1998) determined an increased intensity of biodiffusion just after a bloom in Long Island Sound by a factor of 2 to 3 compared to pre-bloom situation using average D_B values derived by different tracers (chl *a*, ^{234} Th and luminophores). Enhanced mixing was determined 40 days after the bloom. The authors argue that these findings indicate a direct relation between the flux of fresh organic matter and rates of biodiffusion. However, as the authors did not model D_B using chl *a* profiles before the bloom it remains unclear whether sediment mixing is enhanced at their study site using chl as a tracer.

Local sediment mixing intensities (D_B) estimated in the present study combining all stations and seasons ranged from 0.0004 to 4.6 cm² d^{-1} (n = 213). These D_B-values fit other estimates of local mixing in the literature (tab. 13). Boon & Duineveld (1998) investigated sediment mixing on three different stations in the North Sea using chl and applying the model by Soetaert et al. (1996). Two stations present the same sediment type (fine sand and silt). During the same season as the present studies (March), one of these stations is characterized by diffusive mixing with a D_B = 0.015 cm² d^{-1} while the other one was described by non-local mixing with a D_B = 0.022 cm² d^{-1}. The contrasting modes of dominant sediment mixing at two stations with the same sedimentological properties match the results of this study quite well. As the authors did not present data on injection fluxes, it is not possible to compare the non-local transports with each other. Boon & Duineveld (1998) estimated D_B that are as high as at our least mixed station (LB: D_B = 0.02 ± 0.03 cm² 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} that 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 that results in lower concentrations than using the photometric method. D_B of 0.3 ± 0.5 cm² d^{-1} (except least mixed stations LB and OB) of the present study are up to 40 times higher. Mean D_B of 0.5 ± 0.7 cm² d^{-1} were estimated in the present study combining all stations and seasons that is somewhat higher compared to other coastal zone (tab. 13). However, D_B ranges from 0.0004 to 4.6 cm² d^{-1} mainly matching values of different study sites quite well. Wheatcroft & Martin (1996) report a D_B of 0.03 cm² d^{-1} using ^{234}Th near the outfall off the Palos Verdes peninsula and of 0.1 cm² d^{-1} at unimpacted sites. This study carried out in coastal areas indicates lower mixing intensities compared to the present study. Nittrouer et al. (1984) using ^{234}Th found mixing intensities of 0.38 cm² d^{-1} offshore from the mouth Columbia River which match the findings of this study.[1]

Tab. 13: Summary of local bioturbation intensities (D_B) measured at various study sites modified and complemented after Wheatcraft (2006).

Study site	**D_B (cm² d^{-1})**	**tracer**	**reference**
Long Island Sound	0.0008 – 0.1	^{234}Th	Aller et al. (1980)
Long Island Sound	0.001 – 0.03	^{234}Th	Gerino et al. (1998)
Buzzards Bay	0.008 – 0.07	^{234}Th	Martin & Sayles (1987)
Hatteras shelf/slope	0.0008 – 0.3	^{234}Th	Green et al. (2002)
North Carolina slope		^{234}Th	DeMaster et al. (1994)
Site I	0.0005 – 0.05		
Site II	0.001 – 0.05		
Site III	0.01 – 0.08		
North Carolina slope		^{234}Th	Fornes et al. (1999)
Site I	0.0005 – 0.0008		
Site III	0.007 – 0.2		
Palos Verdes shelf	0.02 – 0.2	^{234}Th	Wheatcroft & Martin (1996)
Eel shelf		^{234}Th	Bentley & Nittrouer (2003)
S60	0.01 – 0.1		
S70	0.04 – 0.2		
Offshore Eel River	0.008 – 0.4	^{234}Th	Wheatcroft (2006)
North Sea	0.02	chl	Boon & Duineveld (1998)
Washington continental shelf		^{234}Th	Nittrouer et al. (1984)
Offshore Columbia River	0.4		
Mid-Shelf Silt Deposit	0.1		
New York Bight	0.03 – 0.1	^{234}Th	Cochran & Aller (1979)
Long Island Sound	0.03	^{234}Th	Sun & Wakeham (1999)
Amazon shelf	0.08	^{234}Th	DeMaster et al. (1980)
East China Sea	0.07 – 0.1	^{234}Th	McKee et al. (1982)
Valencia shelf	0.08 – 0.2	^{234}Th	Nittrouer et al. (1982)
West Antarctic continental shelf	0.001 – 0.3	^{234}Th	McClintic et al. (2008)
Venice Lagoon	0002 ± 0.00005 – 0.009 ± 0.003	luminophores	Gerino et al. (2007)
Thau Lagoon	0.001 – 0.008	luminophores	Duport et al. (2007)
Thau Lagoon	0.003 – 0.1	^{234Th}, ^{7}Be	Schmidt et al. (2007)
Gulf of Eilat	0.013– 0.069	chl	Black et al. (2012)
Mediterranean coast	0.006 ± 0.001	luminophores	Grossi et al. (2003)
Debidue Flat	0.15 – 0.28	Inert particle tracer	D'Andrea et al. (2004)
Eckernförde Bay	0.7	^{234}Th	Bentley & Nittrouer (1999)
Baltic Sea	0.0004 – 4.6	chl	Present study

