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Polychaete tubes create ephemeral community patterns: *Lanice conchilega* (Pallas, 1766) associations studied over six years

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Abstract

On intertidal sandflats spatial patterns of benthic communities are influenced by biogenic habitat structures such as mussel beds or seagrass meadows. These structures represent ecological islands hosting a different and often more diverse and abundant community than surrounding sandflats. However, few studies have been carried out on tube aggregations of the polychaete *Lanice conchilega*, although its tube tops are conspicuous habitat features on European intertidal coasts with densities reaching several thousand per m².

The aim of this study was to determine differences between benthic communities associated with tube aggregations and tube-free areas, and to investigate the longevity of community patterns around *L. conchilega* tubes. From 1995 to 2000, the *L. conchilega* population of an intertidal sandflat off the Eastern Friesian coast was sampled annually. Multivariate analysis showed significant differences between the *L. conchilega* and reference communities. Species diversity and abundance were higher among tube aggregations. This pattern developed rapidly after *L. conchilega* colonisation but was also readily destroyed, mainly due to dynamic changes of the *L. conchilega* population.

Five species of benthic macrofauna were exclusively found among *L. conchilega* tubes, and four species were more abundant in tube aggregations than in reference areas. Only one species, the polychaete *Aphelocheata marioni*, was found in lower numbers in dense *L. conchilega* aggregations.

Hence, it is concluded that *L. conchilega* is a habitat engineer, which alters the composition of the benthic community and contributes to its patchy distribution pattern. However, this pattern is dynamic and ephemeral. Effects of tube aggregations depend on the population dynamic of *L. conchilega* itself and the species composition in the surrounding sands. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Macrobenthos; Community pattern; Habitat structure; Tube worms; *Lanice conchilega*; Intertidal sandflats

1. Introduction

In intertidal communities, habitat structures affect recruitment, survival and spatial distribution patterns of benthic species (Dean, 1981; Bell et al., 1991; Archambault and Bourget, 1996; Rilov and Benayahu, 1998). Sand and mudflats, although poor in terms of three-dimensional abiotic features, host

numerous biotic surface structures. Most prominent in temperate regions are mussel and oyster beds and seagrass meadows. Epibenthic bivalves and seagrasses are ecosystem engineers (Jones et al., 1997) and can influence and often enrich the associated benthic community (seagrass: Orth, 1992; Reusch, 1998; Edgar, 1999; mussels: Tsuchiya and Nishihira, 1986; Ragnarsson and Raffaelli, 1999; oysters: Dauer et al., 1982; Meyer and Townsend, 2000). Some studies have examined the importance of polychaete

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tube assemblages and how they influence the distribution and abundance of infaunal species (Woodin, 1978; Eckman et al., 1981; Gallagher et al., 1983; Whitlatch and Zajac, 1985; Trueblood, 1991; Khaitov et al., 1999). However, only a few studies have been carried out on *Janice conchilega* (Feral, 1989; Carey, 1987), a tube-building polychaete widely distributed in temperate sandflats (Hartmann-Schröder, 1996).

Tubes of adult *L. conchilega* have a diameter of about 0.5 cm and are up to 65 cm long (Ziegelmeier, 1952). The tube is built of sand grains and other solid particles such as parts of bivalve shells, foraminifers or ostracods (Ziegelmeier, 1952). The top end protrudes above the sediment by 1–4 cm and terminates with a fringe of filaments of mucus-bound sandgrains, which traps suspended particles. Ziegelmeier (1952) showed that the polychaete increases the height of the tube top with increasing sedimentation. *L. conchilega* can switch between deposit and suspension feeding (Buhr, 1976) and is preyed upon by wading birds (Petersen and Exo, 1999) and fish (Kühl, 1963). Information on the life span of *L. conchilega*, postlarval dispersion and durability of the tubes is sparse. Buhr (1979) speculated that *L. conchilega* reaches an age of 2–3 years. My observations suggest that the tube top with the fringe is destroyed shortly after the death of *L. conchilega* or the abandonment of the tube, but remains of the tubes can still be found in the sediment until several months later. *L. conchilega* has also been reported to be particularly sensitive to cold temperatures (Buhr, 1981). Densities of this polychaete can be high: Buhr and Winter (1977) found up to 20 000 individuals m^{-2} from sublittoral areas off the Friesian coast and Hertweck (1995) found densities between 100 and 10 000 *L. conchilega* m^{-2} in an intertidal area adjacent to the site used in this study.

It was hypothesised that *L. conchilega* tube aggregations affect the other infauna. The aims of the study were

1. to determine the differences between the benthic community amidst tube aggregations and that of tube-free areas, and
2. to investigate the longevity of community patterns associated with *L. conchilega* tubes over a period of several years.

This allowed conclusions on the extent to which the

composition of the benthic community is driven by *L. conchilega*.

