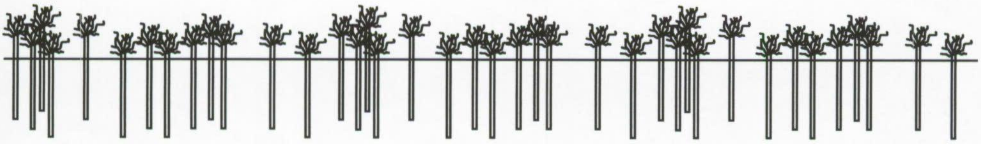
Chapter 6

The impact of *Lanice conchilega* on the soft-bottom benthic ecosystem in the North Sea



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Abstract

The tube building polychaete *Lanice conchilega* has a wide distribution and can form dense aggregations. Unfortunately, the effects of *L. conchilega* on the surrounding benthic community have received little attention, especially in subtidal areas. Therefore, the effects of the presence of *L. conchilega* on the abundance, species richness, diversity and species composition of the North Sea benthos in relation to sedimentology and depth were evaluated in the present paper. The results show that *L. conchilega* does have an effect on the benthic density and species richness in soft-bottom sediments. The density of the benthic species increased and was significantly (positively) correlated with the density of *L. conchilega*. Furthermore, the species richness increased with increasing density of *L. conchilega*. This trend was, however, not consistent: the number of species no longer increased or even decreased after reaching a certain density of *L. conchilega* (> 500 ind/m²). The same overall pattern was detected concerning the expected number of species. The N_1 - diversity index showed similar or slightly higher values in *L. conchilega* patches compared to patches without *L. conchilega*. The effects on density and diversity were most pronounced in shallow fine sands, which are the preferred habitat of *L. conchilega,* and less in deep fine sands. The changes in benthic characteristics result from the alterations of the habitat by *L. conchilega* (hydrodynamics, sediment stability, improved oxygen) and the complex interactions between the benthic organisms and the biogenic structures consisting of *L. conchilega* tubes. A lot of benthic species can profit from the creation, modification and maintenance of that habitat by *L. conchilega*, which results in an increased density and species richness in *L. conchilega* patches compared to the surrounding soft-bottom sediments. Finally, the results indicated that *L. conchilega* has an effect on the benthos present in a particular habitat, rather than forming its own association.

Keywords
Lanice conchilega, diversity, associated species, soft-bottom sediments, North Sea

Introduction

Biogenic habitat structures play a major role in structuring the distribution pattern of benthic fauna by modifying the sediment (Eckman et al., 1981; Carey, 1987) and hydrodynamic parameters (Eckman 1983), or by changing interactions between species (Woodin, 1978). In some cases, those biogenic habitat structures could even be considered as 'biogenic reefs'. 'Biogenic reefs' were defined as rocky marine habitats or biological concretions that rise from the sea bed and were created by the animals themselves (Holt et al., 1998). The best know species forming 'biogenic reefs' and structuring the environment with possible effects on the benthic fauna are *Serpula vermicularis, Mytilus edulis, Sabellaria* species and *Modiolus modiolus* (Holt *et al.*, 1998).

Additionally, some other tube-building polychaetes provide considerable structures in the otherwise relatively unstructured soft-bottom sediments (Woodin, 1978; Zühlke et al., 1998; Zühlke, 2001; Bolam and Fernandes, 2002; Rees et al., 2005). An example of a structuring tube-forming polychaete is the sand mason, *Lanice conchilega*, which lives in a tube of sand or shell breccia attached to an inner thin organic layer. The tube itself is crowned with a sand-fringe, which protrudes 1 - 4 cm above the sediment surface (Ziegelmeier, 1952). This species can reach densities of several thousands of individuals per m² (Buhr and Winter, 1976; Ropert and Dauvin, 2000) and has the ability to influence the surrounding benthic populations (Zühlke et al., 1998; Zühlke, 2001). This ability is mainly due to the following factors: (1) the tubes provide a settlement surface for larval and postlarval benthic organisms (Qian, 1999), (2) there is an improved oxygen supply in the sediments surrounding *L. conchilega* tubes (Forster and Graf, 1995)), (3) the tubes affect the current velocities in the benthic boundary layer (Eckman et al., 1981; Heuers et al, 1998, Hild & Günther, 1999), (4) the tubes have a stabilizing effect on the sediment, and (5) the space between tubes can serve as a refuge from predation (Woodin, 1978). The presence of *L. conchilega* tube aggregations in an intertidal sandflat, for example, resulted in an increase in the species diversity and abundance compared to the surrounding sediment (Zühlke et al., 1998; Zühlke, 2001).

Lanice conchilega has an amphiboreal distribution, is found on all European coasts and colonizes a wide variety of intertidal and subtidal sediments down to about 1900m (Hartmann – Schröder, 1996; Ropert and Dauvin, 2000). Despite its wide distribution and the formation of sometimes dense aggregations, the effects of *L. conchilega* on the surrounding benthic community have received little attention, especially in subtidal areas. The interaction between *L. conchilega* and the benthos was only studied by Zühlke et al., 1998; Zühlke, 2001 and Dittmann (1999) on two sandflats of the East Frisian Waddensea (the Gröninger Plate and the Dornumer Nacken) and included some experiments on the effect of artificial tubes on the benthos. Both studies concluded that the benthos in tidal flats has a temporary and optional association with the biogenic structures of *L. conchilega* and that the presence of such structures enriches the *Arenicola*-dominated sandflat associaton in abundance and species numbers due to a reduction of current velocity.

