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Community bioirrigation potential (BIP_c), an index to quantify the potential for solute exchange at the sediment-water interface

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ABSTRACT

Bioirrigation: the animal-induced exchange of solutes between pore water and overlying water - is a key process in sediments with profound implications for biogeochemical processes such as nutrient cycling and organic matter regeneration at the sediment water interface. There is an urgent need to understand how a changing environment will affect the irrigation activity of macrofauna and *vice versa*. A shift in species composition (e.g. from deep burrowing species to smaller, more opportunistic and shallow burrowing species) will have large effects on bioirrigation and thus on ecosystem function (such as benthic pelagic coupling). Considering the difficulties to determine area-covering rates of bioirrigation (e.g. in terms tracer-based fluxes) and the complexity of interactions of multiple species in the community that prohibit a direct measure of bioirrigation attributable to each species, a mechanistically-based approach is needed to predict relative intensities of bioirrigation activity based on the fundamental functional traits. We propose a conceptual framework to develop an index of bioirrigation that takes into account the biological mechanisms of bioirrigation and provides a simplified, yet functionally based approach to quantify the bioirrigation potential of benthic communities.

We developed the community bioirrigation potential (BIP_c) that provides a biomass- and abundance-weighted scoring system considering functional traits related to pore water and solute exchange. It may be used as a supplement to established methods to assess the function of marine soft sediments related bioirrigation. In analogy to the particle-related community bioturbation potential of Solan et al. (2004), context dependent organismal traits that affect ventilation and bioirrigation (feeding type, morphology of burrows, and burrowing depth) are combined with the data on abundance and biomass of the respective species. These are subsequently summed up to a community bioirrigation potential (BIP_c).

This review considers ecological traits relevant for bioirrigation and their classification into a bioirrigation index. Furthermore the necessary simplifications in the index (e.g. limiting its applicability to interfacial nutrient fluxes) are discussed. We also provide a working example from the southwestern Baltic Sea to illustrate the practical application of the index and a compilation of key species related to this area containing their classification into the considered bioirrigation traits.

1. Introduction

Benthic ecological systems are characterized by an extraordinary level of complexity (Loreau, 2010) caused by a variety of interactions on several biological levels such as species, processes and environments. Due to their unpredictability though, these benthic ecosystems are occasionally treated as a black box and often neglected in large-scale assessments (Woodin et al., 2016). Especially in the context of a changing environment (Bremner et al., 2006) and the progresses made in the management of coastal marine habitats (Frid et al., 2008), an increasing interest in predictability in the function of marine ecosystems has been raised (Gogina et al., 2017). To meet this political and societal demand, scientists have to take up the challenge to translate the contents of directives, e.g. the European Water Framework Directive (WFD) or the European Unions's Marine Strategy Framework Directive (MSFD), into adequate and realistic scientific approaches (Van Hoey et al., 2010). Especially the use of indices complies with easily applicable descriptors as requested e.g. in descriptor 6 (biodiversity and sea floor integrity) of the MSFD, aiming to assess condition and function of benthic communities (European Parliament, 2008).

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Considerable efforts have been undertaken to understand the key role of organisms and their ecological function in benthic ecosystems (Gray, 1981). Beside biomass, size and abundance as well as the environmental setting, the identity of organisms in terms of their activity and function are known to influence both, the magnitude (Törnroos et al., 2015; Woodin et al., 2010) and the variability of ecosystem processes (Belley and Snelgrove, 2016). Considering the functional identity of organisms and grouping them by ecological equivalency (e.g. morphological, physiological, behavioural and reproductive aspects) into functional groups, rather than aggregating benthic animal on the base of their taxonomic identity, is a widely spread approach (Bolam et al., 2002; Bonsdorff and Pearson, 1999; Diaz and Schaffner, 1990; Loreau et al., 2001; Norling et al., 2007; Pearson and Rosenberg, 1986; Rosenberg, 2001) that has led to a better understanding of the role of species within a community (Hale et al., 2014; Hewitt et al., 2008) and the relationship between ecological function, spatial distribution and environmental characteristics (Bolam et al., 2017). However the individual performance of species is not always unambiguous and is closely related to environmental factors, such as habitat or sediment type (Needham et al., 2010; Quintana et al., 2018), food availability (Bernard et al., 2016; Kristensen and Mikkelsen, 2003) or season (Maire et al., 2007; Widdows et al., 2004). Consequently, the classification of individual species into one of two functional groups can be influenced in manifold ways, rendering an implementation of this intraspecific variability into ecological assessments conceivable difficult. That implies, that pooling information to a limited number of categorical traits considered to explain these processes and functions within the ecosystem may lead to an underestimation of the role of species-environment interactions at this level (Hale et al., 2014) and substantially contributes to the blurriness of assessments via trait based indices. Apart from that, the use of such indices might still be a promising tool balancing between detailed scientific considerations (e.g. of process studies) and the practicability for users, given the selection of traits is adequate, depending on the particular functional aspects the traits are related to, the available information on this trait and the specific aim of the investigations (Petchey and Gaston, 2006).

One frequently used approach to assess the ecosystem function related to the sediment reworking activity of macrofauna is the community bioturbation potential (BP_c) (Queirós et al., 2013; Solan et al., 2004; Swift, 1993). This index includes quantitative measures of species biomass and abundance, as well as qualitative considerations for mobility and functional sediment reworking (François et al., 1997). The community bioturbation potential was recently linked to sediment chlorophyll a (Josefson et al., 2012) and total organic carbon (Solan et al., 2012), sediment reworking (Morys et al., 2017), redox metrics (Birchenough et al., 2012), biogeochemical cycling (Braeckman et al., 2014a; Sciberras et al., 2016; Van Colen et al., 2012; Wrede et al., 2017), chemical pollution (Mazik and Elliott, 2000) and the impact of invasive ecosystem engineers (Queirós et al., 2011). It was also used for modelling and mapping spatial differences of ecosystem functioning (Gogina et al., 2017). The wide range of topics applied illustrates the urgent necessity for simple terms, which are required to approximate the complexity of benthic systems. In a recent study, BP_c was also correlated to the bioirrigation activity of benthic organisms (Wrede et al., 2017). However, as the bioturbation potential is related to sediment reworking and therefore only contains traits relevant for that purpose (mobility and reworking mode), it is reasonable to discuss whether the BP_c is the appropriate measure to predict benthic function in all the above mentioned considerations (Queirós et al., 2015).

