Elevation gradient affects the development of macrozoobenthic communities in the Wadden Sea: A field experiment with artificial islands

Gesine Lange[a,*], Olaf R.P. Bininda-Emonds[a], Helmut Hillebrand[b,c], Daniela Meier[b], Stefanie D. Moorthi[b], Jennifer A. Schmitt[b], Oliver Zielinski[b,d], Ingrid Kröncke[e,f]

[a] Institute for Biology and Environmental Sciences, Carl von Ossietzky University Oldenburg, Carl von Ossietzky Str. 9-11, 26111 Oldenburg, Germany
[b] Institute for Chemistry and Biology of the Marine Environment, Carl von Ossietzky University Oldenburg, Schleusenstr. 1, 26382 Wilhelmshaven, Germany
[c] Helmholtz Institute for Functional Marine Biodiversity, Carl von Ossietzky University Oldenburg, Ammerländer Heerstr. 231, 23129 Oldenburg, Germany
[d] Marine Perception Research Group, German Research Center for Artificial Intelligence (DFKI), Marie-Curie-Str. 1, 26129 Oldenburg, Germany
[e] Department for Marine Research, Senckenberg am Meer, Südstrand 40, 26382 Wilhelmshaven, Germany
[f] Institute for Chemistry and Biology of the Marine Environment, Carl von Ossietzky University Oldenburg, Carl von Ossietzky Str. 9-11, 26111 Oldenburg, Germany

ARTICLE INFO

ABSTRACT

Tidal flats are subject to dynamic processes, characterized by sedimentation and erosion, which become more important in times of climate change. To investigate impacts of elevation levels on ecosystem functioning, we focused on macrozoobenthos as an essential ecosystem component that links trophic levels and determines sediment structure. Therefore, three elevation levels of six experimental islands (each 2×6 m) and six natural reference sites (nearby tidal flats) were sampled for species richness, abundance and biomass in the back-barrier system of the island of Spiekeroog (German Wadden Sea, southern North Sea) from 2014 to 2016. Reference sites had constant biodiversity and abundance over time that were higher compared to the three elevations of the experimental islands. At the lowest elevation, the community became more diverse over time, including marine and terrestrial taxa. At the middle elevation, community shifted from a marine species inventory over an opportunist-dominated assemblage to a less diverse community dominated by Enchytraeidae (Oligochaeta). The community of the highest elevation mostly remained constant, resembling the second, opportunistic community from the middle elevation that was dominated by the snail *Peringia ulvae* (Pennant, 1777) and the oligochaetes Enchytraeidae spp. and *Tubificoides benedii* (d'Udekem, 1855). Correspondingly, food web structure was more complex and comprised more trophic interactions at the lowest elevation compared to the other elevations mainly inhabited by deposit feeders. Results demonstrate negative impacts of increased sediment elevation on macrofaunal biodiversity and functional diversity, originating from reduced inundation and vegetation establishment.

1. Introduction

The Wadden Sea ecosystem of the southern North Sea is subject to semidiurnal tides, creating highly dynamic conditions with regard to hydrography, morphology and sedimentology (Hild, 1999; Niesel, 1999). Its coastal areas represent a transition zone between marine and terrestrial boundaries, resulting in gradients and variability of abiotic parameters, which in turn affect species inventory and biodiversity.

During the last decade, the loss of biodiversity and its consequences for ecosystem functioning has become a major focus of international research (Cardinale et al., 2012). Macrozoobenthos has an important impact on the functioning of marine ecosystems, e.g. as ecosystem engineer and trophic link (Braeckman et al., 2014; Kristensen et al., 2014;

Waldbusser et al., 2004). Especially in the Wadden Sea, macro-zoobenthos represents a highly abundant food resource for higher trophic levels, such as fishes (De Vlas, 1979) and birds (Noordhuis and Spaans, 1992). Thus, any decrease in macrozoobenthos (e.g., as caused by habitat modification) could hold serious consequences for a coastal ecosystem (Braeckman et al., 2014).

The recent biodiversity change reflects anthropogenic impacts on nature (Elahi et al., 2015; Hillebrand et al., 2018). Moreover, effects of climate change, such as more frequent storms (Donat et al., 2011) and sea level rise (Kirwan et al., 2010) will alter the natural habitats of the Wadden Sea ecosystem and probably enhance the impacts of sedimentation and erosion. These processes potentially lead to the establishment of segregated habitats, e.g. the formation of small islands and
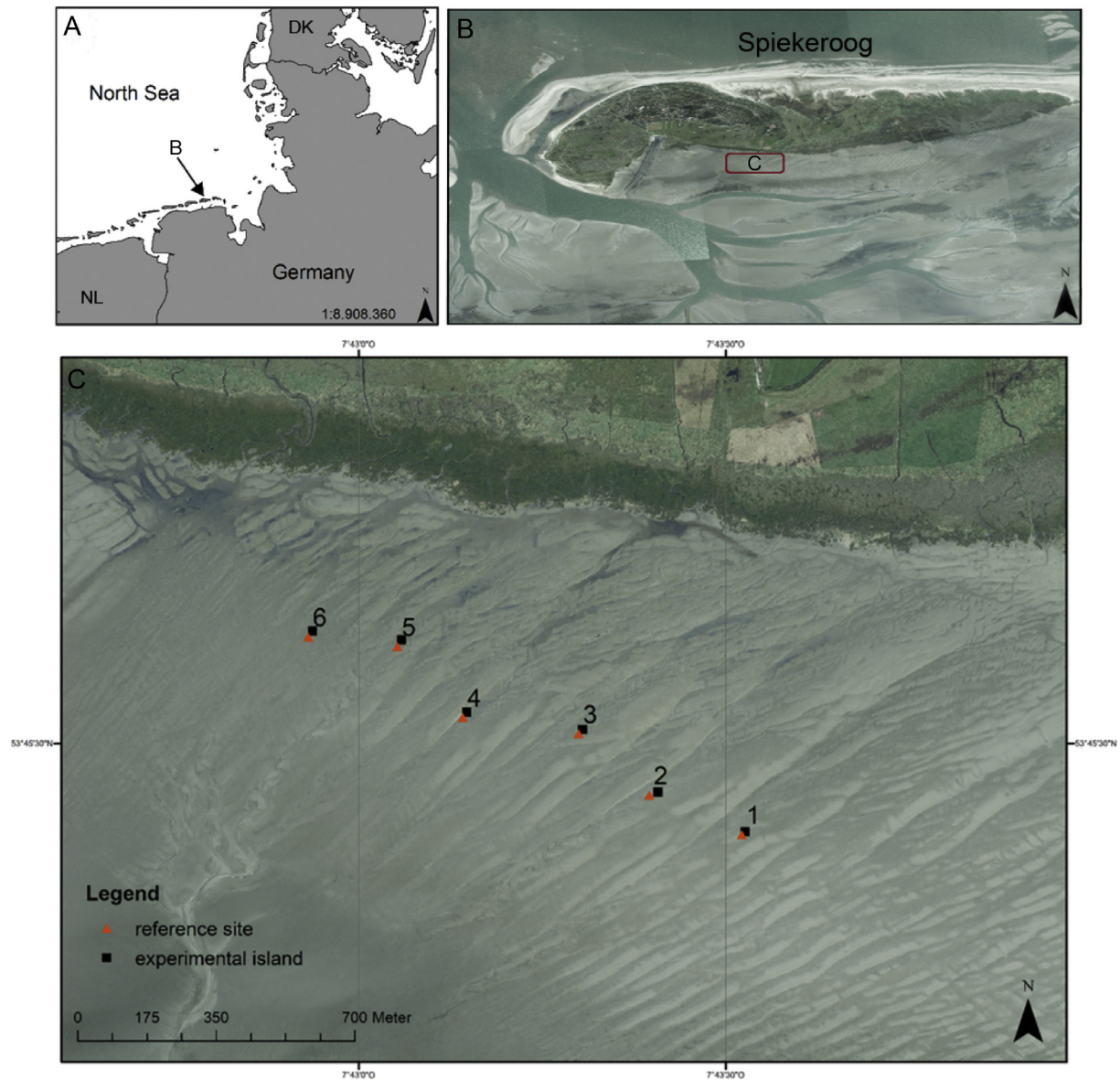

Fig. 1. Study area (A) in the German Wadden Sea (southern North Sea) at (B) the island of Spiekeroog. (C) Back-barrier system of Spiekeroog with sampling sites, comprising six experimental islands (black squares) and six tidal flat reference sites (orange triangles). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

stronger abiotic gradients or frequent environmental changes that require appropriate adaptations of the local organisms (Lange et al., 2018).

Apart from sediment accumulation and stronger environmental gradients, the formation of small islands in the Wadden Sea is characterized by successional changes of macrobenthic community structure involving the colonization of new species and the disappearance of previously established species. However, dynamic systems, such as coastal areas, undergo periodic (daily, seasonally), stochastic (e.g. storm surges, cold winters) and deterministic (e.g. sea level rise) environmental changes with regard to abiotic conditions and resource availability (Brose and Hillebrand, 2016). These perturbations are likely to influence the relationships between biodiversity and ecosystem functioning (BEF). In fact, stochastic disturbances continuously interrupt the direction of community development of isolated habitats and induce successional shifts in species composition that depend on dispersal ability and competitiveness of arriving species as well as on persistence of resident species. Moreover, priority effects by early arriving species influence community development (Loeuille and Leibold,

2008).

In general, succession is affected by diverse biotic interactions, e.g. predation, competition, facilitation and mutualism (Stachowicz, 2001; Wilson, 1990). Furthermore, the presence or absence of certain species during the community development depends on their functional traits, including recruitment success and tolerance against abiotic factors, as well as on the prevailing environmental conditions, such as the species pool present and food availability (Beukema and Dekker, 2005; Schückel et al., 2013). Environmental stress results in less complex communities dominated by *r*-selected, opportunistic species that are usually associated with decreasing biodiversity in marine and terrestrial ecosystems (Pearson and Rosenberg, 1978; Rapport et al., 1985). Consequently, food webs of these ecosystems become simpler and multilevel interactions decrease (Menge and Sutherland, 1987). In fact, the loss of biodiversity affects ecosystem functioning in terms of productivity as it causes a decline in production and biomass in multiple trophic groups, potentially leading to lower decomposition and incomplete resource depletion (Cardinale et al., 2013). Current studies addressed multi-trophic interactions and structural properties of

communities as well as their response to stressors in the context of BEF research (Barnes et al., 2018; O'Gorman et al., 2012).