Under the guidance of the Benthos Ecology Working group of ICES, a large-scale benthos survey was performed in the subtidal of the North Sea in 2000 (Rees et al, 2002). The resulting dataset forms the basis of the description of the impact of *L. conchilega* on the soft-bottom benthic ecosystem in the North Sea. In other words, the present study aims to investigate the effects of the presence of *L. conchilega* on the abundance, species richness, diversity and species composition of the North Sea benthos. These effects of *L. conchilega* will be investigated in relation to depth and sedimentology, and the obtained results will be discussed in the light of the potential environmental and biological effects that *L. conchilega* may cause. Finally, the results will be linked to the arguments used to consider the biogenic structures formed by *L. conchilega* as 'biogenic reefs'.

Materials and Methods

Study area

The study area covers most of the English Channel and the North Sea (delimited by Norway and Denmark in the east, the UK in the west and Germany, the Netherlands, Belgium and northern France in the south). The North Sea (51° to 61° N, 3° W to 9° E) is divided into a number of loosely defined areas: a relatively shallow southern North Sea (Southern Bight and German Bight), the central North Sea (Doggerbank, Oysterground), the Northern North Sea, the Norwegian Trench and the Skaggerak, from which the last two areas are not included in the present study.

Data origin

Under the guidance of the Benthos Ecology Working group of ICES, a total of 2227 macrobenthic samples (1405 stations) were gathered in the North Sea and English Channel in the year 2000 – 2001. These data originate from various projects, including national monitoring surveys (Rees et al., 2002). Most of the sampling was done as agreed beforehand, i.e. collecting infauna (and slowly moving epifauna) with grabs of the Van Veen type (at least 2 grabs of 0.1m² at each station), and sieving alive over a 1 mm sieve. In spite of the initial agreement, some data contributors used other sampling devices, such as Hamon grab, box corer and Day grab. In order to enable detailed analyses on a uniform dataset, only samples, which were taken with a 0.1 m² Van Veen or Day grab and were sieved alive, were included in the present study (except in the description of the distribution of *L. conchilega* in the North Sea). This resulted in a final dataset of 1098 samples (comprising 513 different stations).

All data was incorporated into a database, and taxonomic inter-comparisons were performed (Rees et al, 2002). These data modifications were executed during several workshops of the ICES North Sea Benthos Study group. After taxonomic clearance, a dataset consisting of 717 taxa (further referred to as species) was obtained. The density of *L. conchilega* in the present study is based on individual counts, rather than tube counts.

The sedimentological characteristics of the different samples were coded according to sediment classes: (a) mud, (b) muddy sand, (c) fine to medium sand, (d) medium to coarse sand, (e) sand and gravel, and (f) mixed sediments (Report ICES CM 2004/E:05). Additionally, water depth at each sampling station was recorded. The different habitat types were distinguished by using the sediment classes. Based on the bathymetrical information, those sediment classes were each split up in shallow (< 70 meter) and deep (> 70 meter) (cf. Künitzer et al., 1992).

Data analysis

The effects of *L. conchilega* on the macrobenthos were investigated for every habitat type, in which the species was found and for which a representative amount of samples (> 100) was available (Figure 2). The following univariate indices were used to describe the macrobenthos (excluding *L. conchilega*) in each sample: (1) density N, (2) species richness S, expressed as number of species per sample (i.e. per $0.1m^2$), (3) the exponential form of the Shannon – Wiener index N_1 and (4) expected number of species (ES 50). All indices were calculated with the Primer 5.2.9 software package. The relations between benthic density, species richness, expected number of species or N_1 - diversity and the density of *L. conchilega* in the different habitats were observed and visualised based on different density classes of *L. conchilega,* and were statistically tested using Spearman rank correlations.

In order to identify species which are possibly associated with the presence of *L. conchilega*, three reductions and calculations of the species dataset were performed. Firstly, only species which were present in more than 5 samples per habitat type were selected, thereby excluding rare species. Secondly, 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. Species with an association degree of more than 50% (> 50% of all individuals were found in association with *L. conchilega*) were regarded as associated species. Thirdly, the level of the significance of association was calculated using a Mann – Whitney U test comparing densities of a certain species between *L. conchilega* samples and samples without *L. conchilega*. Finally, species from which the densities showed a positive correlation (Spearman Rank correlation) with the density of *L. conchilega* were retained. Non – parametric test were used because the assumptions for parametric test, even after transformation, were not fullfiled.

Results

Distribution pattern

Lanice conchilega was found in the entire North Sea and English Channel (Figure 1) (25% of the stations). In the central English Channel, *L. conchilega* was seldomly found (< 5% of the samples), whereas the species occurred frequently in the entire North Sea (42% of the samples). The areas with the highest frequency of occurrence and densities were the German Bight, the central part of the North Sea (Dogger Bank) and along the French, Belgian and Dutch coast. In the deeper northern part of the North Sea, *L. conchilega* was frequently found, but in low densities (< 100 ind/m²), whereas in the western North Sea, *L. conchilega* was seldomly found.

