

## ADDENDUM I

### Ecological implications of the presence of the tube building polychaete *Lanice conchilega* on soft-bottom benthic ecosystems



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ADDENDUM I

## Abstract

The common tube building polychaete *Lanice conchilega* is known as a habitat structuring species and can form dense aggregations. The effects of *L. conchilega* on the surrounding benthic community have received little attention, especially in subtidal areas. Therefore, the presence of *L. conchilega* in different habitats in the North Sea and its effect on the abundance, species richness, diversity and community structure in these habitats are evaluated in the present paper, based on data from the ICES North Sea Benthos Survey of 2000.

*Lanice conchilega* has a wide geographical distribution and a low habitat specialization, but optimally occurs in shallow fine sands. In the present study, the presence of *L. conchilega* resulted in a density increase and a significant (positive) correlation of the benthos density with the density of *L. conchilega*. Furthermore, the species richness (number of species) increased with increasing density of *L. conchilega*. This trend was, however, not consistent: the number of species reached more or less an asymptotic value or even decreased after reaching a critical density of *L. conchilega* ( $> 500 - 1000 \text{ ind/m}^2$ ), as observed in shallow fine sands. 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*. From the results of the community analysis, it can be concluded that the species, which were responsible for the increase of the diversity, belonged to the overall species-pool of that habitat. The effects on density and diversity differed between the four discerned habitats (shallow muddy sand, shallow fine sand, shallow medium sand and deep fine sand), and were most pronounced in shallow fine sands. These patterns can be attributed to the habitat structuring capacity of *L. conchilega*. The mechanisms responsible for the increase of the habitat quality in patches of *L. conchilega* can be summarized as (1) changes in the hydrodynamics, (2) increases of the habitat stability and oxygen supply, and (3) a creation of habitat heterogeneity in a uniform environment. In this way, *L. conchilega* alters the habitat characteristics and affects other organisms, and can therefore even be considered as an ecosystem engineer. In other words, *L. conchilega* patches are responsible for an increased habitat quality in an otherwise uniform habitat, which results in a higher survival of the surrounding benthic species.

## Key words

*Lanice conchilega*, geographical distribution, species diversity, benthos, habitat improvement, 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 (Carey, 1987, Eckman *et al.*, 1981) and hydrodynamic parameters (Eckman, 1983), or by changing interactions between species (Woodin, 1978). Some tube-building polychaetes provide considerable structures in the otherwise relatively unstructured soft-bottom sediments (Bolam and Fernandes, 2002, Callaway, 2003b, Rees *et al.*, 2005, Woodin, 1978, Zühlke, 2001, Zühlke *et al.*, 1998). An example of a structuring tube-building polychaete is the sand mason, *Lanice conchilega*, which lives in a tube of sand or shell breccias 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 square meter (Buhr and Winter, 1977, Ropert and Dauvin, 2000, Van Hoey *et al.*, 2006), 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 the presence of *L. conchilega* on the surrounding benthic community have received little attention. The interaction between *L. conchilega* and the benthos was previously described by Zühlke *et al.* (1998), Dittmann (1999) and Zühlke (2001) on two sandflats of the East Frisian Wadden Sea (the Gröninger Plate and the Dornumer Nacken). These studies also described 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 tubes of *L. conchilega* and that the presence of such structures enriched the *Arenicola*-dominated sandflat association in abundance and species numbers. This indicates that *L. conchilega* is a habitat structuring species, which affects the surrounding benthic community. In the study of Callaway (2006), on an exposed beach in South Wales, it was concluded that not only groups of tubes, but also single polychaete tubes affect the environment. This ability can be

attributed to the following mechanisms (Callaway, 2006): (1) the tubes provide a settlement surface for larval and post-larval 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 and 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).

Nevertheless, these conclusions were not confirmed for other habitats, especially in subtidal areas, where *L. conchilega* is widespread. A large-scale benthos survey, performed in the subtidal of the North Sea in 2000-2001 under the guidance of the Benthos Ecology Working group of ICES (Rees *et al.*, 2002, Rees *et al.*, 2007), provided an opportunity to focus on subtidal areas. The resulting dataset formed the basis of the description of the ecological implication of the presence of *L. conchilega* on some soft-bottom benthic ecosystems in the North Sea. In other words, the present study aimed to investigate the effects of the presence of *L. conchilega* on the abundance, species richness, diversity and community structure in different soft-bottom habitats in the North Sea, in view of the ecosystem engineering function of *L. conchilega*.