In Queirós et al. (2015) the limitations of the community bioturbation potential are clearly articulated: although one attribute of bioturbation, in particular the average distance of transported particles, can be predicted well by the index, its power to forecast bioturbation depth, biodiffusive transport of particles (D_b) and activity, especially of individual species, is limited attributable to the multi-faceted processes of bioturbation. Overall, Queirós et al. (2015) emphasise that a successful application of the index requires a careful consideration of predictable bioturbation traits, and especially when using the BP_c to predict benthic function, a combination of physical, chemical and biological parameters complementary to the limited power of single parameters or indices is advantageous (Birchenough et al., 2012).

Bioturbating organisms are known to alter the sediment properties by the translocation of particles by e.g., burrowing or construction activities, feeding and defecation. Simultaneously, burrowing organisms ventilate their burrows while feeding and respiration, causing an exchange of pore water and solutes therein at the sediment-water interface, termed bioirrigation (Kristensen et al., 2012; Meysman et al., 2006b). Burrowing macrofauna influence pore water dynamics with or without reworking the sediment (Jumars, 1993; Woodin et al., 2010) and the less apparent bioirrigation can exceed the transport of particles by several orders of magnitude, as quantitative comparisons of both processes demonstrated (Aller, 1982; Berg et al., 2001). Therefore, bioirrigation must also be taken into account when reflecting the effect of functional diversity (Bale and Kenny, 2005; Belley and Snelgrove, 2016; Braeckman et al., 2014b; Murray et al., 2014; Waldbusser et al., 2004).

Besides influencing the distribution of organic material by both, enhancing the supply and stimulating the degradation, burrowing and feeding activities of organisms increase the sediment water interface and consequently the effective area for solute exchange and biogeochemical reactions. Furthermore, the irrigation of pore water as a consequence of burrow ventilation causes steep chemical gradients and an enhanced exchange of solutes at these interfaces (Forster and Graf, 1992). By providing additional electron acceptors and by removing toxic metabolites, microbial reactions are stimulated. Various aspects concerning benthic infaunal organisms and their bioirrigation in marine sediments, such as burrow ventilation and pore water transport related to different sediment types, effects on biogeochemistry or methods to study these issues are summarized in Volkenborn et al. (2016).

Given that the rates for bioirrigation are not investigated comprehensively for a wide range of benthic species (Kristensen and Kostka, 2005) and the concurrent demand for easily applicable descriptors is strong, we intend to contribute to a conceptual framework for an index based quantification of the bioirrigation potential of benthic macrofauna. Because the integration of scientific data into an index inevitably involves simplification, a balance between applicability in terms of abstraction and extrapolation on the one hand, and a sufficiently precise mechanical description of processes (or activities leading to these processes) on the other hand is indispensable. With the community bioirrigation potential (BIP_c) we provide a scoring system based on the biomass and abundance weighted considerations of functional traits related to solute exchange at the sediment-water interface. In analogy to the BP_c, and as a further development of the functional group approach, bioirrigation will be assigned with a value in an index.

In a practical application example, the BIP_c was assessed for 3 stations in the southwestern Baltic Sea and a compilation of key species for this area, that are classified into the considered bioirrigation traits based on the information from literature and expert knowledge, will be provided.

2. Development of a bioirrigation index

The classification of marine macrofauna into groups was based on the application of biological traits of the respective species for diffusion dominated and advection dominated benthic systems (see section below). Trait scores were derived from an extensive review of published material and expert knowledge. Solely context dependent life modes connected with those purposes of bioirrigation were included. Further considerations leading to the scoring system are provided below. Following Swift (1993), Solan et al. (2004) and Queirós et al. (2013) each species/taxon was scored on increasing categorical scales, reflecting feeding type (FT) burrow type (BT) and environmental position

Table 1
Scoring system of the community bioirrigation potential. Note that deviating scores with regard to the benthic systems (diffusive and advective) within the traits burrow type (BT) and feeding type (FT) are labelled with an asterisk.

Trait	Mode	Scores diff. system	Scores adv. system
FT (Feeding type)	Predator (P), Scavenger (S), Herbivore (H), Omnivore (O)	1	1
	Deposit feeder (DF)	2	2
	Facultative Deposit/ Suspension feeder siphon (fDF/SF I)	2	3*
	Suspension feeder siphon (SF I)	3	3
	Facultative Deposit/ Suspension feeder (fDF/SF II)	2	4*
	Suspension feeder (SF II)	4	4
	Subsurface deposit feeder (SDF)	5	5
	Funnel feeder (FF)	6	6
BT (Burrow type)	Attached, Epifauna	0	0
	Free living	1	2*
	Living in a fixed tube	2	2
	Living in a burrow	3	4*
L (Depth)	Epifauna	0	0
	Depth in cm	cm	cm

(L) (Table 1). Scores were assigned on species level, but when no published information was available, material of species at the nearest taxonomic level was used, always aware of possible differences even of closely related species (Renz and Forster, 2013, 2014).

In cases when trait categories are irrelevant or negligible with regard to solute exchange across the sediment water interface (e.g. epifauna), 'zero' scores are assigned. To calculate a community bioirrigation potential (BIP_c), mean individual biomass (expressed by the relation B_i/A_i, where B_i is ash free dry weight in g m^{-2}, and A_i is abundance in ind. m^{-2}) of each species (i) within a sample is multiplied by the relevant scores for the trait categories feeding type (FT_i), burrow type (BT_i) and depth (L_i), and weighted in turn by species abundance as given in the following equation. Afterwards the results are summed up across all species present in the sample at a particular station.

$$BIP_c = \sum_{i=1}^{n} \sqrt{\frac{B_i}{A_i}} \times A_i \times FT_i \times BT_i \times L_i$$

3. Abundance and biomass

Abundance and biomass are essential characteristics to describe the variability of benthic communities but are subject to considerable fluctuations in time and space (Eklöf et al., 2017; Rosenberg, 2001). In the particle related community bioturbation potential (BP_c), biomass ("body size" sensu Solan et al. (2004)) enters the index as fresh weight (FW) in consistency with its use in literature. Furthermore, biomass in terms of 'living size' is thought to have a major effect on bioturbation (Queirós pers. communication). However, because ash free dry weight (AFDW) only includes biologically active tissue, it is thought to be a more precise measure for macrofaunal biomass (Eklöf et al., 2017). In particular, the use of fresh weight would disproportionally weight the group of bivalves and gastropods by the inclusion of shells. Ash free dry weight can be estimated from fresh weight by the use of species specific conversion factors (Ricciardi and Bourget, 1998), if e.g. only fresh weight for samples is available. In analogy to the bioturbation potential, the individual biomass of the organisms (ratio of biomass per abundance) for the BIP_c was square root transformed to reduce effects of large organisms.