Combining the findings with regard to non-local sediment mixing, LB was also least intense mixed. MB, ST and AB are defined to be of intermediate as well as TW and OB of high intensities. Injection fluxes J in this study ranged from 0.04 to 0.7 µg cm^{-2} d^{-1} (0.3 ± 0.3 µg cm^{-2} d^{-1}, n = 141) and ingestions rates from 0.002 to 10000 d^{-1} with mean value of 363.2 ± 1888.7 d^{-1} (n = 28). As most studies preferably estimate local sediment mixing (D_B) a comparison of non-local mixing intensities is complicated. Some authors in fact ignore subsurface peaks (e.g. Balzer 1996, Gerino et al. 1998, McClintic et al. 2008). Despite the convenience of applying biodiffusive models, one should consider non-local models as these non-local transports are particularly relevant for short time scale investigations and for the benthic fauna thus generating particular tracer profile shapes (Maire et al. 2008). Furthermore, relating injection fluxes J to other marine areas is difficult due to various methods applied in the literature (tab. 14). Injection fluxes estimated by Soetaert et al. (1996) allow a comparison due to the same model applied. Their modeled intensities are lower than in this study, presumably because of the long-lived tracer ^{210}Pb. Non-local mixing (ingestion) rates are comparable with other study sites ignoring the inexplicable high rate of 10000 d^{-1} and taking into account that most rates range from 0.002 to 0.8 d^{-1}.

Tab. 14: Summary of non- local bioturbation intensities (J and r) measured at various study sites

Study site	**J**	**r (d^{-1})**	**tracer**	**reference**
Venice Lagoon	0.02 – 0.02 g cm^{-2} d^{-1}	0.003 – 0.04	luminophores	Mugnai et al. (2003)
Thau Lagoon		0.02 ± 0.1 – 0.03 ± 0.002		Duport et al. (2007)
Carolina continental margin		0.05 ± 0.03	^{234}Th	Fornes et al. (2003)
Equatorial Pacific		0.03 ± 0.02	^{234}Th	Pope et al. (1996)
Ocean margin, NE Atlantic	0.0006 – 0.002 dpm cm^{-2} d^{-1}		^{210}Pb	Soetaert et al. (1996)
NE Atlantic		0.005 – 0.02	^{210}Pb, ^{239,240}Pu	Smith et al. (1986)
Tikehau lagoon			black basaltic	Hily & Fouin (1998)
Inner flat	0.04 ± 0.06 g cm^{-2} d^{-1}		sand	
Inner slope	0.02 ± 0.02 g cm^{-2} d^{-1}			
Lagoon floor	0.001 ± 0.001 g cm^{-2} d^{-1}			
Lake DePue		3.2 – 4.2		Roche et al. (2016)
Baltic Sea	0.04 – 0.7µg cm^{-2} d^{-1}	0.002 - 10000	chl	Present study

Despite the fact of no seasonality, stations along the coast of the Baltic Sea are different in terms of intensities of both local and non-local sediment mixing. In the following section possible explanations will be discussed.