## Material 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 were not included in the present study (Figure 1).

### ***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 years 2000 or 2001. These data originate from various projects, including national monitoring surveys (Rees *et al.*, 2002, Rees *et al.*, 2007). The total dataset was used to describe the spatial distribution of *L. conchilega* in the North Sea. To enable detailed analyses on the effect of *L. conchilega* on the benthos, a uniform dataset was selected with only samples taken with a 0.1 m<sup>2</sup> Van Veen or Day grab and sieved alive on a 1 mm sieve. 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, Rees *et al.*, 2007). These data modifications were executed during several workshops of the ICES study group on the North Sea Benthos Project 2000. 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 and should thus be considered as minimum counts (Van Hoey *et al.*, 2006).

The sedimentological characteristics of the different samples were coded according to the following 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 sediment classes and bathymetrical information (shallow (< 70 meter) and deep (> 70 meter)) (following the benthic community analyses of Kunitzer *et al.* (1992) and Rees *et al.*, (2007)).

### ***Data analysis***

The effects of *L. conchilega* on the benthos were investigated for every habitat type in which the species was found and for which a representative number of samples (> 100) was available (Figure 2). This number of samples was chosen to exclude uncertainties in the results. The following univariate indices were used to describe the benthos (excluding *L. conchilega*) in each sample: (1) density N, (2) species richness S, expressed as number of species per sample (*i.e.* per 0.1 m<sup>2</sup>), (3) the exponential form of the Shannon – Wiener index

$N_1$  (Hill, 1973) and (4) expected number of species (ES 50) (Hurlbert, 1971). The relations between those univariate indices and the density of *L. conchilega* in the different habitats were visualized based on different density classes of *L. conchilega* (defined in such way that they give the best reflection of the observed patterns). A Mann-Whitney U test was used to test for differences in the univariate indices between samples with and without *L. conchilega* and a Spearman rank correlation analysis was done to describe the correlation between the univariate indices and the density of *L. conchilega*. Non-parametric tests were used because the assumptions for parametric tests, even after transformation, were not fulfilled (Conover, 1971).

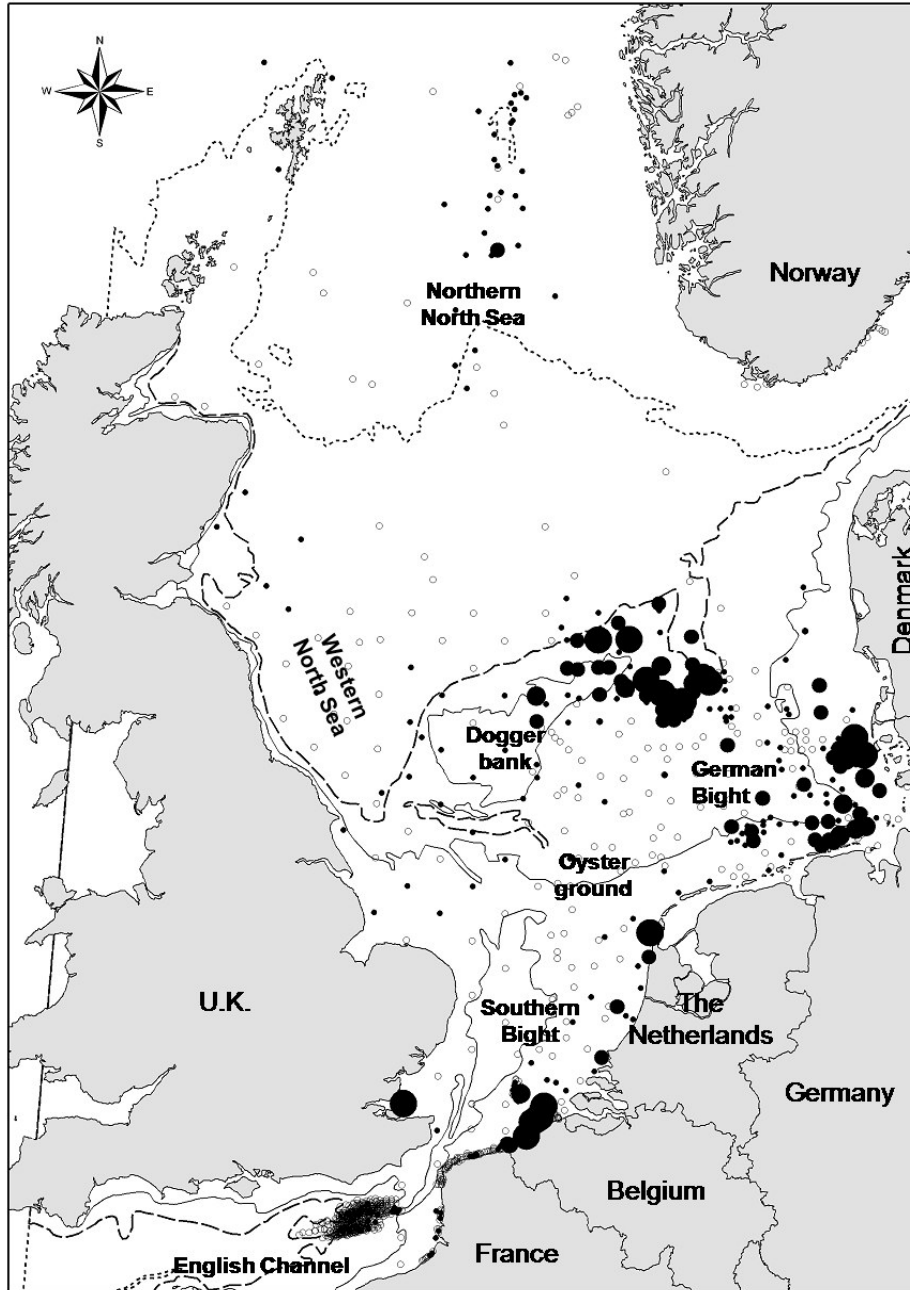
The benthic community structure within the different habitats was analyzed with non-parametric multidimensional scaling (MDS) on the fourth-root transformed dataset, in which the samples containing *L. conchilega* (group 1) and the samples without *L. conchilega* (group 2) were labelled *a priori*. Analysis of similarity (one-way ANOSIM) was used to test for differences between the two groups and SIMPER was used to investigate which species contributed most to the dissimilarity between the groups. These calculations were done with the Primer 5.2.9 software package (Clarke and Warwick, 2001).

