Original Articles

Organism functional traits and ecosystem supporting services – A novel approach to predict bioirrigation

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ABSTRACT

Increasing anthropogenic activities on land and at sea underline the demand for easily applicable indices to effectively predict human mediated changes in ecosystem functioning. Here, we propose a novel bioirrigation index (IP_c) that is based on body mass, abundance, burrow type, feeding type and injection pocket depth of bottom dwelling animals. The index was validated with combined field (in situ communities) and manipulative (single species) experiments. Results from both community and single-species experimental incubations indicate that IP_c is able to predict the bioirrigation rate in different sediment types (mud, fine sand, sand). The trait-based index thus demonstrates robustness in the prediction of animal-mediated functional processes that support biogeochemical functions under variable environmental conditions. Accordingly, we argue that trait-based indices provide a useful tool for the quantitative prediction of ecosystem processes as effect traits provide a direct link to the behavioral mechanisms that drive ecosystem functioning.

1. Introduction

The increasing exploitation of natural resources by mankind proposes a growing threat to many ecosystem functions and associated services (Naeem et al., 2012). In marine systems, rising water temperatures, overexploitation of fisheries, construction of offshore installations and underwater noise are only some of the stressors (i.e. descriptor 6 and 11 in an MSFD context) that progressively change the structure of benthic communities and how benthic organisms influence ecosystem functioning (e.g. biogeochemical cycling, sediment mixing) (Coates et al., 2014; Solan et al., 2016; Tillin et al., 2006). Accordingly, easily applicable descriptors of key ecosystem functions have become of great importance for both policy and science. For example, descriptor 6 (Sea-Floor Integrity) of the EU Marine Strategy Framework Directive (MSFD) specifically calls for multi-metric indices to assess benthic community condition and functionality (European Union, 2008) while the Millennium Ecosystem Assessment (Duraiappah et al., 2005) underlines the urgent need for a broader set of diversity indicators aligned with valued functions. Taxonomic identity, abundance or biomass of species alone have little power in explaining ecosystem processes (e.g. pollination, bioturbation, biocontrol of pests), as these processes are determined by the ecological effect traits of the organisms involved (Díaz and Cabido, 2001; Gagic et al., 2015). The effect traits thereby comprise all characteristics of organisms which may affect their habitat

and thus the functioning of the surrounding ecosystem (Díaz and Cabido, 2001). Recently, trait-based models proved their potential to outperform common ecosystem models in the quantitative prediction of ecosystem functioning (Ghimire et al., 2017; Zwart et al., 2015). Indices based on functional traits may thus be a promising tool to meet the societal, political and environmental demands.

Key services such as biogeochemical cycling, remineralization, soil formation, soil fertility, oxygen and water regulation (e.g. surface water run-off, maintenance of soil humidity) are strongly influenced by the reworking and irrigating (i.e. ventilation and burrow flushing) activities of invertebrates within both terrestrial and aquatic sediment or soil (de Bello et al., 2010; Kristensen et al., 2012; Valença et al., 2017; Wilkinson et al., 2009). Especially in shallow marine areas, the bioirrigation activity of the benthic fauna is of major importance for biogeochemical cycling (Braeckman et al., 2010; Mermillod-Blondin et al., 2004). Bioirrigation promotes the movement of pore water and associated solutes (e.g. O_2, CO_2, dissolved organic matter (DOM), inorganic nutrients) (Kristensen et al., 2012). Accordingly, the oxygenation of deeper, otherwise anoxic layers of the sediment strongly depends on bioirrigation (Aller, 1994; Kristensen, 2000). Hence, bioirrigation enlarges the sediment volume where aerobic processes can take place (e.g. nitrification) (Na et al., 2008) and thus enhances nutrient turnover as well as mineralization (Aller, 1982). Moreover, bioirrigation may stimulate nitrogen cycling by removing inhibiting metabolites, supplying

oxidants, and enhancing denitrification (Aller, 1988). Furthermore, bioirrigation may enhance the remobilization of organic matter compounds such as carbon, nitrogen or manganese (Schaller, 2014). As a result, bioirrigation constitutes a significant driver of ecosystem functioning (primary production, benthic-pelagic coupling, biogeochemical cycling) (Lohrer et al., 2004). Consequently, the loss of bioirrigation activity may have broad implications for overall ecosystem performance (Lohrer et al., 2004).

Bioirrigation is mostly driven by ventilation and suspension feeding activities of benthic species (Aller, 1982; Kristensen, 2001; Kristensen et al., 2012). Consequently, it is primarily dependent on body mass and feeding type (Christensen et al., 2000). In contrast, the depth to which an organism commonly pumps water during bioirrigation (i.e. injection pocket depth) and the general burrow shape (i.e. blind ended or U-shaped burrows) have an indirect effect on bioirrigation and biogeochemical cycling (Kristensen et al., 2012). A deeper injection pocket requires, for a complete exchange of burrow water, the transport of larger volumes of water whereas the burrow shape essentially determines whether water is advectively transported into the surrounding sediment (Kristensen et al., 2012). Additionally the composition of burrow wall may substantially influence water transport, bacterial communities and biogeochemical processes (Laverock et al., 2011). However, only few data exists on specific exchange rates across different wall types.

So far, there is no reliable index or model to predict broad scale changes in bioirrigation activity that are due to shifts in functional community composition or species extinction. The existing models are either only phenomenological descriptions of the bioirrigation process with a weak connection to the underlying biology (i.e. diffusive, non-local and advective one-dimensional models (Meysman et al., 2006b)) or based on complex microenvironment modeling that is dependent on rarely measured parameters (e.g. pumping rate, burrow volume, specific burrow morphology) (i.e. the mechanistic models of Aller (1980) and Meysman et al. (2006a)).