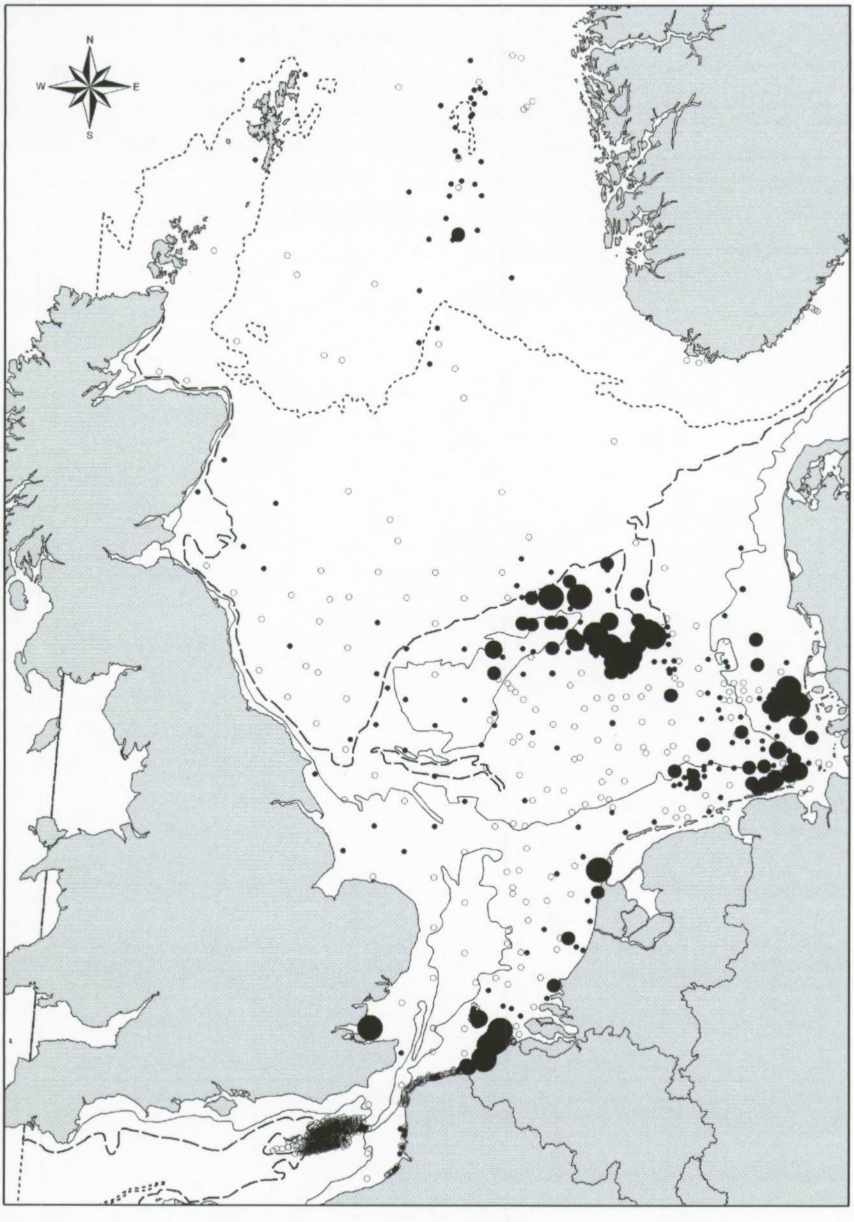

Figure 1. Density distribution of *L. conchilega* in the entire North Sea and English Channel. 0 ind/m²: (○); 1-100 ind/m² (•); 100-500 ind/m² (●); 500-1000 ind/m² (⬤); > 1000 ind/m² (⬤)

Habitat preferences

Lanice conchilega was found in all soft-bottom sediment types in the North Sea; however, with differences in frequency of occurrence and average density between the habitat types discerned (Figure 2). No evaluation of the occurrence of *L. conchilega* in shallow mud, deep muddy sands and deep medium sands could be made, due to the low number of samples in these habitat types (< 30 samples). As for the other habitats, the highest percentages of occurrence (41 - 51 %) and highest densities (138 – 419 ind/m²) of *L. conchilega* in shallow areas were observed in muddy, fine and mixed sediments. In shallow medium and coarse sediments, the frequencies of occurrence (24 and 30%, respectively) and average densities (17 and 12 ind/m², respectively) were much lower. In deep muds and fine sands (> 70 meter), *L. conchilega* occurred frequently (53 and 45%, respectively), but in low average densities (32 and 14 ind/m², respectively). Although *L. conchilega* was found in all habitat types, for reasons of representativeness further detailed analyses were only done for habitats containing more than 100 samples (deep fine sand, shallow muddy sand, shallow fine sand and shallow medium sand).