2. Methods

Between 1995 and 2000 the macro-infauna community in a *L. conchilega* population was investigated on an intertidal sandflat in the German part of the Wadden Sea (Fig. 1). The sandflat, called the ‘Gröninger Plate’, is situated between the mainland and the island of Spiekeroog, one of the East Friesian barrier islands. The mean tidal range is 2.7 m and about 80% of the area between the island and the mainland is emerged during low tide (Hild, 1999). Up to several thousand m^2 of the Gröninger Plate were populated by the tube-dwelling polychaete *L. conchilega*. The study was carried out in an area of about 2500 m^2 at the western side of the Gröninger Plate, centred around position $53^{\circ}43.179'N$ and $7^{\circ}45.266'E$. The Gröninger Plate and the sampling site are described in Hild (1999).

The spatial distribution of *L. conchilega* was patchy in the sampling area; tube aggregations were interspersed with *L. conchilega*-free patches. Replicate core samples (32 cm^2 surface area, 10 cm deep) were taken from *L. conchilega* aggregations as well as from intermediate *L. conchilega*-free patches. *L. conchilega* aggregations were regarded as independent sampling units and only one sample was taken from each haphazardly chosen aggregation. Tube-free areas between *L. conchilega* aggregations were used to obtain reference samples. Again only one sample was taken from any tube-free patch (Table 1). Tube-free patches are also referred to as reference sites.

The size of *L. conchilega* aggregations and the distance between them varied from year to year (see Section 3), but generally they were about 5–20 m apart. Hence, the distance between *L. conchilega* samples as well as the distance between *L. conchilega* and reference samples varied along this range.

Samples were washed through a 0.5 mm mesh sieve. Samples were either processed immediately or preserved in 70% ethanol for later processing. As far as possible, all macrofaunal organisms were identified to species level.

To minimise the influence of seasonal fluctuations in

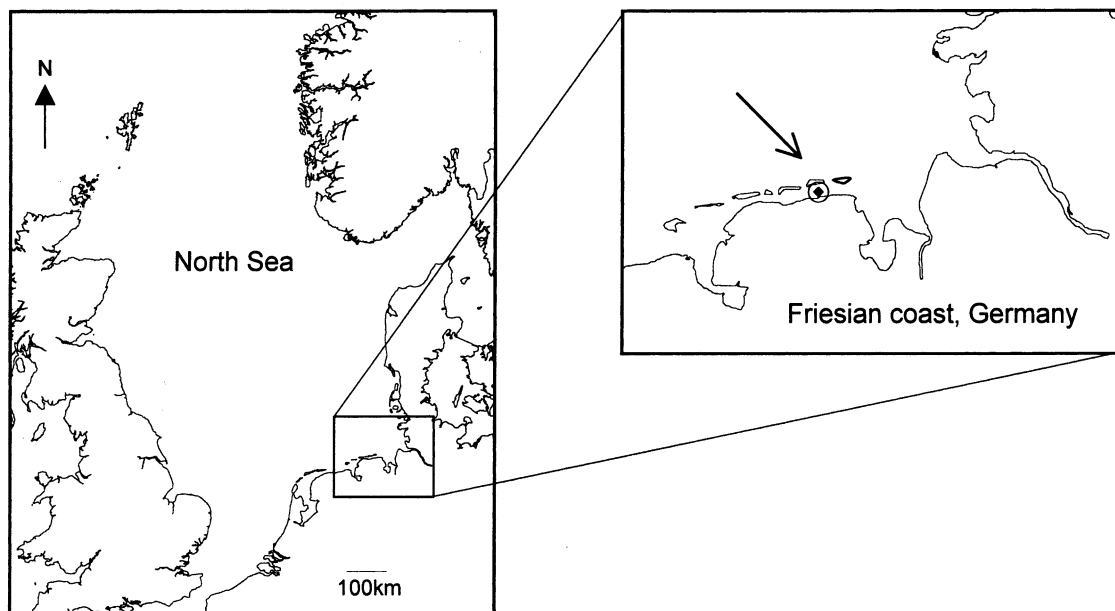


Fig. 1. Location of the study site (◆).

this interannual comparison, sampling was generally carried out in late summer. Initial sampling in both August and September of 1995 established that there was little variation in the abundance and species diversity on such a time scale. Subsequent sampling was annual only. Part of the 1995 data have been published in Zühlke et al. (1998).

In 1997, *L. conchilega* was absent from the study site and only *L. conchilega*-free areas ('reference areas') were sampled. No sampling took place in

1999 and sampling had to be moved to spring in 2000 for logistical reasons.

The tubes of *L. conchilega* were either U- or J-shaped. U-shaped tubes had generally one intact fringe and one opening with 0–3 sand filaments. In samples, only tubes with intact fringes were counted. It was assumed that the number of intact fringes reflected the number of *L. conchilega* in the sediment. Hence, all references to densities of *L. conchilega* are based on numbers of tube tops counted in each sample. The animals themselves are rarely captured by this sampling method since they retreat within their tubes, which may be up to 65 cm in length.

