



Can benthic community structure be used to predict the process of bioturbation in real ecosystems?



Ana M. Queirós^{a,*}, Nicholas Stephens^a, Richard Cook^a, Chiara Ravaglioli^{a,b}, Joana Nunes^a, Sarah Dashfield^a, Carolyn Harris^a, Gavin H. Tilstone^a, James Fishwick^a, Ulrike Braeckman^c, Paul J. Somerfield^a, Stephen Widdicombe^a

^a Plymouth Marine Laboratory, Prospect Place, PL1 3DH Plymouth, United Kingdom

^b Department of Biology, University of Pisa, via Derna 1, Pisa I-56126, Italy

^c Marine Biology Research Group, Ghent University, Krijgslaan 281/S8, 9000 Ghent, Belgium

ARTICLE INFO

Article history:

Available online 19 May 2015

ABSTRACT

Disentangling the roles of environmental change and natural environmental variability on biologically mediated ecosystem processes is paramount to predict future marine ecosystem functioning. Bioturbation, the biogenic mixing of sediments, has a regulating role in marine biogeochemical processes. However, our understanding of bioturbation as a community level process and of its environmental drivers is still limited by loose use of terminology, and a lack of consensus about what bioturbation is. To help resolve these challenges, this empirical study investigated the links between four different attributes of bioturbation (bioturbation depth, activity and distance, and biodiffusive transport); the ability of an index of bioturbation (BP_c) to predict each of them; and their relation to seasonality, in a shallow coastal system – the Western Channel Observatory, UK. Bioturbation distance depended on changes in benthic community structure, while the other three attributes were more directly influenced by seasonality in food availability. In parallel, BP_c successfully predicted bioturbation distance but not the other attributes of bioturbation. This study therefore highlights that community bioturbation results from this combination of processes responding to environmental variability at different time-scales. However, community level measurements of bioturbation across environmental variability are still scarce, and BP_c is calculated using commonly available data on benthic community structure and the functional classification of invertebrates. Therefore, BP_c could be used to support the growth of landscape scale bioturbation research, but future uses of the index need to consider which bioturbation attributes the index actually predicts. As BP_c predicts bioturbation distance, estimated here using a random-walk model applicable to community settings, studies using either of the metrics should be directly comparable and contribute to a more integrated future for bioturbation research.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

The biogenic mixing of sediment and other particulates, i.e. bioturbation (see Meysman et al., 2006 for a review, Richter, 1952), is a key component of benthic-pelagic coupling, and an important mediator of ecosystem functioning in coastal habitats (Teal et al., 2008, 2013). Bioturbation (and associated burrow ventilation) influences sedimentary oxygen, pH and redox gradients (Pischedda et al., 2008; Queirós et al., 2011; Stahl et al., 2006), metal cycling (Teal et al., 2009), sediment granulometry (Montserrat et al., 2009), pollutant release (Gilbert et al., 1994), macrofauna diversity (Volkenborn et al., 2007), bacterial activity

and composition (Gilbertson et al., 2012; Mermillod-Blondin and Rosenberg, 2006), and carbon (Kristensen, 2001) and nitrogen cycling (Bertics et al., 2010). This regulating role of bioturbation in marine biogeochemistry is well recognised, but measuring bioturbation in realistic settings is not always possible, requiring expert knowledge, favourable sampling conditions, and resources that are not always available (Queirós et al., 2013). These shortcomings have led to a paucity of data concerning mechanistic attributes of bioturbation (transport rates, activity, mixing depth) that have actually been measured at the community level, simultaneously covering environmental variability (e.g. seasonality). For example, a worldwide review of the bioturbation literature focusing on the two most widely used bioturbation metrics (bioturbation depth and the biodiffusion coefficient D_b , Goldberg and Koide, 1962; Guinasso and Schink, 1975) and covering four

* Corresponding author. Tel.: +44 (0)1752 633 476; fax: +44 (0)1752 633 101.

E-mail address: anqu@pml.ac.uk (A.M. Queirós).

decades of research, found that these metrics had been estimated less than twenty times during the winter season (Teal et al., 2008). The proportion of reviewed data that covered community level estimates was also low. The majority of data found regarded single species or artificially manipulated assemblages of specific species, or had a geological focus. Observations of artificially manipulated assemblages of single or few species are important routes to isolate particular mechanisms of impact on diagenesis or biogeochemistry, and provide much needed mechanistic understanding (e.g. Michaud et al., 2005). However, they provide little support to predict large-scale patterns of bioturbation in true community settings, where environmental variability, resource availability and species interactions modulate the potential effects of individual species on ecosystem processes (Godbold and Solan, 2009; Teal et al., 2013; Waldbusser et al., 2004). In addition, because bioturbation is an umbrella term for a myriad of processes undertaken by benthic fauna that lead to particle mixing, such as scavenging and burrow formation, numerous methods have been employed to measure it, individually targeting specific attributes (Maire et al., 2008). This leads to significant difficulty in the synthesis of knowledge. Indeed, lack of data and of consensus in the community about what bioturbation is (Kristensen et al., 2012), have stifled the inclusion of this and other benthic processes in macro-scale tools like ecosystem models because of a consequential difficulty in constraining model parameters to describe them (Holt et al., 2014; Queirós et al., 2014). Ecosystem models are routinely used to project abiotic scenarios and ocean productivity in support of the modelling of the distribution of biodiversity, and of the abundance of key species targeted by fisheries, to support management (Barange et al., 2014; Cheung et al., 2009; Fulton et al., 2011). Therefore, such model developments are highly desirable, because bioturbation (and bioirrigation) have fundamental roles in basin scale productivity and ocean chemistry on geological time scales (Boyle et al., 2014; Canfield and Farquhar, 2009). Addressing these gaps in knowledge and reaching of consensus in the literature about what bioturbation is, are therefore urgently needed to improve our ability to project future ocean conditions under unprecedented rates of human pressure.

Alternatively, community bioturbation potential (BP_c) is a metric based on the functional classification of invertebrate taxa into discrete functional groups, that has been used to predict bioturbation where species inventories of biomass and abundance are available (i.e. community structure, Birchenough et al., 2012; Queirós et al., 2013; Solan et al., 2004a). Because benthic community structure data are routinely generated by marine monitoring programs worldwide, a wider use of BP_c could also help support the implementation of bioturbation research, by opening up a larger body of evidence with which to investigate large scale patterns. BP_c has been successfully implemented in a number of applications, correlating well with sedimentary processes in some systems, including nutrient and alkalinity fluxes, redox profiles, oxygen consumption and hypoxia (Braeckman et al., 2014; Queirós et al., 2011; Van Colen et al., 2012). Therefore, this index has good potential as an indicator of bioturbation and benthic ecosystem functioning (Van Hoey et al., 2013). However, the empirical relationships reported in these studies do not provide information about which mechanistic attributes of bioturbation as a community process influence sedimentary systems, other than the functional traits of macrofauna considered in the index (i.e. body size, mobility and reworking mode, Solan et al., 2004a). Specifically, how the index relates to sediment transport rates, or to changes in community bioturbation as a consequence of the response of macrofauna to environmental stimuli remain to be investigated (Queirós et al., 2013). At the landscape scale, the use of BP_c may indeed be the only available option to investigate bioturbation. At that scale, however, environmental parameters such

as food availability and temperature are also most likely to limit invertebrate bioturbation behaviour, despite possible differences in species' functional traits (Maire et al., 2007; Needham et al., 2011; Ouellette et al., 2004). A better understanding of the link between BP_c and mechanistic attributes of community bioturbation, and to their environmental drivers, are therefore important steps towards: (i) the correct interpretation of large scale bioturbation patterns (investigated through the use of BP_c , Birchenough et al., 2012; Braeckman et al., 2014; Solan et al., 2012); (ii) the development of better descriptions of benthic processes in ecosystem models, by providing a larger evidence base at the community level; and (iii) a more informed use of the index as an indicator of benthic function (Van Hoey et al., 2013).