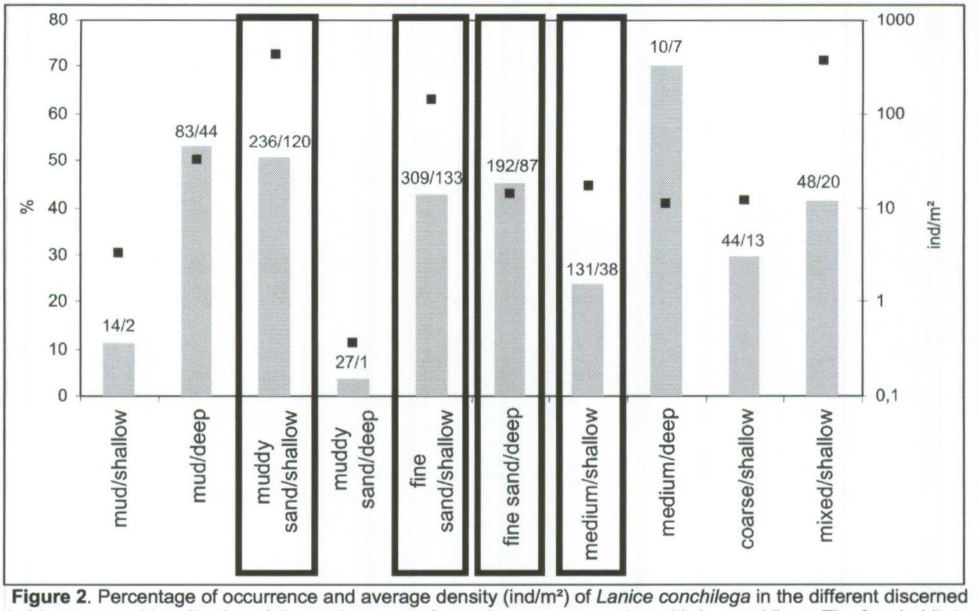

Figure 2. Percentage of occurrence and average density (ind/m²) of *Lanice conchilega* in the different discerned habitat types, with indication of the total amount of samples versus samples with *L. conchilega*. The four habitats, which were represented by more than 100 samples in the database, were encircled.

Effect of *Lanice conchilega* on the benthic characteristics

Presence / absence of Lanice conchilega

A highly significant difference ($p < 0.0001$) in benthic density and species richness (excluding *L. conchilega*) was found between *L. conchilega* samples and samples without *L. conchilega* in shallow muddy sands, fine sands and medium sands (Table 1). Those differences in density and species richness were significant in deep fine sands ($p = 0.0115$ and $p = 0.0027$). The N_1 – diversity index in *L. conchilega* samples differed significantly in shallow fine sands ($p < 0.0001$), medium sands ($p = 0.0012$) and deep fine sands ($p = 0.0225$). Only in shallow muddy sands, no significant differences were found ($p = 0.1299$). The ES (50) was only significantly different in shallow fine sands and medium sands.

Table 1. First, the differences tested in benthic density, species richness, N_1 – diversity and ES (50) by Mann – Whitney U test, between *Lanice conchilega* samples and samples without *L. conchilega* for the different habitats. Second, the Spearman rank correlation between the benthic density, species richness, N_1 – diversity and ES (50) and the density of *L. conchilega* for the different habitats. The number of observations (n) within each habitat where 236 for shallow muddy sand, 309 for shallow fine sand, 192 for deep fine sand and 131 for shallow medium sand.

	HABITATS	Mann - Whitney U- test	Spearman rank correlation R	p
DENSITY	shallow muddy sand	*p < 0,0001*	0,45	*p < 0,0001*
	shallow fine sand	*p < 0,0001*	0,63	*p < 0,0001*
	deep fine sand	*p = 0,0115*	0,23	*p = 0,0013*
	shallow medium sand	*p < 0,0001*	0,39	*p < 0,0001*
SPECIES RICHNESS	shallow muddy sand	*p < 0,0001*	0,4	*p < 0,0001*
	shallow fine sand	*p < 0,0001*	0,65	*p < 0,0001*
	deep fine sand	*p = 0,0027*	0,27	*p = 0,0001*
	shallow medium sand	*p < 0,0001*	0,5	*p < 0,0001*
N_1	shallow muddy sand	p = 0,1299	0,08	p = 0,22
	shallow fine sand	*p < 0,0001*	0,39	*p < 0,0001*
	deep fine sand	*p = 0,0225*	0,158	*p = 0,028*
	shallow medium sand	*p = 0,0012*	0,36	*p < 0,0001*
ES (50)	shallow muddy sand	p = 0,07	0,08	p = 0,22
	shallow fine sand	*p < 0,0001*	0,39	*p < 0,0001*
	deep fine sand	p = 0,16	0,17	p = 0,17
	shallow medium sand	*p < 0,0001*	0,34	*p < 0,0001*

Correlation between benthic structure characteristics and density of Lanice conchilega

In the four habitats, the densities of the surrounding benthos increased with increasing density of *L. conchilega* (Figure 3a). The increasing trend of the density was comparable in the four habitats. The correlation between densities of the benthic fauna and the densities of *L. conchilega* was positive and significant in all habitats, was strongest in shallow fine sands (Spearman R: 0.63) and was lowest in deep fine sands (Spearman R: 0.23) (Table 1).

In shallow muddy sands, the species richness decreased when the density of *L. conchilega* exceeded 1000 ind/m², while in shallow fine sands, the species richness levelled of at 500 ind/m² of *L. conchilega* (Figure 3b). Although species richness differed strongly between habitats, a significant correlation was found between the species richness and the density of *L. conchilega* in all habitats, with the highest value in shallow fine sands (Spearman R: 0.65) and the lowest in deep fine sands (Spearman R: 0.27) (Table 1). In shallow muddy sands, the correlation was atypical: the species richness decreased with higher densities of *L. conchilega*.

The N_1- diversity index and its relation with *L. conchilega* density differed between the habitats (Figure 4a). In shallow muddy sands, the N_1- diversity index did not increased with the *L. conchilega* density and did not show a significant correlation (Spearman R: 0.07; p = 0.28) (Table 1), whereas a minor, through significant to very highly significant correlation was observed in the other three habitats. The strongest correlation was found in shallow fine sands (Spearman R: 0.39) (Table 1).

The trend in the ES(50) was comparable with that of the species richness (Figure 4b), with some small differences: (1) in shallow muddy sands and deep fine sand no increase and no significant correlation in ES(50) with the *L. conchilega* density was observed, (2) in shallow fine and medium sands an increase and a significant correlation (Spearman R: 0.39 – 0.36, respectively) was found, but the curve levelled of at 100 ind/m² in medium sands and slowly increased or even decreased in fine sands (Table 1).