However, BEF experiments have widely ignored the stochastic disturbances that need to be considered during *in situ* community assembly and disassembly in dynamic ecosystems. The present study provides first insights in macrozoobenthic community establishment in newly formed habitats, describing changes in biodiversity and benthic community structure as well as the implications for ecosystem functioning. This process has rarely been studied across marine and terrestrial ecosystems. The Wadden Sea is a dynamic transition zone between land and sea, which is strongly influenced by human activities. Therefore, it represents a suitable system to investigate *in situ* relationships between biodiversity and functional structure of macrozoobenthos from marine to terrestrial environmental conditions.

The objective of our study was to imitate the dynamic emergence of small islands in the Wadden Sea and to show which factors determine the biodiversity and community structure of benthic macrofauna in an ecosystem that is subject to rapid environmental gradients and stochastic disturbances. In this context, we investigated the distribution of feeding types representing functional groups during community establishment to reveal the links between biodiversity and ecosystem functions across the boundary between marine and terrestrial ecosystems. We expect that the succession on new islands primarily depends on the inundation regime. At low elevation, we expect to see a development from *r*-selected opportunists towards a more diverse community of long-living, marine taxa, similar to the tidal flats. At higher elevation, we expect a decline in the abundance of marine species and an increase of terrestrial or opportunistic species. Therefore, we expect a higher food web complexity at lower elevation. Finally, we expect stochastic disturbances to interrupt the direction of community development.

2. Material and methods

2.1. Study area

This study was carried out in the mesotidal back-barrier system of the island of Spiekeroog (E 7°43′30″, N 53°45′31″), which is located in the Wadden Sea National Park of Lower Saxony (southern North Sea), Germany (Fig. 1A,B). The coastal region south of the island is characterized by sandy and mixed tidal flats passing into salt marshes with a high mud content (Flemming and Davis Jr., 1994; Flemming and Ziegler, 1995). Its morphology is subject to semidiurnal tides and storm waves flowing in from the North-West via the tidal inlet "Otzumer Balje" (Hertweck, 1995).

2.2. Experimental islands

Within the framework of a joint research project, a total of 12 experimental islands were built *in situ* in August 2014 (for details, see Balke et al., 2017), in which six islands were completely transplanted with vegetation sods from the lower salt marsh and six islands were filled with circumjacent tidal flat sediment (not treated) down to 10 cm below the top of the island construction and left bare. For our experimental set-up, only the six bare islands (Fig. 1C) were investigated because we wanted to study the development of marine benthic communities depending on environmental changes due to elevation gradients. The islands were positioned at the same tidal elevation approx. 80 cm above standard elevation zero (NHN). All islands were arranged next to shallow tidal creeks running from North-East to South-West and were placed from 240 m (west) to 460 m (east) offshore from the salt marshes on Spiekeroog. Each island had a footprint of 2×6 m and consisted of 12 1-m^2 steel cages (Fig. 2), of which four together formed one of three different elevations (70 cm, 100 cm and 130 cm) corresponding approximately to those of the three naturally occurring salt marsh zones: the pioneer zone ("pio"), the lower salt marsh ("low") and the upper salt marsh ("upp"). The lowest elevation ("pio") faced the

island of Spiekeroog.

2.3. Sampling

Samples were taken every April (t1, t4), July (t2, t5) and October (t0, t3, t6) from October 2014 to October 2016 at each elevation level ("pio", "low", "upp") of each bare island. In addition, natural references were obtained by concurrent sampling of the tidal flats at a distance of approximately 4 m to each of the six islands (Fig. 1C). Macrozoobenthos was collected with hand corers (15 cm in length, 5 cm inner diameter). To better cover the patchy distribution of the macrozoobenthos, two core samples, each of 0.002 m^2, were always taken per elevation level and experimental island, amounting to an area of 0.004 m^2 per sample. Samples were placed in 500-ml Kautex-containers and sieved over a 0.5-mm mesh. The material retained on the mesh was collected and preserved in a 4% buffered formaldehyde solution.

To analyze total organic carbon (TOC) as well as sand (fraction 63–2000 μm) and mud (fraction < 63 μm) contents, surface-sediment samples (< 3 cm depth) were taken with a spoon. All sediment samples were stored in separate plastic bags and immediately frozen at −20 °C until measurement. Sediment samples for the determination of pore-water salinity were also taken with a spoon (< 3 cm depth) and stored in plastic bags at room temperature until measurement (not longer than two months later).

2.4. Macrozoobenthos processing

In the laboratory, samples were washed with tap water through a 0.1-mm sieve mesh and stained with Bengal rose prior to sorting with a stereomicroscope (Leica MZ 95, Leitz, Wetzlar, Germany) and an optical microscope (Leica DM LS 2). All organisms were identified to the lowest possible taxonomic level (standardized to the World Register of Marine Species; http://www.marinespecies.org/index.php), counted and wet-weighed. All taxa were ascribed to the following functional groups according to their feeding type (Fauchald and Jumars, 1979; Jumars et al., 2015; Schückel et al., 2013): surface deposit feeders (SD), subsurface deposit feeders (SSD), suspension feeders (SF), sand lickers (SL), omnivores (O), predators (P), herbivores (H) and interface feeders (IF). Insect larvae were categorized as "other".

2.5. Environmental variables

Samples for TOC measurements were freeze-dried using a Lyovac GT2 (STERIS GmbH, Huerth, Germany) and subsequently ground using a Planetary Ball Mill PM200 (Retsch GmbH, Haan, Germany). Thereafter, pulverized sediment was weighed into silver capsules and treated with HCl until all carbonates were completely removed. TOC content was measured with a CHNS-Elemental-Analyzer "vario EL cube" (ELEMENTAR Analysensysteme GmbH Heraeus, Langenselbold, Germany) that was calibrated with sulfanilic acid. The precision of the measurements was < 0.2%.

To determine sand and mud contents, approximately 100 g sediment of each sample were wet-sieved over a 63–2000 μm mesh cascade to determine the proportion of gravel (> 2000 μm), sand (63–2000 μm) and mud (< 63 μm).

Plant coverage was estimated as the proportion (%) of the complete area of the sampled plots at one elevation level (of 2 m^2). Oxygen concentrations at sediment depths of 0, 0.5, 1.0 and 2.0 cm were measured in the field with an oxygen probe (PreSens®, Regensburg, Germany).

In the laboratory, sediment samples for the determination of pore-water salinity were weighed in pre-weighed tubes. After air-drying, the samples were weighed again to calculate dry weight and water content (= loss in weight). A defined amount of ultrapure water was added before measuring salinity with a HQ40D multi meter and an attached conductivity electrode (Hach Lange GmbH, Germany). Pore-water
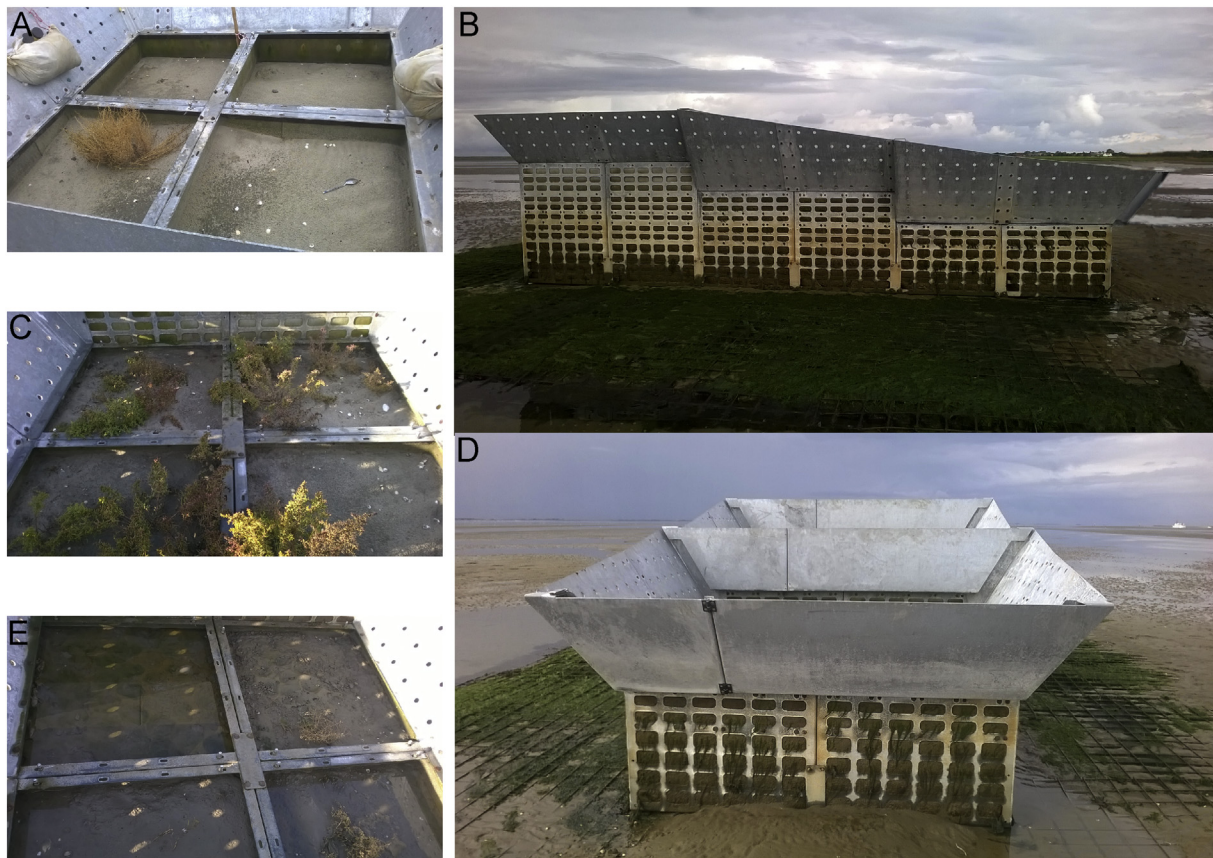
Fig. 2. Photographs of an experimental island at low tide. (A) Highest elevation level "upp" after two years. (B) Side view. (C) Middle elevation "low" after two years. (D) Front view. (E) Lowest elevation "pio" after two years. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

salinity was calculated as the product of the measured salinity and the amount of ultrapure water, all divided by the calculated water content.

