Senckenbergiana maritima | 29 | (1/6) | 131–138 | Frankfurt am Main, 15. 12. 1998

Effects of the Tube-Building Polychaete *Lanice conchilega* (PALLAS) on Benthic Macrofauna and Nematodes in an Intertidal Sandflat

RUTH ZÜHLKE & DIETRICH BLOME & KARL HEINZ VAN BERNEM & SABINE DITTMANN

With 4 Text-Figures and 2 Tables

Key words: *Lanice conchilega*, tube-dwelling, biogenic habitat structures, arificial tube fields, benthic macrofauna, Nematodes.

Abstract

[ZÜHLKE, R. & BLOME, D. & VAN BERNEM, K. H. & DITTMANN, S. (1998): Effects of the tube building polychaete *Lanice conchilega* (PALLAS) on benthic macrofauna and nematodes in an intertidal sandflat. – Senckenbergiana marit., **29** (1/6): 131–138, 4 figs., 2 tabs.; Frankfurt a. M.]

Biogenic habitat structures play a major role for distribution patterns of benthic fauna. Tube-dwelling polychaetes provide one of the main features in the otherwise relatively low structured sandy intertidal. The aim of this study was to investigate the effect of the tube-dwelling sand-mason *Lanice conchilega* on macrofauna and nematodes in an intertidal sandflat in the Wadden Sea area off the German coast. Field studies and experiments were carried out on the associated macrobenthic fauna of natural *L. conchilega* aggregates and of artificial tubes. Furthermore, the distribution of nematode species at increasing distances along transects arising from individual *L. conchilega* tubes, was investigated.

Natural as well as artificial tubes had positive effects on numbers of macrofaunal species and individuals. Yet, juvenile *Mya arenaria* were the only species appearing in higher numbers in both *L. conchilega* aggregates and artificial tube fields. They used the tube structure to attach themselves with their byssus threads. The polychaete *Malmgreniella lunulata* only occurred in natural *L. conchilega* aggregates and was often found inside the polychaetes' tubes. It is possibly a commensal associated to *L. conchilega*. In artificial tube fields, opportunistic spionids and *Capitella capitata* settled in higher numbers. This might be due to colonisation of sediment accumulating in the tube fields, utilisation of the tubes as an attachment surface or refuge from predation. However, two predatory polychaetes, *Eteone longa* and *Nereis diversicolor*, were also found in higher abundance in natural or artificial tube fields.

Nematode abundances were considerably higher next to individual *L. conchilega* tubes at a distance of 0.5 cm. This distribution was mainly caused by a group of threadlike species with a thin cuticle, which are thought to be adapted to epidermal uptake of dissolved organic matter.

It is suggested that there might be a linkage between predatory polychaetes and the distribution pattern found for nematodes around the tubes of *L. conchilega.*

Authors' addresses:
R. ZÜHLKE, University of Swansea, School of Biological Science, Singleton Park, Swansea, SA2 8PP, Great Britain. – D. BLOME, Universität Hamburg, Institut für Hydrobiologie und Fischereiwissenschaft, Zeiseweg 9, D-22765 Hamburg, Germany. – K. H. VAN BERNEM, GKSS-Forschungszentrum Geesthacht, Postfach 1160, D-21494 Geesthacht, Germany. – S. DITTMANN, Forschungszentrum Terramare, Schleusenstraße 1, D-26382 Wilhelmshaven, Germany.

Introduction

The effects of habitat complexity in the benthic system are widely appreciated (Bell 1991). Especially in rather low structured soft sediments, biotic features play a major role for species diversity and distribution patterns. Besides macroalge, mussel- and seagras beds, polychaete dwelling tubes are regarded as a main habitat structure in the intertidal (Bandeira 1995; Everett 1991; Sebens 1991). They potentially modify small-scale hydrodynamics (Eckmann et al. 1981), provide an attachment surface for filamentous algae (Schories & Reise 1993) or serve as a refuge from predation (Woodin 1978). Along the Wadden Sea coast *Lanice conchilega* is the most conspicuous widely distributed tube-dweller which forms extensive populations with densities of up to several thousand individuals per m^2 (Buhr & Winter 1976). The goal of our study was to evaluate (1) whether certain species and functional groups are affected by *L. conchilega* tube aggregates, (2) whether effects are due to the physical structure only and 3) whether effects on the macrofauna and nematodes show any correlation.

Material and Methods

Study Site

Benthic species assemblages associated with *Lanice conchilega* were studied in 1995 at the Gröninger Plate, an intertidal sandflat between the coastline of Lower Saxony, Germany, and the backbarrier island of Spiekeroog (Fig. 1). The northern part of the Gröninger Plate was characterized by a *L. conchilega* population with densities of about 1,000 ind./m^2. The small-scale distribution pattern of *L. conchilega* was patchy: *L. conchilega*-aggregates of approximately 1–5 m^2 alternated with tube-free areas of about the same size. This distribution pattern created a surface structure of gentle mounds with tube-aggregates and shallow depressions in the spaces between.

