A bio-engineered soft-bottom environment: The impact of *Lanice conchilega* on the benthic species-specific densities and community structure

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Abstract

This paper evaluates the effect of the tube-building, habitat structuring polychaete *Lanice conchilega* on the macrobenthic community and sediment characteristics of its habitat. To investigate which factors make species occur in a well-known bio-engineered habitat, macrofaunal and sedimentological data, gathered over a period of 10 years in a shallow, fine sediment bottom of the Belgian Part of the North Sea, were submitted to analyses. Both sediment composition and community structure of the associated macrofaunal matrix were affected by the presence of *L. conchilega*. The effect of the protruding tubes on hydrodynamics clearly resulted in the retention of fine sediment particles, while the increased coarse fraction was assumed to reflect a dynamic population build-up. This study confirmed that tube aggregations of *L. conchilega* expand the realized niche of several species without forming their own association. A species rank list was created according to each species' association with *L. conchilega*. This species rank list is extensively discussed based on all ecological knowledge available. Species are favoured by the habitat modifying ability of the polychaete tubes, which create and regulate refuge for species, alter the interactions between local species and change the physical factors of the environment. This descriptive and correlative data study examines the ecological importance of the bio-engineer *L. conchilega* on species level.
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1. Introduction

Habitat structuring organisms are known to add or alter physical, chemical and biological factors and are therefore often referred to as bio-engineers (Jones et al., 1994). The ecological mechanisms behind the effect of habitat structuring organisms are well described for all kinds of environments: coral reefs (e.g. Holbrook et al., 1990), Darwin mounds (Van Gaever et al., 2004), kelp forests (e.g. Steneck et al., 2002), ascidians (Castilla et al., 2004), seagrass meadows (e.g. Hovel et al., 2002; Alfaro, 2006), mussel banks (e.g. Ragnarsson and Raffaelli, 1999), oyster beds (Lenihan, 1999) and polychaete tubes (e.g. Bolam and Fernandes, 2003; Callaway, 2006). The structural complex framework provided by these emergent features constitutes an important organizing aspect and is critical to the functioning of many ecosystems (Jones et al., 1994). These structures represent important habitats for a variety of marine organisms. They may provide refuge from predation, competition and physical as well as chemical stresses, or may represent important food resources and critical nursery or spawning habitats. In addition, these structures modify the hydrodynamic flow regime near the sea floor, with potentially significant ecological effects on sedimentation, food availability, larval and/or juvenile recruitment, growth and survival. As such, habitat structures and heterogeneity influence the faunal abundance, species richness and species composition

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of invertebrate and fish communities (Turner et al., 1999; Koenig et al., 2000). Though modulation mechanisms are understood quite well, there is often a lack of information on how species assemblages restructure themselves in bio-engineered systems. This study investigates which factors make species to occur in a well-known bio-engineered habitat, based on the autecology of individual species.

The common tube-dwelling polychaete *Lanice conchilega* (Terrebellidae) is the target bio-engineer in this paper. The physiology, tube structure (Ziegelmeier, 1952; Jones and Jago, 1993), hydrodynamic influence (Eckman, 1983; Heuers et al., 1998; Dittmann, 1999), as well as the occurrence of *L. conchilega* patches (Hartmann-Schröder, 1996) have already been extensively described. In intertidal areas, the tube patches are known to have consequences for the distribution and abundance of infaunal species by influencing the habitat structure (Carey, 1987; Feral, 1989; Zühlke et al., 1998; Dittmann, 1999; Zühlke, 2001; Callaway, 2006). The patchy distribution of tube aggregations within a specific habitat is useful to investigate the bio-engineering implications of this polychaete. Recently, bio-engineering influence on faunal abundance, species richness and species composition in subtidal areas has been proved (Van Hoey, 2006). These results indicate that effects on density and diversity are most pronounced in shallow fine sand. Besides, his study shows that rather than forming its own association, *L. conchilega* expands the realized niche of several species.

This study focuses on samples from the Belgian Part of the North Sea (BPNS), a shallow area with a sediment composition of mainly fine sand. The hypothesis that *Lanice conchilega* tube aggregations influence the benthic species assemblage by creating ecological optimal niches for species otherwise living in suboptimal conditions is tested for the specific study area analysed here. This paper provides a species rank list by association degree with *L. conchilega*, based on community and species analyses. This ranking is extensively discussed on the basis of available ecological knowledge of all species. Furthermore, the influence of *L. conchilega* on sediment fractions was tested. In order to do so, macrobenthic data from samples taken in a restricted area of the North Sea, over a period of 10 years, were selected on the basis of physico-chemical habitat characteristics (sedimentology and depth) and submitted to analyses. This allows an assessment of the natural variation in the abundance of *L. conchilega* and its associated community, independent of geographical and temporal variability. This approach enabled us to test for the impact of an ecosystem engineer. However, this is a correlative data study and we are fully aware of the fact that causal relationships cannot be proved here.

2. Materials and methods

2.1. Study area

The study area covers a transect of the BPNS situated in the Southern Bight of the North Sea, close to the Belgian coast

(66 km in length) (Fig. 1). This shallow area (max. 35 m depth) consists of several sandbank systems, more or less oriented parallel to the coast. The characteristic geomorphologic and sedimentological diversity of these soft-bottom habitats is directly responsible for the high biological diversity and species richness, reflected in a mosaic of several distinguishable macrobenthic communities (Degraer et al., 2002; Van Hoey et al., 2004).

2.2. Data origin

Data, gathered on the BPNS, over a period of 10 years (October 1994 until March 2005), were selected on the basis of habitat classification, which takes into account sedimentological characteristics and bathymetrical information. A data set of 657 macrobenthic samples was submitted to analysis. This subset of samples was selected from shallow locations (<25 m according to MLWS level) at which the fine sediment fraction was the largest. Sediment characteristics are known to determine macrobenthic species occurrence (Van Hoey et al., 2004). To test the impact of *Lanice conchilega* as a bio-engineer, samples were selected based on specific median grain size values (125−250 μm) because: (1) a similar macrobenthic species assemblage is expected based on sedimentology and (2) different densities of *L. conchilega* are expected in these sediments (Willems et al., in press).