Sediment samples from *L. conchilega* aggregations and reference areas were taken in order to determine a potential increase in fine sediment among the polychaete tubes (Feral, 1989). In 1995, 1996, 1998 and 2000, samples were taken with a core of 2 cm diameter to a depth of 1–2 cm. Six sediment samples from *L. conchilega* aggregations and reference areas were pooled respectively. In 1995/1996, grain-size distribution was analysed by laser scanning. This method was not available in 1998 and 2000, and dried samples were instead sieved through a series of standard sieves from 2000 to 63 μm mesh size.

Table 1

Numbers of samples taken from *L. conchilega* aggregations and tube-free reference areas. One sample was taken from each *L. conchilega* aggregation or tube-free patch. In August 1997, *L. conchilega* was not present at the study site

	Samples from <i>L. conchilega</i> aggregations (n)	Reference samples (n)
August 1995	6	6
September 1995	6	6
August 1996	6	6
August 1997	–	5
September 1998	6	6
May 2000	6	6

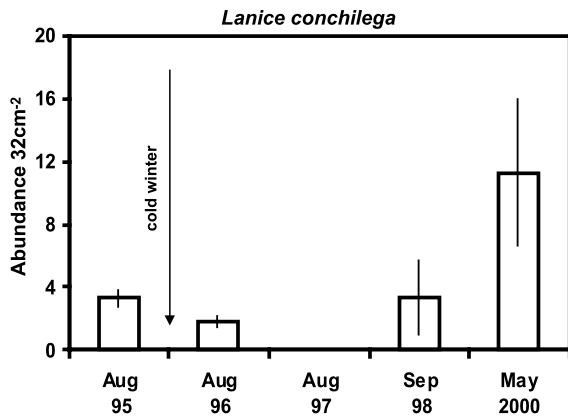


Fig. 2. Number of tubes in *L. conchilega* aggregations ($n = 5-6$, mean \pm S.D.).

2.1. Data analysis

Infaunal species diversity was estimated using Hill's indices (Hill, 1973), where N_0 = number of species (species richness), $N_1 = \exp(H)$, where H is Shannon–Wiener diversity, $N_2 = 1/SI$, where SI is Simpsons' dominance index.

Hill's N_0 is the total number of species in a sample, while N_1 and N_2 incorporate 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.

Non-parametric multidimensional scaling (MDS) and analysis of similarity (one-way ANOSIM) were used to describe temporal and spatial similarities between benthic faunal communities from *L. conchilega* aggregations and reference sites. Two-way crossed ANOSIM was used to test effects of the presence of *L. conchilega* and temporal changes in the community structure simultaneously. The analysis was carried out with the PRIMER statistical package (Clarke and Warwick, 1994). The term 'community' is used here for assemblages of infaunal species found in areas inside and outside *L. conchilega* patches. Ecological interactions are not implied. A community composed of *L. conchilega* tubes plus associated organisms is designated as a *L. conchilega* community.

Differences between abundances of species in *L. conchilega* aggregations and reference areas were tested with the Mann–Whitney U -test. To reduce the risk of a Type 1 error as a result of executing several

U -tests, a p value of 0.03 was attributed. Differences in species diversity between *L. conchilega* aggregations and reference areas as well as temporal changes were tested with two-way ANOVA with (a) presence/absence of *L. conchilega* as the first factor and (b) year as second factor. Pairwise comparisons were carried out with the Tukey-test ($p < 0.05$).

Whether the density of *L. conchilega* tubes correlated with the species richness or individual species abundance was tested with the product moment correlation coefficient.

2.2. Ice-winter

In the Wadden Sea, the intertidal infauna community can be severely effected by cold-winter temperatures, which generate a temporary cover of ice on the sandflats (Dörjes, 1980; Beukema, 1979). During the period of this study, we experienced one particularly cold winter between 1995 and 1996. Long-lasting low temperatures led to ice cover of the intertidal sandflats of the Wadden Sea, including the study site, for 48 days (Günther and Niesel, 1999). This was the longest period of ice cover for 33 years (Niesel, 1999).

3. Results

3.1. Abundance of *Lanice conchilega*

Numbers of *L. conchilega* tubes in the samples reflected their densities within *L. conchilega* patches (Fig. 2). However, patch sizes and distances between *L. conchilega* patches varied over the period of this study. In 1995, *L. conchilega* patches with a diameter of about 1–10 m were found adjacent to similarly sized patches almost free of *L. conchilega*. Up to 1500 tubes m^{-2} were found in *L. conchilega* patches. The unusually cold winter of 1995/1996 obliterated the entire *L. conchilega* population of the Gröninger Plate (Günther and Niesel, 1999) and no live *L. conchilega* were found until July 1996. In August of that year, some *L. conchilega* recolonisation had taken place in the shape of small clusters of 10–70 *L. conchilega* tubes with a patch diameter of about 0.1–0.2 m. The density of *L. conchilega* tubes in these small patches was comparable to those in the larger patches of 1995 (Fig. 2).

L. conchilega did not survive the following year,

and only a few uninhabited tubes were found in 1997. Instead, the area formerly dominated by *L. conchilega* was covered with young *Mytilus edulis* and many of them settled in clusters on empty *L. conchilega* tubes. *L. conchilega* successfully recolonised the Gröninger Plate in 1998 and densities rose steeply until 2000. In May 2000 up to 4000 *L. conchilega* m⁻² were counted.