The present study investigated community bioturbation over a seasonal cycle at the Western Channel Observatory (WCO), building on the observatory's long-term monitoring program in the Plymouth Sound (UK) (Smyth et al., 2010, 2015; Southward et al., 2004). This study was particularly concerned with quantifying variability in community level bioturbation that could be associated with seasonal drivers, such as changes in seawater temperature and the abundance of food available to the benthos. Two mechanistic attributes of bioturbation were measured directly using 2D imaging and particle tracing methods (Gilbert et al., 2003; Solan et al., 2004b): bioturbation depth (typically referred to as L , Meysman et al., 2003), and bioturbation activity. Another two attributes were estimated from these data: biodiffusive transport (i.e. D_b , Goldberg and Koide, 1962; Guinasso and Schink, 1975); and bioturbation distance, the latter estimated using a random-walk bioturbation model (Schiffers et al., 2011). Changes in these four attributes measured at the community level were quantified over the seasonal cycle to determine possible relations to seasonal drivers. Secondly, BP_c was calculated using the community structure data generated from the same sediment cores, enabling the testing of the hypothesis that BP_c replicates potential changes in the mechanistic attributes of bioturbation measured during a seasonal cycle. There was an expectation that bioturbation attributes would vary across a seasonal cycle, but that BP_c would not because the index does not account for the response of organisms to environmental stimuli (Queirós et al., 2013). This has not yet been tested in the literature. However, BP_c is designed to capture variation in the mobility and sediment re-working modes of different types of organisms, which are important aspects of bioturbation (Solan, 2000). Therefore, the same methods were also used to quantify the bioturbation of four invertebrate species individually during the summer, at the same site, to test the hypothesis that BP_c accurately captures variation in the bioturbation of different functional types of bioturbating organisms. It was therefore expected that the predictive ability of BP_c in relation to the four bioturbation attributes measured (bioturbation depth, distance and activity, and D_b) would not vary between species. This work aimed to provide a better understanding of the links between bioturbation attributes, their drivers and BP_c , helping to support the growth of landscape scale bioturbation research.

2. Materials and methods

2.1. Community sampling and holding conditions

Sediment cores were collected during the benthic survey (Dashfield and Queirós, 2014) of the Western Channel Observatory (WCO) at Cawsand (50°19.81N 4°11.50W), in May 2011, July 2011, September 2011 and January 2012, covering one seasonal cycle. The site is a sheltered, sub-tidal, muddy-sand bed, with a typical water depth of 11 m, and average salinity of 34.80 ± 2.24 psu (mean \pm sd overall May 2011 – January 2012;

bottom salinity was 35.20 ± 0.04 psu). Sediments containing natural macrofauna communities were sampled on board the RV Sepia (Marine Biological Association) using a 0.1 m^2 US-NL box-corer. The sediment and overlying water of each core was immediately and gently sub-sampled into clear acrylic aquaria using a rectangular 0.024 m^2 PVC corer that fits tightly into these, preserving sediment structure. The number of cores sampled on each occasion is outlined in Table 1. The aquaria were immediately and gently filled with local, unfiltered, aerated sea-water; covered with a loose black PVC cover; and left to settle in a cool, shaded area of the ship during transport to the Plymouth Marine Laboratory mesocosm laboratory. Transport took approximately one hour. Each aquarium contained sediment to a depth of approximately 22 cm, overlaid by approximately 4.5 l of seawater. The temperature of the water overlaying the sediment cores on arrival to the laboratory was typically within one degree of local temperature at collection. The mesocosm consists of a large temperature controlled room, within which the air temperature is regulated to follow the monthly variability of temperature at the WCO. On arrival to the laboratory, all aquaria were immediately placed in a re-circulating, gentle flow-through system that helped regulate the temperature of the cores, throughout the incubations. Seawater was collected on a weekly basis at the WCO and stored in large reservoirs (16 m^3), and filtered using $10 \mu\text{m}$ and $1 \mu\text{m}$ hydrex block carbon filter before entering the main supply to the aquaria. Sea water was supplied to each aquarium at a rate of $11 \pm 1 \text{ ml min}^{-1}$ and did not cause sediment re-suspension. Each aquarium was individually aerated by use of a small aquarium diffuser stone. Individual aquaria were housed inside individual imaging black boxes ($90(\text{h}), 35(\text{w}) \times 64(\text{d}) \text{ cm}$) following the setup described in Schiffers et al. (2011). Salinity was maintained at 34.65 ± 0.35 psu. Each aquarium was supplied with a daily dilution of microalgae concentrate mix (Instant Algae[®] Marine Microalgae Concentrated Shellfish Diet 1800, 8% dry-weight). Dilutions were prepared to match 20% of macrofauna dry-mass to surface area (0.024 m^2), an estimate based on Cawsand community data for the corresponding time of year in 2008–2009, and on Ricciardi and Bourget (1998). The ration was administered at dusk, when animals were expected to be most active.

2.2. Individual species sampling and holding conditions

Specimens were collected at the same site, on four sampling occasions between June and July 2012, using the protocol described. Individuals of four species were collected on each occasion: the burrowing brittle-star *Amphiura filiformis* (Müller, 1776; henceforth “Amphiura”); the tube-worm *Melinna palmata* (Grube, 1870; henceforth, “Melinna”); the cat-worm *Nephtys hombergii* (Savigny in Lamarck, 1818; henceforth “Nephtys”); and the burrowing holothurian *Oostergrenia* (formerly *Labidoplax*) *digitata* (Montagu, 1815; henceforth “Oostergrenia”). The four species were

chosen because they make an important contribution to the seasonal pattern of BP_{c} at Cawsand (Queirós, 2008–2009 WCO data, unpublished) and because they cover a variety of phyla and bioturbation functional groups. *Amphiura* and *Nephtys* are free living, low mobility biodiffusers; *Melinna* is a head-up tube-dweller, exhibiting conveyor-belt transport of particulates; and *Oostergrenia* is a free-living, low mobility organism observed in this study to exhibit head-up, conveyor-belt particulate transport for long periods of time. On each occasion, sediments containing natural macrofauna communities were manually sorted for live specimens of the four species. All individuals were immediately and carefully placed in a cool, covered, polyethylene container containing aerated seawater, during transport to the laboratory.

Sediments were collected on four occasions from the same site, 21 days prior to each of the live specimen collections, and manually wet-sieved on board using a 1 mm squared mesh for removal of large macrofauna. These sediments were stored in cool, ventilated conditions for 14 days afterwards. They were then mixed in a large pool with aerated seawater before being placed in the mesocosm for a 72 h period, ensuring sediment homogeneity and retention of the fine sediment fraction. These sediments were then transferred to 8 clear acrylic aquaria and filled with aerated seawater. At the end of 72 h, seawater was again replaced with fresh, aerated seawater as above. Each aquarium contained a sediment layer approximately 22 cm deep, overlaid by approximately 2.6 l of seawater. The sediment surface area in these aquaria was 0.014 m^2 . A sample from each prepared sediment batch was frozen and analysed using a Beckman Coulter LS laser particle size analyser, to assess particle size homogeneity across experimental runs. This was verified and sediments characterised as muddy sand as expected (Cook, 2012).

Each aquarium was kept in the same re-circulating flow-through system described (temperature: $13.64 \pm 1.32 \text{ }^\circ\text{C}$; salinity: 34.54 ± 0.32 psu, mean \pm sd). The eight aquaria were housed in pairs side by side inside four individual imaging black boxes, 24 h before the arrival of freshly sampled live specimens.

The blotted wet weight of specimens was recorded on arrival to the laboratory. Individuals of each species were then gently placed on the sediment surface of two aquaria (two aquaria per species), within 2 h of collection. Individuals that did not burry within one hour of introduction to experimental aquaria were removed and replaced by similar sized individuals of the same species. *Melinna* were placed vertically onto the sediment of experimental aquaria in their intact tubes, as close as possible to the visualised wall of the aquarium. Holding conditions were maintained as before, with daily rations calculated to 20% of the dry-mass in each aquarium (wet to dry mass conversions taken from (Brey, 2001)). Individual densities were defined for each species, in each pair of aquaria, based on a balance between the natural abundance ranges at the collection site and the ability to capture a bioturbation signal using 2D imaging and particle tracer methods. Natural abundances

Table 1

Mean assemblage parameters from sediment cores used in the quantification of bioturbation. Community data was estimated from sediment cores with a surface area of 0.024 m^2 , and individual species data are calculated from 0.014 m^2 cores. S is the average number of species in each type of core. H' is the corresponding Shannon diversity index. See Methods for details.

Type	Date	Nr samples	Biomass (g m^{-2})	Abundance (m^{-2})	$S_{(\text{sample})}$	$H'_{(\text{sample})}$	$\text{BP}_{\text{c}(\text{sample})}$
Community	May-11	1	89.44	1333.33	13.00	2.40	37.93
Community	July-11	2	152.49 ± 93.23	4916.67 ± 530.33	31.00 ± 4.24	2.83 ± 0.17	67.44 ± 25.93
Community	September-11	2	160.41 ± 26.80	4833.33 ± 824.96	26.50 ± 9.19	2.26 ± 0.29	68.77 ± 8.52
Community	January-12	1	94.03	4041.67	28.00	2.73	32.30
<i>Amphiura filiformis</i>	June–July 2012	8	106.25 ± 25.55	214.28	1.00	–	25.18 ± 3.08
<i>Melinna palmata</i>	June–July 2012	7	22.64 ± 10.61	459.18	1.00	–	3.95 ± 1.93
<i>Nephtys hombergii</i>	June–July 2012	8	207.74 ± 49.98	214.28	1.00	–	35.21 ± 4.39
<i>Oostergrenia digitata</i>	June–July 2012	8	83.21 ± 36.81	71.42	1.00	–	6.34 ± 1.41

were calculated from unpublished WCO data for 2008–2009. The associated mean biomass and abundances used in these incubations are provided in Table 1.