Temperature were measured using temperature loggers (DEFI-T Miniature Temperature Recorder, JFE Advantech Co., Ltd., Tokyo, Japan) that were locally installed at approximately 5 cm sediment depth within the experimental islands. Data for the surrounding water-level were obtained with a locally installed tide and wave logger (RBRduo T.D / wave, RBR Ltd., Ottawa, Canada) next to the experimental islands. Data for the groundwater-level within the experimental islands were measured with pressure loggers (Hobo U20 L Water Level Loggers, Onset Computer Corporation, Bourne, MA, USA; DEFI-D Miniature Pressure, JFE Advantech Co., Ltd.) that were installed at each of the three elevation levels (Zielinski et al., 2018). For information on data analysis and data quality control steps for temperature and water-level data see Zielinski et al. (2018).

Salinity, temperature and water-level data for the reference sites in 2014 were provided by the Time Series Station Spiekeroog (Reuter et al., 2009) as part of the COSYNA observatory (Baschek et al., 2017). The mean values for all measured environmental parameters are shown in Table 1.

2.6. Statistical analysis

To analyze spatial and temporal differences in macrozoobenthic community structure, multivariate analysis on the square-root-transformed abundances of the found taxa were carried out using PRIMER 6 & PERMANOVA+ (PRIMER-E Ltd., Plymouth, United Kingdom) (Anderson et al., 2008; Clarke and Gorley, 2006). Group average cluster analysis with a similarity profile test (SIMPROF) based on Bray-Curtis similarities were performed initially, followed by multidimensional

scaling (MDS). Thereafter, the dominant taxa and feeding types were identified using the similarity percentage routine (SIMPER). Spearman's rank-order correlation between the macrozoobenthic community structure and all normalized environmental variables were tested using comparative (Mantel-type) tests on similarity matrices (RELATE). Afterwards, the environmental variables that correlated most strongly with community structure were identified using the BEST routine with a BIO-ENV procedure as implemented in PRIMER 6 & PERMANOVA+. Principal coordinates analysis (PCO) was used to show correlation patterns between community structure and environmental variables. Visualization of taxon number, Shannon index, abundance and biomass of the macrozoobenthos as well as respective regression and correlation analyses were performed in R v3.3.0 (The R Foundation for Statistical Computing, Vienna, Austria) (R Core Team, 2016).

3. Results

In total, 55 taxa from six taxonomic groups (18 Polychaeta, 10 Crustacea, 9 Insecta, 8 Mollusca, 6 Oligochaeta, 4 other) were found during our sampling. Thereof, 44 taxa (18 Polychaeta, 9 Crustacea, 2 Insecta, 7 Mollusca, 5 Oligochaeta, 3 other) were present at the tidal flat reference sites. At the elevation level "pio", a total of 22 taxa (8 Polychaeta, 1 Crustacea, 3 Insecta, 3 Mollusca, 4 Oligochaeta, 3 other) occurred. In total, 18 taxa (2 Polychaeta, 5 Insecta, 4 Mollusca, 5 Oligochaeta, 2 other) were found at the elevation level "low" and 17 taxa (2 Polychaeta, 1 Crustacea, 6 Insecta, 2 Mollusca, 4 Oligochaeta, 2 other) were present at the elevation level "upp".

Table 1
Environmental parameters (mean values) at the tidal flat references ("ref") and the three elevations of the experimental islands, corresponding to the salt marsh zonation: pioneer zone ("pio"), lower salt marsh ("low") and upper salt marsh ("upp") at the sampling dates: t0 = October 2014, t1 = April 2015, t2 = July 2015, t3 = October 2015, t4 = April 2016, t5 = July 2016 and t6 = October 2016.

Time/Station	Mud [%]	Sand [%]	Gravel [%]	TOC [%]	Plant cover [%]	Oxygen [mg/L]	Salinity [‰]	Temperature [°C]	Water level [m]
t0ref	2.83	97.13	0.04	0.24	0	7.59	30.78	16.43	0.97
t1ref	0.51	98.55	0.04	0.14	0	9.74	32.92	11.44	1.30
t2ref	1.83	97.50	0.03	0.17	0	9.21	34.25	17.76	1.21
t3ref	0.72	98.27	0.03	0.17	0	10.39	54.37	8.32	1.18
t4ref	0.86	98.06	0.12	0.15	0	9.34	35.60	9.16	1.21
t5ref	1.81	97.26	0.06	0.21	0	8.09	38.49	17.14	0.94
t6ref	1.37	97.19	0.47	0.26	0	7.44	30.35	10.52	1.07
t0pio	2.83	97.13	0.04	0.24	0	8.06	29.11	13.13	0.92
t1pio	2.83	97.13	0.04	0.24	0	10.84	40.87	8.23	1.54
t2pio	2.84	96.33	0.12	0.17	1	9.34	21.73	17.54	1.43
t3pio	2.88	95.88	0.24	0.24	1	10.07	44.45	9.13	1.35
t4pio	4.00	95.15	0.08	0.49	1	8.95	37.95	9.56	1.29
t5pio	11.70	87.76	0.06	0.88	1	7.68	46.19	17.58	1.47
t6pio	14.53	84.17	0.67	0.60	4	9.22	26.62	10.13	1.49
t0low	2.83	97.13	0.04	0.24	0	8.06	32.60	13.50	0.92
t1low	2.83	97.13	0.04	0.24	0	10.54	107.10	8.19	1.13
t2low	1.91	96.97	0.59	0.21	1	9.64	6.02	17.18	1.13
t3low	1.46	97.39	0.66	0.18	1	10.61	46.43	9.31	1.11
t4low	1.36	98.04	0.04	0.22	6	8.57	42.53	9.58	0.24
t5low	1.88	97.51	0.09	0.16	21	7.90	62.66	17.11	0.46
t6low	3.83	95.69	0.07	0.21	31	8.45	35.52	10.20	0.52
t0upp	2.83	97.13	0.04	0.24	0	8.06	26.93	12.78	0.92
t1upp	2.83	97.13	0.04	0.24	0	10.27	118.33	7.05	1.32
t2upp	1.67	97.32	0.35	0.12	0	9.48	3.23	16.47	1.34
t3upp	0.64	99.12	0.01	0.11	1	10.52	40.34	8.94	1.33
t4upp	1.49	98.09	0.12	0.14	3	9.06	54.15	9.62	1.22
t5upp	1.54	97.93	0.10	0.10	6	7.76	76.08	16.78	1.27
t6upp	1.63	98.07	0.04	0.10	20	7.95	25.92	9.66	1.41

3.1. Temporal changes in mean taxon number, abundance, biomass and biodiversity

During our sampling from October 2014 (t0) to October 2016 (t6), mean taxon number was always higher at the reference sites compared to each of the three elevation levels (Fig. 3A). The simple linear regression explained little variance in number of taxa over time ($r^2 = 0.076$, $p = .550$). The mean number of taxa of the elevation level "pio", in contrast, increased in 2016 ($r^2 = 0.642$, $p = .030$). The mean taxon numbers of the elevation levels "low" and "upp" displayed the opposite trend ("low": $r^2 = 0.846$, $p = .003$; "upp": $r^2 = 0.684$, $p = .022$), decreasing to 1 taxon at t6. Shannon diversity (Fig. 3B) correlated with the number of taxa (Pearson's product-moment correlation; $r = 0.715$, $p < .001$).

Like with mean taxon number, mean abundance of the reference sites was always higher compared to each of the three elevation levels (Fig. 3C) without a linear trend over time ($r^2 = 0.354$, $p = .158$). There were also no significant trends in mean abundance of the elevation levels "pio" ($r^2 = 0.076$, $p = .549$) and "low" ($r^2 = 0.547$, $p = .058$) over time. At the elevation level "upp", mean abundance decreased significantly ($r^2 = 0.750$, $p = .012$).

Mean biomass was also always higher at the reference sites compared to each of the three elevation levels (Fig. 3D). There was no significant trend in mean biomass of the reference sites over time ($r^2 = 0.026$, $p = .731$); the same was true for the elevation level "pio" ($r^2 = 0.008$, $p = .852$). By contrast, the mean biomass of the elevation levels "low" ($r^2 = 0.703$, $p = .018$) and "upp" ($r^2 = 0.800$, $p = .007$) both decreased over time.

3.2. Changes in community structure

The SIMPROF test ($p = .001$) and MDS revealed seven different communities (labeled *a* through *g*) during the macrofaunal succession in the entire study site from t0 to t6 (Fig. 4). A schematic illustration of

the community development is given in Fig. 5. At the elevation level "pio", two different communities were present. From t0 to t4, this elevation level was dominated by the oligochaete *Tubificoides benedii*, with additional contributions by the gastropod *Peringia ulvae*, Nematoda spp., the oligochaete *Baltidrilus costatus* (Claparède, 1863), the polychaete *Hediste diversicolor* (O.F. Müller, 1776) and the bivalve *Limecola balthica* (Linnaeus, 1758) (community *d*). After 21 months (t5), the community had significantly changed and biodiversity had increased. This second community (community *e*) was mainly dominated by *T. benedii*, Enchytraeidae spp. and Nematoda spp. together with Dolichopodidae larvae, *H. diversicolor*, the polychaete *Pygospio elegans* Claparède, 1863, *B. costatus*, Collembola spp. and the polychaete *Arenicola marina* (Linnaeus, 1758) (Table 2).

At the elevation level "low", three different communities were found between t0 and t6. From t0 to t1, the first community of this elevation level resembled the first community from the elevation level "pio", representing one statistical unit (community *d*). After these initial nine months, however, both species richness and abundance had declined. The second community from t2 to t4 was dominated by *P. ulvae* and Enchytraeidae spp. together with *T. benedii* and Nematoda spp. (community *f*). Finally, after 21 months (t5), biodiversity had declined so strongly that the community consisted of Enchytraeidae only (community *g*).

Smaller changes in community structure were found for the elevation level "upp", where, except for t1, the community resembled the second one of the elevation level "low" (community *f*). By contrast, the t1-community of the elevation level "upp" resembled the first communities of each of the elevation levels "pio" and "low" (community *d*).