4. Burrow ventilation and feeding type

The ventilation of burrows and associated pore water irrigation of macrofauna serves several objectives, basically ingestion of food, respiration, reproduction and removal of metabolic products (Kristensen et al., 2012). The patterns are highly variable with regard to both, individual variations within one species (e.g. due to body size, age and fitness) as well as differences among taxonomic groups. The ventilation intensity (e.g. the volume of transported water), also related to burrow structure and irrigation rate, is closely linked to these objectives (Kristensen and Kostka, 2005). Deposit feeders ventilate their burrows predominantly for respiration, regardless whether they feed at the sediment – water interface (surface deposit feeder, DF) or below the sediment surface (subsurface deposit feeder, SDF) (Lee and Swartz, 1980). Continuous ventilation of burrows for the sole purpose of respiration is not evident (Christensen et al., 2000) and ventilation activities of deposit feeders are often un-incisive, intermittent and less frequent compared to suspension-feeding organisms (Shull, 2009a). Therefore, portions of burrows of some species may not be ventilated, leading to an overestimation of the irrigation intensity when assessed by burrow length (Koretsky et al., 2002; Sandnes et al., 2000). Conversely, suspension feeders need to process large amounts of water for capturing food and for respiration and these pronounced ventilation activities result in well flushed burrows (Kristensen and Kostka, 2005). In Shull (2009b) burrow ventilation parameters of several species from laboratory studies are summarized. Pumping rates of deposit feeding species typically do not exceed 100 ml h^{-1}, whereas ventilation rates of suspension feeders of > 1000 ml h^{-1} are not uncommon (Volkenborn et al., 2016). On population levels, deposit feeding populations do not exceed 200 l m^{-2} d^{-1} irrespective of taxonomic groups, whereas suspension feeders occasionally surpass 1000 l m^{-2} d^{-1} (Kristensen and Kostka, 2005).

By balancing between biodiversity and ecosystem function, the concept of grouping benthic animals by ecological equivalency into functional groups provides a helpful tool to understand the complexity of ecological systems (Gérino et al., 2003). Within functional groups species share common interspecific and/or intraspecific attributes, such as feeding and mobility (Diaz and Schaffner, 1990; Fauchald and Jumars, 1979; Jumars et al., 2015) or sediment reworking (François et al., 2002). It is generally recognized that the feeding mode of benthic macrofauna plays a key role among variables such as mode of burrowing, locomotion and defecation (Arruda et al., 2003; Diaz and Schaffner, 1990; Fauchald and Jumars, 1979; Jumars et al., 2015; Pagliosa, 2005) and that all other modes may be seen as secondary reflection of the feeding biology and morphology (McLachlan, 1977). Sediment reworking and mobility are typically used to assess bioturbation activities in functional trait analysis, but Belley and Snelgrove (2016) applied the feeding type as biological trait related to bioirrigation activities to explain variations of benthic fluxes at different seafloor locations.

Therefore, we consider the use of the feeding type as the most suitable variable among the variety of functional groups to assess a bioirrigation potential for benthic macrofauna. For the bioirrigation index, 6 different feeding modes (Table 1) are scored in ascending order reflecting their increasing effects on pore water exchange, including (1) species with no or a negligible effect e.g. herbivores (H), scavengers (S), omnivore (O) and predators (P), followed by surface deposit feeders (2). Suspension feeding species were subclassified into species with either indirect (3) or direct contact (4) to pore water exchange. The first group (3) mainly consists of bivalves, whose ventilation activities are restricted to tube-like structures, such as siphons, bounding pore water exchange. The second group (4) contains organisms such as polychaetes that create a water flow, e.g. via undulating body movements and that consequently directly connect pore water with overlying water. Species, that are able to facultatively switch between feeding modes are not uncommon among benthic macrofauna, e.g. many surface deposit

feeding organisms are also capable of practicing suspension feeding (Jumars et al., 2015), and therefore constitute a special case within this classification. The ratio of deposit to suspension feeding may vary considerably among different populations of the same species, depending on a variety of environmental factors such as hydrodynamic conditions and supply of organic material from the water column (Riisgård and Kamermans, 2001; Riisgård and Larsen, 2016). However, data on the frequency of changing feeding modes related to environmental conditions are rather complex and unsuitable for an implementation into the index. Being aware of the roughness of this classification, the feeding mode of species capable of switching between deposit feeding and suspension feeding was related to the respective sediment type (diffusive vs. advective systems) within the index. In case of e.g. *Hediste diversicolor* or *Limecola balthica,* known as representatives for this switching feeding mode (Riisgård and Kamermans, 2001), the dominant feeding mechanism in muddy sediments (diffusive systems) would be deposit feeding, whereas suspension feeding would prevail on sandy sediments (advective systems).

To ensure an applicability and feasibility of the index, we refrain from further differentiations e.g. between selective and non-selective feeding types (Fauchald and Jumars, 1979) or active, passive and obligate suspension feeding organisms (Jumars et al., 2015).

The mechanism of subsurface deposit feeding (5) has pronounced effects on bioirrigation as investigated for *Heteromastus filiformis* (Aller and Yingst, 1985; Quintana et al., 2007). But, since the data situation on bioirrigation activity and related effects of subsurface feeding species are rare, the classification and especially ranking of this group is associated with a certain degree of uncertainty and needs to be confirmed by further investigations. Funnel feeder (6) is a sub-group of deposit feeding organisms mainly represented by a small number of arenicolid, maldanid and pectinariid polychaetes, that feed at the sediment water interface from below the sediment surface (Jumars et al., 2015). Even though the feeding mode is restricted to a small number of taxa and individuals (in the southwestern Baltic Sea primarily *Arenicola marina*), the outstanding influence on pore water exchange and related benthic fluxes of organisms classified within this group (Belley and Snelgrove, 2016) determine its high rating.

