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Long-term effects of imitation polychaete tubes on benthic fauna: they anchor *Mytilus edulis* (L.) banks

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Abstract

Tube-dwelling polychaetes provide habitat structures that potentially affect the composition of the benthic community. This study describes the long-term effects of tubes as a physical structure on the fauna of an intertidal sandflat, based on a field experiment with tubes that mimicked those of the terebellid polychaete *Lanice conchilega*.

Six 1-m^2 plots, each containing 1000 imitation tubes, were set up on an intertidal sandflat off the Eastern Friesian coast (Germany) and sampled annually over 6 years. The imitation tubes had significant effects on the community structure, species diversity and densities of individual species in the plots. In the first year, two opportunistic polychaete species were more abundant in the experimental plots and spat of two bivalves, *Mya arenaria* and *Mytilus edulis*, used the imitation tubes as a settlement surface. *M. edulis* remained attached to the tubes and started to form banks. At the end of the experiment, the size composition of *M. edulis* was similar to that found in natural banks. The mussels had overgrown the imitation tubes and provided a physical habitat structure themselves. Interannual changes in the community among imitation tubes and tubes with attached mussels reflected changes in the fauna of the surrounding sands. The effects of imitation tubes on the benthic fauna were similar to those of natural *L. conchilega* tubes, demonstrating that polychaete tubes themselves can be responsible for structuring the benthic community.
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Keywords: Habitat structure; *Lanice conchilega*; *Mytilus edulis*; Polychaete tubes; Wadden Sea

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1. Introduction

In sandy intertidal areas habitat structures such as seagrass meadows or oyster and mussel banks affect the composition of benthic communities (Reise et al., 1994; DeGrave, 1998; Reusch, 1998; Minchinton and Ross, 1999; Kenyon et al., 1999; Meyer and Townsend, 2000; Hindell et al., 2001). Tube-dwelling polychaetes also provide a three-dimensional structure and have been reported to accommodate a different fauna than tube-free areas (e.g. Woodin, 1978; Gallagher et al., 1983; Hutchings, 1998; Zühlke, 2001). Effects have been shown for a wide size spectrum of tube-dwelling polychaetes ranging from relatively small *Polydora quadrilobata* with a body length up to 2.5 cm (Hartmann-Schröder, 1996; Khaitov et al., 1999) to 5-cm-long *Loimia* sp. and *Axionice* sp. (Trueblood, 1991) and *Diopatra cuprea* with a body length of 30 cm (Woodin, 1978; Ban and Nelson, 1987). Tubes of these species differ in terms of size and shape and the extent to which they protrude the sediment surface (Woodin, 1978; Trueblood, 1991; Hartmann-Schröder, 1996). Tubes were found to influence species diversity and abundance (Luckenbach, 1986; Zühlke, 2001), the dispersal pattern of other polychaetes (Trueblood, 1991) as well as the meiofauna composition (Peachey and Bell, 1997; Netto et al., 1999). Furthermore, Phillips and Lovell (1999) reported elevated levels of microbial biomass and activities in tubes of *D. cuprea*. Whilst most effects on diversity or abundance are positive, tube-dwellers can negatively affect the survival rate of newly recruited bivalves and polychaetes (Luckenbach, 1987; Trueblood, 1991).

Whether the tube-dwelling polychaete or the tube structure itself influences the fauna can only be tested experimentally. Several authors studied the effects of transplanted polychaetes and artificial tubes on the fauna and other environmental properties (e.g. Eckmann et al., 1981; Carey, 1987; Heuers et al., 1998; Friederichs et al., 2000). These
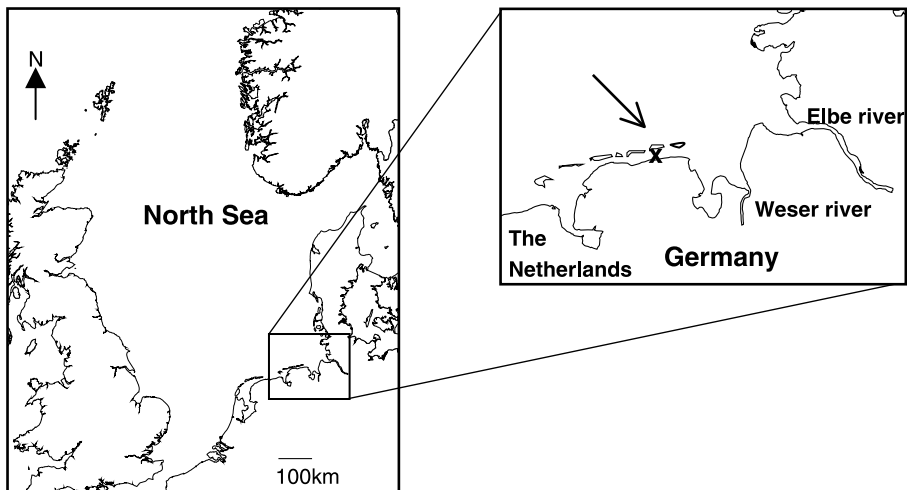

Fig. 1. Location of the study site (✕).

experiments lasted from 1 to 30 days (Eckman, 1983, 1985) to about 8 months (Dauer et al., 1982) and hence investigated short-term effects.

The aim of this study was to investigate long-term effects of tube structures on the benthic fauna. Over a 6-year period, I followed the succession of the benthic community among plots with imitation tubes on a sandflat of the Wadden Sea (Germany). The imitation tubes were supposed to mimic one of the most common tube-dwelling polychaetes in the area, the terebellid *Lanice conchilega*.