Finally, three entirely different communities to those on the islands were found at the tidal-flat reference sites during the sampling period. At t0, the benthic community (community *a*) was dominated by the oligochaete *T. benedii* and the polychaete *P. elegans*, both of which reached high mean abundances (78 ± 61 and 23 ± 24 ind. $0.004 \, \text{m}^{-2}$, respectively), with additional contributions by *L. balthica*,
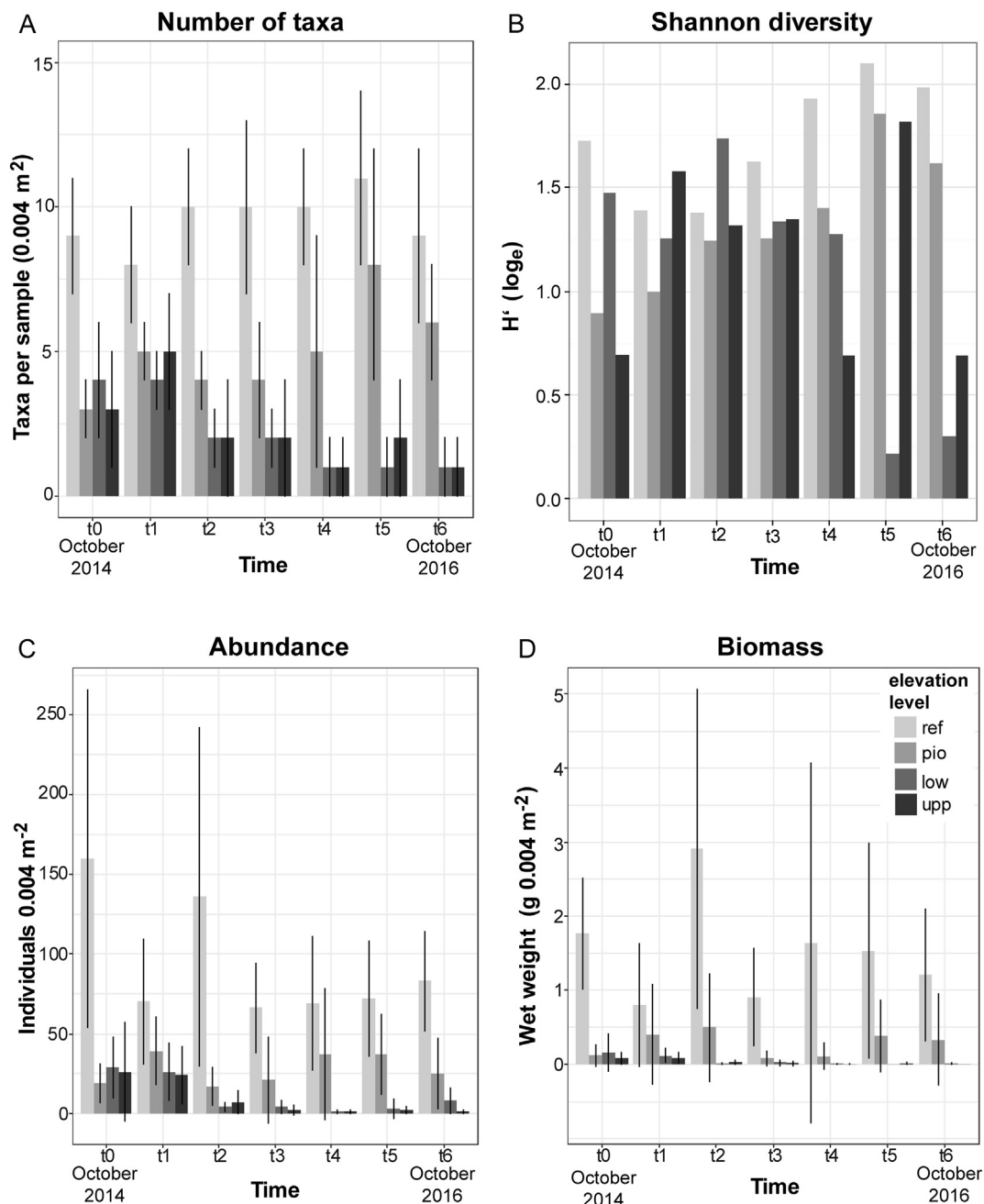
Fig. 3. (A) Mean numbers of taxa per sample ($0.004 \, \text{m}^2$)

(B) Shannon diversity (H'($\log_e$))

(C) mean abundances (individuals $0.004 \, \text{m}^{-2}$) and (D) mean wet weights (g $0.004 \, \text{m}^{-2}$) with standard deviations at the tidal flat references ("ref") and the three elevations of the experimental islands

corresponding to the salt marsh zonation: pioneer zone ("pio")

lower salt marsh ("low") and upper salt marsh ("upp") at the sampling dates: t0 = October 2014

t1 = April 2015

t2 = July 2015

t3 = October 2015

t4 = April 2016

t5 = July 2016 and t6 = October 2016

P. ulvae and *H. diversicolor*. After six months (t1), community composition had significantly changed (community *b*). Although *T. benedii* still dominated the community, the remainder was composed of Nematoda spp., *H. diversicolor*, *L. balthica*, *P. ulvae*, the polychaete *Scoloplos armiger* (Müller, 1776), the gastropod *Retusa obtusa* (Montagu, 1803) and the oligochaete *Tubificoides pseudogaster* (Dahl, 1960). A final significant change in the community structure became visible after 12 months (t3).

Here, in addition to the dominant species of the former time periods, the polychaetes Capitellidae spp., *A. marina* and *Eteone longa* (Fabricius, 1780) as well as the amphipods *Corophium arenarium* Crawford, 1937 and *Urothoe poseidonis* Reibish, 1905 dominated the community (community *c*).

BEST routine with BIO-ENV procedure revealed that plant coverage correlated best with the macrozoobenthic community matrix
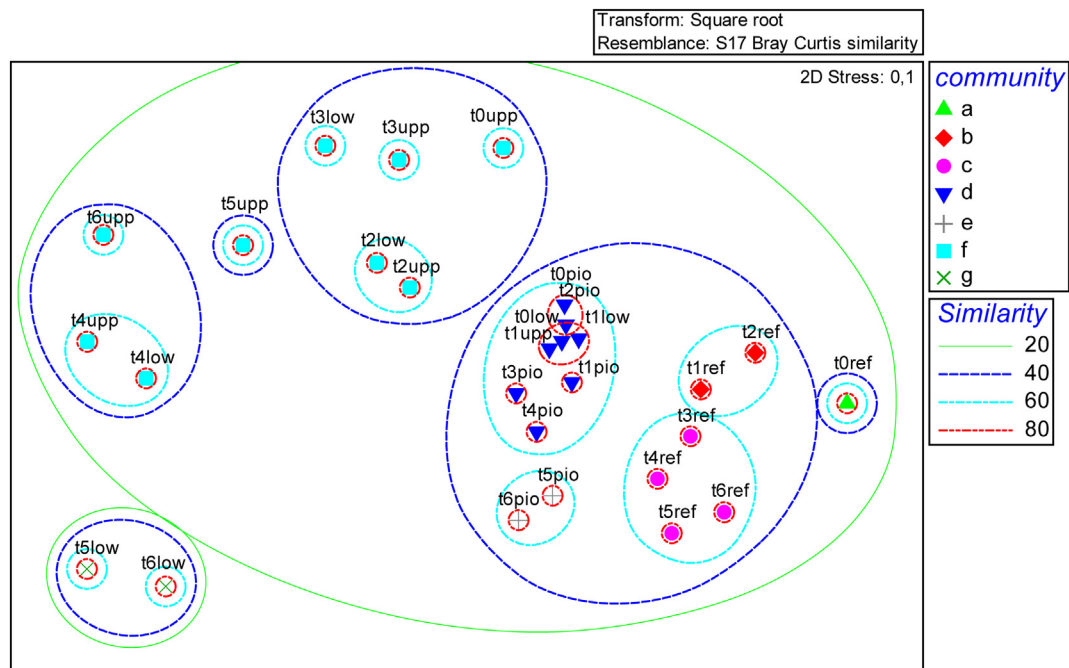
Fig. 4. MDS plot based on the square-root transformed abundances of the taxa present at the tidal flat references ("ref") and the three elevations of the experimental islands, corresponding to the salt marsh zonation: pioneer zone ("pio"), lower salt marsh ("low") and upper salt marsh ("upp") at the sampling dates: t0 = October 2014, t1 = April 2015, t2 = July 2015, t3 = October 2015, t4 = April 2016, t5 = July 2016 and t6 = October 2016. Colored lines indicate percentages of similarity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
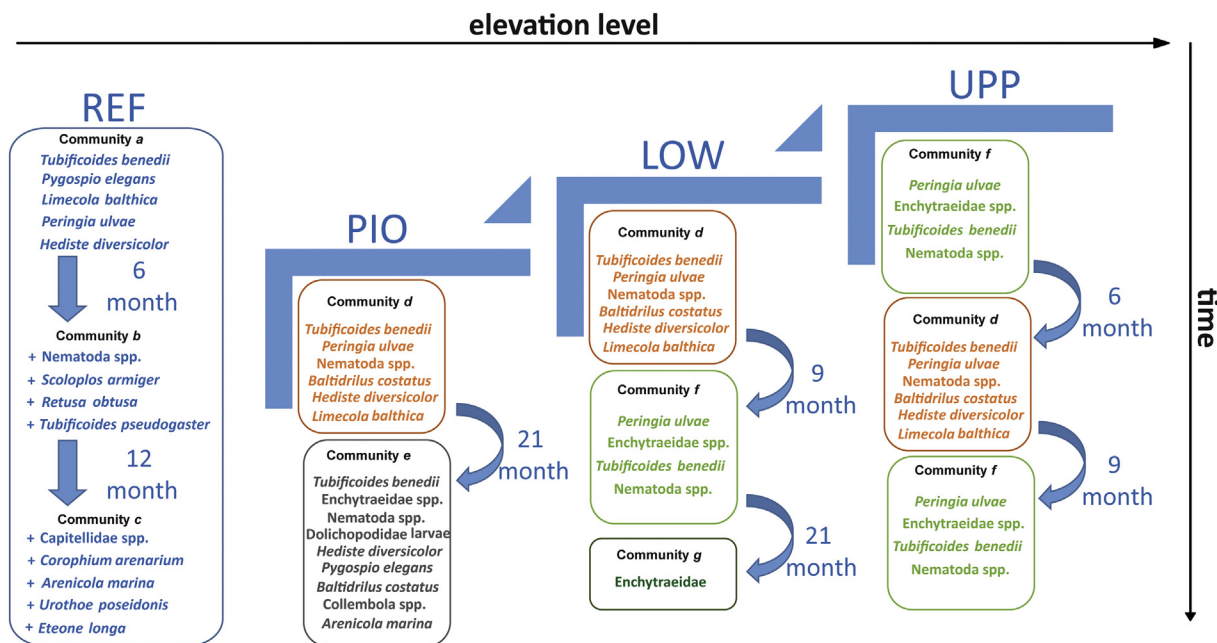

Fig. 5. Schematic representation of the community development at the different elevations of the experimental islands ("pio" "low" "upp") from October 2014 to October 2016 with indication of the surrounding tidal flat communities ("ref"). Communities and their dominant taxa are given as indicated by group average cluster analysis with SIMPROF test and SIMPER analysis, respectively. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

(rho = 0.603). The PCO analysis confirmed this relationship. Here, the first two PCO axes explained 59.0% of the total variation in the similarity matrix of the macrozoobenthic community (Fig. 6). The correlations between these axes and all environmental variables showed that plant coverage had the strongest correlation with PCO1 (61.3%) and PCO2 (49.8%), revealing thereby a strong relationship with community *g*. By contrast, water level correlated with community *d*, (PCO1, 37.2%; PCO2, 31.5%). TOC showed the strongest relationship with community

e (PCO1, 30.2%; PCO2, 15.9%), whereas oxygen showed relationships with the communities *d* and *f*. All remaining environmental variables had correlations < 20% with both of the two major PCO axes.

