52

Influence of the tube-building spionid polychaete *Polydora ciliata* on benthic parameters, associated fauna and transport processes

Carola Ilse-Marie NOJI

Institute of Fisheries and Marine Biology University of Bergen
Thormøhlensgt 55, N-5008 Bergen, Norway
& Institute of Marine Research
P.O. Box 1870, N-5024 Bergen, Norway

ABSTRACT

The influence of the tube-building spionid *Polydora ciliata* Johnston on benthic community, sediment properties and exchange processes through the sediment surface was investigated. Findings showed that spionid tube lawns (eight or more tubes. cm^{-2}) lowered sediment stability and enhanced accumulation of suspended particles. Organic matter was selectively transported into the sediment via feeding, which enriched sediments by up to 100 %. Only a slight increase in fluid transport in the upper sediment layers was attributed to *P. ciliata*. *Polydora* tube lawns significantly increased abundance and diversity of meio- and macrofauna. Further, they increased food input to the sediments and substrate area for colonization by micro- and meiofauna. Their fecal pellets may serve as a food source for meiofauna and chemotrophs in deeper sediment layers. Hence, *Polydora ciliata*, a well known pioneer species, reconditions disturbed sediments, where it may represent a food item for benthic grazers.

RÉSUMÉ

Influence du Polychète Spionidé tubicole *Polydora ciliata* sur les paramètres benthiques, la faune associée et les processus de transport

On a étudié l'influence du polychète Spionidé tubicole *Polydora ciliata* Johnston sur la communauté benthique, sur les propriétés des sédiments et sur les processus d'échange à travers la surface du sédiment. Les résultats ont montré que les pelouses de tubes de spionidés (huit ou plus tubes par cm^2) réduisaient la stabilité du sédiment tandis qu'elles favorisaient l'accumulation des particules en suspension. De la matière organique était sélectivement transportée dans le sédiment à travers le processus de nourrissage, ce qui enrichissait le sédiment jusqu'à 100 %. Seule une faible augmentation du transport des fluides dans les sédiments superficiels a pu être attribuée à *P. ciliata*. Les pelouses de tubes de *Polydora* augmentent significativement l'abondance et la diversité de la méio- et de la macrofaune. De plus, elles augmentent l'apport de nourriture dans les sédiments et créent le substrat pour la colonisation par la micro- et méiofaune. Leurs excréments peuvent servir comme source de nourriture pour la méiofaune et les chémotrophes dans les couches profondes de sédiment. Ainsi, *P. ciliata*, espèce opportuniste bien connue, améliore les sédiments perturbés, où elle peut représenter une source de nourriture pour les

NOJI, C. I.-M., 1994. — Influence of the tube-building spionid polychaete *Polydora ciliata* on benthic parameters, associated fauna and transport processes. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 493-501. Paris ISBN 2-85653-214-4.

brouteurs benthiques.

INTRODUCTION

Tube-building benthic organisms significantly affect processes at the sediment-water interface by their behavior, e.g. feeding, burrowing, defecation and tube irrigation (ALLER, 1978; FÉRAL, 1989; FRITHSEN & DOERING, 1986; MCCALL & TEVESZ, 1982; NOJI & NOJI, 1991; RHOADS, 1974; SCHMAGER, 1988; WEINBERG & WHITLATCH, 1983; WEINBERG, 1984; WHITLATCH & ZAJAK, 1985). Tubes which protrude into the water column influence direction and speed of the laminar bottom current (CAREY, 1983; VOGEL, 1981), the sedimentation rate of sinking particles (CAREY, 1983) and sediment stability (ECKMAN *et al.*, 1981). Therefore, tube-building organisms affect associated fauna (ECKMAN & THISTLE, 1991; OLAFSSON *et al.*, 1990; REICHARDT, 1986, TRUEBLOOD, 1991, WOODIN, 1981). The extent of this influence depends upon tube diameter, density of colonization (NOWELL & CHURCH, 1979), microbial binding of the sediment surface (FAGER, 1964; ECKMAN *et al.*, 1981) and sediment structure (RHOADS *et al.*, 1978).