A first indication could be given by Dauwe et al. (1998) who compared bioturbation potential of macrofauna with contrasting food supply. They report 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 ration (TC/TN) at the sites of the present study is not significantly different Bunke (pers. comm.). TC and TN were analyzed on the same cruise by using the CHNS-O Elemental Analyzer EuroEA 3052 (EuroVecto). After burning of the samples the released gases were separated chromatographically and determined with the aid of a thermoconductivity detector. No general positive correlation between nutritional quality of organic matter in the sediment and bioturbation intensity was found along the coast of the German Baltic Sea.[1]

However, in this study, some hint was found of local mixing depending on surface chl concentrations. 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 correlation of both variables at all their study sites. Additionally, Graf et al. (1982), Christensen & Kanneworff (1985), Boon et al. (1998) and Gerino et al. (1998) report a rapid reaction of benthic macrofauna to spring bloom sedimentation. However, the only sedimented spring bloom situation during the whole sampling campaign took place at OB in spring 2014, but mixing rates were low 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 ocean. The authors state that in some areas in the Arabian Sea 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). Maire et al. (2006) carried out experiments on sediment mixing rates by *Abra ovata* in winter and summer as well as with different food supply using an automated image analysis procedure for luminophore tracer particles. The authors report sediment mixing to be low and not affected by food availability in winter. During summer rates were very high and significantly affected by food availability. The authors state that temperature and not food availability controls sediment mixing in winter. Overall, contrasting evidence of factors controlling sediment mixing intensities (e.g. food quantity and quality, temperature) are reported in the literature.[1]

In this study, highly significant Spearman-correlations were found between D_B and surface chl (0-0.5 cm) concentration ($\rho < 0.001$, r = -0.5) and chl inventory (sum 0-6 cm, $\rho < 0.001$, r = -0.26) estimated at all stations and seasons (n = 213). The higher correlation coefficient of -0.5 indicates a stronger dependency of local mixing (D_B) on surface chl. For that reason, an exponential regression was performed between surface chl and D_B. Results are presented in figure 25. A highly significant negative relationship between the two parameters indicates increasing D_B with decreasing chl. Samples with highest surface chl concentrations display lowest intensities of local sediment mixing. Although the photometric method only gives a hint on the quality of the material, the remarkably green extract gave evidence of fresh food supply, especially at OB owed to the recently sedimented spring bloom in spring 2014. This in turn means that local sediment mixing is highest when food supply is low. Movements while foraging is the most expensive energetic mean 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). These findings were confirmed by Gogina et al. (submitted) who calculated bioturbation potential at the same stations and report lowest BP_c in spring 2014 at OB due to high food supply delivered by the spring bloom.

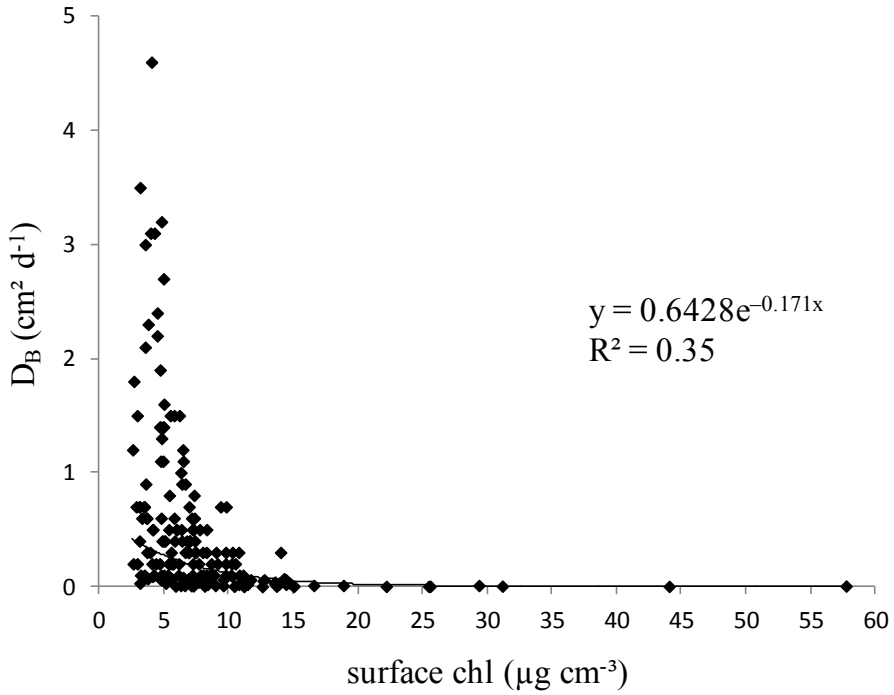


Fig. 25: Exponential regression indicating the relationship of local sediment mixing (D_B = cm² d^{-1}) depending on surface chl concentration (n = 213). Note that the equation derived from this dependency of intermediate quality can be used for calculating D_B.