2.3. Acquisition of bioturbation data

In both sets of runs (community and single species), particle tracing methods were used to quantify bioturbation. These methods typically include the addition of an artificial tracer to sediments containing a community or species of interest *in situ* or under laboratory conditions, followed by an incubation period and subsequent retrieval. In the present study, luminophores were used. These are quartz sand particles coated in such a way as to fluoresce under UV light (Mahaut and Graf, 1987), which were produced to match the sediment grain distribution at the collection site (Cawsand, Partrac Ltd.). 2-D imaging was used to follow the evolution of tracer profiles over time (Gilbert et al., 2003; Maire et al., 2006; Solan et al., 2004b). 0.10 g cm⁻² of homogenised luminophores were gently added to the sediment surface within each aquarium, 24 h after retrieval of community cores to the lab, and 24 h after the additions of specimens to sediments in the single species incubations. At this stage, all circulation and aeration was interrupted to allow the tracer to settle. The tracer formed a layer approximately 0.20 cm thick within one hour, after which time the re-circulation and aeration were re-initiated. The imaging setup described in Schiffers et al. (2011) was used to acquire a time-series of images of the each aquarium under UV lighting, at hourly intervals, for six days ($n_{\text{images per core}} = 144$). UV lights housed inside the imaging boxes stimulated luminophore excitation enabling the tracing of the fluorescent luminophore particles against the dark background sediment. Images were captured using digital SLR cameras (Canon EOS 500D; 15.1 MP; pixel size $\approx 100 \mu\text{m}$) placed at the opposing end of the imaging box, at a fixed distance from the imaged surface of the aquaria. Cameras were set to use 10 s exposure, $f = 5.6$, ISO = 100, and were remotely controlled via a PC using time-lapse software (GB Timelapse, V 3.6.1). Image data extraction was carried out for each each aquarium, using novel standardised, custom-made algorithms for R 2.15.1 (R Foundation, Vienna, Austria) and Image J 1.46 (USA National Institutes of Health), modified from Queirós (2010). The procedure is illustrated in Fig. 1. In summary, after the initial manual delineation of the sediment–water interface in each image, this algorithm enables a standardised automated extraction of luminophore pixel positions in each image, for each time-series dataset, using complete image segmentation (Sonka et al., 1999). The novel principle employed is the automated identification of the area of the images corresponding to luminophores, based on the colour distributions of each image within each image set, compared to that of the image captured at the beginning of the corresponding incubation. Pixels identified as luminophores were accordingly automatically selected by conversion of each image into a binary matrix, and their positions within each image were extracted as 2D arrays. The sediment depth for each luminophore pixel was calculated in relation to the linearised sediment–water interface (depth = 0 cm, Fig. 1b) in each pixel column for each image (Maire et al., 2006). Luminophore pixel counts per pixel line in each image (i.e. luminophore profiles) were compiled per aquarium, in each experimental run, and used in subsequent analyses. All scripts for image data extraction are available from the authors on request.

2.4. Quantification of bioturbation

The luminophore profile time-series' were used to measure the four bioturbation attributes. Firstly, the deepest sediment horizon containing at least five pixels characterised as luminophores was

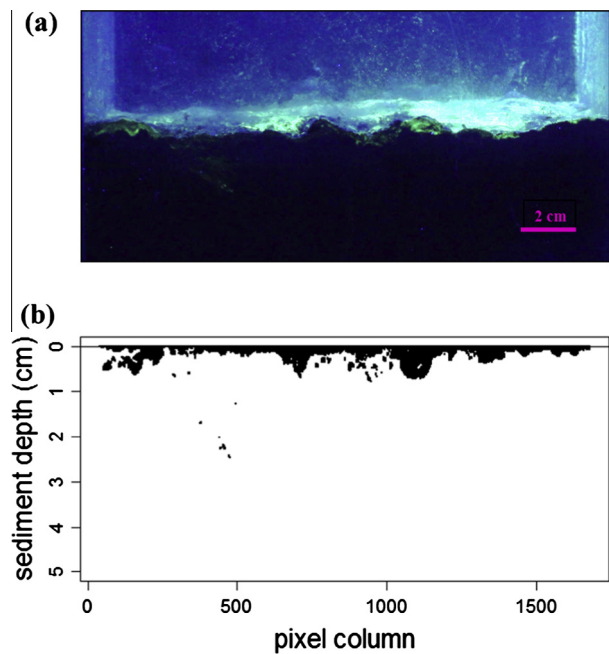


Fig. 1. Example of image segmentation procedure to extract luminophore pixel positions in relation to the linearised sediment–water interface (b) from original image (a).

used as an indicator of the maximum bioturbation depth (henceforth, “depth”). Secondly, the percentage of originally added tracer left at the sediment water interface (the first cm of sediment) was used as a proxy for bioturbation activity (i.e. 100% – % remaining = “activity”). Thirdly, the biodiffusion coefficient D_b was estimated using the solution to the Crank equation for diffusive transport (Crank, 1979) and weighted least-squares regression of predicted tracer concentrations on the observed luminophores profiles. Model cost was quantified as per François et al. (2002) and Maire et al. (2006). Lastly, a random-walk bioturbation model was fitted to the tracer profiles (Schiffers et al., 2011). This model includes three parameters, two of which are important descriptors of bioturbation: “distance”, the average distance travelled by a sediment particle (i.e. a visualised tracer pixel) within one time-step; and “activity”, the probability associated with the displacement of one particle within a time step. As a high correlation between the Schiffers model parameters distance and activity was found in most model runs, model fits were carried out while fixing the parameter “activity” as recommended (Schiffers et al., 2011). Consequently, this analysis focuses on the parameter “distance”.

2.5. Estimation of BP_c

At the end of all incubations, all sediment cores were sieved over a 0.50 mm squared mesh, and macrofauna fixed in 4% buffered formaldehyde. For each core, community macrofauna were sorted and identified to the lowest possible taxonomic level, and biomasses and abundances determined per taxon. The corresponding community abundance, biomass, species number and Shannon-Wiener diversity index (Shannon and Weaver, 1949), averaged across replicates per time-point, are provided in Table 1.

The bioturbation classification of all identified macrofaunal taxa were derived according to the standardised scores for mobility and sediment reworking mode listed in Queirós et al. (2013). These data were used to calculate community bioturbation potential (BP_c), using the equation in Solan et al. (2004a):

$$BP_c = \sum_{i=1}^n \sqrt{B_i/A_i} * A_i * M_i * R_i$$

B_i and A_i are the biomass and abundance of a taxon (i) in a sample; M_i is their standardised score for mobility; and R_i is their standardised score for sediment re-working mode.

2.6. Statistical analyses

Each of the four bioturbation attributes (depth, activity, D_b and distance) was compared to BP_c to test if BP_c reflected their observed pattern of variation, using all datasets (i.e. individual species and community). For this, least-squares linear regressions were calculated using (i) all data, (ii) reworking mode groups and (iii) individual species data. By doing so, the predictive power of BP_c for each of the bioturbation metrics within the groups analysed was discriminated via the coefficient of determination (R^2). Linear model assumptions were verified by inspection of residual distribution plots. Leverage was quantified by observation of Cook's distances (Cook and Weisberg, 1982). All analyses were carried out in R.

2.7. Seasonality at the western channel observatory

Community estimates of bioturbation were then compared with seasonal parameter measurements at the WCO. Bottom seawater temperature at Cawsand was monitored in parallel to the collection of community sediment cores by acquisition of CTD profiles (SeaBird Electronics Inc. SBE19 plus Seacat). Bottom temperature was estimated as the average of the values measured in a 1.50 m bottom water layer. Surface primary production (PP) was estimated over the seasonal cycle to provide an indication of the relative change in food availability to the benthos associated with plankton phenology. PP was chosen instead of other more immediate proxies for benthic primary productivity (like sedimentary productivity or organic carbon) because these are also influenced by bioturbation (Dale and Prego, 2002; Solan et al., 2012). Conversely, surface primary production reflects the effect of environmental drivers on phytoplankton phenology (Atkinson et al., 2015). PP was estimated from January 2011 to April 2012 from the light absorption coefficient of phytoplankton at 665 nm ($aph(665)$, m^{-1}) and photosynthetically active radiation (EPAR) within the WCO at L4, using the equations provided in Barnes et al. (2014). The L4 station is located 5 nm miles from Cawsand Bay, and these estimates were therefore deemed to be a good proxy for the relative timing of changes in food availability at the WCO, during the seasonal cycle covered by the bioturbation monitoring program.