The benthos was sampled using a Van Veen grab of $0.1 \, \text{m}^2$ surface area and the sample was sieved through a 1 mm mesh-sized sieve. Macrofauna was identified to the lowest possible taxonomic level (further referred to as species) and counted. Species abundance data were standardised to a total number of individuals per m^2. Organisms were classified into five trophic groups: (1) suspension feeders; (2) surface-deposit, facultative suspension and interface feeders (capable of alternative suspension- and surface-deposit feeding dependent on flow conditions); (3) subsurface-deposit feeders and grazers; and (4) omnivores, predators and scavengers. Species that forage by more than one feeding mode were classified by their most common feeding mechanism, while species for which information is lacking were grouped together in the category 'unknown'. Parasites (5) occurred coincidentally; they were not adequately sampled and therefore excluded from this study. Information available on the autecology of particular species was also gathered and is considered in the discussion.

In order to study the possible change in benthic community composition due to the presence of *Lanice conchilega* tubes, samples were divided into five classes: (0) samples without tubes and samples with *L. conchilega* densities ranging from: (1) 1−50 ind. m^{-2}; (2) 50−300 ind. m^{-2}; (3) 300−1500 ind. m^{-2}; and (4) >1500 ind. m^{-2}. This division was based on the most significant results obtained by a one-way ANOSIM analysis.

2.3. Data analysis

To investigate potential effects of *Lanice conchilega* tube aggregations on the grain size composition in the patches,
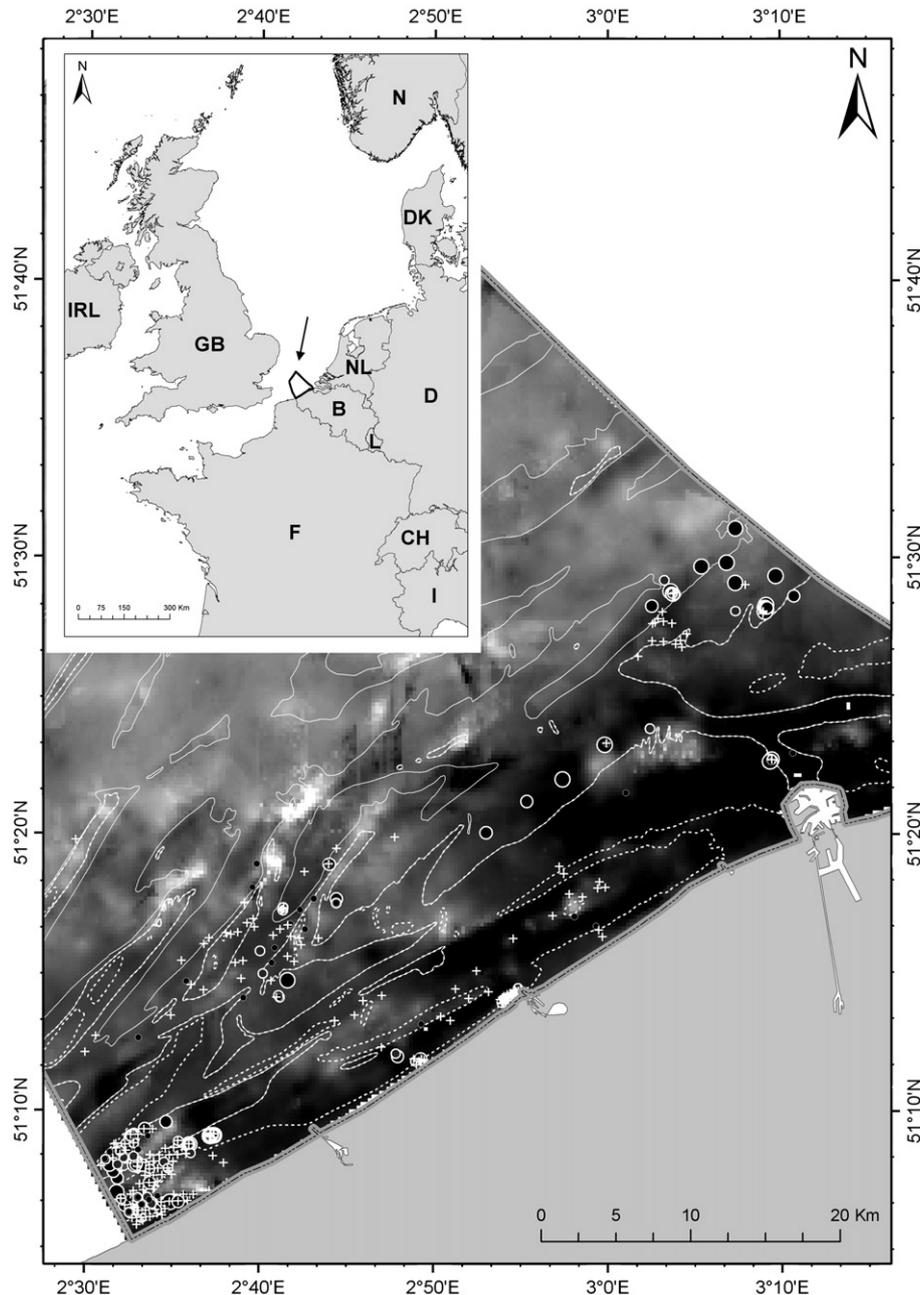
Fig. 1. Distribution of the sample locations in the shallow subtidal and low intertidal areas of the Belgian Part of the North Sea (BPNS). Depth contours of 10 m (white dotted lines) and 20 m (white lines) are visualised. Modelled full coverage sediment characteristics are represented from light grey (coarse median grain size; max. 762 μm) to black (fine median grain size; min. 0.37 μm) (Verfaillie et al., 2006). The 657 samples were selected based on sediment characteristics. Each sample is represented according to *L. conchilega* density class (white edged black dots, dimension of dots from small to large for classes 1—4, respectively); *L. conchilega*-free samples are represented by white crosses.

data on sediment fractions (according to the Udden—Wentworth logarithmic scale (Buchanan, 1984)) obtained by a Coulter LS particle size analyser, were examined. The Mann—Whitney *U*-test was applied to check for differences in median grain size and in allocation of sediment fractions between the *L. conchilega* classes. This non-parametric test was used because the assumptions for parametric tests, even after transformation, were not fulfilled (Conover, 1971).