3.3. Variability in functional trophic groups

The distribution of functional trophic groups, given as feeding types, differed significantly (SIMPROF, *p* = .001) between the different

Table 2
Results of the SIMPER analysis based on square-root transformed abundances (ind. $0.004\,\mathrm{m}^{-2}$) of the taxa that occurred at the tidal flat references ("ref") and the three elevation levels of the experimental islands, corresponding to the salt marsh zonation: pioneer zone ("pio"), lower salt marsh ("low") and upper salt marsh ("upp") at the sampling dates t0 = October 2014, t1 = April 2015, t2 = July 2015, t3 = October 2015, t4 = April 2016, t5 = July 2016 and t6 = October 2016. Av.Abund = average abundance, Av.Sim = average similarity explained by the taxon, Contrib% = contribution to similarity (%), Cum. % = cumulated contribution to similarity (%).

Taxon	Av. Abund	Av. Sim	Contrib%	Cum.%
Community b (t1-2ref), average similarity: 63.01%				
Tubificoides benedii	5.80	20.06	31.83	31,83
Nematoda spp.	3.26	8.97	14.23	46.06
Hediste diversicolor	2.23	8.02	12.73	58.80
Limecola balthica	1.98	6.25	9.92	68.72
Peringia ulvae	5.32	6.25	9.92	78.64
Scoloplos armiger	1.41	3.03	4.81	83.45
Retusa obtusa	0.81	2.63	4.17	87.62
Tubificoides pseudogaster	1.00	2.63	4.17	91.78
Community c (t3-6ref), average similarity: 71.07%				
T. benedii	5.20	17.81	25.06	25.06
Nematoda spp.	3.30	10.29	14.47	39.54
S. armiger	2.86	8.50	11.96	51.49
T. pseudogaster	1.89	4.81	6.77	58.26
L. balthica	1.82	4.49	6.31	64.57
H. diversicolor	1.05	3.46	4.87	69.44
Capitellidae spp.	2.12	3.31	4.66	74.10
Corophium arenarium	0.84	2.57	3.62	77.73
Arenicola marina	0.86	2.55	3.59	81.31
Urothoe poseidonis	0.95	2.50	3.52	84.84
Eteone longa	0.90	2.47	3.47	88.31
P. ulvae	1.13	2.25	3.17	91.48
Community d (t0-4pio, t0-1low, t1upp), average similarity: 74.76%				
T. benedii	3.97	30.07	40.22	40.22
P. ulvae	1.96	13.73	18.37	58.59
Nematoda spp.	1.15	8.02	10.73	69.32
Baltidrilus costatus	1.03	6.68	8.93	78.25
H. diversicolor	0.80	6.22	8.32	86.56
L. balthica	0.68	4.19	5.60	92.16
Community e (t5-6pio), average similarity: 75.76%				
T. benedii	3.54	20.69	27.30	27.30
Enchytraeidae spp.	2.44	13.84	18.27	45.57
Nematoda spp.	2.43	13.37	17.65	63.22
Dolichopodidae larva	0.71	4.38	5.78	69.00
H. diversicolor	0.81	4.38	5.78	74.78
Pygospio elegans	1.06	4.38	5.78	80.56
B. costatus	0.58	3.57	4.72	85.27
Collembola spp.	1.00	3.57	4.72	89.99
A. marina	0.41	2.53	3.34	93.33
Community f (t2-4low, t0 + t2-6upp), average similarity: 38.70%				
P. ulvae	1.30	14.82	38.30	38.30
Enchytraeidae spp.	0.43	10.52	27.19	65.50
T. benedii	0.54	7.98	20.63	86.13
Nematoda spp.	0.40	2.48	6.42	92.54
Community g (t5-6low), average similarity: 55.32%				
Enchytraeidae spp.	2.23	55.32	100	100

elevation levels. At the reference sites, distribution was similar except for the initial sampling (t0) when SSD (e.g. *T. benedii*) and IF (e.g. *P. elegans*) represented the dominant feeding types (SSD, 52.2%; IF, 24.9%) with additional contributions by SD (15.9%) and O (5.8%). After t0, the contributions of both SSD and IF were lower and that of SD also declined slightly. Nevertheless, SSD, SD and IF still represented dominant feeding types, with O and P also having a significant impact on the composition of feeding types (Table 3).

At the elevation level "pio", feeding type distribution was also similar during our sampling. SSD again represented the dominant feeding type although there was a decline in SF and SD compared to the reference sites. Other major feeding types that were present include "other" (e.g. Insecta), SD and IF (Fig. 7). SL were completely absent and

feeding type P did not occur until t4. Among the present taxa, SSD had the highest mean abundances from t0 to t6. However, abundances of "other" increased at the end of our sampling (t5 and t6). By contrast, the highest mean biomasses among the different feeding types did not include SSD at any time but rather IF (t0, t2, t5), SF (t1) or O (t3, t4, t6).

A significant shift in the distribution of feeding types was found for the elevation level "low". Initially (t0 to t1), the distribution resembled that of the elevation level "pio" but thereafter was similar to the single distribution that characterized the elevation level "upp", with increased contributions of SSD and SD and with IF having no importance (Fig. 7). In contrast to the reference sites, SL, SF and P were always absent for "low" and "upp" and the number of O, SD and IF was also comparatively lower. Mean abundances of the elevation level "low" were dominated by SSD, except for t3 when SD were dominant; mean biomasses were dominated by SD, except for t0 when O had the highest biomass and t5 when SSD dominated. At the elevation level "upp", the highest mean abundances were obtained by SD (t0), SSD (t1, and from t3 to t6) and "other" (t2), whereas mean biomass was dominated by SD at all times.

4. Discussion

The species assembly on newly formed islands in the Wadden Sea depends in part on the present species pool. During this study, both salt marsh fauna and the faunal community of the surrounding tidal flats provided potential colonizers and residents. Because of the nature of how the islands were constructed, some fauna on the experimental islands might derive from the untreated tidal flat sediments that were used to fill the islands initially, with others potentially have gone extinct due to the change in habitat and/or competition from other, true colonizers. More importantly, periodic inundation of the islands caused by the tidal cycle supplies their lower elevations with marine taxa and their larval stages, coming from the North Sea into the Wadden Sea. Inundation duration and frequency decreased with increasing elevation (calculated from water-level sensor, for details see Balke et al., 2017). During sampling, average flooding duration per month varied between approximately 9.0 to 12.2% at elevation level "pio" and 1.5 to 2.7% at elevation level "low" and 0.1 to 0.4% at elevation level "upp". Finally, severe disturbances including storm surges will also affect community composition and could suddenly and dramatically change the direction of community development on the experimental islands while also promoting the input of species from the tidal flats.

In general, the Wadden Sea is a dynamic ecosystem that is subject to short-time variability. Furthermore, the shallow tidal flats represent a depositional environment of marine sediments, offering a convenient substratum for microphytobenthic communities (Miller et al., 1996). These communities, which have a high contribution of diatoms, constitute an abundant food resource for deposit feeders (Hagerthey et al., 2002; Miller et al., 1996; Schückel et al., 2013). Accordingly, the present species pool mainly included deposit feeders.

The successional sequence of new habitats or the recolonization of habitats after disturbance is strongly affected by the dispersal of potential colonizers (Negrello Filho et al., 2006). The dispersal of marine fauna and their larval stages primarily depends on hydrological conditions. Importantly, diverse functional traits including post-larval migration, lateral movement and mortality of the organisms will result in faunal variability (Lundquist et al., 2006; Negrello Filho et al., 2006; Whitlatch et al., 1998) that influences the species assembly and community succession in any newly available habitat. In addition, migration of species can be caused by competition for space and food (Wilson, 1990) as well as also by abiotic factors, e.g. sediment properties, currents and waves (Armonies, 1994; Bolam et al., 2004), depending on the ecological tolerances of the species. Thus, marine opportunists dominated the initial benthic communities at all elevation levels of the experimental islands, whereupon subsequent community succession during the next two years developed differently at each elevation level.
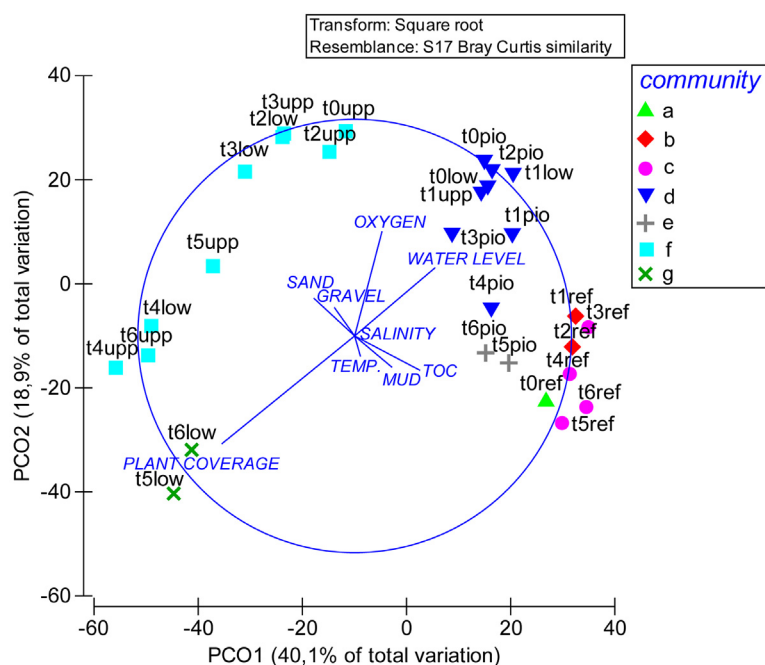
Fig. 6. PCO explaining 59% of the total variation of the macro-zoobenthic community structure based on Bray-Curtis similarities of square-root transformed abundances at the tidal flat references ("ref") and the three elevations of the experimental islands corresponding to the salt marsh zonation: pioneer zone ("pio") lower salt marsh ("low") and upper salt marsh ("upp") at the sampling dates: t0 = October 2014
t1 = April 2015
t2 = July 2015
t3 = October 2015
t4 = April 2016
t5 = July 2016 and t6 = October 2016. PCO axes are correlated with environmental variables (TOC = total organic carbon content
MUD = mud content
SAND = sand content
GRAVEL = gravel content
TEMP. = temperature)
(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3

Results of the SIMPER analysis based on square-root transformed abundances (ind. 0.004 m^{-2}) of the feeding types that occurred at the tidal flat references ("ref") and the three elevation levels of the experimental islands, corresponding to the salt marsh zonation: pioneer zone ("pio"), lower salt marsh ("low") and upper salt marsh ("upp") at the sampling dates t0 = October 2014, t1 = April 2015, t2 = July 2015, t3 = October 2015, t4 = April 2016, t5 = July 2016 and t6 = October 2016. Av.Abund = average abundance, Av.Sim = average similarity explained by the feeding type, Contrib% = contribution to similarity (%), Cum.% = cumulated contribution to similarity (%).