3. Results

3.1. Bioturbation attributes

In general, community incubations had higher BP_c than those of single species (Fig. 2), possibly reflecting the effects of difference in sediment volume between these treatments, and because more species were found in the community cores. However, because we were primarily interested in the relationship between BP_c and each of the bioturbation attributes, this aspect was deemed as having little influence on the results presented. We did not consider that the preparation of the sediments that preceded the single species incubations significantly impacted our results (Michaud et al., 2010) because single species estimates were comparable to the community estimates in the wide majority of our observations (Fig. 2a–d).

At least one of the biodiffusor species (Amphiura or Nephtys) had the highest bioturbation in all of the four attributes measured.

In addition, Melinna and Oestergenia treatments, while exhibiting low BP_c , were observed to have more variable ranks in the four bioturbation attributes, and had particularly low activity. The significance of the relationships between BP_c and each of the four bioturbation attributes are given in Table 2.

The depth of bioturbation was not well predicted by BP_c , when all the data were pooled together (community and single species assemblages), or when community data was analysed separately (Table 2, Fig. 2a). This was also not the case for most species individually, or when species were grouped according to sediment re-working mode (i.e. biodiffusors, Amphiura and Nephtys; and conveyors, Melinna and Oestergenia; Table 2 and Fig. 2a). BP_c only significantly explained the bioturbation depth of Amphiura ($R^2 = 48.88\%$, $p < 0.05$, Table 2), which was the species seen to be reworking sediments the deepest (Fig. 2a).

Bioturbation activity was well predicted by BP_c when we considered all the datasets together ($R^2 = 33.78\%$, $p < 0.05$, Table 2). Differences in this relation between groups of species were, however, apparent: the relationship was positive and stronger when we considered biodiffusor species separately (i.e. Amphiura and Nephtys together, $R^2 = 71.96\%$, $p < 0.05$, Table 2 and Fig. 2b). BP_c also predicted the activity of the surficial modifier/conveyor Oestergenia individually ($R^2 = 42.25\%$, $p < 0.05$), but not after removing one observation with the highest activity which had high leverage (Cook's distance > 1.00 , Fig. 2b). After this, the relationship between activity and BP_c was not significant when we considered the two conveyor species together, or individually. In addition, the bioturbation activity of community cores alone could not be predicted by BP_c (Fig. 2b). Thus, it seems that the significant relationship observed when we pooled all the data together was driven by the inclusion of biodiffusor data, and that BP_c is a poor predictor of bioturbation activity overall.

Biodiffusive transport (D_b) for community cores was comparable to that estimated for the single species cores (Fig. 2c), within the range of density and biomasses used, and despite the use of different surface areas between community and single species incubations (Table 1). The highest values of D_b were observed in the analysis of biodiffusor species data (Amphiura and Nephtys). BP_c did not predict well D_b in any of the cases (D_b , $p > 0.10$, Fig. 2c). A significant relationship between the two was observed when the two conveyor species' data was pooled (Melinna and Oestergenia, $R^2 = 29.66\%$, $p < 0.05$, Table 2 and Fig. 2b), but the removal of a high leverage Oestergenia observation, which also had high D_b , led also to a non-significant relationship. Therefore, overall, BP_c was not a good predictor of biodiffusive transport rates.

Conversely, BP_c was found to be a good predictor of the average distance travelled by sediment particles (Table 2 and Fig. 2d). When we considered the community data collected over the seasonal cycle separately, the relationship between the two metrics was positive and highly significant (Distance (cm) $\sim 0.02 + 9.93 * 10^{-4} * BP_c$, $R^2 = 96.94\%$, $p < 0.05$, Table 2), excluding one high leverage observation collected in the summer, when the distance was highest (Cook's distance > 0.50 , Fig. 2d). The relationship had a stronger slope but was equally positive and significant when we considered the biodiffusor species alone (Amphiura and Nephtys Table 2, Fig. 2d), even after the removal of one high leverage and high distance Nephtys observation (Table 2 and Fig. 2d). BP_c also significantly predicted the bioturbation distance of conveyor species together (Table 2 and Fig. 2d), but not that of any of the species alone.

3.2. Seasonality of bioturbation

PP (Fig. 3a) decreased from May onwards, after the peak observed in April 2011, while average bottom water temperature increased steadily until the end of summer 2011, then declining

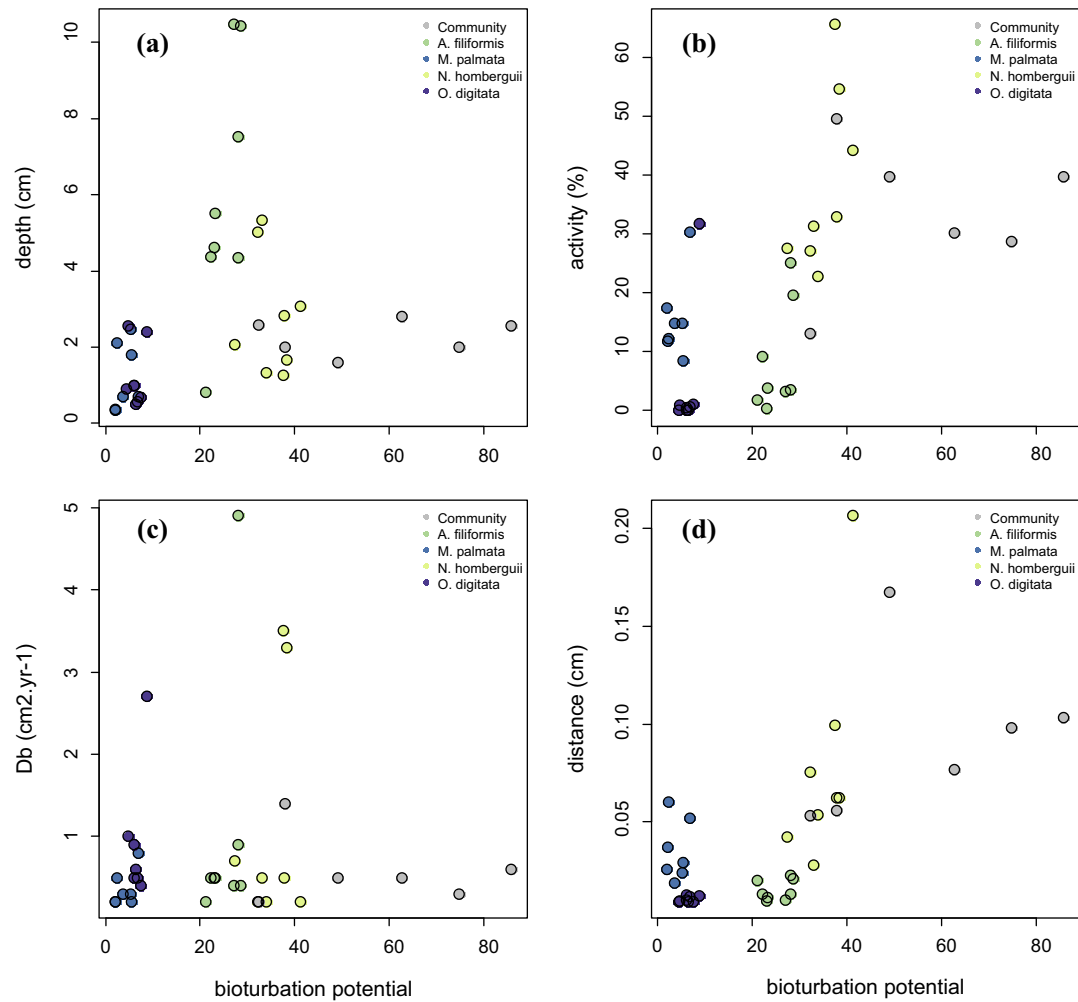


Fig. 2. Relationship between bioturbation potential (BP_c) and quantified metrics of bioturbation: maximum bioturbation depth (a); bioturbation activity (b); biodiffusive transport (D_b , c); and average distance travelled by sediment particles (d).

Table 2

Linear regressions using bioturbation metrics as response variables, and BP_c as predictor. “ R^2 ”: coefficient of determination. “df”: degrees of freedom in F test. “ F ” and “ p ” give the calculated F value and the corresponding probability associated with the null hypothesis.