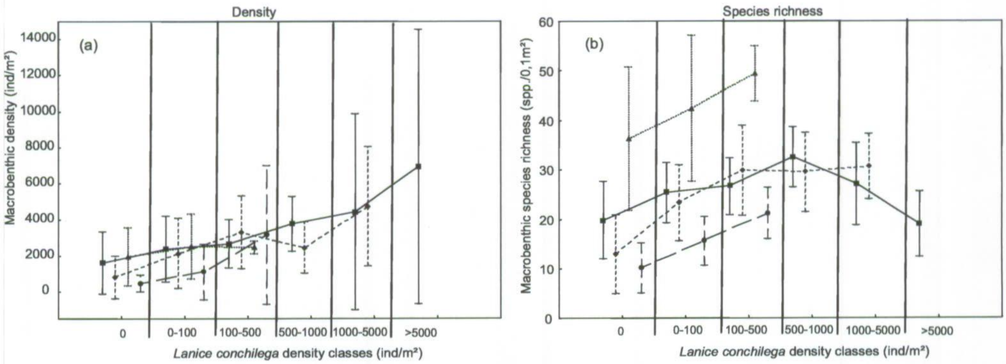

Figure 3. (a) The density (with exclusion of *Lanice conchilega*) of the benthic species, versus the different *L. conchilega* density classes with indication of the standard deviation, and (b) the species richness (with exclusion of *L. conchilega*) of the benthic species, versus the different *L. conchilega* density classes with indication of the standard deviation. Shallow muddy sand: square; shallow fine sand: rhombus; deep fine sand: triangle; shallow medium sand: circle.

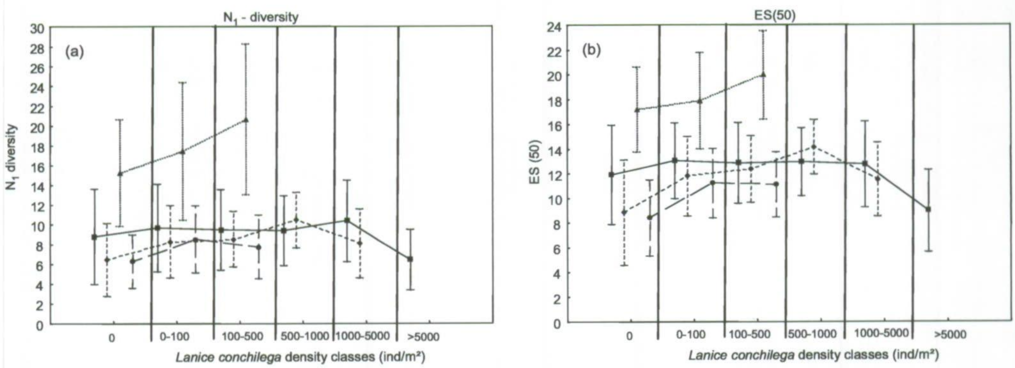

Figure 4. (a) The N_1-diversity (with exclusion of *Lanice conchilega*) of the benthic species, versus the different *L. conchilega* density classes with indication of the standard deviation, and (b) the ES(50) (with exclusion of *L. conchilega*) of the benthic species, versus the different *L. conchilega* density classes with indication of the standard deviation. Shallow muddy sand: square; shallow fine sand: rhombus; deep fine sand: triangle; shallow medium sand: circle.

Species associated with *L. conchilega*

Table 2. First, an overview of the percentage of the species associated with *Lanice conchilega* in relation to the total amount of species (with exclusion of the rare species) is given for the most important higher taxa within each habitat type. Secondly, the amount of associated species of *L. conchilega,* which where also the most frequent occurring species (found in most samples) for that habitat. Thirdly, the percentage of each discerned feeding type within each habitat for the group of samples which contain *L. conchilega* and samples whithout *L. conchilega*.

	shallow muddy sands			shallow fine sands		
Higher taxa	**# associated species**	**total # species**	**%**	**# associated species**	**total # species**	**%**
Anthozoa	1	1	100	1	1	100
Polychaeta	13	54	24	26	54	48
Bivalvia	6	22	27	10	19	53
Gastropoda	2	5	40	3	7	43
Amphipoda	4	16	25	12	20	60
Cumacea	2	9	22	3	8	38
Decapoda	1	5	20	5	6	83
Echinodermata	0	9	0	4	7	57
others	1	8	13	5	11	45
TOTAL	30	129	23	69	133	52
Most frequent occuring species	13	20	65	17	20	85
Feeding type	***Lanice* %**	**no *Lanice* %**		***Lanice* %**	**no *Lanice* %**	
I: suspension feeding	15	14		22	24	
II: surface deposit, facultative suspension and interface feeding	64	54		64	56	
III: subsurface deposit feeding, grazing	11	21		4	5	
IV: omnivore, predator, scavenger	9	8		8	10	
V: unknown	1	3		2	6	

	deep fine sands			shallow medium sands		
Higher taxa	**# associated species**	**total # species**	**%**	**# associated species**	**total # species**	**%**
Anthozoa	1	1	100	1	1	100
Polychaeta	1	107	1	7	32	22
Bivalvia	0	25	0	1	9	11
Gastropoda	0	7	0	0	1	0
Amphipoda	1	26	4	1	10	10
Cumacea	0	6	0	2	3	67
Decapoda	0	2	0	1	3	33
Echinodermata	0	6	0	0	3	0
others	0	12	0	3	3	100
TOTAL	3	192	2	16	65	25
Most frequent occuring species	1	20	5	1	20	5
Feeding type	***Lanice* %**	**no *Lanice* %**		***Lanice* %**	**no *Lanice* %**	
I: suspension feeding	9	8		5	6	
II: surface deposit, facultative suspension and interface feeding	76	77		72	47	
III: subsurface deposit feeding, grazing	4	5		6	12	
IV: omnivore, predator, scavenger	9	8		15	33	
V: unknown	2	2		2	2	

A species was identified as being associated with *L. conchilega* if the association degree was more than 50%, if the species density significantly differed between the samples with and without *L. conchilega* and if a positive correlation with the density of *L. conchilega* was found.