5. Burrow type

The occurrence of tubes and burrow structures of benthic macrofauna significantly contributes to the magnitude of pore water and solute exchange across the sediment water interface (Aller, 1980; Hölker et al., 2015), even if considerable differences with respect to burrow morphology among benthic invertebrates arise. In particular the creation of biogenic structures such as tubes and burrows is known to increase the exchange of pore water and solutes therein, whereas e.g. “free living organisms”, mobile, shallow burrowing macrofauna without distinct burrow linings (e.g. *Nephtys sp*. and many bivalves), have a lower influence on pore water fluxes (Mermillod-Blondin, 2011; Mermillod-Blondin et al., 2004; Michaud et al., 2005, 2006; Pelegri and Blackburn, 1995). The magnitude of pore water exchange is determined by the modality of contact between water transported in the burrow structures and the adjacent pore water. Direct contact is possible through burrow linings, whereas for the flow located within specific body parts such as siphons (Wikander, 1980) minimum effects on bioirrigation are expected.

Notwithstanding the indubitable increase of the sediment water interface by the creation of distinct tube and burrow structures (Kristensen and Kostka, 2005), the contribution of tube building organisms to bioirrigation is controversially discussed. Tubicolous polychaetes (e.g. *Lanice conchilega*, *Pygospio elegans*) construct their permanently inhabited tubes from mud, sand grains or shells cemented together with secreted organic material or from hardened calcium carbonate (O'Clair and O'Clair, 1998). Generally the tubes are considered to be permeable for solute diffusion, although the effective diffusion coefficients are noticeably reduced to 10–40% of the free solution value (Aller, 1983). Woodin et al. (2010) assumed minor effects on bioirrigation based on pressure differences for e.g. *Diopatra cuprea*, a large tube building polychaete, whereas the effects of *L. conchilega* on biogeochemical fluxes are pronounced compared to ‘free living’ organisms (Braeckman et al., 2010; Forster and Graf, 1995; Foshtomi et al., 2018).

Due to permeability effects the shape of irrigated burrows is closely related to sediment characteristics. A detailed description of specific burrow structures and their irrigation is given in Kristensen and Kostka (2005). In muddy sediments where permeability is low, open ending burrows with two or more openings to the sediment surface are common (Kristensen et al., 2012) and radial molecular diffusion is the driving force for pore water exchange. The U-shaped structure allows a unidirectional flushing of burrows that is assumed to be less energy-intensive and to create a more stable environment compared to oscillating conditions of blind ending burrows (Aller, 1994; Forster and Graf, 1992; Gilbert et al., 2016; Kristensen and Kostka, 2005). In contrast, burrow irrigation in sandy, permeable sediments is dominated by advection in the pore water (Meysman et al., 2006a), facilitating the building of blind-ending burrows (Kristensen et al., 2012). Depending on the permeability, blind-ending burrows may be flushed uni- or bidirectionally. Despite knowing that the different shapes of burrows are closely related to both, irrigation pattern and magnitude of pore water exchange, we refrain from the implementation of the burrow geometry into the index, because these structures depend on various and often interdependent factors such as feeding mode, sediment characteristics, environmental conditions as well as size and abundance of macrofauna. Here, the high variability of burrow shapes necessitates simplification.

The diffusion through burrow walls can be reduced by mucus linings (Aller, 1983; Kristensen and Kostka, 2005), characterizing a wide range of burrowing species (Murray et al., 2002). An observed 1.7–6.7 fold reduced diffusivity by the occurrence of 10 μm thin mucus linings (Aller, 1983) suggests that the mucus production may be the controlling factor for diffusion across burrow linings (Meysman et al., 2006b; Zorn et al., 2006).

Therefore, if species are known for a pronounced mucus production consistent with a reduced diffusivity, the scores for the burrow type of the respective species should be adapted and reduced by one, leading to a classification of burrowing species with a pronounced mucus production analogous to organisms living in a fixed tube (see discussion above).

For the bioirrigation potential 4 different context dependent modes of burrowing (BT) were considered (Table 1). Attached species (0) include organisms mostly living above the sediment surface but occasionally burrowing into the sediment a few millimetres deep (e.g. many gastropods). For these species the influence of burrowing type on bioirrigation is assumed to be negligible. ‘Free living organisms’ (1) relates to mobile, shallow burrowing organisms without distinct burrow linings and mostly includes bivalves and a few polychaetes. Their bioirrigation pattern is assumed to be rambling and moderate. The group of ‘tube dwellers’ (2) comprises organisms permanently living in fixed tubes with a reduced permeability. Despite a pronounced ventilation activity referred to as piston pumping (Forster and Graf, 1995), their bioirrigation effect is assumed to be intermediate. For ‘burrow dwellers’ (3), the occurrence of burrow linings is the main characteristic. Regardless of the shape of their burrows, burrow dwellers are considered to have the most pronounced bioirrigation effect.

6. Burrowing depth

Because the magnitude of pore water exchange facilitated at a given sediment depth critically depends on the dimension of burrow wall surface at that depth (Koretsky et al., 2002), the burrowing depth of macrofauna plays a key role when assessing bioirrigation. Beside sediment properties and seasonal patterns (Esselink and Zwarts, 1989),

sizes and feeding types of organisms are relevant parameters determining the burrowing depth. Kristensen and Kostka (2005) substantiated a significant linear correlation between burrow depths of relatively large species and diameter of burrows referring to organism's width, applicable mainly to adult but not small or juvenile species. Furthermore, with regard to e.g. several bivalve species, the burrowing depth of siphon-exhibiting species depends on the length of the siphon (Zwarts and Wanink, 1989) and increases with increasing size of the organism (Zaklan and Ydenberg, 1997). These observations hint at a general positive relation between size/weight and burrowing depth.

Deep burrowing organisms increase the sediment surface available for pore water exchange and locally introduce oxygen into anoxic sediment layers. Consequently, by altering the distribution of redox reactions the biogeochemical heterogeneity of the sediment increases. Therefore the effects of deep burrowing organisms are more pronounced compared to those of shallow burrowers merely reaching oxic or suboxic sediments (Aller, 1988).