A field experiment with artificial tubes was carried out in the vicinity of the *L. conchilega* area at a distance of about 100 m.

Faunal Sampling

Macrofauna in *Lanice conchilega*-Aggregates

In August and September 1995 (31.08., 25.09.) samples were taken from randomly chosen *L. conchilega*-aggregates and intermediate *L. conchilega*-free areas. To avoid pseudoreplication (Hurlbert 1984) just one sample was taken from each aggregate or tube-free area. Samples were taken with a corer of 0.32 cm^2 surface area to a sediment depth of 10 cm. On each sampling day, six replicates were taken from *L. conchilega*-aggregates and intermediate tube-free areas respectively. The samples were taken to the laboratory and sieved using a 0.5 mm mesh. Species of the unpreserved samples were sorted, identified to the lowest practical taxonomic unit and counted.

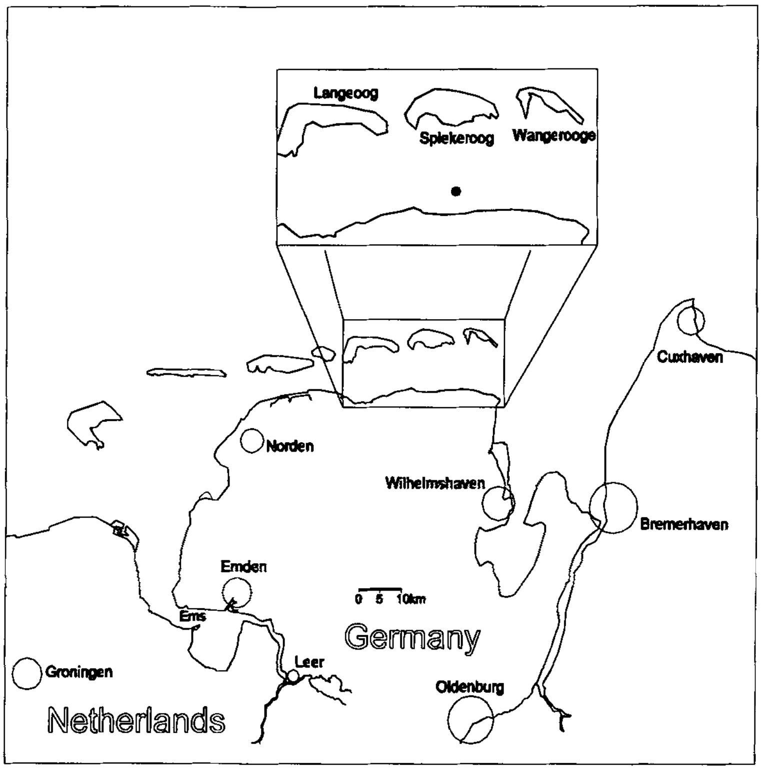

Fig. 1. Location of study site Gröniger Plate (•) between the German coastline and the island of Spiekeroog.

Fig. 2. One of six 1 m^2 fields with 1000 artificial tubes.

Macrofauna in Artificial Tube Fields

In July 1995 six 1 m^2 fields with artificial tubes were established (Fig. 2). Each field consisted of 1,000 metal sticks, 25 cm long with a diameter of 4 mm. They were inserted into the sediment with the upper 2–3 cm protruding from the surface. To take into account the possible impact of the metal, three fields were established with artificial tubes inserted flush with the surface. Furthermore, seven untreated reference fields were staked out. All field variations (artificial tubes, references, controls) were randomly distributed in an area of about 500 m^2. Samples were taken in August and September 1995 (22.08., 12.09.). On each sampling day one sample was taken from every field. Sample size and treatment were as described above. An increase in surface height within the artificial tube fields occurred due to sediment trapping or sedimentation. The increase ranged between 1–3 cm. To avoid covering of the artificial tubes they were regularly adjusted.

Nematodes

Nematodes associated to *Lanice conchilega* tubes with living worms inside were sampled on 15 September 1995. For sampling nematodes, sediment cores were gathered along six transects arising from three *L. conchilega* tubes (two transects each tube) using drinking straws of 0.5 cm diameter (0.2 cm^2 area). Up to a distance of 2 cm from the tubes the straws were inserted into the sediment to a depth of 5 cm. Controls were sampled in the transects at distances of 5 and 10 cm (5 replicates each). All corresponding samples were treated as replicates. Furthermore reference samples were taken in the vicinity of the *L. conchilega* area.

The samples were fixed in 4% formaldehyde (bulk fixation) immediately after retrieval. The total meiofauna was extracted using a beaker, suspending the sediment cores and decanting the fauna. Nematodes were separated and mounted in unhydrous glycerine after dehydration.

Data Analysis

The univariate Mann-Whitney-U-Test was applied to test for differences between numbers of individuals of natural as well as artificial tube fields and their respective references or controls. Additionally differences between species assemblages were tested using the multivariate ANOSIM (CLARKE & WARWICK 1994). Multivariate analysis was carried out using the PRIMER software.