Table 1
Macrobenthic species in plots with imitation tubes and in tube-free reference plots of the Gröninger Plate (Friesian coast, Germany), 1995–2000. Full squares (■) indicate the presence of a species and empty squares (□) their absence

	Imitation tubes					Reference				
	95	96	97	98	00	95	96	97	98	00
Bivalvia										
Cerastoderma edule	■	■	□	□	□	■	■	■	□	■
Ensis sp.	□	□	□	□	□	□	■	□	□	□
Macoma balthica	□	■	■	■	□	□	■	■	■	■
Mya arenaria	■	■	□	□	□	■	■	□	□	□
Mytilus edulis	■	■	■	■	■	■	■	■	□	■
Polychaeta										
Phyllodoce mucosa	□	□	■	□	□	□	□	■	■	□
Aphelochaeta marioni	■	■	■	■	■	■	■	■	■	■
Capitella capitata	■	■	■	■	■	■	■	■	■	□
Eteone longa	■	■	■	□	□	□	■	■	■	■
Eumida sanguinea	□	□	□	□	□	□	□	□	□	■
Hediste diversicolor	■	■	■	■	■	□	□	□	□	■
Heteromastus filiformis	□	■	■	■	■	□	■	■	■	■
Magelona mirabilis	□	□	□	□	□	□	■	□	□	□
Neanthes virens	□	■	□	□	□	□	□	□	□	□
Nephtys hombergii	■	□	□	□	□	□	□	□	□	□
Polydora cornuta	■	■	■	■	■	□	■	■	□	□
Pygospio elegans	■	■	■	■	■	■	■	■	□	■
Scoloplos armiger	□	■	■	■	□	■	■	■	■	■
Spio filicornis	■	■	□	□	□	■	■	□	□	□
Spio martinensis	□	□	■	□	□	□	□	□	□	□
Lanice conchilega	□	□	□	■	□	■	□	■	■	■
Oligochaeta										
Tubificoides benedii	□	■	■	□	■	□	□	□	□	□
Tubificoides pseudogaster	□	■	■	□	■	□	□	□	□	□
Crustacea										
Jaera nordmanni	□	□	□	□	■	□	□	□	□	□
Echinogammarus marinus	□	□	□	■	□	□	□	□	□	□
Urothoe poseidonis	□	□	□	□	□	□	□	□	□	■
Carcinus maenas	□	□	■	■	□	□	□	□	□	□

2. Methods

The experiment was carried out on an intertidal sandflat in the German part of the Wadden Sea (Fig. 1). The sandflat, called Gröninger Plate, is located about 2 km off the mainland coast. The tidal range varies from 2.8 to 3.0 m and the exposure times vary between 1 and 4 h, depending on tidal cycles, wind stress and atmospheric pressure.

In July 1995, six 1-m^2 plots with imitation polychaete tubes were set up in a haphazard pattern around position 53°43.28′N, 07°45.69′E. The distance between plots was 5–10 m. Untreated reference plots of 1 m^2 were staked out between the experimental plots. Metal rods of 25 cm length and a diameter of 0.4 cm were used as tube imitations. They were inserted into the sediment with the upper 2–3 cm protruding from the surface. Each plot consisted of 1000 rods, equivalent to average population densities of *L. conchilega* in other areas of the Gröninger Plate. In the first month after setting up the experiment, sediment accumulated in the plots, which led to an increase in surface height of 1–3 cm. Imitation tubes that were buried by the trapped sediment were raised to maintain the initial height above the sediment surface.

Initially, three control plots were set up with metal rods inserted flush with the sediment surface to test whether the metal of the rods affected the fauna and whether the tube structure below the sediment surface had an effect on the benthic community. However, in the winter of 1995–1996, the tips of the metal rods were exposed by turbulence and this part of the experiment had to be terminated. First results from 1995 indicated that there was no significant difference between communities in control plots and the untreated reference plots (Zühlke et al., 1998).

Infauna samples from experimental plots with imitation tubes and from reference plots were taken in August 1995, 1996, 1997, in September 1998 and in May 2000. Due to logistical constraints, no samples were taken in 1999 and sampling had to be moved to spring rather than late summer in 2000. At the dates of sampling, one benthos sample was
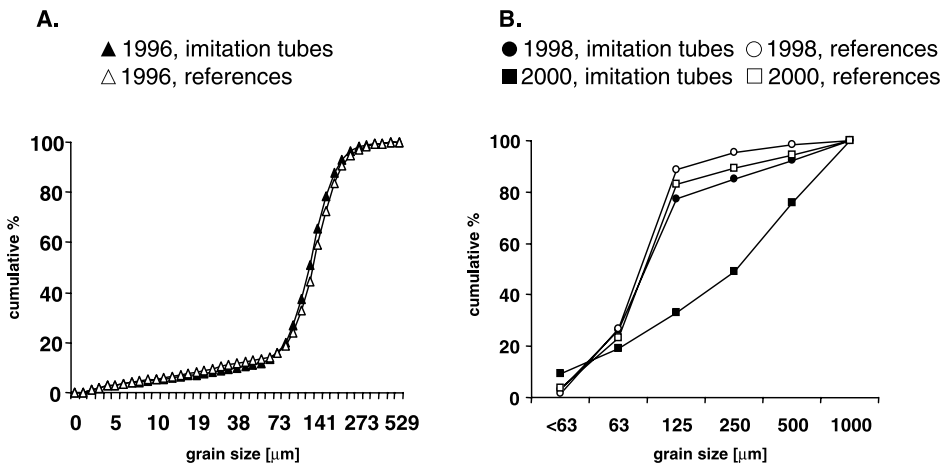

Fig. 2. Grain size distribution of sediment in plots with imitation tubes and reference plots. (A) Samples analysed by laser scanning. (B) Samples analysed by sieving through standardised sieves.

taken from each plot with imitation tubes and from each reference plot. Samples from both experimentally manipulated and untreated plots were treated as replicates. Six replicates were taken each year with the exception of 1998, when only five replicates could be taken due to an unfavourable tide.