The quantitative faunistic data were analysed using a combination of multivariate and univariate methods. Zühlke (2001) and Callaway (2006) designated a species assemblage composed of *Lanice conchilega* tubes plus accompanying organisms as a '*L. conchilega* community'. We emphasise the fact that in our study area *L. conchilega* is part of the well-defined *Abra alba—Mysella bidentata* community (Van Hoey et al., 2004), in which it structures the habitat and thus influences the present species community. We therefore refer to the '*L. conchilega* community *s.s.*', when discussing its community structure. The benthic community structure was analysed with the PRIMER v5 statistical

package (Clarke and Warwick, 2001). Non-parametric multi-dimensional scaling (MDS) and analysis of similarity (one-way ANOSIM) were used to describe (dis)-similarities between benthic faunal communities from *L. conchilega* communities and sites where *L. conchilega* did not occur. The MVDISP algorithm of the PRIMER v5 software was used to quantify the variability in each density class and to calculate the Index of Multivariate Dispersion (IMD). This comparative Index contrasts the average rank of the similarities among samples of a certain density class with the average rank of other density class sample groups (Clarke and Warwick, 2001). With the SIMPER program the (dis)similarity between the communities and the percentage contribution of each species to the similarity within and dissimilarity between communities were examined. Species richness for different *L. conchilega* density classes was calculated using the PRIMER v5 software package and is presented by total number of species (S) and Margalef's index (d) which takes into account the given number of individuals (Clarke and Warwick, 2001).

In order to identify species possibly associated with the presence of *Lanice conchilega*, four criteria were applied. The Indicator Species Analysis (ISA, Pcord4 program) was carried out and an association degree (the percentage of occurrence of a species in samples with *L. conchilega* relative to the total presence of that species in all samples) was calculated. Besides this, the Mann−Whitney U-test was used to compare the abundances of these species between samples with and without *L. conchilega*. Finally, the correlation of the density of *L. conchilega* tubes with individual species abundances was tested with the Spearman rank correlation analysis. A species was defined as positively associated with *L. conchilega* when: (1) a significant indicator value was attributed; (2) the association degree was more than 50%; (3) species density significantly differed between samples with and without *L. conchilega*; and if (4) a positive and significant correlation with the density of *L. conchilega* was found. Based on these results a species list was made in which species are ranked according to a summation of the indicator value and the association degree.

3. Results

3.1. Sediment characteristics

Fine sand (125−250 μm) was the major sediment fraction in all samples, with a contribution ranging from 49 to 65%. The median grain size ranged from 143 to 250 μm (mean ± SD: 206 ± 24 μm), but did not show significant differences according to the presence of *Lanice conchilega*. Comparing the contribution of sediment fractions in samples with and without *L. conchilega*, a significant difference ($p \leq 0.0001$) was found for every fraction, except for the fine and medium sand fractions (respectively, $p = 0.062$ and $p = 0.184$). A comparison between the classes revealed that these differences were mainly caused by significant differences ($p \leq 0.01$) in clay and silt fractions between the *L. conchilega* class of

>1500 ind. m^{-2} and all other classes, and by significant differences ($p \leq 0.02$) in clay, silt and very fine sand fractions between the *L. conchilega* classes of 1−50 ind. m^{-2} and 50−300 ind. m^{-2} and the tube-free patches, with the mentioned fractions always higher in the denser *L. conchilega* patches. The coarse fraction differed rather significantly ($p < 0.001$) between patches with >300 ind. m^{-2} (classes 3 and 4) and all other classes (Fig. 2). Volume percentage of the three finest fractions and the coarsest sediment fraction increased gradually, however not linearly, with increasing *L. conchilega* densities.

3.2. Community analyses

The one-way ANOSIM analysis revealed that the species community around *Lanice conchilega* tubes could be distinguished from the species community in tube-free sediments ($R = 0.237$, $p = 0.001$). A dissimilarity-value of 78.9 was found between samples with and without *L. conchilega* tubes. A global test based on *L. conchilega* classes showed significant ($p = 0.045$) but only slightly distinguishable species communities ($R = 0.028$). The most pronounced community differences were found between samples with >1500 *L. conchilega* ind. m^{-2} and samples without *L. conchilega* individuals ($R = 0.207$, $p = 0.001$), with a dissimilarity-value of 83.6. These results are summarised in Table 1 and visualised in a two-dimensional ordination graph constructed by the MDS-analysis (stress 0.22) (Fig. 3). The benthos composition showed no clear grouping. Nevertheless, communities differed gradually according to increasing abundances of *L. conchilega*, with the community of high *L. conchilega* density sharply defined as the inner circle, enlarging when *L. conchilega* densities are decreasing. This "Babushka" type of community structure was further investigated using the MVDISP algorithm. The highest variability was found in the samples without *L. conchilega* (Dispersion Factor Value 1.135), while lowest variability occurred in the samples with highest *L. conchilega* densities
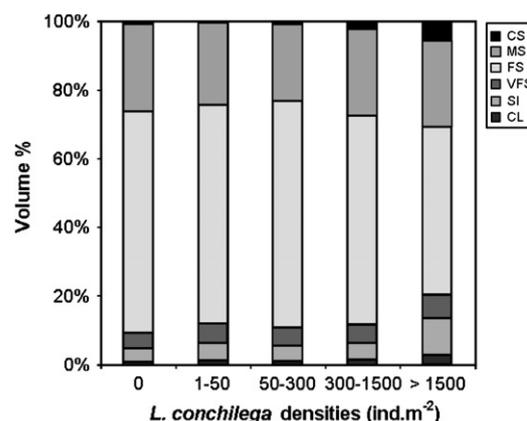

Fig. 2. The grain size distribution (CS: coarse sand 500−1000 μm; MS medium sand 250−500 μm; FS fine sand 125−250 μm; VFS: very find sand 63−125 μm; SI: silt 3.9−63 μm; CL: clay 0.06−3.9 μm) versus the different *L. conchilega* density classes. Clay and silt fractions are significantly larger in the highest density class. Coarse sand fraction is larger in samples with more than 300 *L. conchilega* specimens m^{-2}.

(Dispersion Factor Value 0.242). The Indices of Multivariate Dispersion (IMDs) have negative values, implying that all similarities among samples of a *L. conchilega* density class were greater than the similarities of samples between different density classes. The further the density classes are separated, the closer the IMD is to −1 (Table 2).