In shallow fine sands, 52 % of the species were positively associated with *L. conchilega*, whereas only 23 - 25% of the species were associated in shallow muddy and medium sands. In deep fine sands, only 3 out of 202 species showed an association with *L. conchilega*. In the first three habitats, associated species were found within each higher taxon, except for the Echinodermata. The percentage of associated species within each higher taxon was highest (> 40%) in shallow fine sands. Furthermore, most of the frequently occurring species within that habitat were associated with *L. conchilega* (85%). In shallow muddy sands, only 65% of those species were associated. In deep fine sands and shallow medium sands, the frequently occurring species were not associated with *L. conchilega*.

Differences in the relative abundance of each feeding type within a habitat were observed between samples containing *L. conchilega* and *L. conchilega* free areas (Table 2). In the shallow habitat types, surface deposit feeding was the dominant feeding type and was more dominant in samples containing *L. conchilega*. The dominance of subsurface deposit feeders decreased in *L. conchilega* samples, especially in shallow muddy and medium sands. The percentage of omnivorous and predatory species did not change strongly, except in shallow medium sands, where their dominance was reduced.

Discussion

Distribution

Lanice conchilega has a cosmopolitan distribution, as it is found from the Arctic to the Mediterranean, in the Arabian Gulf and the Pacifc, from the low water neap tide mark down to 1900 m (Hartmann–Schröder, 1996). In our survey, *L. conchilega* was found in the entire North Sea down to a depth of 180 meter (deepest record in the dataset was 380 meter). This tube–building polychaete is known to live mainly in sandy sediments from mud to coarse sand (Hartmann – Schröder, 1996), as was confirmed by the present study. Yet, shallow muddy and fine sands were strongly preferred: *Lanice conchilega* showed its highest frequencies of occurrence and densities in these sediments (more than 1000 individuals per m² compared to maximally 575 ind/m² in shallow medium sands). In the deeper habitats, *L.* conchilega was frequently encountered but only in low abundance (maximally 170 ind/m² in deep fine sand). Hence, it can be concluded that *L. conchilega* has a wide geographical distribution and a low habitat specialization (i.e. eurytopic species), leading to the absence of an obvious relationship between the distribution pattern of *L. conchilega* and the sediment type (cf. Buhr (1979), who assumed that the hydrodynamics are more important). Heuers et al. (1998) also found that the density of *L. conchilega* was related to hydrodynamics: patches of low density occurred in areas with low current velocities (10 cm/s), while patches of high densities were found in areas with high current velocities (20 cm/s). It was, however, not clear which aspect of the hydrodynamics was really relevant. From the distribution map of *L. conchilega* (Figure 1), it can be deducted that the highest densities and percentages of occurrence were observed in the coastal areas of the North Sea (German Bight, French Belgian and Dutch coast) and in the central part of the North Sea (Dogger Bank). Those areas were already characterized as the zones with the highest primary production in the North Sea (McGlade, 2002, Peters et al., 2005). Besides physical factors (sediment type, flow regime), which mainly determine the distribution of a benthic species, the availability of food might also have a positive influence on the abundance of *L. conchilega*. However, for modeling the habitat preferences of *L. conchilega* based on several types of environmental variables (granulometrics, hydrodynamics, pigments, nutrients), only granulometric variables were selected in the final model (Willems et al., submitted).

Effect of *Lanice conchilega* on benthic characteristics

The results of the present study clearly show that *L. conchilega* has the potential to positively affect the benthos, as reflected in the significant and positive correlation between the benthic density and the density of *L. conchilega*. Furthermore, the species richness increased with increasing density of *L. conchilega*. This trend was however not consistent: the number of species no longer increased or even decreased after reaching a certain density of *L. conchilega* (> 500 ind/m²). The trend observed concerning the expected number of species indicates an enrichment of species in *L. conchilega* patches. The N_1 - diversity index, which takes into account species abundances and richness, showed similar or slightly higher values in *L. conchilega* patches compared to patches without *L. conchilega*. This diversity pattern implies that mainly species with low abundance contribute to the higher species richness in samples containing *L. conchilega*. Due to the higher density of a lot of species in *L. conchilega* patches, the chance to catch a certain species increases in those patches compared to the surroundings, which partly explains the increase of species richness in *L. conchilega* patches. The observed increases in species richness and abundances recorded in *L. conchilega* patches have also been discerned around the tubes of other polychaetes (Woodin, 1978; Luckenbach, 1986), in *L. conchilega* patches in intertidal areas (Zühlke et al., 1998; Zühlke, 2001) and even around artificial tubes (Zühlke et al., 1998; Dittmann, 1999).