The benthos was sampled with a core covering a 32-cm^2 surface area, to a depth of 10 cm. Samples were washed through a 0.5-mm sieve and either processed immediately or preserved in 70% ethanol for later processing. All macrofauna organisms were identified to species level and the width and length of bivalves were measured.

Sediment samples for grain size analysis were taken in August 1996, September 1998 and May 2000. One sample from each plot with imitation tubes and from each reference plot was taken with a corer ($\emptyset$ 2 cm, 1–2 cm deep). Replicate samples were pooled for analysis. In 1996, grain size distribution was determined with a laser particle scanner. This method was not available in 1998 and 2000, so dried samples were sieved through a series of standardised sieves from 1000 to 63 μm mesh size.

2.1. Data analysis

Species diversity was estimated from Hill's indices (Hill, 1973). Three indices were calculated:

N_0 = number of species (species richness)
$N_1 = \exp(H)$, where H is Shannon–Wiener diversity
$N_2 = 1/SI$, where SI is Simpson's dominance index.

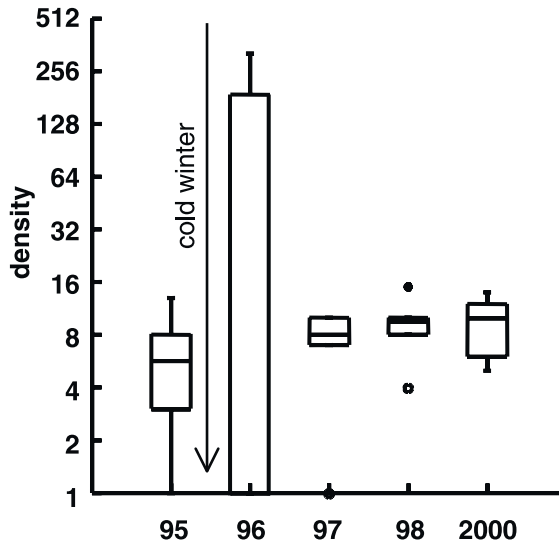Fig. 3. Boxplots of numbers of *M. edulis* on experimental plots with imitation tubes [abundance sample[−1] (32 cm^2)]; median, 25% quartiles and extreme values are shown on a $\log_2$+1 scale (in 1996 the median was 0).

Hill's N_0 merely counts the number of species but N_1 and N_2 incorporate the abundance of individuals. In short, N_1 is an index of the number of abundant species and N_2 the number of very abundant species.

The Mann–Whitney U-test was used to test whether differences between abundances of individuals or diversity in experimental plots and reference plots were significant. To reduce the risk of a type 1 error due to the high number of U-tests carried out, the significance level of 0.05 was adjusted with a Bonferroni procedure, resulting in a significance level of 0.01. Densities of *Mytilus edulis* were $\log_2 + 1$ transformed to allow
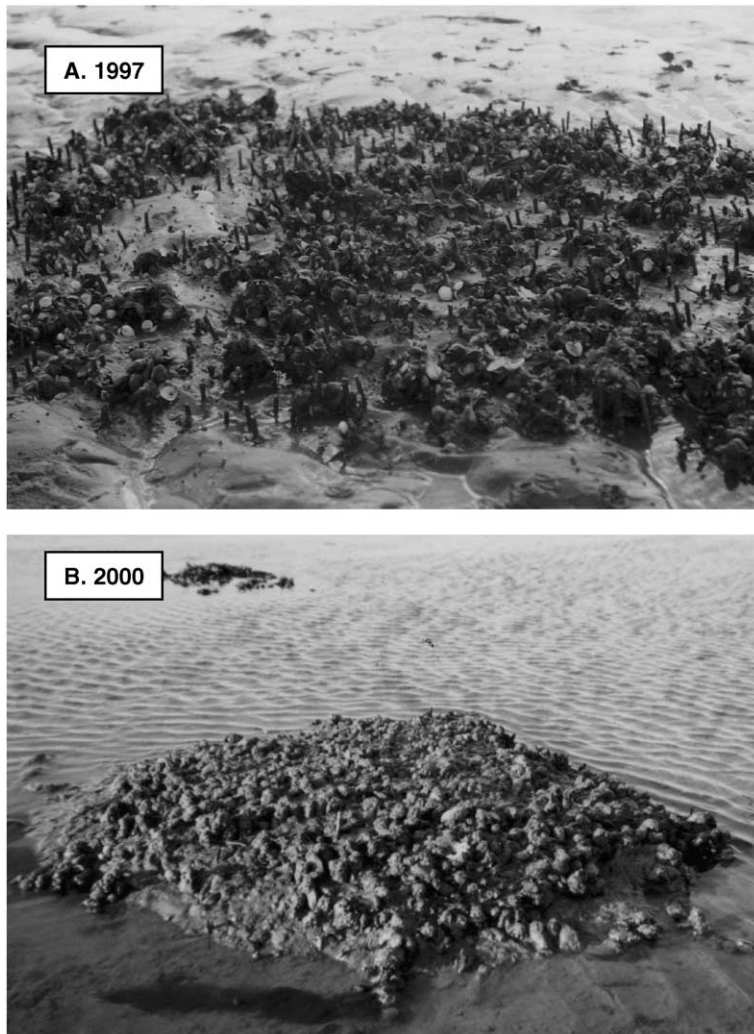

Fig. 4. Experimental plots with imitation tubes: (A) 1997, clumps of 1-year-old *M. edulis* attached to imitation tubes; (B) 2000, *M. edulis* cover the plot.

for zero values and be able to visualise the median and extreme values of all years in one figure.