Response/assemblage	Depth				Activity				D_b				Distance			
	R^2 (%)	df	F	p	R^2	df	F	p	R^2	df	F	p	R^2	df	F	p
All	–	1, 35	–	>0.10	33.78	1, 35	19.37	<0.05	–	1, 35	–	>0.10	29.44	1, 35	9.76	<0.05
Community	–	1, 4	–	>0.10	–	1, 4	–	>0.10	–	1, 4	–	>0.10	96.94	1, 3	127.8	<0.05
Biodiffusers	–	1, 14	–	>0.10	71.96	1, 14	39.50	<0.05	–	1, 14	–	>0.10	63.61	1, 13	25.47	<0.05
Conveyors	–	1, 13	–	>0.10	–	1, 13	–	>0.10	–	1, 12	–	>0.10	14.33	1, 13	3.34	<0.10
Amphiura	48.88	1, 6	7.69	<0.05	–	1, 6	–	>0.10	–	1, 6	–	>0.10	–	1, 6	–	>0.10
Melinna	–	1, 5	–	>0.10	–	1, 5	–	>0.10	–	1, 5	–	>0.10	–	1, 5	–	>0.10
Nephtys	–	1, 6	–	>0.10	28.13	1, 6	3.74	=0.10	–	1, 6	–	>0.10	–	1, 5	–	>0.10
Oestergrenia	–	1, 6	–	>0.10	–	1, 5	–	>0.10	–	1, 6	–	>0.10	–	1, 6	–	>0.10

to the winter levels observed in January (Fig. 3a). As expected from Section 3.1, BP_c appeared to mirror the relative change in bioturbation distance over the seasonal cycle (Fig. 3c and d), but not that of activity, D_b or bioturbation depth, which followed distinct temporal patterns (Fig. 3d–f). Visual inspection of the plots suggests that bioturbation depth, activity and biodiffusive transport appear to follow plankton phenology, peaking when PP is highest. BP_c and bioturbation distance appeared to more closely follow the pattern of seawater temperature.

4. Discussion

4.1. Can community structure be used to predict bioturbation?

This study aimed to facilitate landscape scale bioturbation research by investigating whether BP_c , calculated using community structure and functional classification data, could be used to predict bioturbation as a community level process. This is a relevant issue because bioturbation (and bioirrigation) have

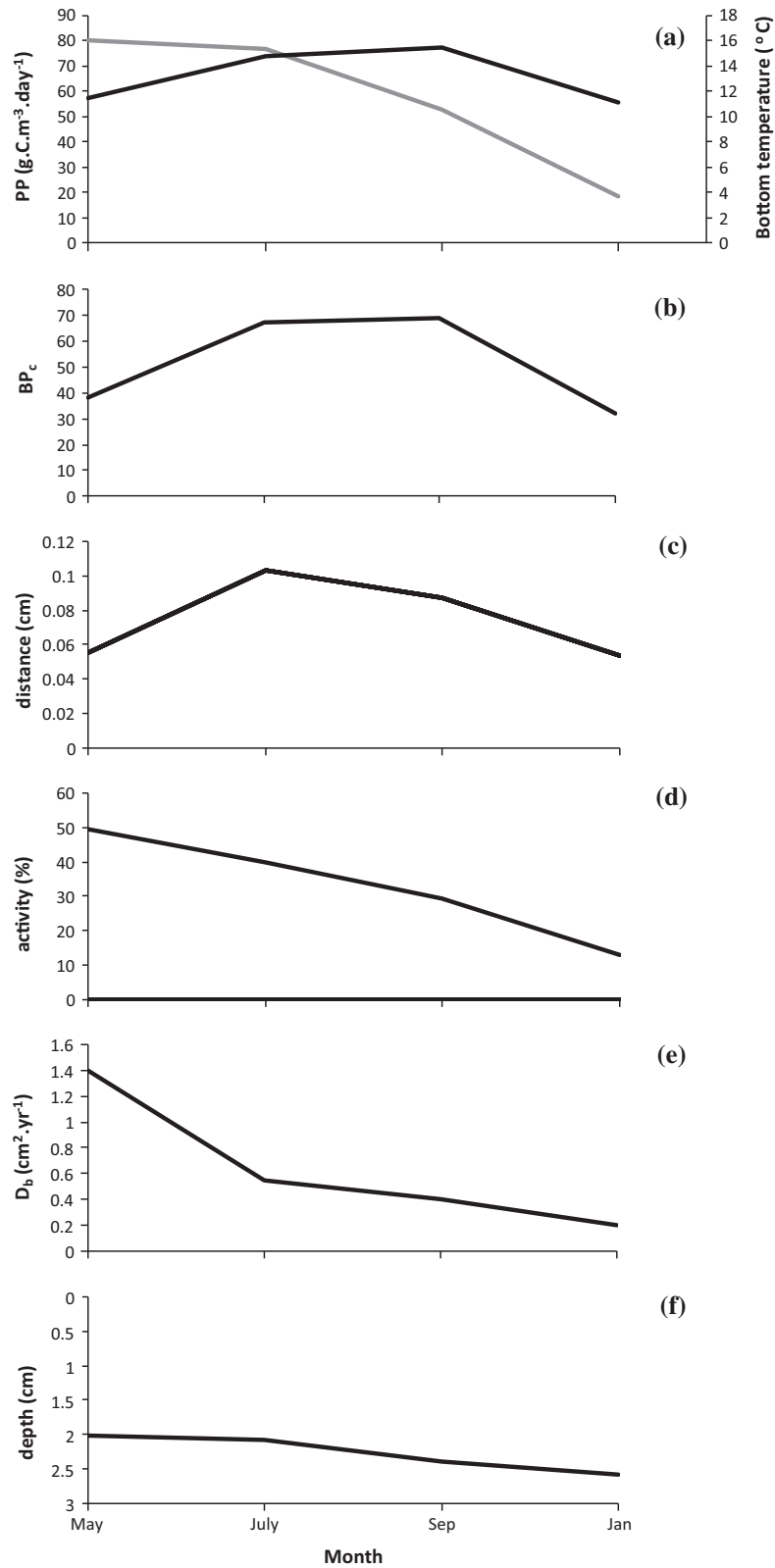


Fig. 3. Monthly trend (average) of bottom seawater temperature (black) and primary productivity (grey, a); and community bioturbation potential (b), Schiffers model distance parameter (c), bioturbation activity (d), biodiffusion (e) and depth (f), measured on community incubations. Data points for May, July and September 2011, and January 2012, linked for illustration purpose.

fundamental roles in productivity and ocean chemistry on geological time scales (Boyle et al., 2014; Canfield and Farquhar, 2009). Community level measurements of bioturbation across

environmental gradients are scarce (Teal et al., 2008), while the types of data required to calculate BP_c are commonly available (Queirós et al., 2013). A better understanding of what aspects of

bioturbation are predicted by the index is therefore needed to better support its use.

Overall the study demonstrated that BP_c successfully predicts one attribute of bioturbation (i.e. distance) over the seasonal cycle, supporting its use for wider scale assessments when bioturbation rates cannot actually be measured. However, BP_c was found not to predict well bioturbation depth, activity or D_b . The index also appeared to be a better predictor of community level estimates than of those of individual species, being particularly poor at predicting the bioturbation of individual, non-biodiffusive type bioturbators. These results support the view that bioturbation is a multi-faceted process, and therefore that the use of BP_c as a predictor of benthic function (Birchenough et al., 2012; Van Hoey et al., 2013) should be done with care.

That BP_c was found to be a good predictor of bioturbation distance (the average distance travelled by a particle in a random-walk bioturbation model, Schiffers et al., 2011) is a particularly promising result, as this is an important parameter for process description (Meysman et al., 2010; Schiffers et al., 2011). The relationship was found to be valid also when we included the community data, even though those data were collected over the seasonal cycle, and therefore included possible effects of changes in seasonal drivers. This result suggests that bioturbation distance may be a fairly conservative attribute of bioturbation as a process, directly linked to the species functional traits considered in the index (body size, reworking mode and mobility) and their distribution within natural assemblages. It suggests that the effects of environmental stimuli may not directly impact upon bioturbation distance, unless such variation would cause a concomitant modification to the structure of the underlying benthic community. It is prudent to suggest that this relationship may vary slightly between habitats, because the effect of bioturbation on particle and solute distributions is context dependent (Braeckman et al., 2014; Mermillod-Blondin and Rosenberg, 2006; Queirós et al., 2011). Given the findings presented here, caution is also advised in possible applications of this relationship to data from communities highly dominated by species exhibiting conveyor type transport, as the strength of the relationship was weaker when estimated from conveyor species alone. Elucidating the specific cause for this difference would require a further application of the random-walk model used here to predict bioturbation distance from other types of bioturbators, and a greater number of species.

The fact that we did not find BP_c to be a particularly good predictor of other attributes of the process of bioturbation, like activity, depth and biodiffusive transport is also significant. This finding may explain why BP_c has been found to be a good predictor of biogeochemical processes in certain contexts but not others. For instance, Braeckman et al. (2014) found BP_c to be a good predictor of denitrification, alkalinity and ammonium fluxes in fine sandy sediments but not in muddy sediments. They primarily attributed this difference to the relative importance of (non-measured) bioirrigation in the different habitats. An alternative interpretation may be that attributes of bioturbation not well captured by BP_c (like bioturbation activity) may be better predictors of those processes and vary between the habitats, or that the communities in the muddy site contained large numbers of conveyor species, in which case BP_c should be used with care. Our findings suggest that poor relationships between BP_c and biogeochemical processes should, in future, not be necessarily attributed to a minor influence of bioturbation as a mediator. Rather, such findings should be interpreted with consideration for what attributes of biogenic mediated sediment transport are and aren't predicted by BP_c . Clearly, similar validation of the index still needs to be undertaken in a greater number of habitat types.