Results

Macrofauna

The macrobenthic fauna at the Gröninger Plate consisted mainly of polychaetes (65–80%) and bivalves (20–30%). Densities of *L. conchilega* varied in aggregates between 600 and 1,800 ind./m^2. The associated fauna of *L. conchilega* was numerically dominated by small species such as the polychaete *Pygospio elegans* or *Tharyx killariensis* and juveniles of the bivalve *Mya arenaria*.

Lanice conchilega-Aggregates

The overall mean macrobenthic abundance as well as total and mean numbers of species were higher in *L. conchilega* aggregates than in the intermediate *L. conchilega* free areas (Tabs 1–2). Altogether about 20 species were identified in *L. conchilega* aggregates whereas only 12 species occurred in the intermediate tube free areas. Mainly mobile polychaete species were missing like *Eumida* spp. or *Scoloplos armiger*, but also tubificoid oligochaetes and amphipodes.

Bivalve abundance was generally higher in *L. conchilega* aggregates whereas overall polychaete abundance was not found to be significantly higher in *L. conchilega* aggregates on either sampling date.

At species level two bivalves and two polychaetes were found to be more abundant in *L. conchilega* aggregates. High numbers of juvenile *Mytilus edulis* and *Mya arenaria* were attached to the tentacle crowns. The predatory polychaete *Eteone longa* appeared in significantly higher abundance in Sep-

Table 1. Mean numbers (per 0.01 m^2) of the most abundant macrobenthic species of *Lanice conchilega* aggrregates and experimental fields with artificial tubes. – Standard deviations are given in parenthesis. Numbers of species were calculated from the original sample size of 32 cm^2. – Functional groups: (F) filterfeeder; (S) surface-feeder; (SS) subsurface-feeder; (C) commensal to *L. conchilega*; (P) predator; (O) omnivor.

	L.conchilega aggregates (LA)/ *L.conchilega* free areas (REF)				Artificial tube fields (ATF)/ Tube free areas (REF)/ Controll with totally inserted tubes (CON)					
	Aug.		Sep.		Aug.			Sep.		
	LA	REF	LA	REF	ATF	REF	CON	ATF	REF	CON
Lanice conchilega (Pallas, 1766)	6.3 (3.4)	-	11.5 (6.5)	-	-	1.8 (2.5)	0.5 (1.3)	0.5 (1.3)	0.4 (1.2)	-
Mytilus edulis (F)$^{(1)}$ Linné	3.6 (3.1)	1.0 (1.6)	3.1 (2.8)	-	10.4 (7.8)	3.1 (7.0)	1.6 (2.6)	8.9 (11.4)	1.3 (2.5)	2.1 (3.6)
Cerastoderma edule (F) (Linné)	4.2 (3.2)	6.3 (3.4)	3.1 (3.4)	4.7 (7.3)	1.0 (1.6)	0.9 (1.5)	0.5 (1.3)	1.6 (1.7)	0.9 (2.4)	1.0 (1.8)
Macoma balthica (S) (Linné)	3.6 (5.0)	2.1 (3.8)	2.6 (3.7)	0.5 (1.3)	-	-	-	-	0.4 (1.2)	-
Mya arenaria (F) Linné	33.9 (17.9)	4.7 (4.7)	28.6 (23.7)	4.2 (5.1)	6.8 (3.1)	1.3 (2.5)	0.5 (1.3)	6.3 (4.4)	0.9 (2.4)	8.3 (4.8)
Malmgreniella lunulata (C) (Delle Chiaje, 1841)	2.6 (2.4)	-	5.7 (4.2)	-	-	-	-	0.5 (1.3)	-	-
Eteone longa (P) (Fabricius, 1780)	0.5 (1.3)	0.5 (1.3)	5.7 (5.7)	0.5 (1.3)	0.5 (1.3)	-	0.5 (1.3)	-	-	1.0 (1.8)
Phyllocode mucosa (P) (Oersted)	0.5 (1.3)	-	-	-	-	-	-	-	-	-
Eumida sanguinea (P) (Oersted, 1843)	0.5 (1.3)	-	2.1 (2.6)	-	-	-	-	-	-	-
Nereis diversicolor (O) O.F. Müller, 1776	1.6 (3.8)	-	-	-	3.6 (4.2)	-	0.5 (1.3)	0.5 (1.3)	-	-
Nephtys hombergi (P) Savigny, 1818	3.6 (4.2)	0.5 (1.3)	1.6 (1.7)	-	1.6 (1.7)	-	1.6 (1.7)	0.5 (1.3)	0.4 (1.2)	-
Pygospio elegans (S) Claparède, 1863	85.4 (62.1)	37.0 (22.7)	30.7 (24.1)	15.6 (12.7)	94.3 (77.1)	23.2 (21.9)	19.8 (17.8)	78.6 (55.0)	17.4 (10.8)	28.1 (17.4)
Polydora cornuta (S) Bosc	9.4 (11.9)	0.5 (1.3)	1.0 (2.6)	-	14.6 (5.8)	0.4 (1.2)	-	4.2 (6.8)	0.4 (1.2)	-
Tharyx killariensis (S) (Saint-Joseph, 1894)	27.1 (22.6)	24.5 (17.5)	29.7 (19.8)	27.6 (26.0)	3.6 (4.6)	4.0 (8.0)	2.1 (2.6)	10.4 (5.8)	4.0 (4.3)	5.2 (6.5)
Capitella capitata (SS) (Fabricius, 1780)	4.7 (1.7)	1.6 (1.7)	0.5 (1.3)	1.6 (1.7)	45.3 (33.7)	3.1 (4.0)	3.6 (3.7)	22.9 (14.9)	0.4 (1.2)	7.3 (12.6)
Heteromastus filiformis (SS) (Claparède, 1864)	-	2.1 (2.6)	0.5 (1.3)	2.1 (2.6)	-	-	-	0.5 (1.3)	-	-
Mean total number of individuals	192.2 (106.0)	81.3 (34.0)	137.5 (69.4)	59.9 (28.0)	182.3 (74.2)	38.4 (28.3)	32.8 (21.0)	141.1 (78.0)	32.6 (13.5)	57.3 (41.3)
Mean number of individuals, *L.conchilega* excluded	185.9 (85.1)	81.3 (34.0)	126.0 (70.3)	59.9 (28.0)	182.3 (74.2)	38.4 (28.3)	32.3 (20.5)	140.6 (78.4)	32.1 (13.9)	57.3 (41.3)
Mean number of species	10.5 (2.6)	5.8 (1.0)	11.0 (2.9)	5.0 1.2)	7.2 (1.3)	3.1 (1.8)	4.4 (2.2)	7.0 (1.8)	4.0 (1.9)	4.2 (2.0)
Total number of species	21	12	22	12	11	9	12	16	15	10