The community structure was analysed with the PRIMER statistical package (Clarke and Warwick, 1994). The term 'community' is used for species assemblages from plots with imitation tubes and reference plots, respectively. Interactions between species in these communities are not implied. The data matrix of all benthic species was square-root-transformed to down-weight abundant species. The Bray–Curtis index was calculated between each possible pair of samples.

The significance of spatial and temporal differences between communities was assessed with two-way analysis of similarity (ANOSIM). They were visualised by nonparametric multidimensional scaling (MDS). Species mainly responsible for differences between communities from plots with imitation tubes and references plots were identified with the PRIMER program SIMPER. This examines the percentage contribution that each species makes to the similarity within and dissimilarity between communities.

3. Results

From 1995 to 2000, 27 benthic species were identified in the study area (Table 1). Polychaetes represented the largest taxonomic group with 16 species. Twenty-three species were recorded in experimental plots with imitation tubes and 19 in reference plots.

The sediment of the study site was characterised by fine and very fine sand (63–250 μm) (Fig. 2). No conspicuous differences were found between the grain size distribution of the experimental plots and reference plots with the exception of the year 2000, where the amount of fine sand was considerably lower in plots with imitation tubes than in reference plots.
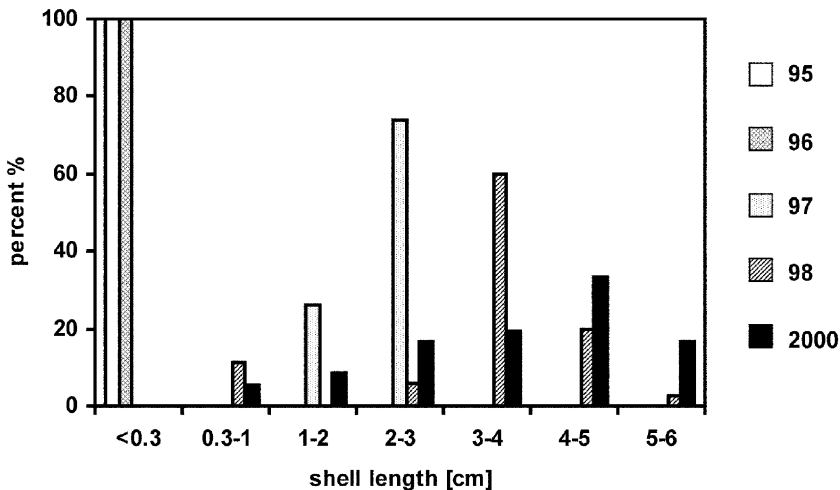

Fig. 5. Size/frequency distribution of *M. edulis* in plots with imitation tubes: 1995, $n = 36$; 1996, $n = 511$; 1997, $n = 35$; 1998, $n = 56$; 2000, $n = 57$.
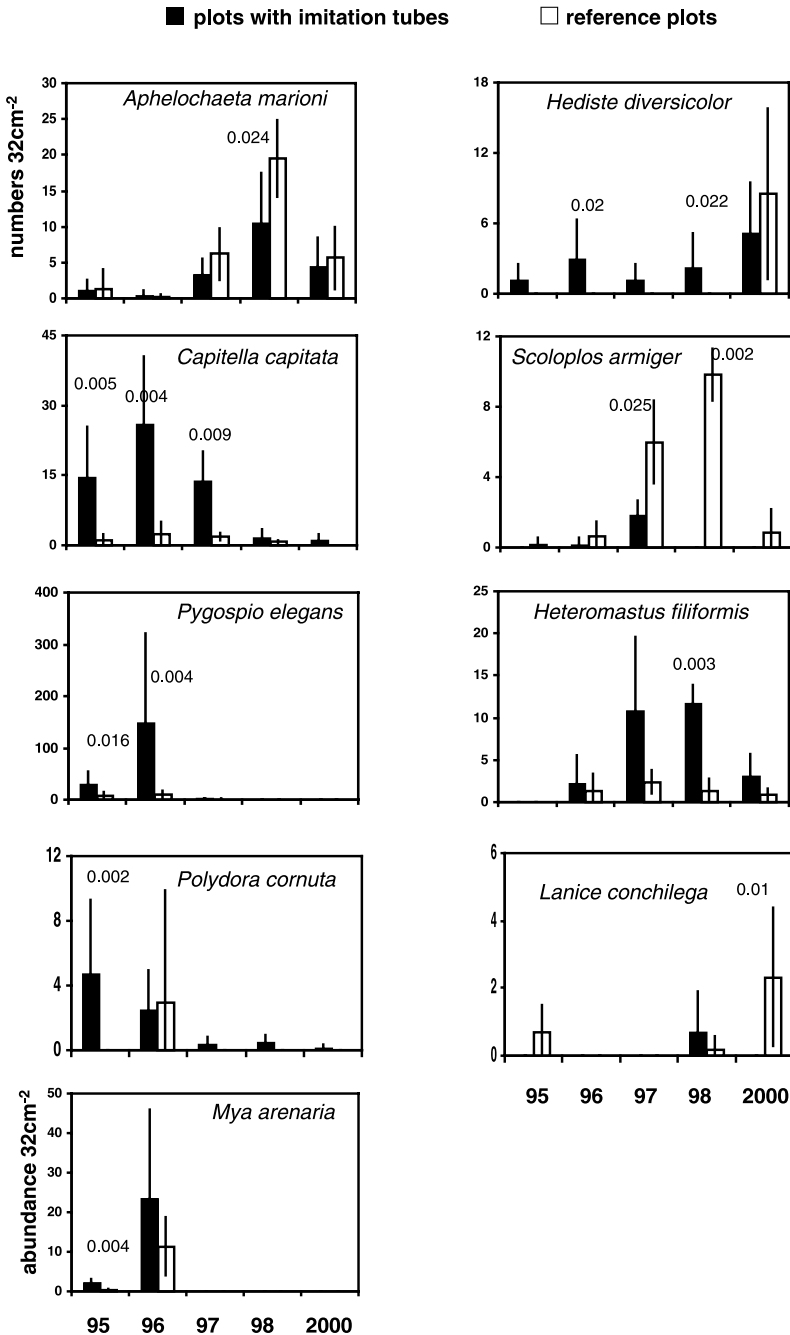
Fig. 6. Abundance of infauna species in plots with imitation tubes (■) and reference plots (□). Means and standard deviations are shown; significant differences are indicated by showing the *p*-values.