Feeding type	Av. Abund	Av. Sim	Contrib%	Cum.%
t1-6ref, average similarity: 80.42%				
Subsurface deposit feeder	6.66	33.58	41.76	41.76
Other	3.28	15.07	18.74	60.50
Surface deposit feeder	3.04	9.20	11.44	71.94
Interface feeder	2.09	8.63	10.73	82.67
Omnivore	1.45	5.73	7.13	89.80
Predator	1.15	4.70	5.85	95.65
t0-6pio, t0-1low, t1upp, average similarity: 82.77%				
Subsurface deposit feeder	4.43	41.49	50.12	50.12
Other	1.66	12.76	15.42	65.54
Surface deposit feeder	1.68	12.68	15.32	80.87
Interface feeder	0.97	7.93	9.58	90.45
t2-6low, t0 + t2-6upp, average similarity: 53.11%				
Subsurface deposit feeder	1.18	30.04	56.56	56.56
Surface deposit feeder	1.11	14.25	26.84	83.40
Other	0.61	7.96	15.00	98.40

The lowest elevation ("pio") of the experimental islands, which corresponded to the elevation of the salt marsh pioneer zone, was long characterized by marine pioneers and opportunistic species (community d). Particularly deposit feeders comprise opportunistic taxa, which are described to be associated with organic enrichment (Pearson and Rosenberg, 1978). Usually, such species are generalists with a broad ecological range and the ability to tolerate disturbances. The elevation gradient of the experimental islands represents a disturbance gradient (decreasing inundation periods, decreasing inundation frequency, silting, increasing vegetation), which changes the predictability of the environment for the organisms. These conditions were reflected by the presence of surface and subsurface deposit feeders (e.g. Oligochaeta), which contributed the most to all recognized communities, at all

elevation levels.

In contrast, other feeding types lost importance or disappeared with increasing disturbance of the middle and the highest elevation, such as predators and suspension feeders, demonstrating the depletion of functional diversity along the elevation gradient. Studies on depth gradients also revealed a functional structuring of benthic communities, at which suspension feeders primarily occurred in shallow waters, while deposit feeders were abundant in deeper, muddy sediments (Pearson and Rosenberg, 1987; Rosenberg, 2001). Investigations on environmental gradients in the Baltic Sea showed a shift from complex to functional poor communities that was associated with a loss of carnivores, while suspension feeders and surface deposit feeders increased importance (Bonsdorff and Pearson, 1999). Investigations at tidal flats in the Dutch Wadden Sea after a period of eutrophication supported these results. Here, the proportion of carnivores decreased, while suspension feeders remained constant and deposit feeders increased (Beukema, 1991).

Deposit-feeding opportunists, such as the oligochaete *T. benedii*, are typically characterized by high reproduction rates (*r*-selected) and fast growth, leading to the high abundances (Pearson and Rosenberg, 1978; Schückel et al., 2013; Vöge et al., 2008) that were observed at all elevation levels, early in the experiment. Moreover, these organisms have different larval and adult dispersal stages, enabling high recolonization potential of newly formed habitats and after disturbances (Bolam et al., 2004; Norkko et al., 2006; Vöge et al., 2008). Reproduction strategies of aquatic Oligochaeta represent adaptations to unpredictable environmental conditions. While asexual reproduction occurs during favorable conditions, sexual reproduction with cocoon deposition allows the survival of populations during periods of stress (Parish, 1981). A similar effect is achieved by the dauer larvae of opportunistic Nematoda (Bongers and Ferris, 1999; Derycke et al., 2013). Since sediment used for the experimental islands was not defaunated prior to the experiment, this adaptive strategy of reproduction likely explains the initial dominance of Nematoda and the oligochaetes *T. benedii* and *B. costatus*.

Other common species with great ecological tolerance, e.g. the polychaete *H. diversicolor* and the snail *P. ulvae* dominated the community during early succession as well. This is consistent with other findings, where these species were described as pioneers of intertidal mudflats (Bolam et al., 2004) and an infilling salt-marsh clay pit (Vöge et al., 2008). The formation of this marine pioneer community requires
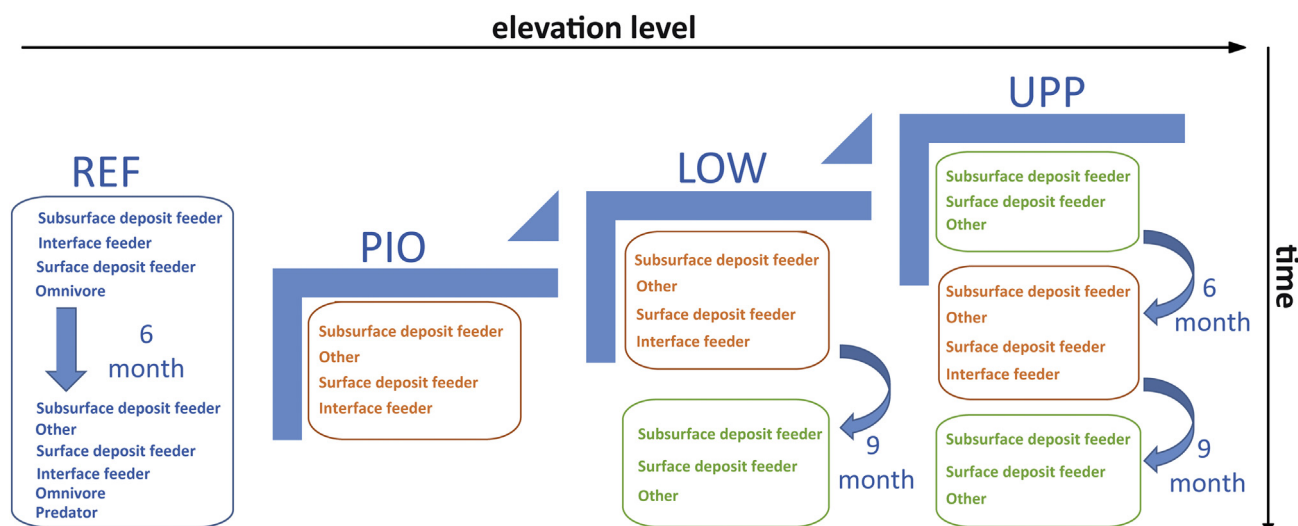
Fig. 7. Schematic representation of the changes in feeding type distribution at the different elevations of the experimental islands ("pio" "low" "upp") and the surrounding tidal flats ("ref") from October 2014 to October 2016. Grouping and dominant feeding types are given as indicated by group average cluster analysis with SIMPROF test and SIMPER analysis, respectively. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

sufficient inundation periods because of the pelagic dispersal of *P. ulvae* via floating (Barnes, 1981) and the short pelagic larval period of *H. diversicolor* (Scaps, 2002). The water level measured during the experiment correlated strongly with the early community of marine pioneer species (community *d*). The high water coverage likely inhibited plant growth and was favorable for the presence of marine species.

After 21 months (t5), community structure of the elevation "pio" changed and the number of taxa, biodiversity and biomass increased, while abundances remained similar. Moreover, 2016 was characterized by increasing biomass of omnivores and the presence of predators. These feeding types were absent at both higher elevation levels. The presence of predators was likely caused by the biodiversity increase as well as by the increase in biomass, providing sufficient prey. Predation indicates a complex food web as it increases the trophic levels within the community. Furthermore, predation is considered to increase biodiversity and ecosystem complexity because it reduces competition between species (Paine, 1966).

This confirms our expectation of a shift towards a more complex community with more competitive species, which are characterized by slower growth and longer life spans as described in the succession model of Pearson and Rosenberg (1978). The biodiversity increase in July (t5) and October 2016 (t6) resulted from the settlement of marine as well as terrestrial taxa. This period was characterized by an abrupt increase in mud content (> 10%) and TOC, offering favorable conditions for terrestrial as well as marine Annelida, e.g. *P. elegans*, which is known from intertidal mudflats (Reise et al., 1994; Schückel et al., 2013). Its ability of asexual reproduction, primarily during summer (Gibson and Harvey, 2000), probably caused the rapid populating and made *P. elegans* one of the dominant taxa of the more diverse community of the elevation level "pio" from July to October 2016 (community *e*). The marine polychaete *A. marina*, which has a relatively long life span, also dominated this community, contributing to the increase in biomass during this period. The lack of a pelagic larval stage disables the dispersal of this polychaete over long distances. However, the highly mobile postlarval stage of *A. marina* likely enabled the increase in juveniles in July and October 2016 after overwintering in subtidal areas (Reise et al., 2001). Successful settlement of the polychaete via postlarval migration is also known from recovery studies in the Dutch Wadden Sea (Beukema et al., 1999). Certainly, inhibitory interactions can limit the establishment of *A. marina* via habitat modification, such as silt accumulation and rooting by patches of salt marsh vegetation

(van Wesenbeeck et al., 2007). At the elevation level "pio", vascular plants had no adverse effect on the presence of *A. marina* because vegetation here was sparse. However, plant coverage increased in July and October 2016 compared to the previous sampling dates. This probably offered sufficient conditions for terrestrial taxa, such as Enchytraeidae, Collembola and Dolichopodidae larvae that dominated the community. These taxa are typical for salt marshes (Haynert et al., 2017; Meyer et al., 1995). The growth of salt marsh vegetation depends on shore height that determines inundation duration and inundation frequency (Balke et al., 2016; Bockelmann et al., 2002). An increase in frequency and duration of inundation and the consequent waterlogging probably led to the sparse vegetation of the lowest elevation of the experimental islands, forcing a different development of the macrofaunal community and feeding type distribution compared to the higher elevation levels.