tember, *Malmgreniella lunulata* at both sampling dates. The latter was regularly found inside the *L. conchilega* tubes whereas no individual was found in the intermediate tube-free areas. Mean abundances of the spionid polychaete *P. elegans* were at least twice as high in *L. conchilega* aggregates as in the intermediate areas. However, due to high variations the differences were not significant. No difference was found for several other abundant species like *T. killariensis*, *Capitella capitata* or *Nephtys hombergi* and no species had higher abundance in the intermediate *L. conchilega* free areas.

Table 2. Mann-Whitney-U-Test results of pairwise comparisons of species abundances or groups of species and ANOSIM results of multivariate comparisons between species assemblages (Bray Curtis index, $\sqrt{}^2$ data transformation). – Tests were conducted between the macrobenthic fauna of (1) *L. conchilega* aggregates and adjacent *L. conchilega* free areas; (2) experimental fields with artificial tubes and tube-free reference areas. Significantly higher numbers in *L. conchilega* aggregates or artificial-tube-fileds: *: $p<0.05$; **: $p<0.01$; ***: $p<0.005$; – no significant difference, – – species not found. Classification of species is shown in Tab. 1.

	L.conchilega-aggregates/ *L.conchilega*-free areas		Artificial tube fields/ Tube-free areas	
	Aug.	Sept.	Aug.	Sept.
ANOSIM	**	**	**	***
Total individuals	*	*	***	***
Total number of species	***	***	***	*
Number of polychaete species	*	*	**	*
Taxonomical Groups				
Bivalves	*	*	*	*
Polychaetes	-	-	***	***
Functional groups(1)				
Surface feeders	-	-	**	*
Subsurface feeders	-	-	***	**
Predators	-	*	-	-
Filter feeders	*	*	*	-
Species				
Mytilus edulis	-	*	-	-
Mya arenaria	**	**	**	*
Malmgreniella lunulata	*	**	--	-
Eteone longa	-	*	--	-
Nereis diversicolor	-	--	*	-
Pygospio elegans	-	-	**	**
Polydora cornuta	-	-	***	-
Capitella capitata	-	-	***	***

Considering functional groups, filterfeeders and predators were more abundant in *L. conchilega* aggregates. The numerically dominating species of these groups were *M. arenaria* and *E. longa* respectively.

The multivariate test ANOSIM (Tab. 2) indicated a significant difference between the faunal assemblages. The corresponding MDS-Plot (Fig. 3) showed a separation of samples from *L. conchilega* aggregates and intermediate *L. conchilega* free areas.

Artificial Tubes

As in natural *Lanice conchilega* aggregates, mean individual abundances and mean numbers of species were significantly higher in the experimental fields with artificial tubes than in untreated reference areas (Tab. 2). In contrast to natural tube areas the total number of species did not differ markedly in comparison to the reference fields. No differences in terms of numbers of species or individual abundance were found between the untreated reference areas and control fields, with *M. arenaria* being the exception in September 1995 (Tab. 1).