3.2. Sediment in *Lanice conchilega* aggregations

Over 50% of the sediment in *L. conchilega* aggregations and the reference areas was fine sand (125–250 µm) and 20–30% was very fine sand (63–125 µm). In 1995 and 1996, the mud content (<63 µm) was marginally higher in *L. conchilega* aggregations than in the reference areas (14 and 16% in comparison to 12 and 11%). The mud content differed by just 1% in *L. conchilega* and reference patches in 1998 and 2000.

3.3. Benthic macrofauna in the study area

Altogether 32 benthic infauna species were recorded during the study, with polychaetes being the largest taxonomic group (Table 2). In 1995/96, the community was numerically dominated by juvenile bivalves and the spionid polychaete *Pygospio elegans*. In 1998/2000, the infauna was poor in terms of numbers of bivalves and apart from *L. conchilega* no suspension-feeding polychaetes were found. Instead, *Hediste diversicolor*, *Scoloplos armiger*, *Heteromastus filiformis* and *Aphelochaeta marioni* dominated the macrobenthos.

3.4. Infaunal species in *Lanice conchilega* aggregations

Four species were found in significantly higher abundances in *L. conchilega* aggregations than in reference areas at some point during the study and one polychaete, *A. marioni*, was found in lower numbers in *L. conchilega* aggregations (Fig. 3). Juvenile *Mya arenaria* and *Mytilus edulis* (0.2–0.5 cm high) were significantly more abundant in *L. conchilega* patches than in tube-free areas in 1995 and 1996, respectively. *M. edulis* had grown up to 2.5 cm high in 1997 but had disappeared in 1998. Furthermore, two carnivorous or scavenging polychaetes were more abundant in *L. conchilega* aggregations:

Phyllodoce mucosa in August 1996 and juvenile *Hediste diversicolor* in 2000 (*P. mucosa* is not shown in Fig. 3 because of low average densities of less than one individual per sample). Abundances of several polychaetes which occurred regularly throughout the study were not significantly different in *L. conchilega* aggregations and the tube-free reference areas (e.g. *Eteone longa*, *Capitella capitata* and *Heteromastus filiformis*).

Five species (*Sagartia troglodytes*, *Harmothoe lunulata*, *Eumida sanguinea*, *Gammarus locusta* and *Microprotopus maculatus*) were found exclusively associated with *L. conchilega* aggregations (Table 2).

3.5. Species diversity in *Lanice conchilega* aggregations

The number of species was highest in 1995 and 1996, and decreased significantly until 2000 (ANOVA, $p < 0.05$). However, species richness was generally higher in *L. conchilega* aggregations than in *L. conchilega*-free areas (ANOVA, Tukey-test, $p < 0.05$) (Fig. 4A). No significant difference between *L. conchilega* aggregations and reference areas was found in 1998.

Diversity indices which take abundances into account (Hill's N_1 , N_2) indicated significantly higher diversity in *L. conchilega* aggregations than in references for 2000 (Fig. 4B and C). Total abundance of individuals was significantly higher in *L. conchilega* aggregations in 1995 and 1996 (Fig. 4D), caused primarily by high numbers of bivalves. In 2000, total abundance was higher in the reference samples, influenced by numbers of the polychaete *A. marioni* (Fig. 3).

No correlation was found between the density of *L. conchilega* tubes and species richness or individual abundances.

3.6. Community structure in *Lanice conchilega* aggregations

The community structure of benthos associated with *L. conchilega* was significantly different from *L. conchilega*-free areas in three out of four investigated years, when *L. conchilega* was present (Fig. 5). The MDS ordination reflects the differences in community structure by grouping samples from *L. conchilega* aggregations and reference samples for 1995, 1996 and 2000. No clustering was found for 1998.

Table 2

Macrobenthic species in *L. conchilega* aggregations and in tube-free patches of the Gröninger Plate (Friesian coast, Germany), 1995–2000. Full squares (■) indicate the presence of species and empty squares (□) their absence. In 1997, no *L. conchilega* were found and consequently no macrofauna associated with *L. conchilega* aggregates was recorded. For 1995, data from August to September were pooled. * Often confused with *Tharyx killariensis*