4.2. Seasonality of bioturbation at the Western Channel Observatory

Despite data availability limiting our analysis of seasonal trends in community bioturbation, this study still represents an important achievement. There are few studies in the literature that have measured so many attributes of bioturbation at the community level simultaneously, covering seasonal variability (Teal et al., 2008). This study and associated ongoing research at the WCO thus provide an important opportunity to link bioturbation as a community level process to macrofauna responses to natural environmental variability, and their associated impacts on coastal biogeochemistry. The present results indicate that not all aspects of bioturbation as a community level process respond to the same drivers equally.

This study supports the view that environmental stimuli such as food availability, driven by plankton phenology, can modify both bioturbation depth and activity in natural settings (Gerino et al., 1998; Teal et al., 2008). Phytoplankton phenology exerts important control over shallow benthic ecosystems because as much as 40 per cent of the phytoplankton biomass produced during a spring bloom may reach the seabed, being a major source of organic matter to the benthos (Graf, 1992; Rudnick and Oviatt, 1986). We did provide a low ration of microalgae to the cores to avoid artificial reduction of bioturbation via food limitation during our laboratory incubations (Maire et al., 2007, 2006). This was seasonally adjusted to match the expected biomass of the benthic community at the site, which is lower in spring than in the summer. Nevertheless, we found that bioturbation activity, D_b and bioturbation depth still appeared to follow the timing of changes in primary production at the WCO, which peaked in spring and decreased through to winter. This signal could not have been reflected in the background availability of phytoplankton in the water supplied to the sediment cores during the incubations, which was filtered down to 1 μm , excluding the largest fraction of the bloom biomass at the WCO (Atkinson et al., 2015). However, at Cawsand, a site with a typical depth of 11 m, plankton blooms at the surface reach the benthos within a few days (Tarran and Bruun, 2015). This has been observed even at deeper sites within the WCO (Zhang et al., 2015). It is therefore likely that in May 2011 when we started the seasonal bioturbation program, the bloom at the surface (which started in April) would have already started accumulating on the seabed. This organic matter would have been picked up in the undisturbed sediments cores we used during the community incubations thus explaining the apparent mirroring of plankton phenology in bioturbation activity, depth and D_b . This aspect highlights the importance of multi-disciplinary, long-term observation programs such as the WCO: without this contextualisation and a good understanding of benthic-pelagic seasonal dynamics at the site, the interpretation of our benthic data would have been limited. Indeed, understanding of the drivers of biologically mediated ecosystem processes can be masked by environmental variability (Godbold and Solan, 2009, 2013; Maire et al., 2007).

Seawater temperature has the potential to impact bioturbation because temperature is a key regulator of metabolic rates in ectotherms such as macrofaunal invertebrates (Brown et al., 2004). As such, the amount of energy required to sustain basic cellular function should increase with higher temperature, within thermal tolerance windows (Pörtner and Farrell, 2008). Seasonal changes in cellular energy requirements thus modulate activities associated with the acquisition of food like foraging and mobility in general. Both of these should contribute to increased bioturbation, as observed by others (Godbold and Solan, 2013; Maire et al., 2007). In parallel, to save energy, bioturbation can be limited in periods of high metabolic energy expenditure (i.e. warm periods) if food availability is low (Maire et al., 2007). This observation

may explain the sharp decrease in D_b we observed between spring and summer, possibly reflecting the decrease in PP while seawater temperature was still rising. Alternatively, BP_c and bioturbation distance appeared to follow the seasonal pattern in seawater temperature, which was highest in summer and autumn. This observation is paradoxical, because as discussed, the present structure of BP_c does not account for the effects of environmental stimuli directly. However, changes in food availability do modify the structure of benthic communities, as different functional groups thrive or perish as a function of the type of food most available (Zhang et al., 2015). In contrast to the close timing of changes in bioturbation depth, activity and D_b in relation to PP (peaking in spring), changes mediated through functional traits may lag behind the timing of the change in the food input, to allow enough time for a tangible change in community structure to take place (Zhang et al., 2015). The same seasonal driver (i.e. food) may therefore cause different scales of response in community bioturbation, depending on which attribute is considered (bioturbation distance c.f. depth, activity or D_b).

4.3. Modelling community bioturbation

The model used here to estimate bioturbation distance includes a random-walk description for active particle displacement, but does not include an exchange function specific to a particular type of transport (Schiffers et al., 2011). This attribute makes this model appealing for applications in natural community settings, where a variety of sediment reworking modes exists (François et al., 1997; Kristensen et al., 2012). The sediment transport model most widely implemented in bioturbation studies is biodiffusion (Boudreau, 1986; Meysman et al., 2010), which is traditionally described as reflecting local particle transport, and isotropic probability of particle displacement (Goldberg and Koide, 1962; Guinasso and Schink, 1975). Biodiffusive transport was also estimated here. However, among other criticisms, biodiffusion estimates are known to depend on the tracer and method used (Gerino et al., 1998; Reed et al., 2006; Teal et al., 2008), and so the comparisons of studies when bioturbation is estimated in that way can be challenging. Furthermore, that model does not enable the accurate depiction of all the different sediment transport mechanisms exhibited by the variety of species which make up natural communities (François et al., 1997); at least not in the length of time typically employed in empirical studies (Meysman et al., 2010). In addition, the biodiffusive model is a particularly bad descriptor of conveyor type transport (Gilbert et al., 2007; Meysman et al., 2010). Other mechanistic modelling approaches exist in the bioturbation literature, explicitly and specifically addressing other types of (“non-local”) transport individually. While elegantly structured, these alternatives are usually underlined by strong mathematical assumptions associated with specific modes of transport, and at times leading to unrealistic estimates of mixing (e.g. continuous mixing versus the discrete activity periods observed in real organisms, Solan et al., 2004b). Other more widely focussed process based simulation models have also been applied to describe bioturbation (Meysman et al., 2008, 2003; Reed et al., 2006), but are typically provided in a context that does not enable fitting to observed (community) data. A wider application of the random-walk model used here therefore has the potential to significantly push the field forward because: the model is applicable to community settings (by definition and as tested here); it can be fitted to observed profiles in a straightforward manner; and its code is openly available. The strong relationship found here between bioturbation distance predicted by the model and BP_c suggests that future applications of this recent model are comparable to other studies where BP_c has been used. This compatibility between the two metrics could increase the ability of community bioturbation research to evolve

from one common base of evidence, resolving problems of terminology and comparability between studies. However because neither this model nor BP_c account for the important role of bioirrigation in organisms–sediment relationships (Volkenborn et al., 2012), it seems that more comprehensive community bioturbation estimates may depend still on further index and model developments. In the meantime, the ability to integrate community level estimates between studies, using these methods applicable to a variety of transport modes, may remain as the best options to predict large scale patterns of bioturbation in real ecosystems.

5. Conclusions

The present study makes an important contribution to the growth of bioturbation research by teasing apart the mechanistic basis of BP_c . The popularity and variety of uses of this index in the literature since its publication ten years ago is testament to its value as a resource to predict bioturbation at the community level, when measuring is not feasible. Its popularity also serves as evidence of the logistic and mathematical challenges involved in the acquisition of quantitative data on bioturbation as a community level process. However, without the type of analysis presented here, the ability to use BP_c as an indicator to investigate the mechanistic role of bioturbation in the mediation of biogeochemical processes is limited. The present analysis re-enforces the idea that bioturbation is a highly dynamic, multi-faceted process mediated by communities of living organisms. These communities respond to environmental stimuli in different ways and time scales, which may be difficult to summarize in one single parameter or mathematical description. However, the finding that one important mechanistic attribute of bioturbation is indeed well predicted by BP_c over the seasonal cycle corroborates future uses of this index, and helps to highlight the importance of functional traits in the regulation of benthic ecosystem processes (like particulate transport). Many of the processes mediated by bioturbation have important contributions to human well-being, like the regulation of climate through burial of carbon in marine sediments (MEA, 2005). Thus, understanding large-scale patterns of bioturbation is of relevance to policy-makers and other stake-holders of the marine environment. The use of BP_c can support the investigation of bioturbation at scales at which direct quantification of this process is not feasible (e.g. decades, basin scale), building on the more available community structure inventories.