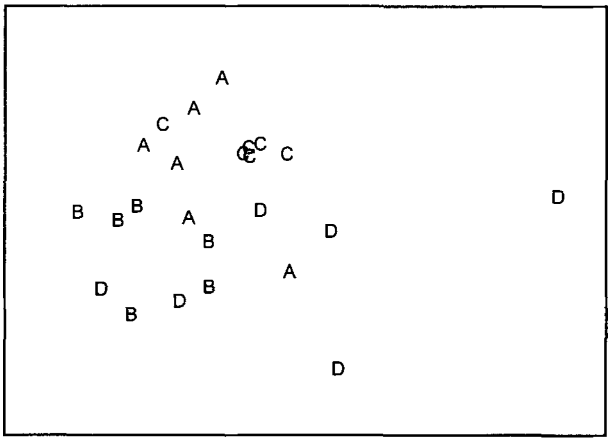

Fig. 3. MDS plot for faunal assemblages of *L. conchilega* aggregates and artficial tube fields, August 1995; stress 0.18 (Bray Curtis index, $\sqrt{}^2$ data transformation). – (A) *L. conchilega* aggregates; (B) Intermediate *L. conchilega* free areas; (C) Artificial tube fields; (D) Reference fields.

In artificial tube fields both polychaete and bivalve abundances were significantly higher than in reference areas. Altogether five species, four polychaetes and one bivalve, were found in higher numbers in artificial tube fields. Mainly juvenile forms smaller than 0.5 cm of *P. elegans* and *C. capitata* were found in higher numbers on both sampling dates; *Polydora cornuta* and *Nereis diversicolor* appeared in higher numbers in August only. Juvenile *M. arenaria* settled preferably at the protruding part of the metal sticks.

The most affected functional groups were surface and subsurface feeders, which was due to the high numbers of the above mentioned spionid polychaetes and *C. capitata*. Similar to the *L. conchilega* aggregates filterfeeders were more abundant in artificial tube fields. This was related to high abundance of *M. arenaria*, although their overall numbers were considerably lower in the artificial than in the natural tube aggregates.

The multivariate comparison (ANOSIM) showed a significant difference between species' assemblages of artificial tube fields and reference fields which is visualized by distinctly separated groups of samples in the MDS plot (Fig. 3). The figure furthermore indicates that the fauna of the artificial tube fields was similar to the natural aggregates.

Nematodes

Nematodes showed considerably higher abundances in samples immediately next to individual *Lanice conchilega* tubes than in controls or in the ambient sandflat without *L. conchilega* tubes. At a distance of 0.5 cm from the tubes 182±171 ind./0.2 cm^2 were found (Fig. 4) – about five times as many as in the vicinity of the *L. conchilega* area with densities of 34.5±14.9 ind./0.2 cm^2. The latter value corresponds to a mean nematode abundance of 34±15 ind./0.2 cm^2 at 5 cm distance from the tubes, serving as control together with samples from 10 cm distance, revealing a value of 58±38 ind./0.2 cm^2.

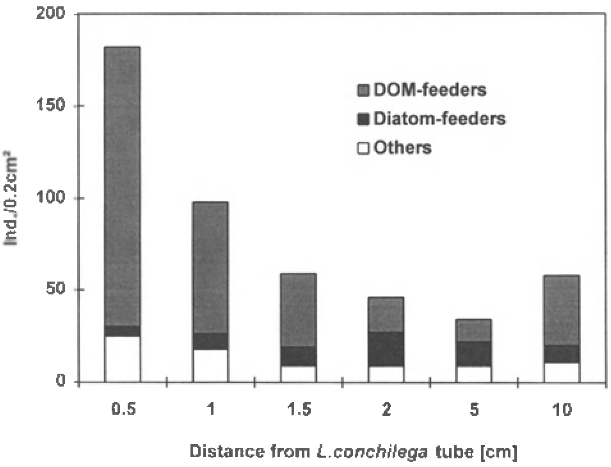

Fig. 4. Mean numbers of nematodes along a transect arising from *L. conchilega* tubes (n = 6).

The nematode density rapidly decreased within 2 cm distance from the worm tube. From about 1.5 cm distance with mean nematode densities ranging from 59±30 to 46±15 ind./0.2 cm², values were similar to the background level.

This general trend was especially due to a group of nematodes characterized by a very long and slender (threadlike) habitus (GIERE 1993) with a thin and weak cuticle. This life form is considered to be an adaptation to epidermal uptake of dissolved organic matter (DOM) (JENSEN 1987). The dominant species of this group were Linhomoeidae like *Metalinhomoeus biformis*, *M. typicus*, *Paralinhomoeus ilenensis* and *P. lepturus*, Molgolaimidae (*Molgolaimus cuanensis*), Microlaimidae like *Calomicrolaimus honestus*, *Calomicrolaimus* sp., *Microlaimus conothelis*, finally *Odontophora rectangula* and, perhaps, *O. armata*.

A reverse trend of higher densities with increasing distance from *L. conchilega* tubes became apparent for another group of nematodes sharing a common food resource: diatoms. Dominant species of this group were *Chromadoropsis vivipara*, *Daptonema oxycerca*, and *D. setosum*.