	<i>L. conchilega</i> aggregations					Reference samples				
	95	96	97	98	00	95	96	97	98	00
Anthozoa										
<i>Sagartia troglodytes</i>	□	□		■	■	□	□	□	□	□
Gastropoda										
<i>Hydrobia ulvae</i>	□	□		□	□	■	■	■	□	□
Bivalvia										
<i>Cerastoderma edule</i>	■	■		■	■	■	■	■	■	■
<i>Ensis</i> sp.	■	■		□	□	■	■	■	□	□
<i>Macoma balthica</i>	■	■		■	■	■	■	■	■	■
<i>Mya arenaria</i>	■	■		□	□	■	■	■	□	□
<i>Mytilus edulis</i>	■	■		□	□	■	■	■	□	□
<i>Scrobicularia plana</i>	■	■		□	□	■	■	■	□	□
Polychaeta										
<i>Phyllodoce mucosa</i>	■	■		■	■	■	■	■	■	■
<i>Aphelochaeta marioni</i> *	■	■		■	■	■	■	■	■	■
<i>Capitella capitata</i>	■	■		■	■	■	■	■	■	■
<i>Eteone longa</i>	■	■		■	■	■	■	■	■	■
<i>Eumida sanguinea</i>	■	■		■	■	■	■	■	■	■
<i>Harmothoe lunulata</i>	■	■		■	■	■	■	■	■	■
<i>Hediste diversicolor</i>	■	■		■	■	■	■	■	■	■
<i>Heteromastus filiformis</i>	■	■		■	■	■	■	■	■	■
<i>Malacoceros tetracerus</i>	■	■		■	■	■	■	■	■	■
<i>Neanthes virens</i>	■	■		■	■	■	■	■	■	■
<i>Nephtys hombergii</i>	■	■		■	■	■	■	■	■	■
<i>Polydora cornuta</i>	■	■		■	■	■	■	■	■	■
<i>Pygospio elegans</i>	■	■		■	■	■	■	■	■	■
<i>Scoloplos armiger</i>	■	■		■	■	■	■	■	■	■
<i>Spio filicornis</i>	■	■		■	■	■	■	■	■	■
<i>Lanice conchilega</i>	■	■		■	■	■	■	■	■	■
Oligochaeta										
<i>Tubificoides benedii</i>	■	■		■	■	■	■	■	■	■
<i>Tubificoides pseudogaster</i>	■	■		■	■	■	■	■	■	■
Crustacea										
<i>Corophium arenarium</i>	■	■		■	■	■	■	■	■	■
<i>Gammarus locusta</i>	■	■		■	■	■	■	■	■	■
<i>Microprotopus maculatus</i>	■	■		■	■	■	■	■	■	■
<i>Urothoe poseidonis</i>	■	■		■	■	■	■	■	■	■
<i>Crangon crangon</i>	■	■		■	■	■	■	■	■	■
<i>Carcinus maenas</i>	■	■		■	■	■	■	■	■	■

In Fig. 6 the community structure of each date of sampling was compared, based on means of individual abundances of each date. Two-way ANOSIM indicated significant differences for both factors, (a)

the presence or absence of *L. conchilega* and (b) interannual changes ($p < 0.001$ for both factors, based on all samples, not mean values, from 1995 to 1998). The MDS shows a gradual change in the

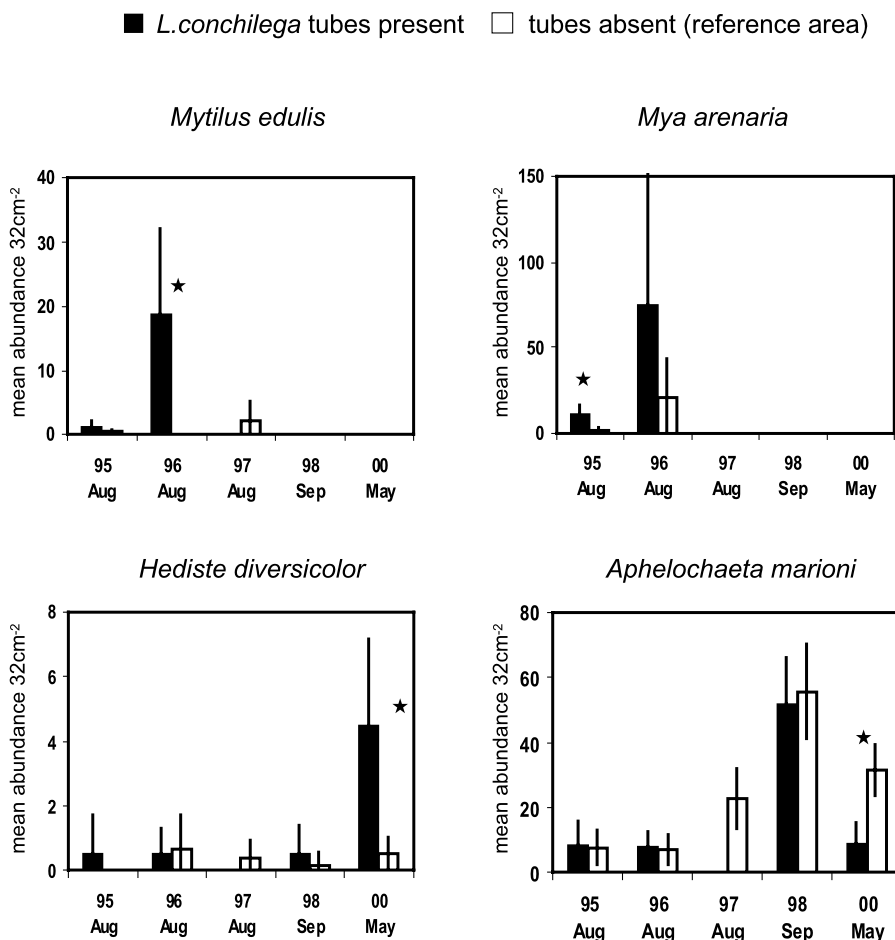


Fig. 3. Abundance of infauna species in *L. conchilega* aggregations (■) and reference samples (□); means and standard deviations are shown. Significant differences between abundances of species in *L. conchilega* aggregates and reference samples are indicated by an asterisk. No values are shown for 1997 *L. conchilega* aggregations since no *L. conchilega* were present that year.