However, insufficient periods of inundation probably caused the decrease in mean taxa numbers at the middle elevation ("low") and the highest elevation ("upp") over time. Suspension feeders, for instance, depend on a minimum of inundation time for sufficient filter feeding (Asmus and Asmus, 2005). Consequently, they were rare at the lowest elevation level ("pio") and absent at both higher elevation levels ("low", "upp"), while they regularly occurred at the periodically flooded tidal flat references. By contrast, interface feeders were also regularly present at the elevation level "pio" and declined only at the elevation levels "low" and "upp". Interface feeders are able to switch between suspension feeding and deposit feeding (Dauer et al., 1981; Ólafsson, 1986). The organisms probably compensate the short inundation periods that are inadequate for suspension feeding with the deposit-feeding mode. This may enable life in upper intertidal zones (Asmus and Asmus, 2005; Lange et al., 2018).

Furthermore, the community of the elevation "low", corresponding to the lower salt marsh level, was dominated by small opportunists, such as Enchytraeidae (Oligochaeta) that have terrestrial affinities. They usually dominate higher marsh habitats, where they tolerate less tidal inundation (Lange et al., 2018; Vöge et al., 2008). Thus, a shift from marine to terrestrial conditions was indicated early. After 21 months (t5), biodiversity of the middle elevation strongly declined, while mean abundances showed a slight increase. This increase was caused only by Enchytraeidae, which predominated the community (community *g*). The shift from several opportunistic species towards an Enchytraeidae assemblage was associated with increased coverage of

vascular plants. This is consistent with the assumption that Enchytraeidae are associated with salt marsh vegetation (Healy and Walters, 1994).

In contrast to both lower elevation levels, the rarely inundated, highest elevation level ("upp"), corresponding to the upper salt marsh level, was constantly poor in species because of the prompt extinction of marine taxa due to desiccation. The species inventory of this elevation level remained constant during the experiment, except for April 2015 (t1), where more marine pioneer species occurred. This likely resulted from the storm events at the beginning of the year, which increased inundation frequency and the supply of marine taxa during this period. Such an event represents a typical example for stochastic disturbances in the Wadden Sea that forces interruptions in community establishment.

Overall, species richness, abundances and biomasses at the experimental islands remained low compared to the tidal flats references. However, the number of different feeding types at the lowest elevation level ("pio") was similar to the adjacent tidal flats, although the total number of taxa and abundances of omnivores and predators were lower at the elevation level "pio". Sand lickers, which feed on organic matter while individual sand grains are rotated by the mouthparts, were completely absent. Species of different feeding types show dissimilar affinities to biotic factors such as food availability (Dauwe et al., 1998) and food quality (Lange et al., 2019; Wieking and Kröncke, 2005), leading to different communities. Sand lickers and interface feeders, for example, benefit from intermediate amounts of high-quality food (Wieking and Kröncke, 2005). Competition for food probably led to the disappearance of sand lickers at the experimental islands in favor of the more flexible and partly opportunistic interface-feeding taxa.

Apart from feeding type distribution, the communities of the tidal flats and those of the experimental islands significantly differed in the proportion of taxa and, therefore, in their dominant traits. Especially, the contribution of typical Wadden Sea species, such as *S. armiger*, *R. obtusa* and *C. arenarium* was higher at the tidal flats than at the experimental islands. This suggests that the elevation gradient and the resulting differences in environmental conditions represent disturbances that cannot be tolerated by all marine invertebrates from the species pool of the tidal flats. Thus, results point to adverse effects of increased sediment elevation on macrofaunal biodiversity in the Wadden Sea, suggesting impacts on ecosystem functioning in terms of decreasing productivity as shown for marine and terrestrial systems (Cardinale et al., 2013).

Moreover, the different communities of the experimental island elevations did not fully resemble the natural salt marsh communities of the island of Spiekeroog (Haynert et al., 2017; Lange et al., 2018). The pioneer zone elevation of the experimental islands had a more diverse community compared to the pioneer zone of the natural salt marsh because of the higher proportion of marine taxa. In contrast, the diversity of the elevation levels "low" and "upp" were low compared to the natural lower and upper salt marsh, which are inhabited by several (semi-) terrestrial Arthropoda (Lange et al., 2018). Admittedly, the study period of two years is insufficient for the formation of a mature salt marsh and the upper levels of the experimental islands will have difficulties in receiving migrants due to the spatial distance to the natural salt marshes. Nevertheless, these results indicate functional differences of macrofaunal communities during the different stages of salt marsh succession, which are dissimilar to older natural marshes. Findings about macrofaunal succession in young artificial marshes in North Carolina, USA that were studied for four years confirm these results (Levin et al., 1996) and long-term investigations on ecosystem assembly in the Netherlands describe functional changes, indicating that successional development is not driven by vegetation alone but also depends on food web dynamics (Schrama et al., 2012).

5. Conclusions

This study demonstrates the negative effects of increased sediment elevation, which may result from strong sedimentation, on biodiversity and functional diversity of macrozoobenthos on tidal flats. Elevation gradients in the Wadden Sea substantially alter hydrodynamic conditions, which potentially change vegetation zonation and sediment composition. Such changes affect overall biodiversity patterns and species assembly of coastal zones that determine the functional traits within the ecosystem.

Authors' contributions

Gesine Lange conceived the idea for the study; collected data regarding the macrozoobenthos, mud, sand, gravel and total organic carbon content; analyzed all the data and wrote the manuscript. Jennifer Schmitt provided the oxygen data and Daniela Meier and Oliver Zielinski provided the salinity, temperature and water-level data. Olaf Bininda-Emonds, Helmut Hillebrand, Stefanie Moorthi, Oliver Zielinski and Ingrid Kröncke were all involved in the planning and coordination of the BEFmate project, thereby enabling this field campaign. Ingrid Kröncke also supervised the work and all authors discussed the results and commented on the manuscript.

Author declaration

The authors wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

The funding source had no involvement in study design; in the collection, analysis and interpretation of data; in the writing of the report; and in the decision to submit the article for publication.

Declaration of Competing Interest

None.

References

Reise, K., Simon, M., Herre, E., 2001. Density-dependent recruitment after winter disturbance on tidal flats by the lugworm *Arenicola marina*. Helgol. Mar. Res. 55, 161–165.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to software and statistical methods. In: PRIMER-E. Plymouth Marine Laboratory, Plymouth UK.

Armonies, W., 1994. Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. Helgol. Meeresunters. 48, 299–320.

Asmus, H., Asmus, R.M., 2005. Significance of suspension-feeder systems on different spatial scales. In: Dame, R.F., Olenin, S. (Eds.), The Comparative Roles of Suspension-Feeders in Ecosystems. Springer, The Netherlands, pp. 199–219.

Balke, T., Stock, M., Jensen, K., Bouma, T.J., Kleyer, M., 2016. A global analysis of the seaward salt marsh extent: the importance of tidal range. Water Resour. Res. 52, 3775–3786.

Balke, T., Lõhmus, K., Hillebrand, H., Zielinski, O., Haynert, K., Meier, D., Hodapp, D., Minden, V., Kleyer, M., 2017. Experimental salt marsh islands: a model system for novel metacommunity experiments. Estuar. Coast. Shelf Sci. 198, 288–298.

Barnes, R.S.K., 1981. An experimental study of the pattern and significance of the climbing behaviour of *Hydrobia ulvae*. J. Mar. Biol. Assoc. U. K. 61, 285–299.

Barnes, A.D., Jochum, M., Lefcheck, J.S., Eisenhauer, N., Scherber, C., O'Connor, M.I., de Ruiter, P., Brose, U., 2018. Energy flux: the link between multitrophic biodiversity and ecosystem functioning. Trends Ecol. Evol. 33, 186–197.

Baschek, B., Schroeder, F., Brix, H., Riethmüller, R., Badewien, T.H., Breitbach, G., Brügge, B., Colijn, F., Doerffer, R., Eschenbach, C., Friedrich, J., Fischer, P., Garthe, S., Horstmann, J., Krasemann, H., Metfies, K., Merckelbach, L., Ohle, N., Petersen, W., Pröfrock, D., Röttgers, R., Schlüter, M., Schulz, J., Schulz-Stellenfleth, J., Stanev, E., Staneva, J., Winter, C., Wirtz, K., Wollschläger, J., Zielinski, O., Ziemer, F., 2017. The coastal observing system for northern and arctic seas (COSYNA). Ocean Sci. 13, 379–410.

Beukema, J.J., 1991. Changes in composition of bottom fauna of a tidal-flat area during a period of eutrophication. Mar. Biol. 111, 293–301.

Beukema, J.J., Dekker, R., 2005. Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. Mar. Ecol. Prog. Ser. 287, 149–167.

Beukema, J.J., Flach, E.C., Dekker, R., Starink, M., 1999. A long-term study of the recovery of the macrozoobenthos on large defaunated plots on a tidal flat in the Wadden Sea. J. Sea Res. 42, 235–254.

Bockelmann, A.-C., Bakker, J.P., Neuhaus, R., Lage, J., 2002. The relation between vegetation zonation, elevation and inundation frequency in a Wadden Sea salt marsh. Aquat. Bot. 73, 211–221.

Bolam, S.G., Whomersley, P., Schratzberger, M., 2004. Macrofaunal recolonization on intertidal mudflats: effect of sediment organic and sand content. J. Exp. Mar. Biol. Ecol. 306, 157–180.

Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends Ecol. Evol. 14, 224–228.

Bonsdorff, E., Pearson, T.H., 1999. Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: a functional-group approach. Aust. J. Ecol. 24, 312–326.

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 17, 720–737.

Brose, U., Hillebrand, H., 2016. Biodiversity and ecosystem functioning in dynamic landscapes. Philos. Trans. R. Soc. B 371, 2015026710 1098/rstb.2015.0267.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67.

Cardinale, B.J., Gross, K., Fritsche, K., Flombaum, P., Fox, J.W., Rixen, C., van Ruijven, J., Reich, P.B., Scherer-Lorenzen, M., Wilsey, B.J., 2013. Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. Ecology 94, 1697–1707.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: user manual/tutorial. In: PRIMER-E. Plymouth Marine Laboratory, Plymouth UK.

Dauer, D.M., Maybury, C.A., Ewing, R.M., 1981. Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 54, 21–38.