Discussion

This study showed significant effects of the tubes built by the polychaete *Lanice conchilega* on the distribution of macrofaunal species and meiobenthic nematodes. Effects on macrofauna were confirmed by the experiment with artificial tubes.

Macrofauna

Natural as well as artificial tubes were accompanied by higher numbers of species and individuals in comparison with tube free reference areas. WOODIN (1978) described similar findings when comparing the effect of *Diopatra cuprea* tubes and plastic straws and concluded that physical and biogenic entities affected infaunal abundance in the same way. However, in this study, juvenile *Mya arenaria* were the only species appearing in higher numbers with both *L. conchilega* aggregates and artificial tubes. Most other species appearing in higher numbers in artificial tube fields were opportunistic polychaetes, whereas natural *L. conchilega* aggregates were inhabited by higher numbers of a potentially commensal polychaete and juvenile *Mytilus edulis*. Furthermore, two predatory polychaetes were found in higher abundance: *Eteone longa* in the *L. conchilega* aggregates and *Nereis diversicolor* in artificial tube fields.

Juvenile *M. arenaria* and *M. edulis* used the tube structures as a primary settlement surface. Both bivalves are able to anchor in the sediment or attach to hard substratum with byssus-threads (GÜNTHER 1992; LINKE 1939).

Malmgreniella lunulata was the only species presumably exhibiting an interspecific relationship to *L. conchilega*. Numerous individuals of the mobile polychaete were found in *L. conchilega* aggregates but none in fields with artificial tubes or reference areas. HARTMANN-SCHRÖDER (1996) mentioned that *M. lunulata* lives as a commensal to other polychaetes including *L. conchilega*. It was found regularly inside *L. conchilega* tubes (pers. observation). The artificial tubes were not hollow, which might have distorted the result. The exact character of the relationship between *L. conchilega* and *M. lunulata* still remains unclear.

Higher numbers of opportunistic polychaetes in artificial tube fields were presumably mainly related to sediment accumulation inside the experimental fields. *P. elegans*, *P. ligni* and *C. capitata* are all known to be primary colonizers (MCCALL 1977; GRASSLE & GRASSLE 1974). They might either be passively trapped, as ECKMANN (1979) suggests for *Tanais* sp. and *Manayunkia aestuarina* around simulated tubes, or migrate actively (ARMONIES 1994). Just as the already mentioned bivalves, they might also use tubes as a settlement substrate, as BELL & COEN (1982b) found for *P. ligni*.

They presumably also benefit from decreased predatory pressure as WOODIN (1978) stated in her refuge-hypothesis. *P. elegans* for example is exposed to damage from 0-group plaice and flounder (MUUS 1967) which were certainly inhibited in their preying activities by the artificial tubes. Weaker sediment trapping and less effective refuge from predation by the more flexible natural *L. conchilega* tubes can explain the moderate effect of *L. conchilega* aggregates on the surface- and subsurface feeding opportunistic polychaetes. Again, the studies of WOODIN (1978) and own observations at sites with higher *L. conchilega* densities showed that spionids can also be affected by natural tube aggregates.

While tube structures provide shelter from epibenthic predation, endobenthic predatores have access to abundant prey. In our study the predatory polychaetes *E. longa* and *N. diversicolor* were found in higher numbers in natural or artificial tube aggregates, respectively. Thus, tube aggregates are by no means perfect refuges from predation.

Nematodes

Effects of macrofaunal burrows, tubes or trails on meiofauna organisms have been reported from tidal flats around the world (BELL & COEN 1982a, b; DITTMANN 1996; REIDENAUER 1989). Especially small-scale differences in distribution of meiofauna, and thereof nematodes, with polychaetes are well documented (ALONGI 1985; BELL 1983; JENSEN 1980, 1983; Reise 1981a; Warwick et al. 1986) and the *Arenicola marina*-system of the German Wadden Sea became a classic case (Reise 1981b, 1985, 1987; Scherer 1985; Wetzel et al. 1995). Wetzel et al. (1995) provide data on nematode species from the tail shaft of *A. marina* and report distribution patterns similar to those found in this study, for both total numbers of nematodes and the groups "slender nematodes" (DOM-feeders) and "stout nematodes" (diatom feeders).

L. conchilega potentially produce bromophenols (Goerke & Weber 1990, 1991), which are known to negatively effect meiofauna (Alongi 1987; Jensen et al. 1992; Steward et al. 1992). Prior to the investigations it was hypothesized that nematode distribution patterns might correspond to concentrations of this substance. However, sediment samples revealed that bromophenol concentrations were of the same level as in the water column and showed no gradient associated to *L. conchilega* tubes (unpubl. own data). Due to these results and high nematode abundance close to the *L. conchilega* tubes it appears to be most unlikely that bromophenols had any effect on the nematode distribution pattern.