3.3. Species analyses

3.3.1. Associated species

Hundred and sixty-two macrobenthic species (*Lanice conchilega* excluded) were recorded in this study of which 66 were found to be positively associated with *L. conchilega* (i.e. 41%). Of these associated species, polychaetes constituted the highest number of species (30 species or 45%), and were the most abundant taxonomic group (63%), followed by bivalves (25%), amphipods (7%), oligochaetes (2%), ophiuroids (1%) and others (2%). A ranking list of the positively and negatively associated species is given in Table 3. Positively associated bivalves were *Donax vittatus*, *Ensis* spp., *Mysella bidentata*, *Spisula subtruncata*, *Abra alba*, *Tellina fabula* and others. For polychaetes, *Pygospio elegans*, *Eumida sanguinea*, *Harmothoe* spp., *Spiophanes bombyx*, etc. were found to be strongly associated, whereas some of the most associated amphipods were *Pariambus typicus*, *Urothoe poseidonis*, *Gammarus* spp., etc. Based on association degree only, eight species were exclusively associated (100%) with *L. conchilega* tubes: *Gattyana cirrhosa*, *Asterias rubens*, *Bodotria arenosa*, *Gammarus* spp., *Leucothoe lilljeborgii*, *Liocarcinus arcuatus*, *Amphilochus neopolitanus* and *Pagurus bernhardus*. However, due to their presence in a low number of samples (max. 19) and/or low densities, their indicator value never exceeded 5. Five species were found to be negatively associated with *L. conchilega* (Table 3). Besides the negative (significant) correlation values, these species were significantly more abundant in samples without *L. conchilega* ($p < 0.01$).

Table 1
Results of the global and pairwise ANOSIM and SIMPER analysis for differences between the macrofauna community composition of *L. conchilega* patches with different classes of densities (1–4) and *L. conchilega*-free patches (0)

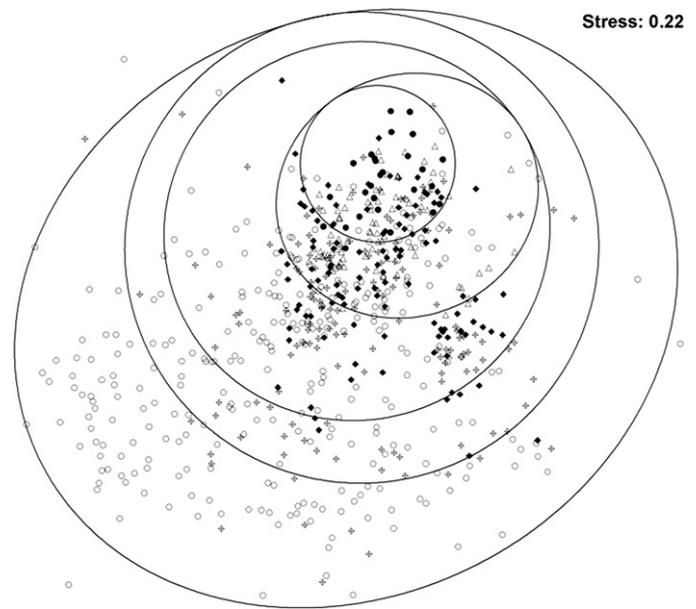|	R	p	Dissimilarity
L. conchilega presence/absence			
Global test	0.238	0.001	78.9
L. conchilega classes			
Global test	0.028	0.045	
Pairwise test			
1–0	0.029	0.025	78.2
2–0	0.054	0.016	78.4
2–1	0.002	0.420	70.6
3–0	0.095	0.002	80.0
3–1	0.047	0.030	71.2
3–2	0.033	0.027	63.2
4–0	0.207	0.001	83.3
4–1	0.129	0.013	76.2
4–2	0.113	0.010	67.9
4–3	0.090	0.043	57.5

Stress: 0.22

Fig. 3. Two-dimensional MDS ordination plot of similarities between species assemblages of different density classes of *L. conchilega* aggregations (classes 1–4, respectively, crossed squares, filled grey squares, open triangles and black filled dots) and *L. conchilega*-free samples (open dots) (using Bray–Curtis similarity measure of square root transformed data). The "Babushka" like organisation of the samples indicates that *L. conchilega* restructures the species assemblage by expanding the realized niche of several species.

Average macrobenthos densities (mean ± SE) of 8080 ± 1032 ind. m^{-2} were found in the presence of *Lanice conchilega*, while 1608 ± 146 ind. m^{-2} were found in samples without *L. conchilega*. There was a positive correlation between the steadily increasing macrobenthic densities and densities of *L. conchilega* ($R = 0.59$; $p < 0.001$). Species richness was increasing with *L. conchilega* densities, except for the highest *L. conchilega* density class (Table 4).

3.3.2. Trophic composition

Trophic group analysis showed a gradual increase in density for every trophic group, with increasing densities of *Lanice conchilega*, except for the suspension feeders. The

Table 2
Indices of Multivariate Dispersion (IMDs) show that all similarities among samples of a *L. conchilega* density class were greater than the similarities of samples between different density classes. The further the density classes are separated, the closer the IMD is to −1

Density class	Density class compared with	IMD value
1	0	−0.278
2	0	−0.608
2	1	−0.406
3	0	−0.802
3	1	−0.647
3	2	−0.29
4	0	−0.838
4	1	−0.694
4	2	−0.352
4	3	−0.057

Table 3
Rank list of the associated species. Species are ranked based on the summation of the indicator value (ISA) and the association degree