For the BIP_c the burrowing depth (or 'environmental position' sensu Törnroos and Bonsdorff (2012)) is implemented in the index as depth in centimetres and we desist transferring these depths into scores, because the translation of the vertical distribution of macrofauna into scores cannot be validated sufficiently based on literature. Burrowing depth of macrofauna may enter the bioirrigation potential via either a mean effective burrowing depth (L_{eff}), directly determined from samples (layer, where the respective species was found) or a theoretical burrowing depth (L_{max}) that is given in the literature. Furthermore a differentiation between burrowing depth of juvenile and adult organisms could be implemented. When no data on actual position of species is given (e.g. due to the sampling design), literature values can be applied. It should be noted however, that the application of these maximum burrowing depths leads to higher overall BIP_c.

7. Diffusive vs. advective systems

The physical and hydrological properties of sediments are decisive factors determining the magnitude of pore water exchange in benthic ecosystems (Palmer et al., 1997). In both, sandy and muddy sediments, the ventilation activities of macrofauna that are the driving mechanisms for bioirrigation are the same, increasing the transport of solutes within the pore water and its exchange at the sediment water interface. But the underlying physical processes in mud and sand are very different. Diffusion dominated systems are characterized by fine grained, muddy sediments, a low permeability and molecular diffusion as driving mechanism for solute exchange across the burrow wall. In contrast, in advection dominated systems, coarse grained, sandy sediments and a high permeability enable an advective flow of water across burrow walls (Aller, 1980; Huettel and Webster, 2001; Kristensen and Hansen, 1999; Meysman et al., 2006b). Advection dominated systems showed a more than 20 fold higher microbial respiration at the burrow wall-sediment interface compared to diffusion dominated systems (Mermillod-Blondin and Rosenberg, 2006). Permeable sediments associated with an advective transport of pore water are typically characterized by permeability above $10^{-12}\,m^2$ (Glud et al., 1996; Huettel et al., 2014). Below this critical threshold, advection becomes negligible. In association with the bioirrigation the permeability threshold is controversially discussed (Brand et al., 2013; Woodin et al., 2010). The permeability effects on bioirrigation are likely to be gradual rather than starting at a threshold value, however the proposed BIP_c is far from including such subtlety.

Following Mermillod-Blondin and Rosenberg (2006), we distinguish between diffusion dominated and advection dominated benthic environments, being aware of the crudeness of this classification. In the BIP_c, the two different systems are taken into account by increasing the relevant scores for the 'free living' and 'living in a burrow' burrow type traits by 1 within the advective system (Table 1). For the remaining category 'living in a fixed tube', an adjustment of scores from diffusion to advection dominated systems is not necessary because the permeability of the tubes is independent from the ambient system.

Table 2
Selected biotic and abiotic characteristics of the sampling stations Lübeck Bay (LB), Mecklenburg Bay (MB) and Stoltera (ST). Slight deviations from Morys et al. (2016) and (2017) are caused by rounding errors. Abundance and biomass are given as mean values with standard error (se).

	LB	MB	ST
Sediment type	mud	mud	sand
Median grain size (μm)	19.4	17.4	148.8
Water depth (m)	23	25	18
Number of cores	23	22	24
Total number of species (per station)	13	9	28
Abundance (ind. m^{-2})	1961 ± 259	3098 ± 478	5080 ± 565
Biomass (afdw m^{-2})	0.31 ± 0.16	13.70 ± 4.01	44.76 ± 9.37

8. Application

To illustrate the practical application and the range of numbers obtained by the index, the community bioirrigation potential was calculated on the base of a data set published in Morys et al. (2016) and Morys et al. (2017). The part of the data set used here comprises 3 sampling stations in the southwestern Baltic Sea that differ in their biotic and abiotic properties (Table 2 and Fig. 1). Each station was sectored in 6 locations (S1−S6) and each location was sampled with 4 cores (inner diameter of 10 cm) by deploying a multicorer, leading to a total of 24 cores per station. Macrofauna was extracted by slicing the cores in 0.5 cm intervals to 3 cm and at 1 cm intervals to 10 cm depth. The advantage of the use of these data is the information on the vertical distribution of macrofauna within the samples. Being aware of methodical uncertainties and smaller sampling areas due to the sampling procedure (using multicorer cores instead of e.g. a van Veen grab), the calculated BIP_c from real observed burrowing depths (L_{eff}) can be compared to literature depths (L_{max}) based values in the workout example. For the practical application of the BIP_c we refer to the stations Lübeck Bay (LB), Mecklenburg Bay (MB) and Stoltera (ST). Detailed information on station characteristics, sampling and analyses are given in Morys et al. (2016).

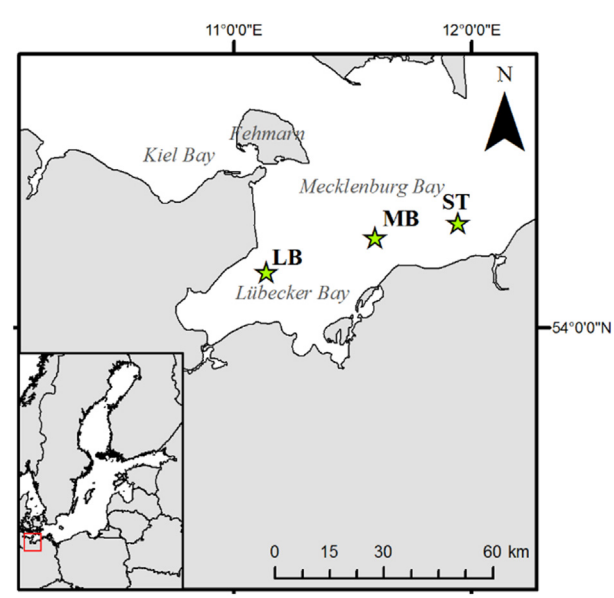

Fig. 1. Sampling stations in the southwestern Baltic Sea.