Dauwe, B., Herman, P.M.J., Heip, C.H.R., 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. Mar. Ecol. Prog. Ser. 173, 67–83.

De Vlas, J., 1979. Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey. Neth. J. Sea Res. 13, 117–153.

Derycke, S., Backeljau, T., Moens, T., 2013. Dispersal and gene flow in free-living marine nematodes. Front. Zool. 10. https://doi.org/10.1186/1742-9994-10-1.

Donat, M.G., Renggli, D., Wild, S., Alexander, L.V., Leckebusch, G.C., Ulbrich, U., 2011. Reanalysis suggests long-term upward trends in European storminess since 1871. Geophys. Res. Lett. 38. https://doi.org/10.1029/2011GL047995.

Elahi, R., O'Connor, M.I., Byrnes, J.E.K., Dunic, J., Eriksson, B.K., Hensel, M.J.S., Kearns, P.J., 2015. Recent trends in local-scale marine biodiversity reflect community structure and human impacts. Curr. Biol. 25, 1938–1943.

Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Annu. Rev. 17, 193–284.

Flemming, B.W., Davis Jr., R.A., 1994. Holocene evolution, morphodynamics and sedimentology of the Spiekeroog barrier island system (southern North Sea). Senckenberg. Marit. 24, 117–155.

Flemming, B.W., Ziegler, K., 1995. High-resolution grain size distribution patterns and textural trends in the backbarrier environment of Spiekeroog Island (southern North Sea). Senckenberg. Marit. 26, 1–24.

Gibson, G.D., Harvey, J.M.L., 2000. Morphogenesis during asexual reproduction in *Pygospio elegans* Claparede (Annelida, Polychaeta). Biol. Bull. 199, 41–49.

Hagerthey, S.E., Defew, E.C., Paterson, D.M., 2002. Influence of *Corophium volutator* and *Hydrobia ulvae* on intertidal benthic diatom assemblages under different nutrient and temperature regimes. Mar. Ecol. Prog. Ser. 245, 47–59.

Haynert, K., Kiggen, M., Klarner, B., Maraun, M., Scheu, S., 2017. The structure of salt marsh soil mesofauna food webs – the prevalence of disturbance. PLoS One 12, e0189645. https://doi.org/10.1371/journal.pone.0189645.

Healy, B., Walters, K., 1994. Oligochaeta in *Spartina* stems: the microdistribution of Enchytraeidae and Tubificidae in a salt marsh, Sapelo Island, USA. Hydrobiol. 278, 111–123.

Hertweck, G., 1995. Verteilung charakteristischer Sedimentkörper und Benthossiedlungen im Rückseitenwatt der Insel Spiekeroog, südliche Nordsee. I. Ergebnisse der Wattkartierung 1988-92. Senckenberg. Marit. 26, 81–94.

Hild, A., 1999. Morphology and sedimentology of the Spiekeroog backbarrier system. In: Dittmann, S. (Ed.), The Wadden Sea Ecosystem: Stability Properties and Mechanisms. Springer-Verlag, Berlin, pp. 31–35.

Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A., Eriksson, B.K., Filstrup, C.T., Harpole, W.S., Hodapp, D., Larsen, S., Lewandowska, A.M., Seabloom, E.W., Van de Waal, D.B., Ryabov, A.B., 2018. Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. J. Appl. Ecol. 55, 169–184.

Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: an update of polychaete feeding guilds. Annu. Rev. Mar. Sci. 7, 497–520.

Kirwan, M.L., Guntenspergen, G.R., D'Alpaos, A., Morris, J.T., Mudd, S.M., Temmerman, S., 2010. Limits on the adaptability of coastal marshes to rising sea level. Geophys. Res. Lett. 37. https://doi.org/10.1029/2010GL045489.

Kristensen, E., Delefosse, M., Quintana, C.O., Flindt, M.R., Valdemarsen, T., 2014. Influence of benthic macrofauna community shifts on ecosystem functioning in shallow estuaries. Front. Mar. Sci. 1 (41). https://doi.org/10.3389/fmars.2014.00041.

Lange, G., Haynert, K., Dinter, T., Scheu, S., Kröncke, I., 2018. Adaptation of benthic invertebrates to food sources along marine-terrestrial boundaries as indicated by carbon and nitrogen stable isotopes. J. Sea Res. 131, 12–21.

Lange, G., Schmitt, J.A., Kröncke, I., Moorthi, S.D., Rohde, S., Scheu, S., Schupp, P.J., 2019. The role of invasive marine plants for macrofauna nutrition in the Wadden Sea. J. Exp. Mar. Biol. Ecol. 512 (1–11).

Levin, L.A., Talley, D., Thayer, G., 1996. Succession of macrobenthos in a created salt marsh. Mar. Ecol. Prog. Ser. 141, 67–82.

Loeuille, N., Leibold, M.A., 2008. Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. Am. Nat. 171, 788–799.

Lundquist, C.J., Thrush, S.F., Hewitt, J.E., Halliday, J., MacDonald, I., Cummings, V.J., 2006. Spatial variability in recolonisation potential: influence of organism behaviour and hydrodynamics on the distribution of macrofaunal colonists. Mar. Ecol. Prog. Ser. 324, 67–81.

Menge, B.A., Sutherland, J.P., 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. 130, 730–757.

Meyer, H., Fock, H., Haase, A., Reinke, H.D., Tulowitzki, I., 1995. Structure of the invertebrate fauna in salt marshes of the Wadden Sea coast of Schleswig-Holstein influenced by sheep-grazing. Helgol. Meeresunters. 49, 563–589.

Miller, D.C., Geider, R.J., MacIntyre, H.L., 1996. Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. II. Role in sediment stability and shallow-water food webs. Estuaries 19, 202–212.

Negrello Filho, O.A., Underwood, A.J., Chapman, M.G., 2006. Recolonization of infauna on a tidal flat: an experimental analysis of modes of dispersal. J. Exp. Mar. Biol. Ecol. 328, 240–250.

Niesel, V., 1999. Hydrographic conditions in the Spiekeroog backbarrier system. In: Dittmann, S. (Ed.), The Wadden Sea Ecosystem: Stability Properties and Mechanisms. Springer-Verlag, Berlin, pp. 26–30.

Noordhuis, R., Spaans, A.L., 1992. Interspecific competition for food between herring *Larus argentatus* and lesser black-backed Gulls *L. fuscus* in the Dutch Wadden Sea area. ARDEA 80, 115–132.

Norkko, A., Rosenberg, R., Thrush, S.F., Whitlatch, R.B., 2006. Scale- and intensity-dependent disturbance determines the magnitude of opportunistic response. J. Exp. Mar. Biol. Ecol. 330, 195–207.

O'Gorman, E.J., Fitch, J.E., Crowe, T.P., 2012. Multiple anthropogenic stressors and the structural properties of food webs. Ecology 93, 441–448.

Ólafsson, E.B., 1986. Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. J. Anim. Ecol. 55, 517–526.

Paine, R.T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65–75.

Parish, J., 1981. Reproductive ecology of Naididae (Oligochaeta). Hydrobiol. 83, 115–123.

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Annu. Rev. 16, 229–311.

Pearson, T.H., Rosenberg, R., 1987. Feast and famine: Structuring factors in marine benthic communities. In: Gee, J.H.R., Giller, P.S. (Eds.), Organization of Communities Past and Present. Blackwell Scientific Publishers, Oxford, pp. 373–395.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ (accessed 7 March 2017).

Rapport, D.J., Regier, H.A., Hutchinson, T.C., 1985. Ecosystem behavior under stress. Am. Nat. 125, 617–640.

Reise, K., Herre, E., Sturm, M., 1994. Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the northern Wadden Sea. Helgol. Meeresunters. 48, 201–215.

Reuter, R., Badewien, T.H., Bartholomä, A., Braun, A., Lübben, A., Rullkötter, J., 2009. A hydrographic time series station in the Wadden Sea (southern North Sea). Ocean Dyn. 59, 195–211.

Rosenberg, R., 2001. Marine benthic faunal successional stages and related sedimentary activity. Sci. Mar. 65, 107–119.

Scaps, P., 2002. A review of the biology, ecology and potential use of the common ragworm *Hediste diversicolor* (O. F. Müller) (Annelida: Polychaeta). Hydrobiol. 470, 203–218.

Schrama, M., Berg, M.P., Olff, H., 2012. Ecosystem assembly rules: the interplay of green and brown webs during salt marsh succession. Ecology 93, 2353–2364.

Schückel, U., Beck, M., Kröncke, I., 2013. Spatial variability in structural and functional aspects of macrofauna communities and their environmental parameters in the Jade Bay (Wadden Sea Lower Saxony, southern North Sea). Helgol. Mar. Res. 67, 121–136.

Stachowicz, J.J., 2001. Mutualism, facilitation, and the structure of ecological communities: positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. BioScience 51, 235–246.

Van Wesenbeeck, B.K., Van de Koppel, J., Herman, P.M.J., Bakker, J.P., Bouma, T.J., 2007. Biomechanical warfare in ecology; negative interactions between species by habitat modification. Oikos 116, 742–750.

Vöge, S., Reiss, H., Kröncke, I., 2008. Macrofauna succession in an infilling salt marsh clay pit. Senckenberg. Marit. 38, 93–106.

Waldbusser, G.G., Marinelli, R.L., Whitlatch, R.B., Visscher, P.T., 2004. The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. Limnol. Oceanogr. 49, 1482–1492.

Whitlatch, R.B., Lohrer, A.M., Thrush, S.F., Pridmore, R.D., Hewitt, J.E., Cummings, V.J., Zajac, R.N., 1998. Scale-dependent benthic recolonization dynamics: life stage-based dispersal and demographic consequences. Hydrobiol. 375, 217–226.

Wieking, G., Kröncke, I., 2005. Is benthic trophic structure affected by food quality? The Dogger Bank example. Mar. Biol. 146, 387–400.

Wilson, W.H., 1990. Competition and predation in marine soft-sediment communities. Annu. Rev. Ecol. Syst. 21, 221–241.

Zielinski, O., Meier, D., Lõhmus, K., Balke, T., Kleyer, M., Hillebrand, H., 2018. Environmental conditions of a salt-marsh biodiversity experiment on the island of Spiekeroog (Germany). Earth Syst. Sci. Data 10, 1843–1858.

Glossary

Abbreviation: Definition
BEF: Biodiversity – Ecosystem functioning
pio: elevation level, corresponding to the salt-marsh pioneer zone
low: elevation level, corresponding to the lower salt marsh
upp: elevation level, corresponding to the upper salt marsh
TOC: total organic carbon