## Results

### *Distribution pattern*

In 2000 - 2001, *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 seldom 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 (east of the 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/m<sup>2</sup>), whereas in the western North Sea, *L. conchilega* was seldom found and only in very low densities (< 100 ind/m<sup>2</sup>).

ADDENDUM I



**Figure 1.** Density distribution of *Lanice conchilegia* in the entire North Sea and English Channel. 0 ind/m<sup>2</sup>: (○); 1-100 ind/m<sup>2</sup> (◐); 100-500 ind/m<sup>2</sup> (◑); 500-1000 ind/m<sup>2</sup> (◒); > 1000 ind/m<sup>2</sup> (◓)



### Habitat preferences

*Lanice conchilega* was found in most soft-bottom sediment types in the North Sea, with differences in frequency of occurrence and average densities between the discerned habitat types (Figure 2). No definitive conclusion 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 average densities (138 – 419 ind/m<sup>2</sup>) of *L. conchilega* in shallow areas were observed in mixed sediments, muddy and fine sand. In shallow medium and coarse sediments, the frequencies of occurrence (24 and 30%, respectively) and average densities (17 and 12 ind/m<sup>2</sup>, 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/m<sup>2</sup>, 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).

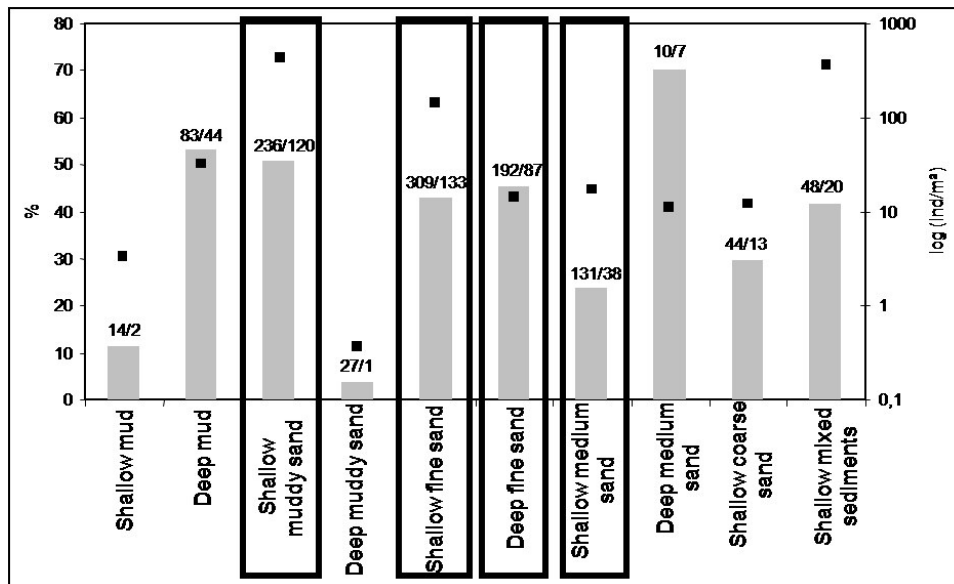


Figure 2. Percentage of occurrence (bars, left axis) and average density (log ind/m<sup>2</sup>) (squares, right axis) of *Lanice conchilega* in the different habitat types (with indication of the total number of samples) versus samples with *L. conchilega*. The four habitats, which were represented 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 difference was found ( $p = 0.1299$ ). The ES(50) was only significantly different in shallow fine sands and medium sands ( $p < 0.0001$ ).