Nematodes might have utilized the dwelling tubes themselves as a nutrient source e.g. polypeptides or polysacharides (Franke 1994) or benefited from improved oxygen conditions through ventilation activities of *L. conchilega*.

Nematode-Macrofauna Relationship

Dauer et al. (1982) found significantly higher numbers of nematodes in experiments with artificial tubes and concluded that this was due to spatial refuge from macrofaunal predation. Schubert & Reise (1986) and Muus (1967) mentioned that juvenile *Nephtys hombergi* and *N. diversicolor* possibly prey on nematodes. Thus, the distribution of endobenthic predators could be related to higher numbers of nematodes associated with tube structures.

In our study, the predatory polychaetes *E. longa* was more abundant in natural tube fields. This suggests that endobenthic predators might benefit from high nematode densities.

Tubes may be an obstacle for subsurface predation as well, which might explain the higher numbers of nematodes in the immediate vicinity of the tubes, in addition to a distribution of food resources for nematodes.

However, several studies on the effect of tube structures could not find a clear correspondence between meio- and macrofaunal results (Bell & Woodin 1984; Dauer et al. 1982) and the same certainly applies to the findings of this investigation. Further studies are needed to resolve meio- and macrobenthic interactions on the various spatial scales of this intertidal assemblage.

Acknowledgements

Special thanks to Ingrid Linkenbach who diligently assisted the macrofaunal part of the project, Michael Grotjahn for his support and to the Company Gerdes & Wenk (Norden, Germany), which donated 10.000 metal sticks for the experiment.

This work was supported by the Bundesministerium für Bildung, Wissenschaft, Forschung und Technologie (BMBF) under grant 03F0112A. Responsibility for the content of this publication rests with the authors. This is publication number 245 of the "Ecosystem Research Wadden Sea".

References

Alongi, D. M. (1985): Microbes, meiofauna, and bacterial productivity on tubes constructed by the polychaete *Capitella capitata*. – Mar. Ecol. Progr. Ser., **23**: 207–208.

– – – M. (1987): The influence of mangrove-derived tannins on intertidal meiobenthos in tropical estuaries. – Oecol., **71**: 537–540.

Armonies, W. (1994): Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. – Helgoländer Meeresunters., **48**: 299–320.

Bandeira, S. O. (1995): Marine botanical communities in southern Mozambique: Sea grass and seaweed diversity and conservation. – Ambio, **24** (7–8): 506–509.

Bell, S. S. (1983): An experimental study of the relationship between below-ground structure and meiofaunal taxa. – Mar. Biol., **76**: 33–39.

– – – (1991) [Ed.]: Habitat Structure. – (Chapmann & Hall).

Bell, S. S. & Coen, L. D. (1982a): Investigations on Epibenthic Meiofauna I. Abundances on and Repopulation of the Tube-Caps of *Diopatra cuprea* (Polychaeta: Onuphidae) in a Subtropical System. – Mar. Biol., **67**: 303–309.

– & – (1982b): Investigations on epibenthic meiofauna. II. Influence of microhabitat and macrolgae on abundance of small invertebrates on *Diopatra cuprea* (BOSC) (Polychaeta: Onuphidae) tube-caps in Virginia. – J. exper. mar. Biol. Ecol., **61**: 175–188.

Bell, S. & Woodin, S. (1984): Community unity: Experimental evidence for meiofauna and macrofauna. – J. mar. Res., **42**: 605–632.

Buhr, K. J. & Winter, J. E. (1976): Distribution and maintenance of a *Lanice conchilega* association in the Weser estuary (FRG), with special reference to the suspension-feeding behaviour of *Lanice conchilega*. – In: Keegan, B. F. & O'Ceidigh, P. O. & Boaden, P. J. S. [Eds.]: Biology of Benthic Organisms: 101–113; (Pergamon Press).

Clarke, K. R. & Warwick, R. M. (1994): Changes in Marine Communities: an Approach to Statistical Analysis and Interpretation. – 144pp.; (Natural Environmental Research Council, UK).

Dauer, D. M. & Tourtelotte, G. H. & Ewing R. M. (1982): Oyster shells and artificial worm tubes: The role of refuges in structuring benthic communities of the Lower Chesapeake Bay. – Int. Rev. ges. Hydrobiol., **67** (5): 661–677.

Dittmann, S. (1996): Effects of macrobenthic burrows on infaunal communities in tropical tidal flats. – Mar. Ecol. Progr. Ser., **134**: 119–130.

Eckmann, J. E. (1979): Small-scale patterns and processes in a soft-substratum, intertidal community. – J. mar. Res., **37**: 437–457.

Eckmann, J. E. & Nowell, A. R. M. & Jumar, P. A. (1981): Sediment destabilisation by animal tubes. – J. mar. Res., **39**: 361–374.

Everett, R. A. (1991): Intertidal distribution of infauna in a central California lagoon: the role of seasonal blooms of macroalgae. – J. exper. Biol. Ecol., **150**: 223–247.

Franke, P. (1994): *Lanice*-Zement: ein calciumstabilisierter Heteropolymer. – (unpubl.)