	ISA		Association degree (%)	Mann–Whitney U-test	Spearman rank correlation	
	Indicator value	p		p	R	p
L. conchilega patches						
Eumida sanguinea	65	0.001	83	0.000	0.730	0.000
Spiophanes bombyx	72	0.001	63	0.000	0.558	0.000
Phyllodoce maculata-mucosa	59	0.001	76	0.000	0.614	0.000
Pariambus typicus	56	0.001	78	0.000	0.610	0.000
Tellina fabula	61	0.001	62	0.000	0.397	0.000
Capitella spp.	52	0.001	68	0.000	0.418	0.000
Pectinaria spp.	44	0.001	75	0.000	0.507	0.000
Nephtys hombergii	61	0.001	57	0.000	0.375	0.000
Ensis spp.	51	0.001	67	0.000	0.388	0.000
Oligochaeta spp.	49	0.001	69	0.000	0.401	0.000
Abra alba	52	0.001	65	0.000	0.441	0.000
Nereis spp.	41	0.001	72	0.000	0.417	0.000
Spisula subtruncata	53	0.001	55	0.000	0.124	0.001
Polydora spp.	10	0.001	97	0.000	0.296	0.000
Mysella bidentata	45	0.001	61	0.000	0.303	0.000
Magelona spp.	49	0.005	56	0.000	0.333	0.000
Gattyana cirrhosa	5	0.001	100	0.000	0.246	0.000
Microprotopus maculatus	19	0.001	86	0.000	0.370	0.000
Notomastus latericeus	34	0.001	70	0.000	0.372	0.000
Spio spp.	43	0.001	61	0.000	0.261	0.000
Liocarcinus arcuatus	3	0.004	100	0.002	0.178	0.000
Harmothoe spp.	22	0.001	82	0.000	0.354	0.000
Amphilochus neopolitanus	3	0.003	100	0.003	0.209	0.000
Leucothoe lilljeborgii	3	0.005	100	0.003	0.142	0.000
Melita obtusata	21	0.001	82	0.000	0.361	0.000
Bodotria arenosa	3	0.011	100	0.005	0.108	0.005
Sigalion mathildae	32	0.001	71	0.000	0.270	0.000
Asterias rubens	3	0.014	100	0.007	0.148	0.000
Gammarus spp.	2	0.024	100	0.011	0.088	0.024
Cirratulidae spp.	38	0.001	64	0.000	0.324	0.000
Pagurus bernhardus	2	0.031	100	0.028	0.129	0.001
Leucothoe incisa	28	0.001	73	0.000	0.361	0.000
Bodotria scorpioides	12	0.001	88	0.000	0.321	0.000
Atylus swammerdami	13	0.001	87	0.000	0.284	0.000
Eteone longa	25	0.001	75	0.000	0.353	0.000
Hinia reticulata	29	0.001	70	0.000	0.236	0.000
Liocarcinus pusillus	5	0.002	94	0.000	0.239	0.000
Stenothoe marina	7	0.002	91	0.000	0.252	0.000
Megaluropus agilis	6	0.001	91	0.000	0.226	0.000
Autolytus spp.	18	0.001	78	0.000	0.226	0.000
Owenia fusiformis	29	0.001	66	0.000	0.276	0.000
Scoloplos armiger	41	0.00	53	0.000	0.218	0.000
Ophiura spp.	30	0.001	64	0.000	0.214	0.000
Phtisica marina	3	0.020	91	0.007	0.174	0.000
Poecilochaetus serpens	18	0.001	75	0.000	0.230	0.000
Liocarcinus holsatus	16	0.001	77	0.000	0.316	0.000
Orchomene spp.	3	0.015	90	0.012	0.123	0.002
Sthenelais boa	20	0.001	72	0.000	0.253	0.000
Pseudocuma spp.	21	0.001	71	0.000	0.265	0.000
Perioculodes longimanus	17	0.001	76	0.000	0.241	0.000
Donax vittatus	19	0.001	72	0.000	0.186	0.000
Heteromastus filiformis	13	0.001	78	0.000	0.236	0.000
Diastylis bradyi	25	0.001	65	0.000	0.270	0.000
Ampelisca brevicornis	15	0.001	76	0.000	0.250	0.000
Actiniaria spp.	25	0.001	65	0.000	0.195	0.000
Arenicola marina	5	0.005	84	0.002	0.092	0.018
Pholoe minuta	15	0.001	73	0.000	0.248	0.000
Urothoe poseidonis	28	0.005	58	0.000	0.163	0.000
Glycera alba	17	0.001	67	0.000	0.199	0.000
Corophium spp.	3	0.045	81	0.034	0.118	0.002
Glycera convoluta	5	0.013	79	0.008	0.125	0.001
Phyllodoce rosea	4	0.020	77	0.017	0.156	0.000

Table 3 (*continued*)

	ISA		Association degree (%)	Mann–Whitney *U*-test	Spearman rank correlation	
	Indicator value	*p*		*p*	*R*	*p*
Venerupis pullastra	12	0.001	69	0.001	0.156	0.000
Eteone flava	4	0.026	75	0.019	0.155	0.000
Crangon crangon	8	0.003	70	0.004	0.181	0.000
Phyllodoce groenlandica	5	0.045	67	0.039	0.150	0.000
L. conchilega-free patches						
Nephtys cirrosa	33	0.001	38	0.000	−0.198	0.000
Bathyporeia spp.	25	0.001	27	0.000	−0.218	0.000
Pontocrates altamarinus	10	0.001	20	0.000	−0.180	0.000
Urothoe brevicornis	4	0.027	17	0.002	−0.131	0.001
Scolelepis bonnieri	5	0.001	14	0.001	−0.127	0.001

suspension feeders reached their maximum density within the range of 1–50 *L. conchilega* ind. m^{-2}. Yet their relative abundance did not strongly vary, as is also the case for subsurface-deposit feeders. The overall most successful trophic groups were the groups of surface-deposit, facultative suspension and interface feeders, followed by the omnivores, predators and scavengers. They dominated both in *L. conchilega* patches and in *L. conchilega*-free patches; surface-deposit feeders however dominated stronger in *L. conchilega*-free patches, while predators gained dominance in the vicinity of *L. conchilega*.

When considering density distributions of all macrobenthic species, in samples with >1500 *Lanice conchilega* ind. m^{-2}, densities of other benthic species tended to decline; this trend was, however, not found to be statistically significant. Only 11 out of the 162 species, all polychaetes and decapods, seemed to bear the highest *L. conchilega* densities and are listed in Table 5. Their density increased significantly ($p \leq 0.032$) and contributed to the overall increase of macrobenthic density. Among these tolerant species, predators and scavengers were particularly numerous (eight species).