Acknowledgments

This work was supported by the Western Channel Observatory and Plymouth Marine Laboratory’s Ecosystem Modelling, as part of the UK Natural Environment Research Council’s National Capability (all authors). AMQ, NS, PJS and SW were also funded by the Marine Ecosystems Research Programme (jointly funded by the UK Natural Environment Research Council and the UK Department for Environment, Food and Rural Affairs, contract agreement NE/L003279/1). GHT was additionally supported by the EU project Information System on the Eutrophication of our Coastal Seas (ISECA) (Contract No. 07-027-FR-ISECA) funded by INTERREG IVA 2 Mers Seas Zeen Cross-border Cooperation Programme 2007–2013. A warm thank you is due to Adam Cowles, Allan Bettinson, Amanda Beesley, Caroline Louise McNeill, Denise Cummings, Trish Frickers, Roger Pawley, Andy Pawley, Andy Perkin and other crew of the RVs Quest and Sepia during the benthic monitoring work. We thank Angus Atkinson and Glen Tarran for useful advice in the interpretation of plankton phenology at the WCO. Rachel Harmer and Claire Widdicombe are

thanked for the collation of the L4 zooplankton and phytoplankton time-series, respectively.

References

- Atkinson, A., Harmer, R., Widdicombe, C., Mcevoy, A., Smyth, T., Somerfield, P., Cummings, D., 2015. Questioning the Role of Phenology Shifts and Trophic Mismatching in a Planktonic Food Web. *Progress in Oceanography* 137, 498–512.
- Barange, M., Merino, G., Blanchard, J.L., et al., 2014. Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Climate Change* 4, 211–216.
- Barnes, M.K., Tilstone, G.H., Smyth, T.J., Suggett, D.J., Astoreca, R., Lancelot, C., Kromkamp, J.C., 2014. Absorption-based algorithm of primary production for total and size-fractionated phytoplankton in coastal waters. *Marine Ecology Progress Series* 504, 73–89.
- Bertics, V.J., Sohm, J.A., Treude, T., Chow, C.-E.T., Capone, D.G., Fuhrman, J.A., Ziebis, W., 2010. Burrowing deeper into benthic nitrogen cycling: the impact of bioturbation on nitrogen fixation coupled to sulfate reduction. *Marine Ecology Progress Series* 409, 1–15.
- Birchenough, S., Parker, R., Mcmanus, E., Barry, J., 2012. Combining bioturbation and redox metrics: potential tools for assessing seabed function. *Ecological Indicators* 12, 8–16.
- Boudreau, B.P., 1986. Mathematics of tracer mixing in sediments; I, Spatially-dependent, diffusive mixing. *American Journal of Science* 286, 161–198.
- Boyle, R., Dahl, T.W., Dale, A.W., et al., 2014. Stabilization of the coupled oxygen and phosphorus cycles by the evolution of bioturbation. *Nature Geoscience* 7, 671–676.
- Braeckman, U., Foshtomi, M.Y., Van Gansbeke, D., Meysman, F., Soetaert, K., Vincx, M., Vanaverbeke, J., 2014. Variable importance of macrofaunal functional biodiversity for biogeochemical cycling in temperate coastal sediments. *Ecosystems*, 1–18.
- Brey, T., 2001. Population dynamics in benthic invertebrates. A Virtual Handbook. <<http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html>>. Alfred Wegener Institute for Polar and Marine Research, Germany.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Canfield, D.E., Farquhar, J., 2009. Animal evolution, bioturbation, and the sulfate concentration of the oceans. *Proceedings of the National Academy of Sciences* 106, 8123–8127.
- Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Pauly, D., 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* 10, 235–251.
- Cook, R., 2012. Single species bioturbation. Unpublished Master's thesis. MSc Environmental Consultancy, Plymouth University, in Collaboration with Plymouth Marine Laboratory, 85 pp.
- Cook, R.D., Weisberg, S., 1982. *Residuals and Influence in Regression*. Chapman and Hall, New York, USA.
- Crank, J., 1979. *The Mathematics of Diffusion*. Oxford University Press.
- Dale, A.W., Prego, R., 2002. Physico-biogeochemical controls on benthic-pelagic coupling of nutrient fluxes and recycling in a coastal upwelling system. *Marine Ecology Progress Series* 235, 15–28.
- Dashfield, S., Queirós, A.M., 2014. In: Smyth, T., (Ed.). *The Western Channel Observatory: Benthic Survey*. Plymouth Marine Laboratory. <http://www.westernchannelobservatory.org.uk/benthic_survey.php>.
- François, F., Poggiale, J.-C., Durbec, J.-P., Stora, G., 1997. A new approach for the modelling of sediment reworking induced by a macrobenthic community. *Acta Biotheoretica* 45, 295–319.
- François, F., Gerino, M., Stora, G., Durbec, J.-P., Poggiale, J.-C., 2002. Functional approach to sediment reworking by gallery-forming macrobenthic organisms: modeling and application with the polychaete *Nereis diversicolor*. *Marine Ecology Progress Series* 229, 127–136.
- Fulton, E.A., Link, J.S., Kaplan, I.C., et al., 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries* 12, 171–188.
- Gerino, M., Aller, R., Lee, C., Cochran, J., Aller, J., Green, M., Hirschberg, D., 1998. Comparison of different tracers and methods used to quantify bioturbation during a spring bloom: 234-thorium, luminophores and chlorophyll a. *Estuarine, Coastal and Shelf Science* 46, 531–547.
- Gilbert, F., Rivet, L., Bertrand, J., 1994. The in vitro influence of the burrowing polychaete *Nereis diversicolor* on the fate of petroleum hydrocarbons in marine sediments. *Chemosphere* 29, 1–12.
- Gilbert, F., Hulth, S., Strömberg, N., Ringdahl, K., Poggiale, J.-C., 2003. 2-D optical quantification of particle reworking activities in marine surface sediments. *Journal of Experimental Marine Biology and Ecology* 285, 251–263.
- Gilbert, F., Hulth, S., Grossi, V., et al., 2007. Sediment reworking by marine benthic species from the Gullmar Fjord (Western Sweden): importance of faunal biovolume. *Journal of Experimental Marine Biology and Ecology* 348, 133–144.
- Gilbertson, W.W., Solan, M., Prosser, J.L., 2012. Differential effects of microorganism–invertebrate interactions on benthic nitrogen cycling. *FEMS Microbiology Ecology* 82, 11–22.
- Godbold, J., Solan, M., 2009. Relative importance of biodiversity and the abiotic environment in mediating an ecosystem process. *Marine Ecology Progress Series* 396, 273–282.
- Godbold, J.A., Solan, M., 2013. Long-term effects of warming and ocean acidification are modified by short-term responses to seasonal change. *Transactions of the Royal Society B* 368, 20130186.
- Goldberg, E.D., Koide, M., 1962. Geochronological studies of deep sea sediments by the ionium/thorium method. *Geochimica et Cosmochimica Acta* 26, 417–450.
- Graf, G., 1992. Benthic-pelagic coupling: a benthic view. *Oceanography and Marine Biology* 30, 149–190.
- Guinasso, N., Schink, D., 1975. Quantitative estimates of biological mixing rates in abyssal sediments. *Journal of Geophysical Research* 80, 3032–3043.
- Holt, J., Icarus Allen, J., Anderson, T.R., et al., 2014. Challenges in integrative approaches to modelling the marine ecosystems of the North Atlantic: physics to fish and coasts to ocean. *Progress in Oceanography*.
- Kristensen, E., 2001. Impact of polychaetes (*Nereis* spp. and *Arenicola marina*) on carbon biogeochemistry in coastal marine sediments. *Geochemical Transactions* 12, 1–28.
- Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T.B., Quintana, C.O., Banta, G.T., 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology-Progress Series* 446, 285–302.
- Mahaut, M., Graf, G., 1987. A luminophore tracer technique for bioturbation studies. *Oceanologica Acta* 10, 323–328.
- Maire, O., Duchene, J.C., Rosenberg, R., De Mendonca, J.B., Gremare, A., 2006. Effects of food availability on sediment reworking in *Abra ovata* and *A. nitida*. *Marine Ecology-Progress Series* 319, 135–153.
- Maire, O., Duchêne, J.C., Grémare, A., Malyuga, V.S., Meysman, F.J.R., 2007. A comparison of sediment reworking rates by the surface deposit-feeding bivalve *Abra ovata* during summertime and wintertime, with a comparison between two models of sediment reworking. *Journal of Experimental Marine Biology and Ecology* 343, 21–36.
- Maire, O., Lecroart, P., Meysman, F., Rosenberg, R., Duchêne, J.-C., Grémare, A., 2008. Quantification of sediment reworking rates in bioturbation research: a review. *Aquatic Biology* 2, 219–238.
- Mea, 2005. *Ecosystems and Human Well-Being: Our Human Planet: Summary for Decision Makers*. Island Press.
- Mermillod-Blondin, F., Rosenberg, R., 2006. Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. *Aquatic Sciences* 68, 434–442.
- Meysman, F.J.R., Boudreau, B.P., Middelburg, J.J., 2003. Relations between local, nonlocal, discrete and continuous models of bioturbation. *Journal of Marine Research* 61, 391–410.
- Meysman, F.J.R., Middelburg, J.J., Heip, C.H.R., 2006. Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology & Evolution*, 688–695.
- Meysman, F.J., Malyuga, V.S., Boudreau, B.P., Middelburg, J.J., 2008. A generalized stochastic approach to particle dispersal in soils and sediments. *Geochimica et Cosmochimica Acta* 72, 3460–3478.
- Meysman, F.J., Boudreau, B.P., Middelburg, J.J., 2010. When and why does bioturbation lead to diffusive mixing? *Journal of Marine Research* 68, 881–920.
- Michaud, E., Desrosiers, G., Mermillod-Blondin, F., Sundby, B., Stora, G., 2005. The functional group approach to bioturbation: The effects of biodiffusers and gallery-diffusers of the *Macoma balthica* community on sediment oxygen uptake. *Journal of Experimental Marine Biology and Ecology* 326, 77–88.
- Michaud, E., Aller, R., Stora, G., 2010. Sedimentary organic matter distributions, burrowing activity, and biogeochemical cycling: natural patterns and experimental artifacts. *Estuarine, Coastal and Shelf Science* 90, 21–34.
- Montserrat, F., Van Colen, C., Provoost, P., et al., 2009. Sediment segregation by biodiffusing bivalves. *Estuarine, Coastal and Shelf Science* 83, 379–391.
- Needham, H.R., Pilditch, C.A., Lohrer, A.M., Thrush, S.F., 2011. Context-specific bioturbation mediates changes to ecosystem functioning. *Ecosystems* 14, 1096–1109.
- Ouellette, D., Desrosiers, G., Gagne, J.P., Gilbert, F., Poggiale, J.C., Blier, P.U., Stora, G., 2004. Effects of temperature on in vitro sediment reworking processes by a gallery biodiffuser, the polychaete *Neanthes virens*. *Marine Ecology-Progress Series* 266, 185–193.
- Pischedda, L., Poggiale, J.C., Cuny, P., Gilbert, F., 2008. Imaging oxygen distribution in marine sediments. The importance of bioturbation and sediment heterogeneity. *Acta Biotheoretica* 56, 123–135.
- Pörtner, H.O., Farrell, A.P., 2008. Physiology and climate change. *Science* 322, 690–692.
- Queirós, A.M., 2010. *Ecosystem Engineers in Diversity and Process Relationships*. PhD, Bangor University, Menai Bridge, 163 pp.
- Queirós, A.M., Hiddink, J.G., Johnson, G., Cabral, H.N., Kaiser, M.J., 2011. Context dependence of marine ecosystem engineer invasion impacts on benthic ecosystem functioning. *Biological Invasions* 13, 1059–1075.
- Queirós, A.M., Birchenough, S.N., Bremner, J., et al., 2013. A bioturbation classification of European marine infaunal invertebrates. *Ecology and Evolution* 3, 3958–3985.
- Queirós, A.M., Bruggeman, J., Stephens, N., et al., 2014. Placing biodiversity in ecosystem models without getting lost in translation. *Journal of Sea Research*.
- Reed, D.C., Huang, K., Boudreau, B.P., Meysman, F.J., 2006. Steady-state tracer dynamics in a lattice-automaton model of bioturbation. *Geochimica et Cosmochimica Acta* 70, 5855–5867.
- Ricciardi, A., Bourget, E., 1998. Weight-to-weight conversion factors for marine benthic macroinvertebrates. *Marine Ecology Progress Series* 163, 245–251.
- Richter, R., 1952. Fluidal-texture in Sediment-Gesteinen und ober Sedifikation überhaupt. *Notizbl. Hess. L.-Amt. Bodenforsch* 3, 67–81.