Table 3
Classified key species of the southwestern Baltic Sea. (X) indicates the presence of the respective species at the stations Lübeck Bay (LB), Mecklenburg Bay (MB) and Stoltera (ST). The most dominant species with regard to abundance and/or biomass (> 8% of total abundance/biomass) have been adopted from Morys et al. (2017). Note that feeding type (FT) and burrow type (BT) of the respective species are displayed in scores, whereas L_{max} (maximum literature values; references are given in appendix in Table 5) and mean L_{eff} (obtained from core samples) are given in cm. Species specific standard deviation (sd) for mean L_{eff} refers to the total number of cores that is given in Table 2. If scores for the two different systems (diff. vs. adv.) related to FT, BT and L_{eff} deviate, the respective information for the advective system is given in parentheses. The list was extended by **Arenicola marina,* due to its key function with regard to bioirrigation and its occasional occurrence at ST. For L_{eff} and sd labelled with (**) no information on burrowing depth from core samples can be given due to methodological reasons.

	Species	LB	MB	ST	Feeding type	FT	BT	L_{max}	L_{eff} ± sd
Bivalvia	***Abra alba***	x	x	16.7%/0.1%	DF, SF (I)	2(3)	1(2)	7	1.6 ± 1.2 (1.5 ± 0.6)
	Arctica islandica		3.9%/99%		DF, SF (I)	2(3)	1(2)	10	3.4 ± 2.4
	Cerastoderma sp.				SF (I)	3	1(2)	3	**
	Corbula gibba			x	SF (I)	3	1(2)	5	1.4 ± 0.8
	Kurtiella bidentata	34.2%/5.3%	x	28.3%/0.1%	DF, SF (I)	2(3)	1(2)	3	0.9 ± 0.3 (1.9 ± 1.3)
	Limecola balthica			6.4%/9.1%	DF, SF (I)	2(3)	1(2)	6	(2.7 ± 1.2)
	Mya arenaria				SF (I)	3	1(2)	25	**
	Parvicardium pinnulatum	x			SF (I)	3	1(2)	3	1.0 ± 0.0
Crustacea	*Corophium volutator*				DF, SF (II)	2(4)	3(4)	5	**
	Diastylis rathkei	14.3%/8.8%	84.9%/0.4	24.9%/0.1%	DF	2	1(2)	3	1.0 ± 1.2 (1.4 ± 0.7)
	Microdeutopus gryllotalpa	x			H, DF	2	2	2	1.5 ± 0.0
	Pontoporeia fermorata				DF, SF (II)	2(4)	1(2)	2	**
Gastropoda	*Peringia ulvae*			x	G, DF	2	1(2)	1	(1.3 ± 0.5)
	Retusa truncatula	x		x	P	1	1(2)	1.5	1.0 ± 0.0 (1.1 ± 0.2)
Polychaeta	*Ampharete sp.*			x	DF	2	2	5	(2.1 ± 2.3)
	*Arenicola marina**				FF	6	3(4)	40	**
	Aricidea minuta				SDF	5	1(2)	6.5	(3.9 ± 1.4)
	Bylgides sarsi	x	x		P	1	1(2)	2	0.8 ± 0.5
	Capitella capitata	24.6%/71.6%			SDF	5	3(4)	9	1.3 ± 0.6
	Dipolydora quadrilobata			x	DF, SF (II)	2(4)	2	4	(2.2 ± 1.2)
	Eteone longa	x	x		P, S	1	1(2)	6.5	1.0 ± 0.0 (3.0 ± 3.0)
	Hediste diversicolor				DF, SF (II)	2(4)	3(4)	15	**
	Lagis koreni			x	SDF	5	2	10	(2.3 ± 0.9)
	Marenzelleria neglecta				DF, SF (II)	2(4)	3(4)	35	**
	Neoamphitrite figulus			x	DF, SF (II)	2(4)	2	3	(2.5 ± 0.0)
	Nephtys hombergii		x		P, S	1	1(2)	15	3.1 ± 2.8
	Paraonis fulgens		x		SDF	5	1(2)	10	2.0 ± 0.5
	Phyllodoce mucosa	x		x	P, S	1	1(2)	4.5	1.0 (1.3 ± 0.4)
	Polydora sp.			x	S, DF, SF (II)	2(4)	2	6.5	(1.0)
	Pygospio elegans				DF, SF (II)	2(4)	2	8	**
	Scoloplos armiger			x	SDF	5	1(2)	15	(2.8 ± 1.8)
	Sphaerodoropsis baltica			x	SDF	5	1(2)	1.5	(1.2 ± 0.5)
	Terebellides stroemii				DF	2	2	10	**
	Trochochaeta multisetosa				DF, SF (II)	2(4)	2	2	**
Priapulida	***Halicryptus spinulosus***	together 14%/7.5%		x	P	1	1(2)	25	1.2 ± 0.5 (1.6 ± 0.9)
	Priapulus caudatus		x		P, S	1	1(2)	15	1.4 ± 0.7 (1.9 ± 1.1)

9. Classified key species of the southwestern Baltic Sea

Table 3 provides the classification for the bioirrigation potential (feeding type (FT)), burrowing type (BT) and burrowing depth (L) assigned to 36 species of the southwestern Baltic Sea for the stations Lübeck Bay (LB), Mecklenburg Bay (MB), both muddy sites (diffusive systems) and a sandy site (advective system) Stoltera (ST), selected based on Morys et al. (2017).

The species specific classification for the southwestern Baltic Sea taxa that will be weighted by abundance and biomass afterwards is shown in Fig. 2. Thereby, the classification of species into groups is fraught with a certain level of uncertainty that is different among the used three traits of the BIP_c due to the different nature of the traits. Possible errors within the traits FT and BT potentially arise from a misjudgement of either score or biological trait classification. Thus, they may reflect inter- and intraspecific variations in the behaviour of organisms. Contrarily, the depth L_{eff} derived from e.g. mean value of all individuals of one species within one core can be quantified and associated with a statistical error, as shown by the standard deviation of L_{eff} in Fig. 2. By comparing these error bars with the magnitude of the other traits (BT and FT) the level of uncertainty of L_{eff} can be assessed in comparison to e.g. the feeding type.

Overall, the data set contains a total of 36 species from 5 classes (Table 3) and for each species, information on biomass (dry weight) and abundance in relation to the respective sediment layer from which they were extracted, are given in the data set from Morys et al. (2016) and Morys et al. (2017). Ash free dry weight was estimated from dry weight by the application of species specific conversion factors (internal conversion factor list from the Leibniz Institute for Baltic Sea Research, Warnemünde including 500 species and about 15000 measurements).