Giere, O. (1993): Meiobenthology. The Microscopic Fauna in Aquatic Sediments. – Berlin (Springer).

Goerke, H. & Weber, K. (1990): Locality-dependent concentrations of bromophenols in *Lanice conchilega* (Polychaeta: Terebellidae). – Comp. Biochem. Physiol., **97B**: 741–744.

– & – (1991): Bromophenols in *Lanice conchilega* (Polychaeta, Terebellidae): the influence of sex, weight and season. – Bull. mar. Sci., **48**: 517–523.

Grassle, J. F. & Grassle, J. P. (1974): Opportunistic life histories and genetic systems in marine benthic polychaetes. – J. mar. Res., **32**: 253–284.

Günther, C. P. (1992): Settlement and recruitment of *Mya arenaria* L. in the Wadden Sea. – J. exper. mar. Biol. Ecol., **159**: 203–215.

Hartmann-Schröder, G. (1996): Die Tierwelt Deutschlands, Polychaeta. – 648 pp.; Jena (Fischer).

Hurlbert, S. H. (1984): Pseudoreplication and the design of ecological field experiments. – Ecol. Monogr., **72**: 93–102.

Jensen, P. (1980): Description of the marine free-living nematode *Chromadora lorenzeni* n. sp. with notes on its microhabitats. – Zool. Anz., **205**: 213–218.

– – – (1983): Meiofaunal abundance and vertical zonation in a sublittoral soft bottom, with a test of the Haps corer. – Mar. Biol., **74**: 319–326.

– – – (1987): Differences in microhabitat, abundance, biomass and body size between oxybiotic and thiobiotic free-living marine nematodes. – Oecol., **71**: 564–567.

Jensen, P. & Emrich, R. & Weber, K. (1992): Brominated metabolites and reduced numbers of meiofauna organisms in the burrow wall lining of the deep-sea enteropneust *Stereobalanus canadensis*. – Deep-Sea Res., **39**: 1247–1253.

Linke, O. (1939): Die Biota des Jadebusenwattes. – Helgol. wiss. Meersesunters., **1** (3): 201–348.

McCall, P. C. (1977): Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. – J. mar. Res., **35** (2): 221–266.

Muus, B. J. (1967): The fauna of Danish estuaries and lagoons: distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. – Medd. Danm. Fiskeri Havunders., **5** (1): 1–316.

Reidenauer, J. A. (1989): Sand-dollar *Mellita quinqiesperforata* (Leske) burrow trails: Site of harpacticoid disturbance and nematode attraction. – J. exper. mar. Biol. Ecol., **130**: 223–235.

Reise, K. (1981a): High abundance of small zoobenthos around biogenic structures in tidal sediments of the Wadden Sea. – Helgol. Meeresunters., **34**: 413–425.

– – – (1981b): Gnathostomulida abundant alongside polychaete burrows. – Mar. Ecol. Progr. Ser., **6**: 329–333.

– – – (1985): Tidal Flat Ecology. – 191 pp; Berlin (Springer).

– – – Spatial niches and long-term performance in meiobenthic Plathelminthes of an intertidal lugworm flat. – Mar. Ecol. Progr. Ser., **38**: 1–11.

Scherer, B. (1985): Annual dynamics of a meiofauna community from the sulfide layer of a North Sea sand flat. – Microfauna mar., **2**: 117–161.

Schories, D. & Reise, K. (1993): Germination and anchorage of Enteromorpha spp. in sediments of the Wadden Sea. – Helgol. Meeresunters., **47**: 275–285.

Schubert, A. & Reise, K. (1986): Predatory effects of *Nephtys hombergii* on other polychaetes in tidal flat sediments. – Mar. Ecol. Progr. Ser., **34**: 117–124.

Sebens, K. P. (1991): Habitat structure and community dynamics in marine benthic systems. – In: Bell, S. S. [Ed.]: Habitat Structure: 211–234; (Chapmann & Hall).

Steward, C. C. & Pinckney, J. & Piceno, Y. & Lovell, C. R. (1992): Bacterial numbers and activity, microalgal biomass and productivity, and meiofaunal distribution in sediments naturally contaminated with biogenic bromophenols. – Mar. Ecol. Progr. Ser., **90**: 61–71.

Warwick, R. M. &. Gee, J. M & Berge, J. A. & Ambrose Jr, W. (1986): Effects of the feeding activity of the polychaete *Streblosoma bairdi* (Malmgren) on meiofaunal abundance and community structure. – Sarsia, **71**: 11–16.

Wetzel, M. A. & Jensen , P. & Giere, O. (1995): Oxygen/sulfide regime and nematode fauna associated with *Arenicola marina* burrows: new insights in the thiobios case. – Mar. Biol., **124**: 301–312.

Woodin, S. A. (1978): Refuges, disturbance, and community structure: a marine soft-bottom example. – Ecol., **59** (2): 274–284.

Submitted: 12.09.1997
Reviewed: 15.10.1997
Accepted: 14.11.1997