The observed trends in density, species richness and diversity were most pronounced in shallow fine sands and were less pronounced in deep fine sands. The strong effect of *L. conchilega* in shallow fine sands indicates that the habitat structuring capacity of *L. conchilega* has an optimal effect in shallow fine sands. In deep fine sands, which were already characterized by a high benthic diversity and low densities of *L. conchilega*, the effect on benthic species was minimal. It is not kown if the effect on the benthos increases whit even higher densities of *L. conchilega*. It can be hypothesized that the habitat structuring effect of *L. conchilega* in deeper environments has a less optimal result, due to the lower environmental variability in such habitats; less species can profit from the improved conditions around *L. conchilega* tube aggregates. *Lanice conchilega* had an effect on the density of some benthic species in shallow muddy sands, but no real increases of the species richness and diversity were observed. On the contrary, very high densities of *L. conchilega* (> 1000 ind/m²) had a decreasing effect. In shallow medium sands, the effects of *L. conchilega* on benthic density and diversity were not strongly pronounced, but were present, due to the lower maximal densities of *L. conchilega*.

The patterns in density and species richness observed in the present study were in agreement with the results on the species composition. In the habitat where the effect of *L. conchilega* was most pronounced (shallow fine sands), most associated species were found, which belonged to different higher taxa. These associated species mostly belonged to the overall species–pool of a certain habitat, rather than being commensals of *L. conchilega*. It was thus demonstrated that *L. conchilega* has an effect on the benthos present in a particular habitat, rather than forming its own community (see also Zühlke et al, 1998, Dittmann, 1999). It seems that the effect of *L. conchilega* tubes on the benthic fauna is highly dependent on the native species present in the surrounding sands at any moment and on their susceptibility to tube effects. Therefore, it is logical that the species richness and diversity levelled off in some habitats: no new species for that habitat were attracted but *L. conchilega* rather affected the habitat quality, which led to increases of the densities of otherwise seldom species in that habitat.

It can be argued that underlying factors (e.g. food availability) determine the densities of *L. conchilega* and therefore also the densities of other benthic species. However, the results of the present study clearly show that *L. conchilega* has the potential to affect the surrounding benthic species. The effects of *L. conchilega* on the surrounding benthos result from alterations of some habitat characteristics (cf. other studies on effects of biogenic habitat structures). Changes in following environmental and biological characteristics were induced by the presence of *L. conchilega*: (1) hydrodynamics, (2) sediment modifications and (3) species interactions.

Effect of Lanice conchilega on hydrodynamics

High densities of *L. conchilega* can influence the hydrodynamics, as has been shown in flume experiments, in which dense assemblages of tubes significantly reduced the current velocity of the near-bottom flow and in which normal, laminar near-bottom flow was deflected around and across the assemblages (turbulence effect) (Heuers et al., 1998). The effect of *L. conchilega* on the benthic density and diversity in intertidal areas is partially attributed to those reductions of the current velocities around the tubes (Zühlke et al, 1998). It can be expected that *L. conchilega* tube aggregations also have an effect on the near-bottom flow in shallow coastal areas. These hydrodyamical changes could have an effect on the sedimentation of particles, detrital food and on the settling of larvae and benthic species.

It is known that *L. conchilega* tubes can provide a settlement surface for larval and post-larval benthic organisms (Qian, 1999). First, the increased settling rate could be caused by the reduction of the current speed and the turbulence around the tubes. These factors are responsible for the higher preference of settling of the *L. conchilega* aulophore larvae nearby adult tubes (Heuers et al., 1998, Callaway, 2003). Similarly, larvae of other benthic species can profit of the changes in hydrodynamics to settle within *L. conchilega* patches. Second, larvae can directly attach to *L. conchilega* tubes, which act as a hard substrate. Zühlke et al. (2001), for example, observed that individual *Mytilus edulis* attached to the *L. conchilega* tubes, but the tubes did not provide secure anchorage for *M. edulis* clumps.

Reduced currents do not only have an effect on larvae, but they also influence the sedimentation of particles and detritus. Sedimentation leading to elevation of the sediment surface occurs in high density patches of *L. conchilega* in intertidal as well as in subtidal areas (Heuers et al., 1998; Seys & Musschoot, 2001, Degraer et al., 2002). On the other hand, the accretion of fine and organic detritus between the tubes promotes the formation of a stable and productive sediment, suitable for both suspension and deposit feeders (Eagle, 1975). *Lanice conchilega* itself is a deposit feeder when occurring in low densities and switches to suspension feeding when present in high densities (cf. increased competition) (Buhr and Winter, 1976). In shallow muddy and fine sands, an increase of surface deposit feeders or facultative suspension feeders in *L. conchilega* patches was observed, probably profiting from the higher deposition rate of detrital organic matter between the tubes. On the other hand, suspension feeders were not found in increased percentage in *L. conchilega* patches, which could be caused by the competition with *L. conchilega*.

Effect of Lanice conchilega on sediment modifications

Other habitat changes resulting from the presence of tube aggregations include increased or decreased sediment stability (Eckman et al., 1981; Luckenbach, 1986). The effect of a tube dweller on the physical modifications of sediments depends on its density, spacing and on the length of the tubes (Rhoads & Boyer, 1982). The dense aggregations of *L. conchilega* cause sedimentation, leading to elevations of the sediment surface and to an increase of the bottom roughness. These processes indicate that dense aggregations cause a "skimming flow" (protecting the bed within the tube field from higher-energy turbulence, Morris, 1955) with reduced shear stress near the bottom (Heuers et al., 1998). High densities of *L. conchilega* probably create stability in the soft-bottom sediments, due to the reduced shear stress near the bottom. This stability could be a very important factor for the benthos to increase their survival in shallow coastal areas, which are characterized by a high environmental variability and a lot of disturbance. At low densities, animal tubes can create destabilization of sediments by scouring around single tubes (Luckenbach, 1986). This was recently observed nearby single tubes of *L. conchilega*, but they still act as bio-engineers, affecting their environment in a positive way (Callaway, 2006). The sediment stabilizing effect of tubes is also strongly influenced by the activity of other organisms, which can have a destabilizing effect (high bioturbation by depositfeeders) or can increase the stability (fecal pellets, sediment-binding exudates from surface-living bacteria and diatoms) (Rhoads & Boyer, 1982). It can be concluded that the presence and activities of both tube building species and surrounding benthic fauna play a role in the sediment stability, but that the effects are expected to be positive in the case of high density *L. conchilega* patches.