The following equation is derived from the exponential regression highlighting the relationship between local sediment mixing intensities and surface chl concentration:

$$y = 0.6428\ e^{-0.171x} \quad (9)$$

where y is D_B ($cm^2\ d^{-1}$) and x the surface chl concentration ($\mu g\ cm^{-3}$). This dependency is of intermediate quality, however, this approach delivers an opportunity of easily calculating D_B for a rough assessment of large scale distribution of local sediment mixing. When applying this equation, we have to keep in mind that it is based on chl concentrations measured photometrically that results in an overestimation of true chl *a* and therefore in an overestiamtion of D_B. Neverthelss, it is a useful approach for a general characterization of a marine area with regard to local sediment mixing intensities and the focus on either comparing different areas, estimating temporal variability or even reconstructing local sediment mixing intensities. It is necessary to use the same method for analyzing chl when applying this equation.

Similarly, no general pattern of seasonality in bioturbation intensities of non-local sediment mixing within and between was found along the coast of the southwestern Baltic Sea. These findings were confirmed by Duport et al. (2007) who also did not find significant differences in non-local transports over time at Thau Lagoon. Mugnai et al. (2003) carried out luminophore experiments during autumn 1998 and spring 1999 at Venice Lagoon. The authors did not report any significant differences in non-local mixing (generated by surface deposit feeders or regenerators transporting particulate matter from the surface to depth) between the two seasons. On the other hand, they found seasonal differences in bioadvection (caused by head-down oriented organisms transferring sediment from the ingestion zone in the sediment through their guts to the surface) with a possible explanation of increasing temperature enhancing biological activities.

As a significant dependency of D_B on food supply was found in this study, the same relationship was tested using quantities of injection fluxes J (fig. 26). No significant correlation was found between J and surface chl ($\rho = 0.591$, $n = 141$) but between J and chl inventory ($\rho < 0.001$, $n = 141$). A Spearman-correlation coefficient of $r = 0.29$, however, indicates a relationship of low quality and thus no strong dependency.

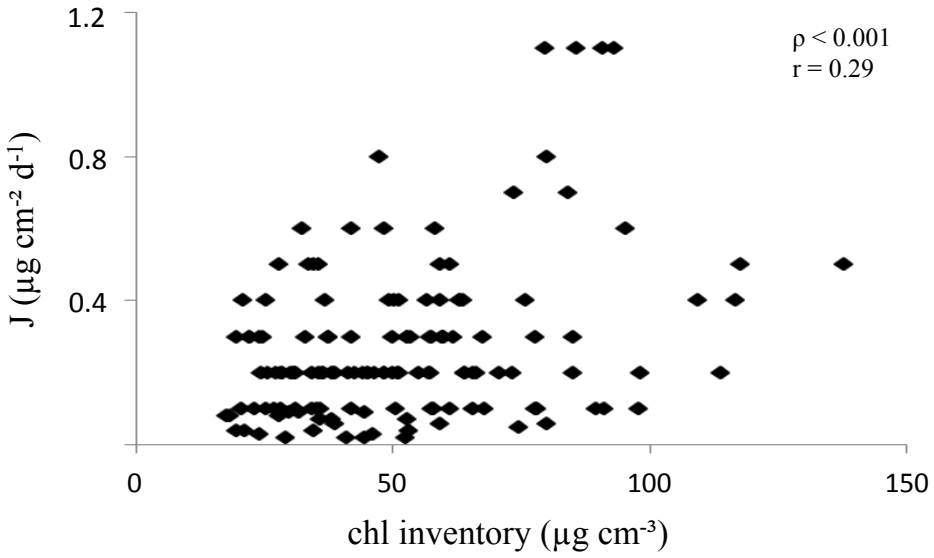


Fig. 26: Spearman-correlation indicating the highly significant relationship of non-local sediment mixing (injection flux J = µg cm^{-2} d^{-1}) depending on chl inventory (n = 141) of low quality.