*Table 1. First, the differences tested in benthic density, species richness,  $N_1$ -diversity and ES (50) by Mann-Whitney U test, between samples with and without Lanice 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	Spearman rank	
	U- test	correlation	
	$p$	R	$p$
Density			
shallow muddy sand	< 0.0001	0.45	< 0.0001
shallow fine sand	< 0.0001	0.63	< 0.0001
deep fine sand	0.011500	0.23	0.0013
shallow medium sand	< 0.0001	0.39	< 0.0001
Species richness			
shallow muddy sand	< 0.0001	0.4	< 0.0001
shallow fine sand	< 0.0001	0.65	< 0.0001
deep fine sand	0.002700	0.27	0.0001
shallow medium sand	< 0.0001	0.5	< 0.0001
$N_1$			
shallow muddy sand	0.129900	0.08	0.22
shallow fine sand	< 0.0001	0.39	< 0.0001
deep fine sand	0.022500	0.158	0.028
shallow medium sand	0.001200	0.36	< 0.0001
ES (50)			
shallow muddy sand	0.070000	0.08	0.22
shallow fine sand	< 0.0001	0.39	< 0.0001
deep fine sand	0.160000	0.17	0.17
shallow medium sand	< 0.0001	0.34	< 0.0001

***Correlation between benthic univariate indices and density of *Lanice conchilega****

In the four habitats, the density 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 the density of the benthic fauna and the density of *L. conchilega* was positive and significant in all habitats, but was strongest in shallow fine sands (Spearman R: 0.63) and was lowest in deep fine sands (Spearman R: 0.23) (Table 1).

Although species richness differed strongly between habitats, a significant positive 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*. In shallow muddy sands, the species richness decreased when the density of *L. conchilega* exceeded 1000 ind/m<sup>2</sup>, while in shallow fine sands, the species richness levelled off at 500 ind/m<sup>2</sup> of *L. conchilega* (Figure 3b).

The N<sub>1</sub>-diversity index and its relation with *L. conchilega* density differed between the habitats (Figure 4a). In shallow muddy sands, the N<sub>1</sub>-diversity index did not increase with the *L. conchilega* density and did not show a significant correlation (Spearman R: 0.08; p = 0.22) (Table 1), whereas a minor, through significant to very high 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 – 0.34, respectively) was found, but the curve levelled off at 100 ind/m<sup>2</sup> in medium sands and decreased in fine sands when the density of *L. conchilega* exceeded 1000 ind/m<sup>2</sup>.

ADDENDUM I

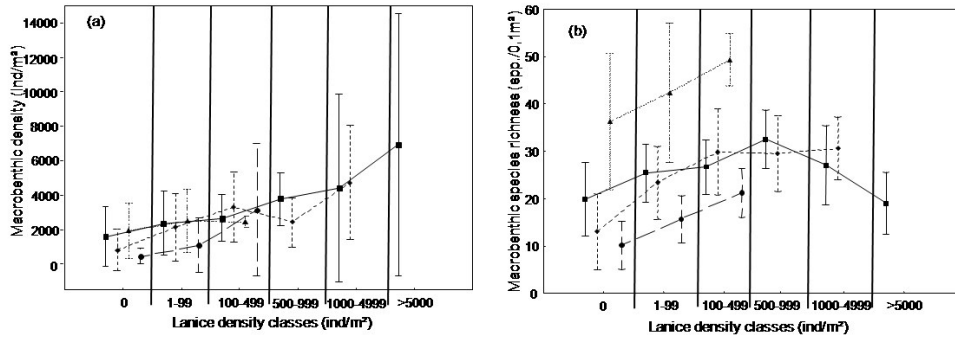


Figure 3. (a) The density (with exclusion of *Lanice conchilega*) of the benthic species, versus the different *L. conchilega* density classes with indication of the standard deviation, and (b) the species richness (with exclusion of *L. conchilega*) of the benthic species, versus the different *L. conchilega*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