3.1. Abundance of individual species

M. edulis spat attached to the imitation tubes soon after setting up the experiment. In 1995, 6.0 ± 4.6 juvenile mussels shorter than 0.3 cm were found in samples (32 cm^{-2}) (Fig. 3). In 1996, after a particularly cold winter, large clumps of mussel spat were patchily distributed between the imitation tubes. In two replicates, 190 and 330 juvenile mussels were counted, while none were found in the other replicates. During the subsequent years, the mussels grew in size, spread and formed beds over the plots with imitation tubes. In 1998 and 2000, the majority had grown to a size between 3 and 6 cm length (Figs. 4 and 5).

In the reference plots, a total of six *M. edulis* < 0.3 cm were found in 1995 and single *M. edulis* only were recorded in one replicate in 1996, 1997 and 2000.

Four polychaete species and one other bivalve species were significantly more abundant in plots with imitation tubes than in reference plots (Fig. 6, $p < 0.01$). Within
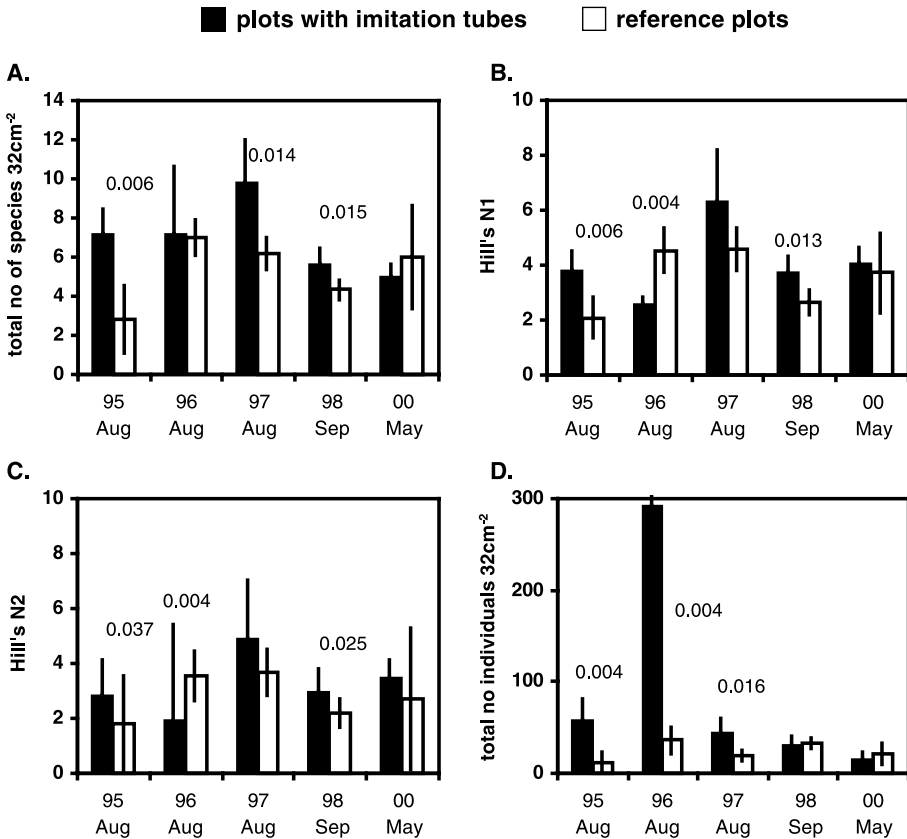

Fig. 7. Species diversity and abundance of benthic fauna in plots with imitation tubes (■) and reference plots (□). (A) Hill's N_0 (total number of species); (B) Hill's N_1; (C) Hill's N_2; (D) total number of individuals. Significant differences are indicated by showing the *p*-values.