Mugnai et al. (2003) state that the macrofaunal community is the major responsible for non-local transports and that seasonal differences in bioadvection could also be attributed to changes in the functional composition of the benthic community. Additionally, there seems not to be a strong relationship between the total number of species and ecosystem functioning, but instead key-species will essentially determine the health of the ecosystem (Johannesson et al. 2010, Gamfeldt et al. 2015). These findings were confirmed by the present study. Injection fluxes J were found to correlate significantly with abundance (fig. 17 a) and biomass (fig. 17 b). This fact highlights that non-local sediment mixing depends on the number and size of organisms. Additionally, gallery-biodiffusors (GB) and upward/downward conveyors (UC/DC) were found to induce non-local sediment mixing in the Baltic Sea. For that reason it was now tested whether injection fluxes J depend on the number of GB and/or UC/DC. On the basis of the findings of AL434 cruise in spring 2014, each modeled injection flux J was plotted against the number of GB (fig. 27 a) and UC/DC (fig. 27 b) found in the corresponding core. No significant correlation was found, however, a tendency towards increasing injection fluxes with increasing number of GB is visible (fig 27 a).

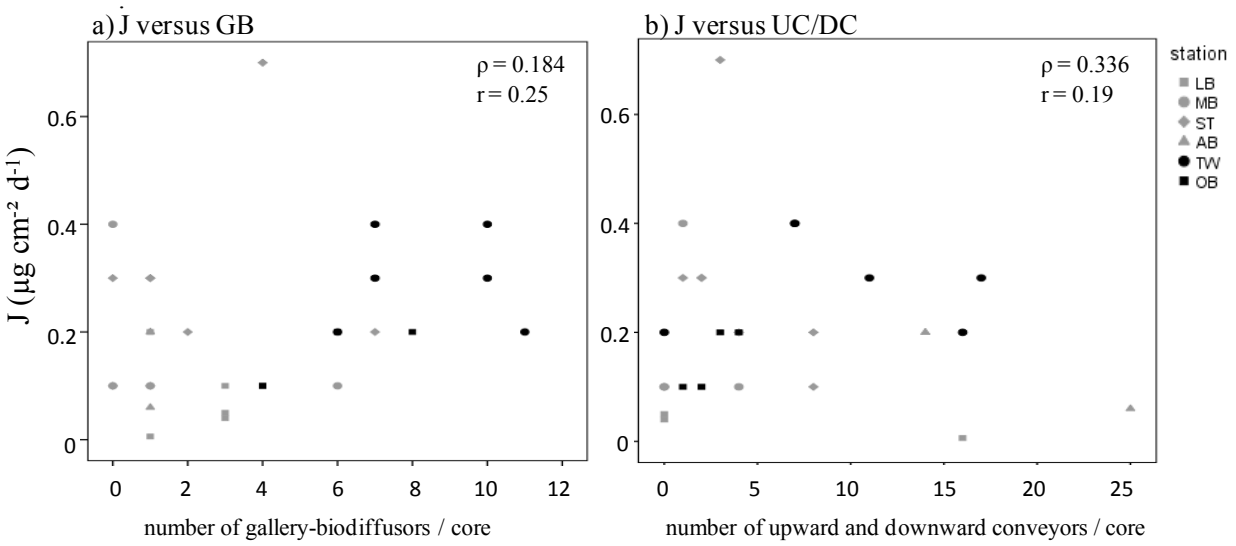


Fig. 27: Plot of non-local sediment mixing events in single cores (injection flux J = µg cm^{-2} d^{-1}) in relation to the number of (a) gallery-biodiffusors (GB) and (b) upward and downward conveyors (UC/DC) found in the same cores. Spearman-correlation with ρ-value and correlation coefficient r indicate no significant relationship.