The trait-based non-quantitative concept of community bioturbation potential (BP_c) was originally introduced as an approach to estimate the effects of species extinctions on sediment reworking and ecosystem properties (Solan et al., 2004). Recently, BP_c was linked to biogenic mixing depth, total organic carbon content, chlorophyll concentrations, oxygenation depth, sediment oxygen consumption, ammonium efflux and denitrification (Birchenough et al., 2012; Braeckman et al., 2014; Gogina et al., 2017). Additionally Queirós et al. (2015) demonstrated that BP_c predicts sediment reworking distance and Gogina et al. (2017) observed a moderate but significant correlation with sediment reworking rates in Balthic Sea communities. Further a recent study (Wrede et al., 2017) showed that BPc may also correlate with bioirrigation activity as it contains, next to sediment reworking traits, a term that describes the body mass of macrofaunal organisms. Yet, considered, that BP_c was not specifically designed to predict bioirrigation and that it uses only effect traits (i.e. body mass, mobility and reworking mode) that describe macrofaunal sediment reworking activity and particle transport it may be an ambiguous tool for the prediction of macrofaunal bioirrigation. Especially the mobility trait of BP_c is likely to underestimate the contribution of sessile species, with low mobility but high bioirrigation, to biogeochemical processes whereas the contribution of highly mobile species with low bioirrigation is overestimated (Braeckman et al., 2010).

To overcome this ambiguity we propose a novel trait-based index in the style of BP_c, the irrigation potential IP_c, which incorporates specific bioirrigation effect traits (i.e. burrow shape, injection pocket depth and feeding type). Furthermore, we validated IP_c with a multi-factorial experiment. We hypothesize that IP_c will allow for quantitative modelling of macrofaunal bioirrigation activity over large spatial scales. Additionally we hypothesize that IP_c is a predictor of bioirrigation activity in contrast to BP_c, and can thus complement the assessment of benthic community condition and functionality in the context of MSFD.

Table 1
Irrigation potential effect traits burrow type, feeding type and injection pocket depth with the respective categories and scores.

Effect trait	Category	Score
Burrow type	Epifauna, internal irrigation (e.g. siphons)	1
	Open irrigation (e.g. U- or Y- shaped burrows)	2
	Blind ended irrigation (e.g. blind ended burrows, no burrow systems)	3
Feeding type	Surface filter feeder	1
	Predator	2
	Deposit feeder	3
	Sub surface filter feeder	4
Injection pocket depth	0–2 cm	1
	2–5 cm	2
	5–10 cm	3
	> 10 cm	4

2. Material and methods

2.1. Irrigation potential (IP_c)

We adapted the bioturbation potential (BP_c) of Solan et al. (2004) and replaced the traits mobility and reworking mode (defined in more detail by Queirós et al., 2013) by traits that characterize the irrigation behaviour of benthic macrofaunal organisms and its effects on ecosystem functioning: burrow type (BT_i), feeding type (FT_i), injection pocket depth (ID_i). The index now reads as follows:

$$IP_c = \sum_{i=1}^{n} \left(\frac{B_i}{A_i} \right)^{0.75} \times A_i \times BT_i \times FT_i \times ID_i \tag{1}$$

where B_i is the biomass of species i and A_i its abundance. Following the approach of Solan et al. (2004), the traits are subdivided in categories that describe the species specific expression of the respective trait (Table 1). Each category is assigned a descriptive numerical score. A low score indicates low bioirrigation and associated effects whereas a high value indicates high bioirrigation and associated effects (for example: "feeding type: predator – score: 2, sub surface filter feeder – score: 4"). The body mass term is weighted by an exponent of 0.75 to account for the scaling of metabolic activity with body mass (Brey, 2010; West and Brown, 2005) which we consider to be more appropriate than the square root scaling applied by Solan et al. (2004).

2.2. Experiment

Single and multispecies laboratory experiments were run to test IP_c performance. Sediments and macrofaunal organisms were collected from three different sedimentary habitats within the German Bight (mud, fine sand and sand (Table 2)) (54°7′21″N 8°12′96″E; 54°0′50″N 7°48′51″E; 55°01′32″N 8°26′10″E). The muddy habitat was inhabited by a *Nucula nitidosa*-community (Salzwedel et al., 1985), the fine sand habitat by an *Amphiura filiformis*-community (Salzwedel et al., 1985) and the sand habitat by a *Lanice conchilega*-reef (Rabaut et al., 2008). The *Nucula*- and *Amphiura*-communities were sampled in April 2016 by ship while the *Lanice*-reef was sampled in March 2016 by foot during low tide. From each of these communities, 10 cylindrical in situ cores (h: 35 cm, d: 9.4 cm) were taken. In the case of the *Lanice*-reef, cores were randomly sampled from a 12 m² area within the reef. For the other two communities, the cores were carefully extracted from 0.1 m² box cores to maintain an undisturbed sediment column. The cores were then transferred to a climate controlled room (on board of the research vessel for the *Nucula*- and *Amphiura*-community and to the Wadden Sea Station of the Alfred Wegener Institute (AWI) at the island of Sylt for the *Lanice*-community) where they were constantly aerated through an air stone. Experimental temperature was 8 °C which is about the annual mean bottom temperature in the southern North Sea (Dulvy et al.,