community structure from 1995 to 1998 parallel to a separation of *L. conchilega* associations from reference communities. Data from 2000 indicate that the temporal change in the community structure continued, but samples were taken in spring rather than autumn and seasonal effects might have biased the result.

4. Discussion

4.1. The *Lanice conchilega* population

The *L. conchilega* population experienced

dynamic changes between 1995 and 2000. It collapsed during the cold winter of 1995/1996 (Günther and Niesel, 1999), but *L. conchilega* recolonised the site in summer 1996. In 1997, the population collapsed again, but recruitment thereafter led to densities up to 4000 *L. conchilega* m⁻² in 2000.

Cold winters are known to have severe effects on *L. conchilega* populations in intertidal areas (Beukema, 1979; Crisp, 1964) and Buhr (1981) described the obliteration of a dense *L. conchilega* population in the sublittoral of the Weser estuary after an unusually cold winter. According to

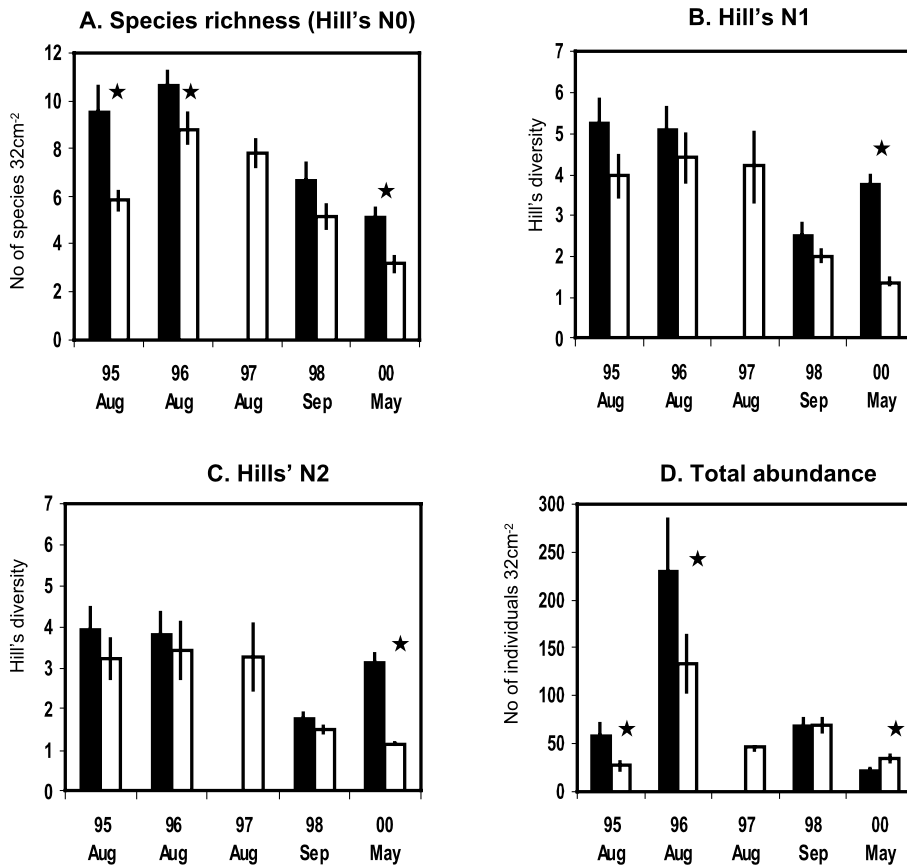


Fig. 4. Species diversity (Hill's diversity indices) and total abundance of benthic fauna in *L. conchilega* aggregations (■) and reference samples (□). Significant differences are indicated by an asterisk. In 1997, no *L. conchilega* were found.

Günther (1999) recolonisation of *L. conchilega* on the Gröninger Plate was achieved by secondary dispersal of juveniles.

The development of a dense *L. conchilega* population by 2000 was probably due to the ice-free winters of 1998/1999 and 1999/2000, which ranked among the mildest of winters for the past 100 years (Bundesamt für Seeschifffahrt und Hydrographie, 2001). High standing stocks of *L. conchilega* after several successive mild winters were also described for the Dutch Wadden Sea (Beukema, 1992). Furthermore, juvenile *L. conchilega* preferentially settle in areas already populated by *L. conchilega* (Carey, 1987; Heuers et al., 1998), which might be the cause of the thickening lawn of *L. conchilega* tubes from 1998 to 2000.