4. Discussion

4.1. Effect of Lanice conchilega on sediment properties

Lanice conchilega occurred at different population densities at the sample sites of the BPNS and small-scale density

variations were recorded where replicates were taken. The distribution of different density classes is shown in Fig. 1. This indicates that mosaic distribution patterns in which patches of low and high density alternate on a scale of meters, are formed in a similar way to what is found in some parts of the intertidal areas (Carey, 1987; Heuers et al., 1998), where dense aggregations of *L. conchilega* have been described as distinguishable mounds (Heuers et al., 1998). These mounds are formed because high densities of *L. conchilega* locally influence the hydrodynamics (Eckman, 1983). In dense tube assemblages the velocity of the near-bottom flow is reduced and normal, laminar near-bottom flow is deflected around and across the assemblages (Heuers et al., 1998). The reduced current velocities in the patches increase the residence time of particles (Friederichs et al., 2000) and thus facilitate the deposition of silt, clay and very fine sand particles as observed in this study. These findings were consistent with results from studies conducted on other tube-building polychaete patches (e.g. Eckman et al., 1981; Noji, 1994; Bolam and Fernandes, 2003). As differences in hydrodynamics are related to tube density, sediment composition changed with a variation in density of *L. conchilega*. However, the significant though moderate increase in the finest sediment fractions in the *L. conchilega* patches might be limited due to the activity of burrowing and crawling infauna and predating epifauna. Their presence

Table 4

Species richness for different *L. conchilega* density classes, represented by average number of species per sample in each density class (*S*) and by Margalef's index (*d*). Species richness increases with increasing *L. conchilega* densities, except for the highest *L. conchilega* density class

Density class	*S*	*d*
0	12.80	1.71
1–50	17.66	2.15
51–150	22.89	2.65
151–300	25.76	2.95
301–500	29.23	3.27
501–1000	32.83	3.59
1001–1500	35.57	3.89
>1500	33.93	3.66

Table 5

List of species found to be tolerant for the highest *L. conchilega* densities (>1500 ind. m^{-2}). (P: polychaete, D: decapod)

Surface-deposit, facultative suspension and interface feeders (2)
  Spiophanes bombyx (P)

Subsurface-deposit feeders and grazers (3)
  Pectinaria spp. (P)
  Scoloplos armiger (P)

Omnivores, predators and scavengers (4)
  Crangon crangon (D)
  Eteone longa (P)
  Eumida sanguinea (P)
  Gattyana cirrosa (P)
  Harmothoe spp. (P)
  Liocarcinus holsatus (D)
  Liocarcinus pusillus (D)
  Phyllodoce maculata-mucosa (P)

can lower the resistance of sediments to erosion (the stability of the sediment) and promote resuspension of the finest fractions into the water column (Rhoads and Young, 1970). Though our results support the current knowledge of sedimentation impact, we point out that this correlative data study cannot distinguish this effect from the preference of the worm for a certain sediment type.

A gradual increase in the coarse sand fraction with increasing densities of a tube-building polychaete has never been recorded before. Therefore, it can only be hypothesised that this fraction is a residue of *Lanice conchilega* tubes, as this species is known to line the walls of its burrow with coarse particles, firmly incorporated into an elastic mucous membrane (Jones and Jago, 1993). The tubes could get buried and biodegraded underneath accumulating finer sediments, after the inhabiting polychaetes died or left their tubes due to growth or disturbance (Carey, 1987). As this fraction of coarser sand increases with increasing *L. conchilega* densities, this could reveal some information on the age and dynamics of these patches. It is known that *L. conchilega* aulophore larvae prefer the vicinity of tubes of conspecific adults for initial settlement (Carey, 1987; Heuers et al., 1998; Zühlke, 2001; Callaway, 2006). Moreover, it has been reported to be more successful in areas with adults present than in areas without adults (Heuers and Jaklin, 1999). In environmental favourable and stable conditions, the interactions between adults and larvae could result in a successful build-up of a dense population, of which the succession process could be reflected in the sedimentary environment.

The parallel increase of the volume percentages of the finest and the coarsest sediment fraction might balance the median grain size, which possibly explains why there was no difference between the *Lanice conchilega* classes.

4.2. Effect of Lanice conchilega on the benthic community

Results indicated that even low densities of 1−50 ind. m^{-2} had a significant effect on the macrobenthic community. When all classes are taken into account, total density of the macrobenthic fauna significantly augmented with the presence of *L. conchilega*. These findings support the results of previous studies on *L. conchilega* (Zühlke et al., 1998; Dittmann, 1999; Zühlke, 2001; Callaway, 2006), other polychaete tube patches (Woodin, 1978; Luckenbach, 1987; Noji, 1994; Bolam and Fernandes, 2003) and even imitations of polychaete tubes (Zühlke et al., 1998; Dittmann, 1999; Callaway, 2003).

The MDS ordination clearly illustrates this shift in community composition and indicates that *Lanice conchilega* alters the community structure of the benthic fauna, even when present at low densities. Further the plot clearly shows that the structuring effect creates communities that consist entirely of species sampled out of the same species-pool. Based on the enlarged difficulty to compress the relationship of this large quantity of data into two dimensions, we obtained a relatively high, though acceptable stress value of 0.22.

An explanation for the overall increase in species richness can be partially found in the fact that there is a greater chance to catch a species when it occurs in higher densities (Downes et al., 2000). However, the driving force that allows these higher densities to evolve can be attributed to the capacity of *Lanice conchilega* to create or modify the habitat in a way that is favourable and generates good living conditions, for many species. The result is an increased habitat complexity and heterogeneity (niche diversification) that facilitates the evolution of a more diverse community (Bell et al., 1991 as cited in: Downes et al., 2000). This confirms that *L. conchilega* not only alters the physical but also the biological factors and is therefore referred to as a bio-engineer (Jones et al., 1994). The ability of *L. conchilega* to enhance the survival of certain species in more optimal conditions is reflected in a gradual community shift, based on changes in relative abundances of macrobenthic species. However, the MDS results, as well as the indicator values (max. 72) clearly show that the species found to be positively associated with *L. conchilega*, belonged to the overall species-pool of the habitat. Though we selected samples from one habitat type (fine sediment) and hence worked within one macrobenthic community, significant ANOSIM results were found. The relatively low *R* value indicates that all samples belong to the same community. The structuring effect is shown in the decreasing Dispersion Factor Values with increasing *L. conchilega* densities which is visualised in the ''Babushka'' like pattern of the MDS. Furthermore, Indices of Multivariate Dispersion (IMDs) show that density classes differ, emphasising the structuring effect. These results confirm that this bio-engineer shapes the community structure considerably by expanding the realized niche of several species, without forming its own community *s.l.* (see also Zühlke et al., 1998; Dittmann, 1999).