Tube building species are also known to control the pumping of water into and out of the bottom. Consequently, some species might benefit from an improved oxygen supply in the sediment surrounding *L. conchilega* tubes. Forster & Graf (1995) suggested that *L. conchilega* acts as a piston when moving in its tube, exchanging burrow water with the overlying water and providing oxygen to the adjacent sediment along the whole length of the tube.

In this way (by increasing the habitat stability and oxygen supply), *L. conchilega* alters the habitat characteristics and affects other organisms. Therefore, the species can be considered as an ecosystem engineer (Jones et al., 1994).

Effect of Lanice conchilega on species interactions

The interactions between benthic species and *L. conchilega* itself or its tubes can be important factors in explaining the effect of *L. conchilega* on the surrounding benthos. Some species were exclusively associated with *L. conchilega* tubes (e.g. *Harmothoe species*, *Eumida sanguinea, Eteone longa, Malmgreniella lunulata, Gammarus species* and *Microprotopus maculates*) in intertidal areas, while some were found in significantly higher abundances in *L. conchilega* aggregations (e.g. *Mya arenaria*, *Mytilus edulis* and *Phyllodoce mucosa*) (Zühlke et al., 1998, Zühlke, 2001). A lot of these exclusively associated species in intertidal areas were also found associated with *L. conchilega* in subtidal habitats, however not exclusively. No species is known to be commensal with *L. conchilega*, but numerous species do interact with *L. conchilega* and are therefore preferentially found in association with *L. conchilega*. A lot of species were observed in or attached to the tubes of *L. conchilega*: *Phyllodoce* spp., *Eumida sanguinea* and species of the family of the Polynoidae (like *Malmgreniella* and *Harmothoe* species) were generally found inside the tubes or among the ragged fringes (pers. obs.). Similarly, a lot of amphipods were found associated with *L. conchilega*, suggesting that feeding conditions might be facilitated among *L. conchilega* tubes for species that are at least partly epibenthic. Furthermore, a lot of surface deposit feeders can profit from the increased food supply, as mentioned higher. Other species, like epibenthic and infaunal predators, can profit from the abundant prey in *L. conchilega* patches. Epibenthic predatory species are recorded in association with *L. conchilega* (e.g. some Decapoda), and a lot of infaunal predatory species, like *Eteone longa* and *E. sanguinea* were found in higher numbers and frequencies in *L. conchilega* patches. These polychaetes probably prey on macrofauna but might also benefit from an enriched meiofauna, which can develop around tubes (Zühlke et al, 1998). Due to the presence of a lot of predatory species, tube aggregates are by no means perfect refuges from predation.

***Lanice conchilega* as 'biogenic reef'-builder?**

'Biogenic reefs' were defined as biological concretions that rise from the sea bed and were created by the animals themselves (Holt et al., 1998). In both intertidal and subtidal areas, *L. conchilega* accretions, which rise from the sea bed (10 – 40 cm), were found (pers. obs.). These reefs were formed by sediment trapping in dense aggregations of *L. conchilega* tubes, which is a different mechanism than in *Sabellaria alveolata* reefs (real concretions of animal tubes) (Holt et al., 1998). *Lanice conchilega* aggregations were characterized by a constant renewal of the population due to the high turn-over of *L. conchilega* (Van Hoey et al., in prep.). This is different from the real biogenic reef builders where the reef increases with settling juveniles on the older static structures. However, the biogenic structures of *L. conchilega* do affect the environment by increasing the habitat heterogeneity, which in turn affects the density and species richness of the surrounding benthos, even at low densities (few individuals per m²) of *L. conchilega*. Although, in many cases, it is probably more realistic to refer to these aggregations as *L. conchilega* beds rather than reefs, their characteristics and effects are, in some cases (rise from the sea bed at high densities), likely to be very similar to those of really protruding 'biogenic reefs'. Consequently, *L. conchilega* beds can be considered as important habitat structuring features in the soft – bottom sediments of the North Sea.

Conclusion

It can be concluded that *Lanice conchilega* has an effect on the benthic density and diversity in soft-bottom sediments. This effect is most pronounced in shallow fine sand, which is its preferred habitat. The changes in benthic characteristics result from the alterations of the habitat by *L. conchilega* (hydrodynamics, sediment stability, improved oxygen) and the complex interactions between the benthic organisms and the biogenic structures consisting of *L. conchilega* tubes. A lot of benthic species can profit from the creation, modification and maintenance of that habitat by *L. conchilega*, which results in an increased density and species richness in *L. conchilega* patches compared to the surrounding soft-bottom sediments. It was further demonstrated that *L. conchilega* only has an effect on the benthos present in a particular habitat, rather than forming its own association. Consequently, *L. conchilega* beds can be considered as important habitat structuring features in the soft – bottom sediments of the North Sea.

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