4.2. The benthic community associated with *Lanice conchilega* aggregations

Five species were found exclusively in *L. conchilega* aggregations. While the single recording of the sea anemone *S. troglodytes* in a *L. conchilega* aggregation occurred possibly by chance, other species might be dependent on the presence of *L. conchilega* tubes. The polychaete *H. lunulata*, for example, was generally found inside the tubes and *E. sanguinea* among the sand fringe. Dependence of species on biogenic structure was also reported for oyster and mussel beds (Minchinton and Ross, 1999; Ragnarsson and Raffaelli, 1999).

Species richness was found to be higher in *L. conchilega* aggregations than in tube-free areas

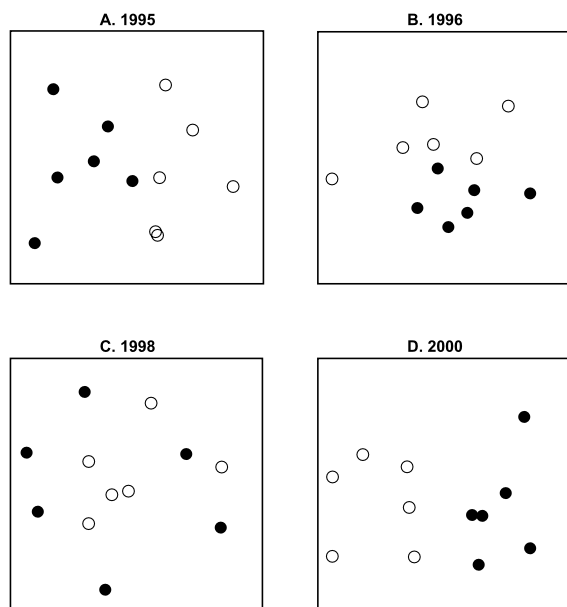


Fig. 5. MDS ordination of similarities (Bray Curtis index, $\sqrt{\sqrt{\text{data}}}$ transformation) between species assemblages of *L. conchilega* aggregations (●) and tube-free reference samples (○). (A) August 1995, stress 0.15, $p = 0.006$; (B) August 1996, stress 0.14, $p = 0.004$; (C) September 1998, stress 0.13, $p = 0.91$; and (D) May 2000, stress 0.07, $p = 0.02$.

in three of the five years investigated, and total abundance was higher in the presence of *L. conchilega* in two of the years. Higher macrofaunal densities in tube aggregations were also found by Dauer et al. (1982) and Luckenbach (1986). Other diversity indices, which take species abundances into account, showed higher diversity in the presence of *L. conchilega* only for 2000. This indicates that mainly species with low abundances contributed to the higher species richness in the *L. conchilega* community in 1995 and 1996.

4.3. Effects of tubes on the benthic community

Whether or not *L. conchilega* was responsible for differences in the faunal composition in tube aggregations in comparison to tube-free areas, or whether another underlying factor determined the distribution pattern of the *L. conchilega* community could only be tested by experimental transplantation of *L. conchilega* tubes. However, the composition of the community amongst *L. conchilega* tubes, and

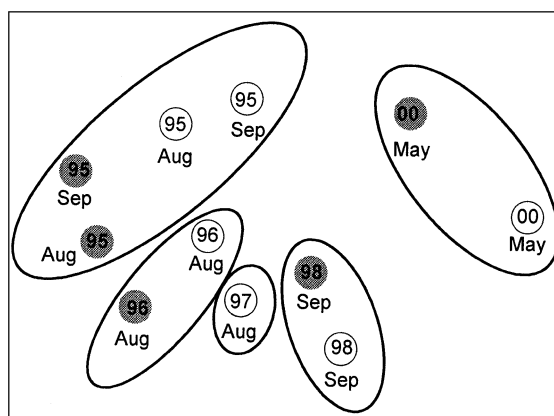


Fig. 6. MDS ordination of similarities of macrobenthic species associations of the Gröninger Plate between 1995 and 2000 (Bray Curtis index, $\sqrt{\sqrt{\text{data}}}$ -transformation of mean abundances of the respective year and month; stress 0.07). (●) Fauna in *L. conchilega* aggregations; (○) fauna in reference areas. In August 1997, no *L. conchilega* was found at the study site. The ovals group consecutive years of sampling.

evidence from other studies on effects of biogenic habitat structures suggest that tubes of *L. conchilega* add to or alter some habitat characteristics which affect the benthic community.

Similar to other structuring species, *L. conchilega* tubes provide primarily a settlement surface for larval and postlarval benthic organisms (Qian, 1999). Juvenile bivalves, *M. edulis* in particular, settle preferentially on complex habitat structures (Buhr, 1981; Dean, 1981; Bourget et al., 1994; Hunt and Scheibling, 1998; Reusch, 1998). Juvenile *M. edulis* stayed attached to the *L. conchilega* tubes for 1 year and grew to a size of 0.5–2.5 cm, forming dense clusters. However, *L. conchilega* tubes obviously did not provide secure anchorage for *M. edulis* clumps, because two years later in 1998, all mussels had disappeared. Presumably, they were uprooted and washed away by hydrodynamic forces during a storm (Harger and Landenberger, 1971; Hertweck, 1995), were subjected to predation or were removed by fisheries.