- Rudnick, D.T., Oviatt, C.A., 1986. Seasonal lags between organic carbon deposition and mineralization in marine sediments. *Journal of Marine Research* 44, 815–837.
- Schiffers, K., Teal, L.R., Mark, J., Travis, J., Solan, M., 2011. An open source simulation model for soil and sediment bioturbation. *PLoS ONE* 6, e28028. <http://dx.doi.org/10.1371/journal.pone.0028028>.
- Shannon, C.E., Weaver, W., 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Urbana, Illinois.
- Smyth, T.J., Fishwick, J.R., Lisa, A.-M., et al., 2010. A broad spatio-temporal view of the Western English Channel observatory. *Journal of Plankton Research* 32, 585–601.
- Smyth, T., Atkinson, A., Widdicombe, S., Frost, M., Allen, J.I., Fishwick, J., Queirós, A.M., Sims, D., Barange, M., 2015. The Western Channel Observatory. *Progress in Oceanography* 137, 335–341.
- Solan, M., 2000. The concerted use of 'traditional' and Sediment Profile Imagery (SPI) methodologies in marine benthic characterisation and monitoring. Unpublished PhD thesis, Department of Zoology, National University of Ireland, Galway.
- Solan, M., Cardinale, B.J., Downing, A.L., KaM, Engelhardt, Ruesink, J.L., Srivastava, D.S., 2004a. Extinction and ecosystem function in the marine benthos. *Science* 306, 1177–1180.
- Solan, M., Wigham, B.D., Hudson, I.R., et al., 2004b. In situ quantification of bioturbation using time-lapse fluorescent sediment profile imaging (f-SPI), luminophore tracers and model simulation. *Marine Ecology Progress Series* 271, 1–12.
- Solan, M., Scott, F., Dulvy, N.K., Godbold, J.A., Parker, R., 2012. Incorporating extinction risk and realistic biodiversity futures: implementation of trait-based extinction scenarios. *Marine Biodiversity and Ecosystem Functioning: Frameworks, Methodologies, and Integration*, p. 127.
- Sonka, M., Hlavac, V., Boyle, R., 1999. *Image Processing, Analysis and Machine Vision*. PWS Publishing.
- Southward, A.J., Langmead, O., Hardman-Mountford, N.J., et al., 2004. Long-term oceanographic and ecological research in the western English Channel. *Advances in Marine Biology* 47, 1–105.
- Stahl, H., Glud, A., Schroder, C.R., Klimant, I., Tengberg, A., Glud, R.N., 2006. Time-resolved pH imaging in marine sediments with a luminescent planar optode. *Limnology and Oceanography: Methods* 4, 336–345.
- Tarran, G.A., Bruun, J.T., 2015. Nanoplankton and picoplankton in the Western English Channel: seasonality and variability from 2007–2013. *Progress in Oceanography* 137, 446–455.
- Teal, L., Bulling, M., Parker, E., Solan, M., 2008. Global patterns of bioturbation intensity and mixed depth of marine soft sediment. *Aquatic Biology* 2, 207–218.
- Teal, L.R., Parker, R., Fones, G., Solan, M., 2009. Simultaneous determination of in situ vertical transitions of color, pore-water metals, and visualization of infaunal activity in marine sediments. *Limnology and Oceanography* 54, 1801–1810.
- Teal, L., Parker, E., Solan, M., 2013. Coupling bioturbation activity to metal (Fe and Mn) profiles in situ. *Biogeosciences* 10, 2365–2378.
- Van Colen, C., Rossi, F., Montserrat, F., et al., 2012. Organism-sediment interactions govern post-hypoxia recovery of ecosystem functioning. *PLoS ONE* 7, e49795.
- Van Hoey, G., Permy, D.C., Vandendriessche, S., Vincx, M., Hostens, K., 2013. An ecological quality status assessment procedure for soft-sediment benthic habitats: weighing alternative approaches. *Ecological Indicators* 25, 266–278.
- Volkenborn, N., Polerecky, L., Hedtkamp, S.I.C., Van Beusekom, J.E.E., De Beer, D., 2007. Bioturbation and bioirrigation extend the open exchange regions in permeable sediments. *Limnology and Oceanography* 52, 1898–1909.
- Volkenborn, N., Polerecky, L., Wetthey, D., Dewitt, T., Woodin, S., 2012. Hydraulic activities by ghost shrimp *Neotrypaea californiensis* induce oxic-anoxic oscillations in sediments. *Marine Ecology Progress Series* 455, 141–156.
- Waldbusser, G.G., Marinelli, R.L., Whitlatch, R.B., Visscher, P.T., 2004. The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. *Limnology and Oceanography* 49, 1482–1492.
- Zhang, Q., Warwick, R.M., Mcneill, C.L., Widdicombe, C.E., Sheehan, A., Widdicombe, S., 2015. An unusually large phytoplankton spring bloom drives rapid changes in benthic diversity and ecosystem function. *Progress in Oceanography* 137, 533–545.