Continuatively, injection fluxes J were averaged for all stations/seasons and correlated with numbers of GB and UC/DC derived from 3 to 10 van Veen grabs. Data on abundance were provided by M. Gogina. Results are presented in figure 28. Highly significant Spearman-correlations were found between J and GB ($\rho = 0.004$) as well as J and UC/DC ($\rho = 0.032$). The correlation with GB provides a better correlation-coefficient indicating a stronger dependency of GB on J rather than of UC/DC on J. Considering the high variability of sediment mixing previously described one should especially pay attention to this highly significant correlation. This significant correlation is a strong sign of a cause-effect relation. Firstly, both GB and UC/DC were determined to induce non-local sediment mixing in the Baltic Sea. Secondly, there is evidence of increasing intensities with increasing abundance. Thirdly, when comparing J and GB from the same cores a tendency towards a dependency is visible. Again the pattern becomes visible when averaged data are used and not individual cores. Combining all these findings and considering the highly significant correlation between J and GB (taken from grabs) it becomes obvious that non-local sediment mixing depends on the abundance of GB. More work should be investigated in order to obtain a larger dataset for the direct comparison of injection flux J and number of GB in the same core.

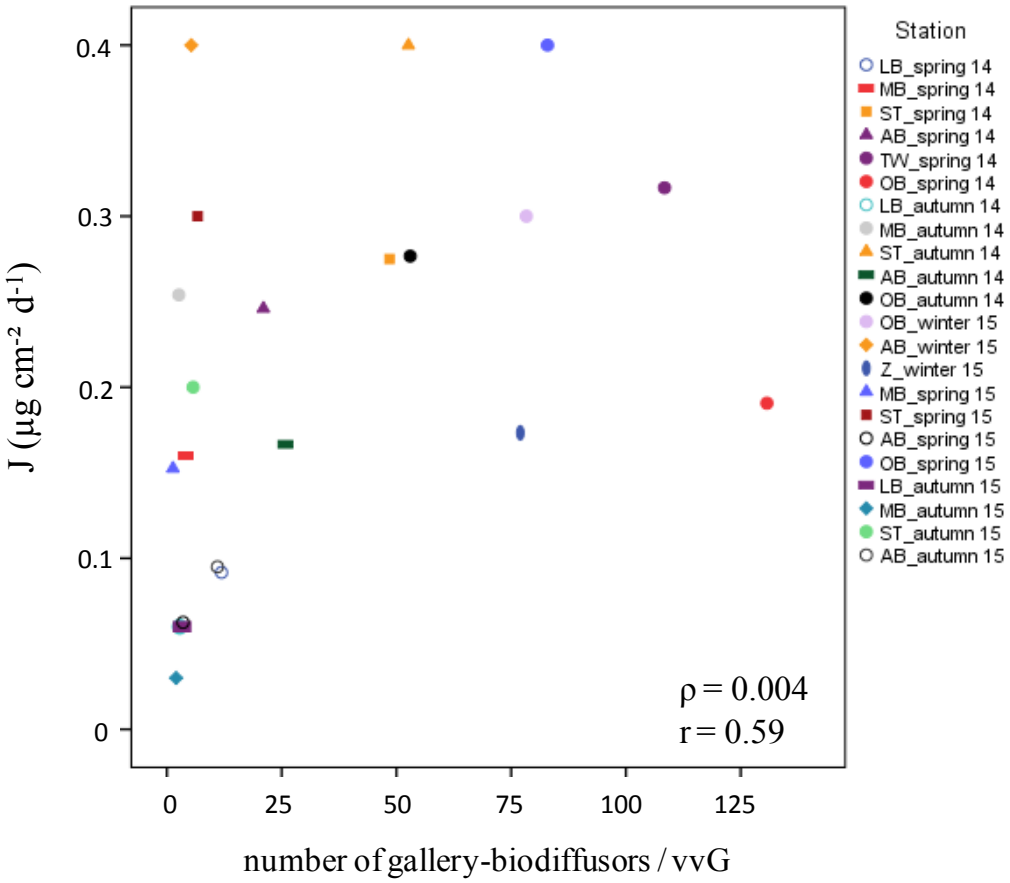


Fig. 28: Relationship between number of gallery-biodiffusors (from vvG) and mean bioturbation intensity ofnon-local sediment mixing (injection flux J) estimated during various seasons at the stations of investment along the southwestern Baltic Sea highlighting highly significant Spearman-correlation ($\rho = 0.004$) with a correlation coefficient of $r = 0.59$. Data on abundance were provided by M. Gogina and present mean values analyzed by 3 to 10 van Veen grabs. Injection fluxes J were also averaged using all J modeled at each station/season (n is presented in table 10). Significant Spearman-correlation between upward/downward conveyors and J with $\rho = 0.032$ and $r = 0.46$.