4.3. Effect of Lanice conchilega on species' abundances

All positively associated species obviously take advantage from the favourable conditions within the patches. This section explains the presence or absence of species, based on the available knowledge on the autecology and species interactions. In general, the presence or absence of associated species can be considered to be a result of the habitat modifying ability of *L. conchilega* and/or direct interaction with the tubes, or as rather accidental.

All but one of the exclusively associated species have never been reported elsewhere as being exclusively found in the presence of *Lanice conchilega* tubes. Therefore, their exclusive presence in the *L. conchilega* samples can be regarded as accidental, even more so as they are only found in a few samples (6 to max. 19 samples). Only the amphipod species *Gammarus locusta* has previously been reported as exclusively associated with *L. conchilega* in an intertidal area (Callaway, 2006). *Gammarus* is known as a genus of amphipods of which certain species actively enter the water column and have a high mobility on the scale of tens of meters (Ragnarsson and Raffaelli, 1999). Perhaps, in this case the more stable *L. conchilega* beds are actively preferred and may facilitate the

existence of this species that otherwise could not occur within that flow and sediment regime.

Direct interaction with the tubes includes the settlement of larval and postlarval benthic organisms (Qian, 1999). Juvenile bivalves are known to settle on the worm tubes, as they provide attachment facilities in a relatively protected area. This settlement is a passive process facilitated by the hydrodynamic regime (''skimming flow'') around the tubes (Eckman, 1983; Heuers et al., 1998). Increasing densities of *L. conchilega* could provide more and secure settlement surface, which partially explains the increasing presence of positively associated bivalves in this study area. Based on a comparable phenomenon observed in patches of the tube-building polychaete *Pygospio elegans*, it is assumed that once established, the juvenile bivalves may have benefited from the indirect effects of the tubes slowing down the water flow across the beds, promoting the feeding and increasing protection from erosion and predation (Bolam and Fernandes, 2003). This increased protection may also favour the presence of species earlier observed in or attached to the tubes (Zühlke, 2001; Callaway, 2006) and found to be positively associated with *L. conchilega* in this study: *Eumida sanguinea* and *Harmothoe* spp. In previous studies, *E. sanguinea* (probably juveniles) was almost exclusively found among the sand fringes at the top-end of the tubes, where it may share its food source and profit from the shelter in these so called miniature hatcheries (Zühlke, 2001; Callaway, 2006). The scale worm *Harmothoe* spp. was found inside the tubes (Callaway, 2006). *Harmothoe* spp. are also known to live commensally with other species that construct burrows and cavities, such as the lugworm *Arenicola marina* (Reise, 2002).

Amphipods were abundantly represented among the positively associated species (16 species). Callaway (2006) suggests that all amphipods may benefit from the loosened sediment around single tubes, as this facilitates penetration of the sediment surface and could explain their success. Higher densities of bioturbating species might also contribute to a looser structure of the sediment in between the tubes. While most amphipod species migrate between the water column and the sediment and were exclusively found in the upper 0−2 cm surface layers of the sand, *Urothoe poseidonis* seemed to live (without migrating) at a depth of 4 cm or below, down to about 15 cm, in close proximity to the tubes (Callaway, 2006). The actual benefit for *U. poseidonis* may be an improved oxygen supply in the sediments surrounding the tubes, mediated by the mobility of *Lanice conchilega* in its tube. Forster and Graf (1995) found increased oxygen concentrations in the sediment along the whole length of the tube and suggested that *L. conchilega* acts as a piston, exchanging burrow water with the overlying water. Besides crawling over and in the sediment, two positively associated free-living amphipod species *Pariambus typicus* and *Phtisica marina* may also interact directly with the tubes. They have previously been observed to perform a clinging behaviour in which they attach to algae with adapted grasping appendages (Guerra-Garcia et al., 2002). Aikins and Kikuchi (2001) showed that the preference of a tube-dwelling *Corophium* amphipod species for algal and artificial filamentous structure habitat, was explained by decreased current velocity, increased detritus trapping (and thus food availability) and increased shelter provision. Analogous phenomena are encountered in the *L. conchilega* reefs and may likewise facilitate the success of amphipods clinging to the tubes.

While the space between the tubes serves as a refuge from epibenthic predators or impact of physiological stress (Woodin, 1978; Bolam and Fernandes, 2002), infaunal predators are certainly not inhibited and seem on the contrary to be rather attracted to the species rich tube patches. Polychaetes and amphipods constituted the highest numbers of predatory species positively associated with *Lanice conchilega*. Some of these species were at least found once in higher abundances in the presence of *L. conchilega* in previous studies: *Eumida sanguinea*, *Eteone longa*, *Phyllodoce maculata-mucosa*, *Nephtys hombergii* (Zühlke et al., 1998; Dittmann, 1999; Zühlke, 2001; Callaway, 2006). The fact that the three most positively associated species (*E. sanguinea*, *Spiophanes bombyx* and *P. maculata-mucosa*) also occurred as species tolerant to the highest *L. conchilega* densities, indicates a very close association with the tubes.

The five negatively associated species are part of the *Nephtys cirrosa* community which is characterised by clean mobile sands (Van Hoey et al., 2004). Therefore, it can be assumed that sediment related factors are responsible for the habitat preference of these species in our study. As the presence of *Lanice conchilega* implies an increase in the finest sediment fractions, the absence of *N. cirrosa* and *Bathyporeia* spp. in the tube patches can be considered as a *L. conchilega* mediated effect. Moreover, in this study area, the *N. cirrosa* community seems to border the *L. conchilega* communities *s.s.*, which is considered to be part of the *Abra alba−Mysella bidentata* community *s.l.* (Van Hoey et al., 2004).

In general, the response pattern of a particular species to a factor induced by *L. conchilega*, e.g. potential refuge, will not only reflect the consequences of the exclusion of large predators or disturbers, but will also mirror the interactions with the assemblages around the refuge (Luckenbach, 1987). Besides the direct or indirect physical impact of the tubes' presence, interactions among species take place based on the activities of crawling, burrowing and irrigating, and providing or competing for habitat structures or food. In order to further explain the species interactions in this highly complicated coexistence, we analysed the trophic group composition of the *L. conchilega* community *s.s.*

4.4. Effect of trophic interactions on the Lanice conchilega community s.s.

Trophic interactions may at least equal habitat engineering in importance, and both are linked and affected by differential mobility of the organisms and by their physical environment (Reise, 2002). As protruding structures, the tubes reduce the near-bottom flow velocity which enhances particle settlement. This implies increased food availability, as clay particles tend to bind higher quantities of organic matter (Nichols, 1970).