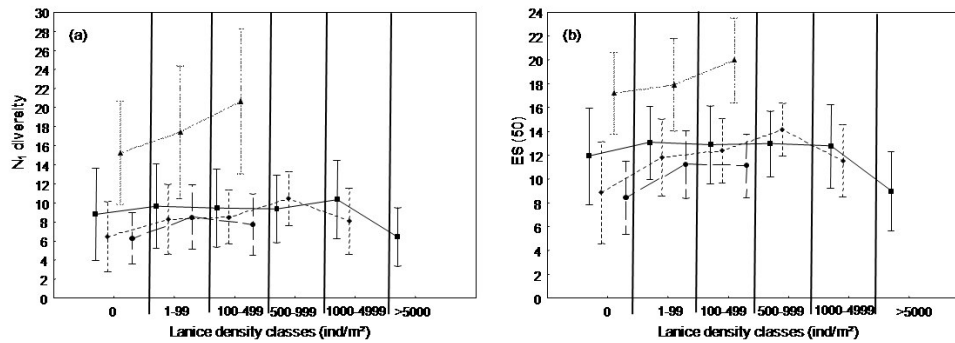


Figure 4. (a) The N<sub>1</sub>-diversity (with exclusion of *Lanice conchilega*) of the benthic species, versus the different *L. conchilega* density classes with indication of the standard deviation, and (b) the ES(50) (with exclusion of *L. conchilega*) of the benthic species, versus the different *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.

**Effect of *Lanice conchilega* on the community structure**

When the community structure in the different habitats was visualized by MDS, it was clear that the samples containing *L. conchilega* individuals (group 1) were not clearly separated from the samples without *L. conchilega* (group 2), due to their central position in the MDS (Figure 5). The one-way ANOSIM analysis revealed that, for the four habitats, the two groups could be significantly distinguished ( $p < 0.05$ ). The R value was low, indicating a high

overlap between the groups in all habitats ( $R = 0.125$  for shallow fine sands [ $p = 0.001$ ],  $R = 0.098$  for shallow medium sands [ $p = 0.039$ ],  $R = 0.097$  for shallow muddy sands [ $p = 0.001$ ] and  $R = 0.018$  for deep fine sands [ $p = 0.048$ ]). Based on the SIMPER results (Table 2), it became clear that the two groups were dominated by the same species, but with differences in their densities between the two groups. For most species their density was higher in the samples containing *L. conchilega* individuals. The average density of the species was 3 to 10 times higher in the samples with *L. conchilega* compared to the samples without *L. conchilega*, except in deep fine sand where the density differences were much lower (1.4 times) (Table 2).

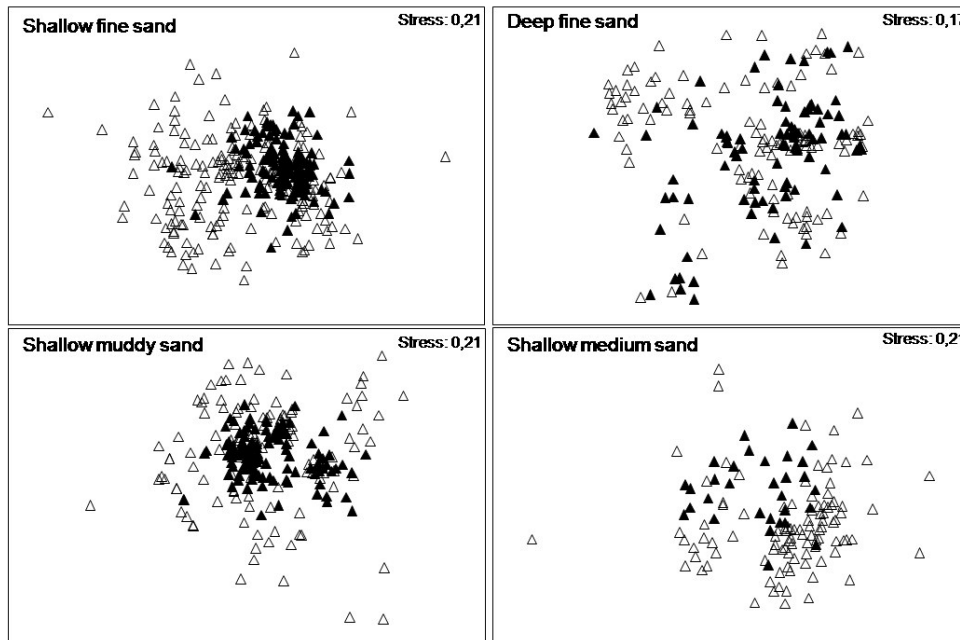


Figure 5. Two-dimensional MDS (Multi dimensional scaling) plot of similarities for the four habitats between samples with *Lanice conchilega* individuals (black triangles) and samples without *L. conchilega* individuals (open triangles), with exclusion of the *L. conchilega* individuals.