Fornes et al. (2003) investigated in situ tracer experiments for short-term sediment mixing processes at two Carolina continental margin sites both dominated by non-local mixing but characterized by different benthic assemblages. The authors added tagged sand-size glass beads to the sediment-water interface and after 1.5 days, tagged particles were observed 5 cm below the sediment surface at Site I and 12 cm below at Site III. As Fornes et al. (2003) were not able to provide confident non-local mixing intensities; this difference in burrowing velocity implies more intense non-local sediment mixing (injection fluxes). At Site III the authors report subsurface peaks often coinciding with burrows observed during sampling. Subsurface maxima were located at 2–3 cm depth that may be from feeding activities of *Scalibregma inflatum* (Blair et al. 1996). Abundance of *S. inflatum*, most likely a gallery-biodiffusor due to its assignment to biodiffusors (Queirós et al. 2013) and its effect on non-local transports (Fornes et al. 2003), is 126 times higher at Site III than at Site I. These findings of apparently more intense or rather more rapid

non-local sediment mixing rates at Site III where gallery-biodiffusors are more abundant match the results of this study well. In contrast, Gerino et al. (2007) report increased intensities of non-local sediment mixing in spring 1999 compared to autumn 1998 in the Venice Lagoon due to increasing abundance of the upward conveyor *C. capitata*. Gilbert et al. (2007) also state that functional groups assemblage in community play a major role in the intensity of sediment mixing. The authors analyzed the relationships between macrobenthos and sediment mixing in the Thau Lagoon and report differences between two sampling times estimated in summer 2002 and spring 2003. Duport et al. (2007) explain the lower intensities of both local and non-local mixing in spring 2003 by the bioturbation functional composition of the communities. In contrast to the findings in the present study, the authors report a decrease of gallery-biodiffusors causing lower rates.

On the basis of non-local mixing intensities depending on the number of GB and considering the stations separately, it becomes obvious that the number of UC/DC and GB follow the salinity gradient from west to east. Beyond AB a border exists and TW as well as OB display lower salinities. UC/DC are more abundant at the more saline stations in the west and GB take over at less saline stations in the east (tab. 15). In fact, stations in the east are more intense non-locally mixed due to greater abundance of GB.

Tab. 15: Abundance of gallery-biodiffusors (GB) and upward/downward conveyors (UD/DC) estimated from cores in this study, chl inventory (sum of chl concentration of top 6 cm sediment (n = 24 per station) and near bottom salinity at each station.

Station	GB m^{-2}	UC/DC m^{-2}	chl inventory µg 6 cm^{-3}	Salinity near bottom
LB	281	467	76.6	22
MB	101	159	54.3	23
ST	388	520	36.2	23
AB	361	2293	81.6	19
TW	2236	1231	53.4	10
OB	573	340	62.2	8

At the less saline stations both the extent and intensity of non-local sediment mixing is enhanced. These findings give a hint that in the context of global warming resulting in a decrease in salinity in many oceanic areas, GB may generally become more abundant. It can then be expected that the sediments of our oceans will be mixed more intensely and that the extent of non-local transports will increase.

Depth distribution of functional groups

Depth distribution of functional groups within the sediment indicated vertical zoning at most stations (except LB and TW) with SB being most abundant within the top centimeter. GB inhabit the sediment in depth layers below followed by UC/DC. However, there is no general pattern apparent whether the vertical zoning of functional groups within the sediment has any effect on the bioturbation patterns found in the southwestern Baltic Sea.

At LB, chl peaks and injection depths of up to 6 cm indicate the presence of organisms in deeper horizons, however, no fauna was found in these depth layers. Zwicker (2014) found *A. islandica* and *L. balthica* in van Veen grab samples during the same cruise. This leads to the assumption that these two DC-species inhabit the sediment below GB, thus, achieving vertical zoning at LB. The missing evidence for vertical zoning at TW is primarily explained by sampling many organisms in juvenile stages that results in the loss of information in which depth horizons UC/DC settle once they are grown up.