In total, the calculated bioirrigation potential (Table 4) shows clear variations among the 3 stations. BIP_c was lowest at LB (62 ± 23), intermediate at MB (432 ± 115) and highest at ST (1739 ± 235). In general, the BIP_c at LB was low when compared to MB, a station with similar biotic and abiotic characteristics. This may be owed to recurring hypoxia and a high organic content of the sediment as well as the fact that the area was used as an industrial dumping site until 1971 (Leipe et al., 1998; Zettler et al., 2000).

Large differences in the BIP_c within the locations emerge, reflecting the spatial heterogeneity and patchy distribution of species within benthic communities (Morrisey et al., 1992). Dominant species in terms of abundance and biomass of the sampling stations (Morys et al., 2017) are displayed in Table 3. At station LB, biomass was clearly dominated by *Capitella capitata* (71.6%), *Diastylis rathkei* (8.8%) and the priapulids *Halicryptus spinulosus* und *Priapulus caudatus* (7.5% collectively). The smallest BIP_c (1 ± 0) at location S4 (LB) can be attributed to a comparatively low biomass of 0.24 ± 0.11 g afdw m^{-2} and a shallow mean burrowing depth of the organisms (0.5 ± 0.3 cm). Compared to a BIP_c of 44 ± 14 at S1 (LB), the differences result from a considerably higher biomass (58.6 ± 31.0 g afdw m^{-2}) in the respective cores, but apart

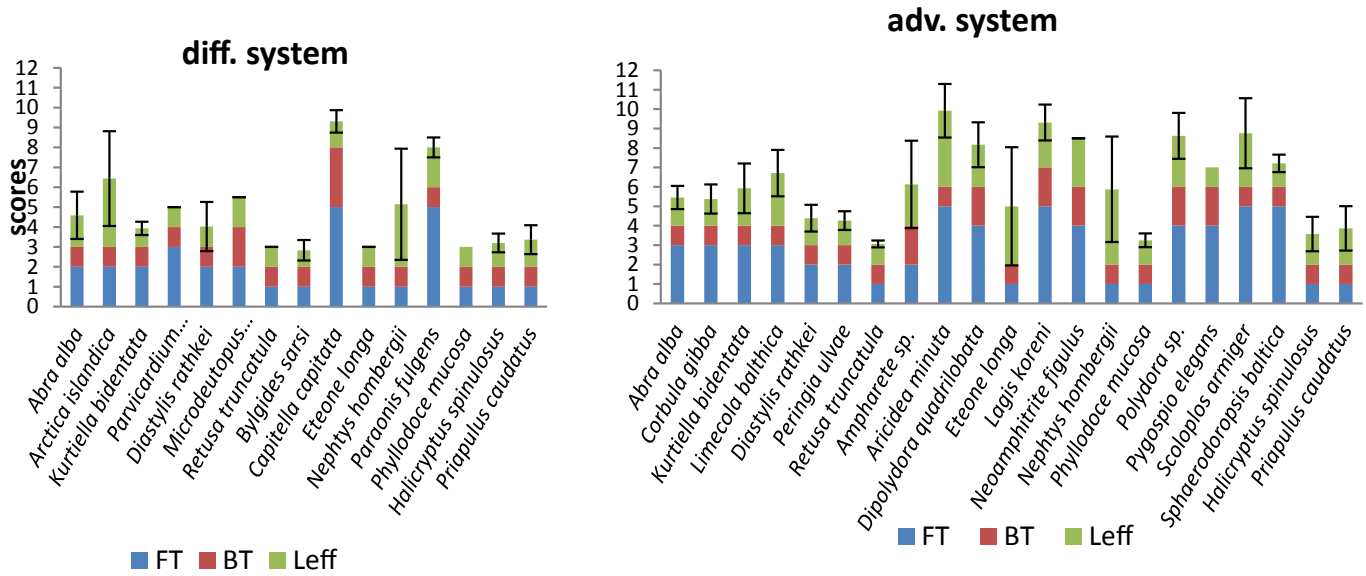

Fig. 2. Scores for FT_i, BT_i and L_{eff} of the BIP_c in the respective diffusive and advective systems; Note that the displayed standard deviation (sd) relates to the burrowing depth L_{eff} as assessed from mean values from the data set of Morys et al. (2016) and (2017), see also Table 3 and appendix Table 5. For the diff. system L_{eff} was calculated from stations LB and MB, whereas for the adv. system L_{eff} refers to ST. Species are sorted by class (Bivalvia, Crustacea, Gastropoda, Polychaeta, Priapulida) and within classes in alphabetical order.

Table 4
Mean BIP_c (referring to afdw (g m^{-2})) with standard error (se) from 6 locations (S1 − S6) of Lübeck Bay (LB, n = 23 cores), Mecklenburg Bay (MB, n = 22 cores) and Stoltera (ST, n = 24 cores).

location	LB	MB	ST
S1	44 ± 14	47 ± 24	1125 ± 579
S2	52 ± 36	491 ± 245	1816 ± 267
S3	191 ± 112	531 ± 244	1977 ± 487
S4	1 ± 0	170 ± 84	2545 ± 245
S5	285 ± 268	265 ± 231	1019 ± 243
S6	396 ± 134	269 ± 252	1953 ± 635
mean	**162 ± 64**	**295 ± 76**	**1739 ± 235**

from that the range of species within the cores of the subsamples is comparable and the mean burrowing depth is similar (0.5 ± 0.3 cm). The high BIP_c at the sandy station ST reflects the higher biomass as well as the different species inventory, with *Arctica islandica* and *Limecola balthica* dominating the BIP_c (Table 3). Furthermore the additional accentuation of free living and burrow building organisms by adjusting the scores of BT for an advective dominated system leads to a 1.9-fold increased BIP_c (1739 ± 235) at ST, compared to a calculated BIP_c based on the scores for a diffusion dominated system (897 ± 123).

The results clearly emphasise the dominance of biomass and abundance of the bioirrigation potential given by the mathematical formulation of the index. Both parameters are important in reflecting activity rates of benthic macrofauna (Woodin et al., 2016), but the addition of functional traits information for bioirrigation facilitates a more precise assessment of functioning of marine sediments. However, it is conceivable to refine the index by e.g. modifying the individual weighting term, i.e. biomass/abundance term. In a similar approach to capture bioirrigation with an index, Wrede et al. (2018) modified the biomass/abundance term by applying an exponent of 0.75 instead of the square root scaling as suggested by Solan et al. (2004) to account for the mass dependency of the metabolic rate. This is an interesting approach, however as the allometric exponent may vary considerably both, on intra- and interspecific levels (Brey, 2010), further investigations are needed to assess the appropriateness of this relation.