ADDENDUM I

Table 2. SIMPER analysis: The first 25 species of the SIMPER species list, which contribute to the dissimilarity between group 1 (samples with *Lanice conchilega*) and group 2 (samples without *L. conchilega*) for each habitat with indication of their average abundance (ind/m<sup>2</sup>) per group.

Species	Shallow fine sand		Deep fine sand		Shallow muddy sand		Shallow medium sand		
	Group 1 Av.Abund	Group 2 Av.Abund	Group 1 Av.Abund	Group 2 Av.Abund	Group 1 Av.Abund	Group 2 Av.Abund	Group 1 Av.Abund	Group 2 Av.Abund	
<i>Spiophanes</i>	601.01	66.15	497.47	452.76	<i>Amphicteis gunneri</i>	484.5	222.07	<i>Spiophanes</i>	651.06
<i>Magelona</i>	246.42	117.13	335.06	231.43	<i>Spiophanes</i>	388.08	102.4	<i>Gastrosaccus spinifer</i>	49.35
<i>Bathyporeia</i>	150.47	68.4	279.66	220.38	<i>Mysella</i>	331.86	127.61	<i>Aonides paucibranchiata</i>	76.71
<i>Tellina</i>	145.6	29.2	252.3	172.95	<i>Nucula nitidosa</i>	125.08	234.05	<i>Bathyporeia</i>	45.1
<i>Ensis directus</i>	263.18	23.73	138.05	102.19	<i>Abra alba</i>	130.5	102.69	<i>Nephtys cirrosa</i>	35.58
<i>Phoronida</i>	115.49	124.32	100	44.95	<i>Corbula gibba</i>	75.5	92.59	<i>Scoloplos</i>	33.61
<i>Echiurida</i>	34.14	47.9	42.07	28.57	<i>Phoronida</i>	136.17	32.84	<i>Spio</i>	30.48
<i>Urothoe poseidonis</i>	72.29	19.02	32.87	23.9	<i>Pectinidae</i>	109.12	29.01	<i>Urothoe brevicornis</i>	14.13
<i>Mysella</i>	105.03	11.44	33.1	24.1	<i>Magelona</i>	49.37	48.13	<i>Tellina</i>	9.26
<i>Amphicteis gunneri</i>	71.2	26.93	29.89	12	<i>Myriochele</i>	54.25	48.79	<i>Ophelia rathkei</i>	17.77
<i>Scoloplos</i>	33.32	14.07	32.3	23.9	<i>Pholoe baltica</i>	78.88	11.47	<i>Goniadella</i>	14.84
<i>Pectinidae</i>	45.2	12.05	22.64	14.38	<i>Tellina</i>	62.98	25.13	<i>Hydroides norvegicus</i>	20.32
<i>Acrocnida brachiata</i>	64.96	3.58	38.62	13.24	<i>Scoloplos</i>	82.81	11.07	<i>Echiurida</i>	15.71
<i>Nephtys cirrosa</i>	15.61	18.07	29.77	20.86	<i>Chaetozone</i>	22.27	37.6	<i>Thracia</i>	15.48
<i>Corbula gibba</i>	72.33	7.84	28.05	17.71	<i>Montacuta</i>	45.64	10.05	<i>Magelona</i>	18.55
<i>Nemeritina</i>	36.32	4.33	33.91	27.05	<i>Phaxas pellucidus</i>	95.58	10.69	<i>Spisula</i>	11.77
<i>Abra alba</i>	45.79	15.01	5.98	14.19	<i>Nephtys hombergii</i>	42.83	32.71	<i>Abra alba</i>	13.84
<i>Nephtys hombergii</i>	20.61	12.77	21.49	19.81	<i>Owenia fusiformis</i>	31.63	14.18	<i>Urothoe poseidonis</i>	11.23
<i>Hexacorallia</i>	31.2	5.99	19.2	18.86	<i>Harpinia antennaria</i>	27.58	8.71	<i>Stenothoe marina</i>	21.06
<i>Polinices</i>	19.49	3.02	12.76	18	<i>Scalibregma</i>	12.25	21.72	<i>Notomastus</i>	15.06
<i>Chaetozone</i>	24.9	7.24	16.09	17.14	<i>Hexacorallia</i>	16.94	17.94	<i>Glycera lapidum</i>	8.9
<i>Montacuta</i>	18.65	5.86	15.63	15.52	<i>Bathyporeia</i>	19.58	8.18	<i>Pisone remota</i>	4.81
<i>Ophelia rathkei</i>	8.14	7.24	7.36	14.67	<i>Notomastus</i>	18.65	20.27	<i>Hexacorallia</i>	9.65
<i>Goniada</i>	17.97	5.28	15.98	11.62	<i>Eudorella emarginata</i>	20	4.48	<i>Poecilochaetus serpens</i>	10.71
<i>Spio</i>	13.63	6.9	4.48	8.48	<i>Chamelea gallina</i>	21.17	3.88	<i>Branchiostoma lanceolatum</i>	6.06
Density of species at average 5 times			Density of species at average 1.4 times		Density of species at average 3 times			Density of species at average 10 times	
higher in group 1 compared to group 2			higher in group 1 compared to group 2		higher in group 1 compared to group 2			higher in group 1 compared to group 2	