Additionally, evenness was found to increase with decreasing chl (except at LB). At LB, no significant correlation was found due to missing organisms below 4 cm depth making the calculation of evenness impossible. However, as previously discussed, there are hints of *A. islandica* and *L. balthica* inhabiting the sediment in these horizons which would then result in high values of evenness because of a homogenous distribution of both species and presumably a significant correlation.

Combining these findings, UC/DC seem to be organisms that are specialized to living in deeper horizons of the sediment by, for example, long siphons that enable them to feed at the sediment surface. In turn, the advantage of inhabiting deeper parts of the sediment is protection from predators and prevention of competition for food and space.

It was found that at the muddy stations (LB, MB, AB) UC/DC inhabit the sediment 2 - 4 cm deeper than at sandy stations. One would assume to find non-local transports to deeper horizons of the sediment. This is the case for MB with mean injection depth of $L = 4.6 \pm 2.2$ cm ($n = 18$). However, LB and AB belong to stations where lower injection depths were estimated.

All in all, there is evidence that the various organisms are adapted of coexisting by inhabiting different layers of the sediment. In muddy sediments animals are able to move up to 4 cm deeper.

Ecosystem services

The main bioturbation pattern found in the southwestern Baltic Sea is the increasing extent of non-local sediment mixing from west to east. Most abundant organisms, the way animals are distributed within the sediment and their assignment to functional groups explain this pattern. In the west, surficial biodiffusors inducing local mixing were generally most abundant as well as all most organisms were found at the sediment surface and their numbers decreases exponentially with depth. In the east, depth distribution of chl and organisms indicate non-local transports to be dominant and gallery-biodiffusors become more important. Local mixing depends on food supply while non-local transports increase with increasing abundance of gallery-biodiffusors.

Variability within stations indicated some stations being more heterogeneous (i.e. OB) than others (i.e. TW). Modeled D_B and injection fluxes J gained from the investigated locations indicate strong differences with factors varying from 3 (both sandy stations) to 30 (Mecklenburg Bay) within one station. This fact illustrates the importance of investigating 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.[1] No general seasonal patterns in bioturbation were found. Intensities of local sediment mixing depend on surface chl concentrations with increasing D_B when food supply is low. In turn, D_B decreases when food supply is high due to extended resting periods of organisms. Intensities of non-local sediment mixing rather depend on the abundance of gallery-biodiffusors. As GB become more abundant at the less saline stations more intense non-local sediment mixing can be expected in the context of global warming.

As a consequence, no general value for bioturbation can be assigned, as assumed, but rather each station has to be investigated separately. These 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 derive more realistic ecosystem services.[1]

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Declaration / Selbständigkeitserklärung

I hereby declare that I have completed the work submitted here independently and have composed it without outside assistance. Furthermore, I have not used anything other than the resources and sources stated and where I have taken sections from these works in terms of content or text, I have identified this appropriately.

Ich versichere hiermit an Eides statt, dass ich die vorliegende Arbeit selbstständig angefertigt und ohne fremde Hilfe verfasst habe. Dazu habe ich keine außer den von mir angegebenen Hilfsmitteln und Quellen verwendet und die den benutzten Werken inhaltlich und wörtlich entnommenen Stellen habe ich als solche kenntlich gemacht.

Rostock, den 29.09.2016

Appendix I

Appendix I: Bioturbation potential allocations for all macrozoobenthic species found in the present study for calculating BP_i after Solan et al. (2004 a). Mi and Ri are the reworking and mobility traits, mainly taken from Queirós et al. (2013). M scores: 1 for organisms in fixed tubes, 2 limited movement, 3 slow/free movement through the sediment matrix, 4 free movement via burrow system. R scores: 1 epifauna, 2 surficial modifiers, 3 upward and downward conveyors, 4 for biodiffusors, 5 regenerators. Assignment to functional groups after Kristensen et al. 2012.

species	M	R	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	Francois (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)
Neoamhitrite 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	Zettler, Gogina (pers. comm.)