4 weeks of setting up the experiment in 1995, the polychaetes *Pygospio elegans*, *Polydora cornuta* and *Capitella capitata* as well as spat of *Mya arenaria* (< 0.3 cm) were more abundant among the imitation tubes. Following the development of mussel banks on the imitation tubes (1998–2000), the polychaete *Heteromastus filiformis* was found in significantly higher numbers in plots with imitation tubes ($p < 0.01$), and *Hediste diversi-*
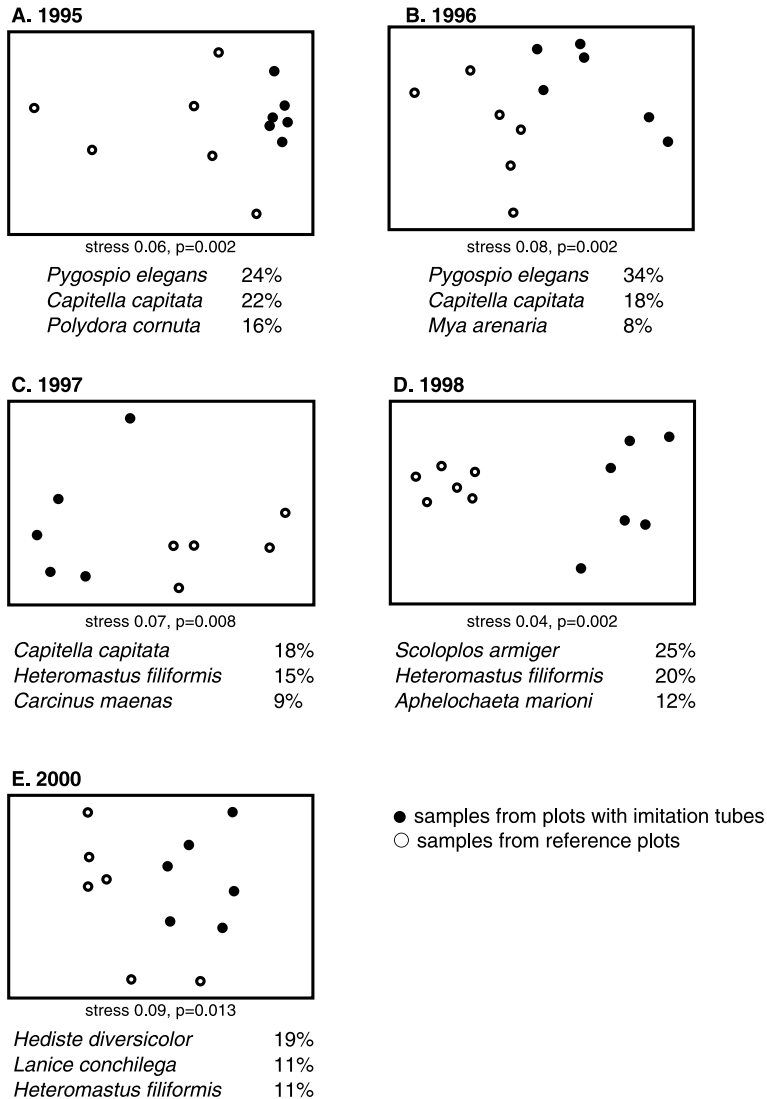

Fig. 8. MDS ordination for infauna communities from plots with imitation tubes and reference plots. *M. edulis* was excluded from the data. Significance levels (p) for the difference between the communities are given for each year. The species contributing most to the dissimilarity are shown, as well as their respective percentage contribution to the dissimilarity.

color at a significance level of 0.02. The polychaete *Scoloplos armiger* was significantly more abundant in reference plots in 1998 (Fig. 6, $p < 0.01$). Single individuals of mobile epibenthic crustaceans (*Jaera nordmanni*, *Echinogammarus marinus* and juvenile *Carcinus maenas*) and oligochaetes were exclusively found in *M. edulis* banks (Table 1).

In 1995, only single juvenile individuals of the tube-dwelling polychaete *L. conchilega* were found in some reference samples, but in 1998 their numbers started to increase. Densities reached 730 individuals m^{-2} in references plots in 2000, while no *L. conchilega* were found in plots with imitation tubes, which were overgrown by *M. edulis*.

3.2. Diversity and abundance

Species richness was significantly higher in plots with imitation tubes than in reference plots in 1995, 1997 and 1998 (Fig. 7). Hill's indices N_1 and N_2 indicated higher diversity in plots with imitation tubes in 1995, but higher diversity in reference plots in 1996. Total abundance was significantly higher in plots with imitation tubes in 1995 and 1996.

3.3. Community structure

There were significant differences in the infaunal community structure between plots with imitation tubes and reference plots. *M. edulis* were largely responsible for differences during the period 1997–2000, although differences were still significant with *M. edulis* removed from the data set (Fig. 8). The main source of dissimilarity between communities was those species with significantly higher or lower abundance in the plots with imitation tubes (Fig. 6). Pooling all data for all years showed that interannual changes of the benthic
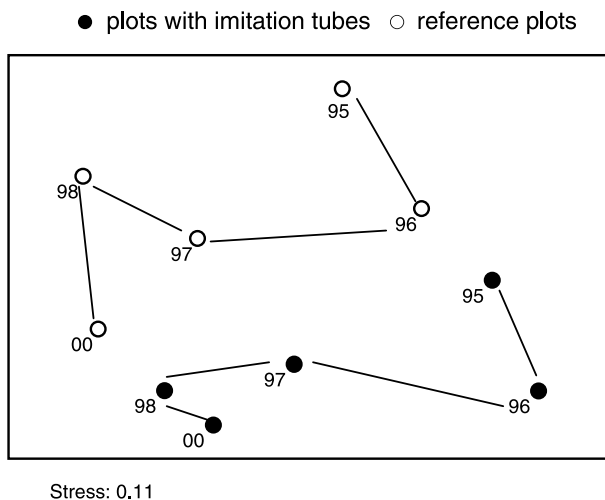

Fig. 9. MDS ordination for benthic communities from experimental plots (●) and reference plots (○) based on mean values for the respective year. Lines connect consecutive years of sampling to indicate interannual changes.

community were significant as well as the overall difference between plots with imitation tubes and reference plots (two-way ANOSIM, $p < 0.001$ for both factors). The general direction of interannual change was similar for both the plots with imitation tubes and the reference plots (Fig. 9). SIMPER analyses indicated that the high numbers of opportunistic polychaetes and spat of *M. arenaria* in 1996 were responsible for the dissimilarity between communities in 1995 and 1996. In 1997, these species were absent or their numbers were low, but other polychaetes had successful recruitments (*Aphelochaeta marioni*, *H. filiformis*, *S. armiger*). These polychaetes established themselves and were found in considerable numbers until the end of the study. The change between 1998 and 2000 might have been influenced by seasonal differences, because samples were taken in spring rather than late summer in the year 2000.