Prolonged sedimentation of relatively fresh organic matter will promote the growth of suspension and interface feeders in the first place, while extended deposition is beneficial to (sub)surface-deposit feeders as well and promotes a higher diversity of feeding types (Wieking and Kröncke, 2005). It is remarkable however that the abundance of associated suspension feeders remains relatively low and even declines when >50 L. conchilega ind. m^{-2} are present, while all other trophic groups increase in abundance with increasing L. conchilega densities. This observation can be explained by several factors.

Surface dwelling and burrowing polychaetes are known to have a direct and/or indirect negative effect on the survival of e.g. bivalve recruits (which make up the majority of the positively associated suspension feeders) by, respectively, predation and/or burial due to high resuspension of the sediment (Luckenbach, 1987). Lanice conchilega itself is less affected by predation and resuspended particles as it can withdraw within its tube and is known to be able to switch to deposit feeding when occurring in low densities. Moreover, tubes protrude up to 4 cm from the sediment surface and they have the ability to burrow through newly deposited sediment. They may also be less susceptible to suffocation by clogging of the filter apparatus than bivalves, a trend observed in areas subject to higher inputs of particulate organic matter (Pearson and Rosenberg, 1978). In addition, a potential competition for food and/or space between L. conchilega and other suspension feeders could result in favour of L. conchilega. The fact that no other positively associated suspension-feeding polychaete was found possibly reflects the success of L. conchilega in competition.

The success of surface-deposit or facultative suspension feeders can be attributed to the higher deposition rate of detrital organic matter between the tubes and the increased bacterial biomass, due to enhanced nutrient fluxes occurring around the tubes (Eckman, 1985). They even may increase their own food supply by stimulation of microbial growth by feeding and irrigation (''microbial gardening'') (Hylleberg, 1975; Miller et al., 1984; Grossmann and Reichardt, 1991 as cited in: Snelgrove and Butman, 1994). Furthermore, their relative ability to resist lower oxygen tensions and higher acidities and sulphide concentrations favours them to withstand higher organic matter inputs (Pearson and Rosenberg, 1978), which co-occur with increased sedimentation of the finest sediment fractions.

While tube structures provide shelter from large, mobile epibenthic predators/disturbers, endobenthic predators have access to abundant prey. The higher densities of infaunal predators in Lanice conchilega patches could primarily be a response to higher meio- and macrobenthic densities at these sites (Luckenbach, 1987; Dittmann, 1999; Zühlke, 2001). However, in accordance with the cage experiment studies of Ambrose (1984) and Sardá et al. (1998), an increased total density of infaunal predators and ratio of predatory to non-predatory infauna ($\sum$ Predators/$\sum$ non-predators ratios were for classes 0–4, respectively, in percentages 15; 14; 18; 28 and 48) was found, following the presence and increased densities of L. conchilega tubes. This indicates that the tube aggregations can be considered as natural epibenthic predator/disturber exclusion structures, comparable to what Ambrose (1984) assumed for seagrass beds, with increasing refuge efficiency as densities of the tubes increase. As the ratio is notably higher in samples containing >1500 L. conchilega individuals per m^2, predation by infaunal predators on non-predatory infauna may be considered as a more important structuring force in these dense patches than in the less dense patches. This is based on the assumption that predatory infauna are preferentially preyed upon by epibenthic predators or that predatory and non-predatory infauna are preyed upon equally but predatory infauna reduce the abundance of other infauna (Ambrose, 1984).

The observed community shift to lower diversity and higher densities in the highest class could also be an effect of exclusion of epibenthic predation/disturbance according to the intermediate disturbance hypothesis, as proposed by Connell (1978). This hypothesis predicts that at low disturbance, in our case due to epibenthic predators/disturbers, diversity declines as competitive dominants monopolize the habitat (Peterson, 1982). These competitive dominants were identified as bearing the highest L. conchilega densities. They were mainly represented by relatively large-sized infaunal predators. In this study, decapods were also considered as infaunal predators or scavengers since they are known to be an important food source for demersal fishes (e.g. Mauchline, 1982; Dauvin, 1988, as cited in: Wang and Dauvin, 1994) and they or their juveniles can certainly profit from the tube reefs as a refuge. The increase of these relatively large-sized infaunal predators can be explained by the fact that shallow-dwelling species are more susceptible to epibenthic predation than deeper-dwelling species (Virnstein, 1977; Holland et al., 1980; Blundon and Kennedy, 1982; as cited in: Wilson, 1991). The increased survivorship of decapod crustaceans (shrimp and brachyuran crabs), which reduces infaunal abundances significantly, was also found in seagrass beds where fish were excluded (Wilson, 1991). In general, the dense polychaete tube reefs directly and positively increase the density of primarily predatory infauna by giving them shelter. At a certain density, however, they also indirectly and negatively affect macroinfaunal organisms which are preyed upon by these predators, or excluded due to competition for food or space.

5. Conclusion

This study supports the findings of other studies on bio-engineering organisms. Lanice conchilega positively influences macrofaunal density, species richness and community composition. This paper provides information on the specific mechanisms that lead to species aggregation in a well-defined bio-engineered habitat. A rank order of associated species was produced, based on an in situ sampling design. This rank list of associated species, combined with the available ecological knowledge, allows explaining functional group interactions. Nevertheless, we admit that the exact nature of the relationships between species, and with the tube patches remains uncertain in some cases. We conclude that knowledge

on the autecology of species is crucial to reach full explanation of this particular system. This requires controlled experiments in which the influence of dynamic variables, e.g. recruitment success, competition for space, trophic interactions, inter-related variables such as grain size, organic content, microbial content and food supply, is examined systematically, as it is unlikely that one of these factors alone can explain the presence of species in a particular habitat. We believe that this descriptive and correlative data study points out the ecological implications of *L. conchilega* on species level and serves as a solid basis for research on mechanistic relationships between the observed species.

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