## Discussion

### *Distribution and habitat preferences*

*Lanice conchilega* has a cosmopolitan distribution, as it is found from the Arctic to the Mediterranean, in the Arabian Gulf and the Pacific, 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 (Degraer *et al.*, 2006, 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 those sediments (more than 1000 individuals per m<sup>2</sup> compared to maximal 575 ind/m<sup>2</sup> in shallow medium sands). In the deeper habitats, *L. conchilega* was frequently encountered but only in low abundance (max. 170 ind/m<sup>2</sup> in deep fine sand).

The distribution of *L. conchilega* is mainly determined by the sedimentology as was shown in Willems *et al.* (2008). This study tried to model the habitat preferences of *L. conchilega* based on several types of environmental variables (granulometrics, hydrodynamics, pigments and nutrients), and only granulometric variables were selected in the final model. However, the hydrodynamics were assumed to be more important following the study of Buhr (1976) and Heuers *et al.* (1998), but sedimentology and hydrodynamics were more or less related. From the distribution map of *L. conchilega* (Figure 1), it can be deduced 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 (east of the Dogger Bank). Those areas were characterized as zones with very high primary production in the North Sea (McGlade, 2002, Peters *et al.*, 2005). Next to physical factors (sediment type, flow regime), which mainly determine the distribution of benthic species, the availability of food might also have a positive influence on the abundance and occurrence of *L. conchilega*. Additionally, the occurrence of *L. conchilega* also depends on the recruitment success, which is highly variable (Van Hoey, 2006), but seemed to be successful in 2000 - 2001.

Hence, it can be concluded that *L. conchilega* has a wide geographical distribution and a low habitat specialization (*i.e.* eurytopic species), but optimally occurs in shallow fine sands and shallow muddy sands in the subtidal.

### ***Ecological implications of the presence of Lanice conchilega***

The results of the present study clearly show that *L. conchilega* has the potential to positively affect the surrounding benthos, which is 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 critical density of *L. conchilega* (> 500 - 1000 ind/m<sup>2</sup>), as observed in shallow fine sands. A similar, but weaker trend was observed concerning the expected number of species and indicated an enrichment of species in *L. conchilega* patches. The N<sub>1</sub>-diversity index, which takes into account species dominance and richness, showed similar or slightly higher values in *L. conchilega* patches compared to patches without *L. conchilega*. These diversity patterns imply that mainly species with low abundance contribute to the higher species richness in samples containing *L. conchilega*. In other words, the chance to encounter a certain species increases in *L. conchilega* patches, due to the higher density of a lot of benthic species in those patches (see SIMPER results, Table 2), compared to the surroundings. The observed increases in species richness and abundances recorded in *L. conchilega* patches have also been discerned around the tubes of other polychaetes (Luckenbach, 1986, Woodin, 1978), in *L. conchilega* patches in intertidal areas (Callaway, 2003a, 2003b, 2006, Zühlke, 2001, Zühlke *et al.*, 1998) and even around artificial tubes (Dittmann, 1999, Zühlke *et al.*, 1998).

The MDS results visualized that in every investigated habitat the two groups (samples with (group 1) and without (group 2) *L. conchilega*) consisted mostly of species from the same species pool. This was confirmed by the ANOSIM and SIMPER results, where a significant difference between the two groups was found, but with a very low R value and a similar species dominance in the two groups. This indicates that there was a high overlap in species composition between the two groups, but the density of the species differed. These results confirmed the hypothesis that the species, which are affected by *L. conchilega* belong to the overall species pool of that habitat. This aspect is described more elaborately in Rabaut *et al.*



(2007). It was thus demonstrated that *L. conchilega* is affecting the benthos present in a particular habitat in the subtidal, rather than forming its own community (see also Zühlke *et al.* (1998) and Dittmann (1999)). In this way, 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. This could be a reason why species richness and diversity levelled off in some habitats: almost no new species for that habitat were attracted. *Lanice conchilega* was considered to improve the habitat quality (e.g. habitat heterogeneity, food availability, flow velocity reduction), which led to increases of the densities of otherwise rare species in that habitat. In contrast, the decrease in species richness and diversity from a critical density of *L. conchilega* can be related to the competition for space and food in the *L. conchilega* patches.