4. Discussion

This experiment showed that the presence of tube structures changed the composition of benthic fauna. Most conspicuously they supplied juvenile mussels with an attachment surface anchoring them securely as they matured. The presence of imitation tubes allowed the development of mussel banks. However, beyond *M. edulis* the dissimilarity between the benthic community structure in experimental and reference plots did not increase over the years. Interannual changes in the reference plots were reflected in the benthic community of imitation tube plots. It appears that tube structures do not create islands where benthic communities evolve increasingly independently from the outside community.

In the following, effects of imitation tubes and mussels attached to tubes are discussed, and the degree to which the tube mimics reflected the physical presence of *L. conchilega*.

4.1. Effects of imitation tubes on benthic fauna

The effects of imitation tubes will be considered in the first 2 years of the experiment since they were subsequently overgrown with mussels and the effects of mussel banks could no longer be distinguished from tube effects. Imitation tubes had a significant effect on the benthic fauna in respect of overall community structure, species diversity, total abundance and abundance of individual species.

Generally tube structures may affect four main factors: sediment properties, the hydrodynamic regime, the availability of refuge from predation and the availability of attachment surfaces. While tubes may destabilise the sediment (Eckmann et al., 1981; Carey, 1983; Luckenbach, 1986), Eckman (1983) showed that effects of tubes on hydrodynamic processes depend on their numerical density. Friederichs et al. (2000) found that the sediment was only destabilised at tube densities of less than 870 tubes m^{-2}. Their results showed that current velocity decreased at high and low tube densities and they concluded that the residence time of particles within tube plots is higher than in tube-free sands, thus facilitating deposition. This process is most likely to be responsible for the sediment accumulation observed in plots with imitation tubes after they were set up in 1995 and might also have led to some of the changes in the benthic fauna. During the first

year of the experiment small opportunistic polychaete species, namely *P. elegans*, *P. cornuta* and *C. capitata*, were found in higher numbers among the imitation tubes than in the surrounding sand. Dauer et al. (1982) reported similar results for *P. cornuta* (then called *Polydora ligni*). Polychaetes, especially juveniles, are known to be negatively affected by bedload movement (Zühlke and Reise, 1994) and more stable sediment among tubes might have promoted denser spionid populations. *P. elegans* and *P. cornuta* are both also known to use postlarval migration to disperse (Günther, 1992a), which explains the rapid colonisation of the plots with imitation tubes.

Tubes provide a refuge from predation (Woodin, 1978) and the rigid imitation tubes possibly presented an impediment to the foraging activities of fish. Predation by fish has been shown to potentially shape benthic communities (Connell and Anderson, 1999; Hindell et al., 2001). However, the imitation tubes did not function as a refuge from predatory polychaetes, such as *Nephtys hombergii*, *Eteone longa* and *H. diversicolor*. These may have preyed on juvenile polychaetes and bivalves (Goerke, 1971), and may also have benefited from higher abundance of meiofauna among the imitation tubes (Zühlke et al., 1998; Peachey and Bell, 1997; Dauer et al., 1982).

Imitation tubes improved the availability of settlement surfaces for juvenile bivalves. Spat of *M. arenaria* and *M. edulis* was found attached to the imitation tubes 1 month after setting up the experiment. Several authors report the preference of *M. edulis* to settle on structured surfaces rather than smooth substratum (e.g. Dean, 1981; Bourget et al., 1994; Hunt and Scheibling, 1998) and Günther (1992b) mentioned the ability of small *M. arenaria* to anchor to substrata with byssus threads, similar to *M. edulis*. Spat fall was high after the particularly cold winter 1995–1996 (Herlyn and Millat, 2000), which coincides with studies on bivalves from other parts of the Wadden Sea (Strasser et al., 2001). From 1996 to 2000, the mussels grew to a size range found in mature mussel banks on intertidal sands (Buschbaum and Saier, 2001).

4.2. Effects of imitation tubes with attached mussels on benthic fauna

In 1998 and 2000, mussels had formed dense banks covering the plots with imitation tubes. Their effect on the benthic fauna was probably stronger than that of the tubes. *M. edulis* banks are among the most important habitat structures on intertidal sandflats, and Ragnarsson and Raffaelli (1999) showed that they host a different fauna than surrounding sands. In agreement with their results, some polychaete species were found in significantly higher and some in lower abundance among mussels in 1998. The mechanisms leading to higher densities of *H. filiformis* and *H. diversicolor* were probably similar to those discussed for the initial imitation tube plots. Changes in the sediment composition among mussels, the hydrodynamic regime and their function as a refuge from predation have all been proposed as responsible for the species composition in mussel banks (Dauer et al., 1982; Tsuchiya and Nishihira, 1986; Kautsky and Evans, 1987; Hatcher et al., 1994; Widdows et al., 1998). Low densities of the polychaetes *S. armiger* and *A. marioni* in the mussel banks are most likely to be related to spatial restrictions and/or competition for food with *M. edulis*.

Ragnarsson and Raffaelli (1999) emphasised the importance of mussels for mobile epibenthic crustaceans. In accordance with their results, three species of mobile crusta-

ceans were recorded exclusively in the mussel banks (*J. nordmanni*, *E. marinus* and juvenile *C. maenas*), but only as single individuals. The low numbers are probably due to the absence of natural mussel banks in the close vicinity (Hertweck, 1995; Herlyn and Millat, 2000), which would be the most likely source of colonists, at least for the isopod and amphipod.