The quality of information on burrowing depth (depth obtained from samples L_{eff} vs. theoretical depth L_{max}) furthermore determines the magnitude of the BIP_c values. When using a depth (L_{max}) from literature that mainly refers to the maximum burrowing depth (see appendix Table 5) the calculated bioirrigation potential will be higher. Compared to a mean BIP_c of 162 ± 64 at LB, calculated with the L_{eff} from the samples, the potential estimated on the base of literature values (L_{max}) is 7.95 fold higher (1284 ± 711). This indicates that the theoretical depth L_{max} is only suitable to a limited extend for the implementation in the index e.g. when the appropriate information on individual effective burrowing depth is not given. The use of L_{eff}, however, enables a more differentiated view by better reflecting the vertical distribution of macrofauna e.g. the shallow burrowing depth of juvenile or relatively small organisms compared to deeper burrowing large, adult animals in the sediment.

The wide variety of approaches to realize the principles of directives is an ongoing process, that requires continuous research and permanent updates based on scientific progresses (Van Hoey et al., 2010). Being aware, that the assessment of ecosystem functions such as bioirrigation in terms of a potential is an evolving process, the presented theoretical and conceptual framework of the bioirrigation index needs further validation e.g. in terms of a comparison of measured pore water exchange of communities with the calculated bioirrigation potential. Furthermore, new scientific insights related to the individual behaviour and ecology of benthic animals may cause a shift in the classification of single species as e.g. shown for the particle transport behaviour of *L. balthica* or *A. alba* (Morys et al., 2017).

The advantage of the index is in its simplicity that allows a wide applicability owning to its reliance of largely available macrofaunal data. If validation will confirm the improved usability of the proposed index as a proxy for bioirrigation-driven processes, it will be a highly valuable metric suitable for spatial full coverage estimates. But even though the bioirrigation potential is funded and derived from a mechanistic view of processes involved in bioirrigation, the index is not the appropriate tool to mechanistically explain e.g. complex biogeochemical processes at the sediment-water interface. Accepting the limitations imposed by bundling information on a large variety of life modes to single traits, the provided bioirrigation potential allows capturing the variability in the function of communities in marine sediments. With the current study used as a baseline to expand upon, and keeping in mind the habitat and species-specific nature of reflected

biogeochemical processes, the bioirrigation index may then be used as a supplement to existing methods, e.g. the particle related bioturbation potential (Solan et al., 2004) to assess the function of benthic communities in terms of the MSFD more comprehensively. Furthermore, the presented considerations based on a reduction of bioirrigation to three basic functional traits enable the implementation of bioirrigation in ecological models because models rely on simplifications that rarely exist in the present form.

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Appendix

Table 5
List of references related to the theoretical maximum burrowing depth L_{max} (cm) of the classified key species of the southwestern Baltic Sea. Note when Morys et al. (2016) and (2017) is given, maximum burrowing depth was extracted from the data set.

	Species	L_{max} (cm) Literature	Reference
Bivalvia	*Abra alba*	7	(Braeckman et al., 2010; Rosenberg, 1993)
	Arctica islandica	10	(Cargnelli et al., 1999; Strahl et al., 2011; Taylor, 1976)
	Cerastoderma sp.	3	(Flach, 1996; Zwarts and Wanink, 1989)
	Corbula gibba	5	(Rosenberg, 1974; Yonge, 1946)
	Kurtiella bidentata	3	(Ockelmann and Muus, 1978)
	Limecola balthica	6	(Virtasalo et al., 2011) and references therein
	Mya arenaria	25	(Forster and Zettler, 2004; Zaklan and Ydenberg, 1997; Zwarts and Wanink, 1989)
	Parvicardium pinnulatum	3	Zettler (expert knowledge)
Crustacea	*Corophium volutator*	5	(Jensen and Kristensen, 1990)
	Diastylis rathkei	3	(Virtasalo et al., 2011) and references therein
	Microdeutopus gryllotalpa	2	(Borowsky, 1989)
	Pontoporeia fermorata	2	(Lopez and Elmgren, 1989)
Gastropoda	*Peringia ulvae*	1	(Huxham et al., 1995)
	Retusa truncatula	1,5	(Morys et al., 2016, 2017)
Polychaeta	*Ampharete sp.*	5	(Hartmann-Schröder, 1996)
	Arenicola marina	40	(Kristensen and Kostka, 2005) and references therein
	Aricidea minuta	6,5	(Morys et al., 2016, 2017)
	Bylgides sarsi	2	(Virtasalo et al., 2011) and references therein
	Capitella capitata	9	(Gamenick et al., 1998)
	Dipolydora quadrilobata	4	(Morys et al., 2016, 2017)
	Eteone longa	6,5	(Morys et al., 2016, 2017)
	Hediste diversicolor	15	(Kristensen and Kostka, 2005) and references therein
	Lagis koreni	10	(Dobbs and Scholly, 1986; Mayhew, 2007)
	Marenzelleria neglecta	35	(Renz and Forster, 2013; Zettler et al., 1994)
	Neoamphitrite figulus	3	(Morys et al., 2016, 2017)
	Nephtys hombergii	15	(Braeckman et al., 2010)
	Paraonis fulgens	10	(D'Andrea et al., 2004)
	Phyllodoce mucosa	4,5	(Morys et al., 2016))
	Polydora sp.	6,5	(Morys et al., 2016, 2017)
	Pygospio elegans	8	(Virtasalo et al., 2011) and references therein
	Scoloplos armiger	15	(Kruse et al., 2004)
	Sphaerodoropsis baltica	1,5	(Morys et al., 2016, 2017)
	Terebellides stroemii	10	(Virtasalo et al., 2011) and references therein
	Trochochaeta multisetosa	1,75	(Morys et al., 2016, 2017)
Priapulida	*Halicryptus spinulosus*	25	(Powilleit et al., 1994)
	Priapulus caudatus	15	(Virtasalo et al., 2011) and references therein

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