It can also 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, the studies of Rabaut *et al.* (2007), Zühlke *et al.* (1998) and Callaway (2003a, 2003b, 2006) clearly show that *L. conchilega* has the potential to affect the surrounding benthic species.

Nevertheless, differences in the effect of the presence of *L. conchilega* on the surrounding benthic species in the trends of density, species richness and diversity were observed between the investigated soft-bottom habitats in the North Sea. The strongest expression of the trend was observed in shallow fine sands, and the weakest in deep fine sands. The positive trend in shallow fine sands, can be attributed to the fact (1) that fine sands were the optimal habitat for *L. conchilega* and (2) that many species can profit from the habitat structuring capacity of *L. conchilega* in that environment. Shallow coastal areas were characterized by strong dynamics and a lot of disturbance and it can be hypothesized that *L. conchilega* patches create a certain stability that increases the survival of other benthic species. In deep fine sands, the effect of *L. conchilega* on benthic species was minimal. This might relate to the naturally higher benthic diversity (Künitzer *et al.*, 1992) and the lower impact of the habitat modifying capacity of *L. conchilega* on the other benthic species in deep soft-bottoms. It has to be mentioned that *L. conchilega* was found in low densities, which make it impossible to predict the effect of dense patches (not yet found in those areas). *Lanice*

## ADDENDUM I

*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/m<sup>2</sup>) had a negative effect. The reasons for this were not clear and further investigation is needed to draw conclusions for this habitat. In contrary, the habitat structuring capacity is more effective in shallow medium sands, where the benthic density and diversity increased even by lower densities of *L. conchilega*. This can be attributed to the fact that the occurrence of *L. conchilega* creates a 3D structure in the otherwise poor sandy environment.

It can be concluded that the presence of *L. conchilega* has ecological implications on the benthos in soft-bottom sediments, expressed in an increase of density and diversity of the benthos in the nearness of *L. conchilega*.

### ***Lanice conchilega as ecosystem engineer?***

The mechanisms responsible for the increase of the habitat quality in patches of *L. conchilega* can be summarized as (1) changes in the hydrodynamics, (2) increases of the habitat stability and oxygen supply, and (3) a creation of habitat heterogeneity in a uniform environment.

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). These hydrodynamic changes have an effect on the sedimentation of particles, detrital food (Degraer *et al.*, 2002, Féral, 1989, Heuers *et al.*, 1998, Seys and Musschoot, 2001) and on the settling of larvae and benthic species (Callaway, 2003a, 2003b, Heuers *et al.*, 1998, Qian, 1999, Zühlke, 2001). The patches of *L. conchilega* caused sedimentation, sometimes 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” (Morris, 1955) with reduced shear stress near the bottom (Heuers *et al.*, 1998) leading to a higher stability in the soft-bottom sediments. Tube building species are also known to control the pumping of water into and out of the bottom, by “piston pumping” in the case of *L. conchilega*, and provide oxygen to the adjacent sediment along the whole length of the tube (Forster and Graf, 1995).

Consequently, some species might benefit from an improved oxygen supply in the sediment surrounding *L. conchilega* tubes (Callaway, 2006). Due to the creation of tubes, extending out of the sediment, the habitat heterogeneity of the environment will increase, which leads to more niches for a wider variety of species. Specific species will not only interact with the tubes, but some species (predators) will be attracted by the higher food availability.

In this way (changing hydrodynamics, increasing the habitat stability and oxygen supply, habitat heterogeneity), *L. conchilega* alters the habitat characteristics and affects other organisms. Therefore, the species can be considered as an ecosystem engineer (Jones *et al.*, 1994). *Lanice conchilega* patches can even be considered as 'biogenic reefs', because *L. conchilega* is sometimes found in patches, which rise from the sea bed (10-40cm), in both intertidal and subtidal areas (Van Hoey, 2006). 'Biogenic reefs' were defined as biological concretions that rise from the sea bed and were created by the animals themselves (Holt *et al.*, 1998). The *L. conchilega* reefs were formed by sediment trapping in dense aggregations of *L. conchilega* tubes, which is a different mechanism than, for example, in *Sabellaria alveolata* reefs (real concretions of animal tubes) (Holt *et al.*, 1998). *Lanice conchilega* aggregations were also characterized by a constant renewal of the population due to the high turn-over of *L. conchilega* (Van Hoey, 2006). 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* affect the density and species richness of the surrounding benthos, even at low densities (few individuals per m<sup>2</sup>) (this study; Callaway (2006)). 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 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. In other words, *L. conchilega* patches were responsible for the increased habitat quality in an otherwise uniform habitat and result in a higher survival of the surrounding benthic species.

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## ADDENDUM I

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