In 2000, no significant differences were found between mussel banks and reference plots in terms of species diversity and abundance of individual species with one exception, *L. conchilega*. The tube-dwelling polychaete had colonised the reference area and reached densities of more than 700 individuals m^{-2}. No *L. conchilega* were found in mussel banks. The presence of this polychaete in reference plots compromised the experimental design. From the initial comparison between plots with imitation tubes and tube-free plots, the experiment developed into a comparison between imitation tubes covered by mussel banks and reference plots with natural tubes. It cannot be ruled out that effects of *L. conchilega* tubes on the fauna (Zühlke, 2001) masked or weakened differences that would have emerged in the absence of *L. conchilega*.

4.3. Comparison between effects of imitation tubes and tubes of L. conchilega

The fauna associated with *L. conchilega* tubes has also been studied on the Gröninger Plate sandflat (Zühlke, 2001). The imitation tubes differed in many aspects from natural tubes of *L. conchilega*, which they were supposed to mimic; they were more rigid, solid rather than hollow, did not have a tentacle fringe and were more persistent over time, since *L. conchilega* lives no longer than about 3 years (Buhr, 1979). Despite these differences, imitation tubes and *L. conchilega* tubes had similar effects on some fauna. Similarly to the imitation tubes, *L. conchilega* tubes had positive effects on the densities of two polychaete species and were also used as an attachment surface by juvenile *M. arenaria* and *M. edulis*.

Conversely, two polychaete species, which had been found inside *L. conchilega* tubes and among the tentacle fringe (Zühlke, 2001), were not recorded from plots with imitation tubes. This indicates that these species can have a closer interspecific relationship with *L. conchilega*, or that they depend on the cavity of the tube and the sand fringe.

Imitation tubes actually affected more species than *L. conchilega* tubes. While densities of spionid polychaetes and *C. capitata* were significantly higher among imitation tubes than in reference plots, these differences were not found for aggregations of *L. conchilega*. The rigid imitation tubes might have had a more pronounced effect on hydrodynamic properties and provided more secure shelter from predation, which benefited the polychaetes.

4.4. The possible connection between L. conchilega tubes and mussel banks

Imitation tubes anchored the growing mussel clumps and allowed the development of mussel banks. This generates the question, whether or not *L. conchilega* tubes could also be the foundation of mussel banks. Any extrapolation from the results of this experiment to natural tubes has to be regarded with caution, since the experiment was carried out in a small part of a sandflat, there was no replication in other areas and the physical characters of natural tubes and mimics were different. However, similar to imitation tubes, *L.*
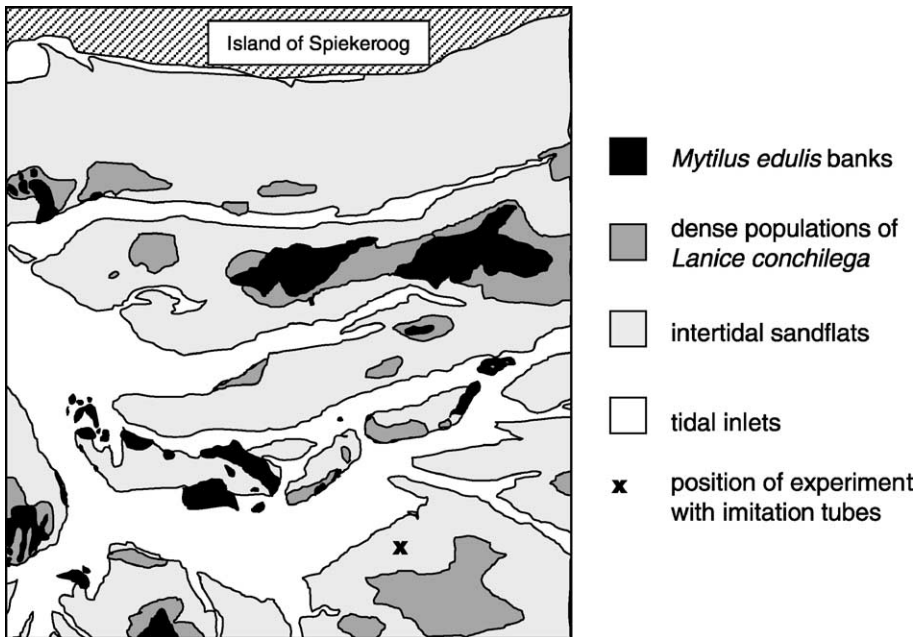
Fig. 10. Positions of mussel banks and dense populations of *L. conchilega* in the study area after Hertweck (1995).

conchilega tubes encouraged large numbers of mussel spat to settle (Zühlke, 2001), but after 2 years the growing clumps of mussels were removed from the area, most likely washed away by storms (Harger and Landenberger, 1971; Nehls and Thiel, 1993). Between 1991 and 1993, Hertweck (1995) made identical observations at a sandflat 3 km further west. Thus, based on the present evidence, it can be concluded that *L. conchilega* does not provide secure anchorage for juvenile mussels. On the other hand, distribution maps of *L. conchilega* and *M. edulis* in Hertweck (1995) (Fig. 10) show similar spatial patterns of the two species. Mussel banks were generally located in the centre of dense *L. conchilega* populations. I hypothesise that under favourable conditions, namely the absence of severe storms for a period of time, mussel banks may develop on top of *L. conchilega* aggregations. Although their vulnerability to hydrodynamic forces increases with body size, they become more resistant once they form dense banks (Denny et al., 1985; Hunt and Scheibling, 2001). However, whether *L. conchilega* aggregations indeed promote the establishment of new mussel banks has yet to be established.

Acknowledgements

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