These mussel clumps might have had an adverse effect on *L. conchilega*. Remains of empty *L. conchilega* tubes were found among and underneath *M. edulis* clumps and it is assumed that they overgrew *L. conchilega* aggregations. *M. edulis* clumps can accumulate organically enriched sediment

through biodeposition of faeces and pseudofaeces (Tsuchiya and Nishihira, 1986; Kautsky and Evans, 1987), which might have buried *L. conchilega* or forced the polychaete to constantly extend its tube. A similar interaction was described for ascidians and sponges, which used bryozoans as settlement surface and smothered them through overgrowth (Russ, 1980). Furthermore, both species possibly compete for food, as Ropert et al. (1996) suggested for *L. conchilega* and *Crassostrea gigas*.

Competition for food and/or space might also have been responsible for low numbers of the polychaete *A. marioni* in 2000, when *L. conchilega* occurred in particularly high densities. Both species use detritus and diatoms on the sediment surface as a source of food (Hartmann-Schröder, 1996).

Other habitat changes associated with tube aggregations include varied sediment conditions (Feral, 1989), increased or decreased sediment stability (Eckman et al., 1981; Luckenbach, 1986) and a varied hydrodynamic and chemical regime (Aller, 1980; Friederichs et al., 2000). The sediment composition, in particular the mud content, was almost identical in *L. conchilega* aggregations and tube-free areas and hence seems unlikely to be related to differences in the faunal composition. It can only be speculated that small-scale changes of the hydrodynamic regime and the sediment stability might have had effects on the fauna.

Some species might also have benefited from improved oxygen supply in the sediment surrounding *L. conchilega* tubes. Forster and Graf (1995) suggested that *L. conchilega* acts as a piston when moving in its tube, exchanging burrow water with the overlying water. They found oxygen at all depths in the adjacent sediment along the tube. Lackschewitz and Reise (1998) drew similar conclusions for *Arenicola marina* and its associated fauna.

An important characteristic attributed to the biogenic habitat structures is their function as refuge from predation (Woodin, 1978; Crowder and Cooper, 1982; Lubchenco, 1983). This generally relates to epibenthic predators, and to my knowledge no studies have been carried out on the relationship between epibenthic fauna and *L. conchilega*. In the present study two amphipods, *G. locusta* and *M. maculatus*, were exclusively found in *L. conchilega* aggregations, which suggests that feeding conditions might even be

facilitated among *L. conchilega* tubes for species that are at least partly epibenthic.

L. conchilega aggregations certainly did not inhibit infaunal predators. The predatory polychaete *Eteone longa* was found in equally high numbers in and outside *L. conchilega* aggregations and juvenile *H. diversicolor* were found in higher numbers among *L. conchilega* tubes. *E. sanguinea*, a carnivorous polychaete, was even exclusive to *L. conchilega* aggregations. These polychaetes might prey on macrofauna but might also benefit from an enriched meiofauna, which can develop around tubes (Dauer et al., 1982; Peachey and Bell, 1997; Zühlke et al., 1998). Luckenbach (1984) suggested that among tubes of *Ditrupa cuprea* increased predation or disturbance by other associated species rather than *D. cuprea* itself caused low postlarval survival rates of some benthic species.

4.4. Ephemeral patterns

L. conchilega qualifies as an ‘ecosystem engineer’ in that it changes and/or creates a habitat, which affects other organisms (Jones et al., 1997). However, the spatial pattern of benthic fauna related to *L. conchilega* aggregations was ephemeral. It was recurrently destroyed due to breakdowns of the *L. conchilega* population, but developed rapidly after *L. conchilega* recolonisation. In this respect, polychaete tubes differ from other biogenic habitat structures. *M. edulis* communities, for example, have been reported to be relatively stable and to a great extent dependent on the age structure of the mussels (Tsuchiya and Nishihira, 1986).

Furthermore, effects of *L. conchilega* tubes on the benthic fauna seemed to be highly dependent on the species present in the surrounding sands at any one time and on their susceptibility to tube effects. Changes in this species composition increased or decreased the engineering force of *L. conchilega*.

5. Conclusion

The results of this study indicate that *L. conchilega* tube aggregations have a marked, but often short-lived effect on the benthic community. Tube aggregations create ecological islands, which generally host a more

diverse and abundant fauna and hence contribute to a patchy distribution pattern of the benthic community. However, in comparison with other habitat-structuring species such as mussels, patterns are more dynamic and ephemeral. Given the dynamic changes in density of the *L. conchilega* population and the susceptibility of the *L. conchilega* community to changes in the species assemblage outside tube aggregations, *L. conchilega* seems to be a moderately influential ecosystem engineer in intertidal sandflats of the Wadden Sea.

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