In Kiel Bight (western Baltic Sea) the spionid polychaete *Polydora ciliata* Johnston is one of the most important opportunistic species (KÖLMEL, 1979). After deterioration of environmental conditions *P. ciliata* can occur in high densities. Eight or more tubes per cm^2 sediment surface are here defined as *Polydora* tube lawns. In a study by WEIGELT (1991) a mass occurrence of opportunistic species (*Polydora* sp., *Capitella capitata*, *Diastylis rathkei*, *Harmothoe sarsi*) was used to indicate oxygen depletion.

This study concentrated on the influence of this spionid on benthic organisms, sediment parameters and transport processes through the sediment-water interface. A comparison of natural sediments from Kiel Bight with and without *Polydora* lawns addressed the following questions: 1. Does a dense tube lawn stabilize or destabilize the sediment ? 2. Do the activities of *P. ciliata* have an impact on other organisms ? 3. What is the influence on processes of fluid transport ?

MATERIAL AND METHODS

Sediment and fauna were sampled 10 times between May and November 1987 at a fixed station (54°33'N,10°14'E) with a depth of 19 m in Kiel Bight, Baltic Sea. Sediment with and without tube lawns was collected using a Reineck grab (20 x 30cm opening). Subsamples were extracted with cylindrical Plexiglas cores of 10 cm (redox and biomass analyses) and 5 cm (meiofauna) diameter. Macrofauna was collected with a Van Veen grab (0.1 m^2 collecting area). Fluid transport rates in the sediment were studied in 30 cm long Plexiglas cores (10 cm in diameter) containing "artificial" sediment prepared by sieving through 500 µm mesh, incubation without aeration for 5.5 weeks and homogenization. *Polydora* was added to half the samples, and tube lawns were soon established.

In 1-cm intervals relative sediment stability using a fall cone penetrometer (Geonor AS, Oslo, EKMAN, 1947), grain size (ATTERBERG, 1905, modified) and water content (gravimetric) were measured. Relative stability was estimated from the penetration depth of a vertically falling cone which is released directly above the surface of the studied sediment layer. The measurements were conducted shipboard to avoid transport related artifacts. Redox potential was measured with a platinum Eh-electrode (Ingold. Pt-4800-M5) in 0.5 cm intervals.

For biomass analyses sediment was cut into 0.5 and 1 cm layers for intervals above and below 3 cm, respectively. five parallels for chlorophyll *a* and pheopigments (UNESCO method, JEFFREY & HUMPHREY, 1975), adenosine triphosphate (ATP ; PAMATMAT *et al.*, 1981) and organic matter (POM) (combustion at 500 °C for 24 h) were measured for respective intervals from five cores. Individuals of *P. ciliata* were randomly selected and measured for ATP.

For meiofauna analyses defined volumes of sediment from 1 cm intervals were preserved in a buffered formalin/seawater solution (4 %) with Rose Bengal (stains protoplasm). Meiofauna (> 45 µm) was extracted according to JENSEN (1983). Macrofauna was sieved (500 µm) and preserved in a buffered formalin/seawater solution (4 %). Numeration and identification of major taxa were made using a dissecting microscope.

Fluid transport (DICKE, 1986; KITLAR, 1991) in the sediment was measured using sodium bromide solution added to water above the sediment to a concentration about 50 times higher than natural. For four days water was regularly monitored for changes in concentration, after which sediments were sectioned, porosity determined and bromide concentration in the porewater measured (KREMLING, 1983).

RESULTS

Analyses of grain size and redox potential revealed that the sediment was silty sand (SHEPARD, 1954) and became anoxic (JØRGENSEN & FENCHEL, 1974) below 1 cm depth. The data for redox potential and grain size spectra showed no related differences over time or between the sediments with and without *Polydora* lawns. For all sampling dates relative sediment stability increased with depth, reflecting an increase in sand content from about 42 to 55 % from the surface to 8 cm depth. Relative stability of sediment with tube lawns was slightly lower, i.e. the fall cone penetrated 1 to 3 mm deeper into the sediment. The porewater content generally decreased from about 60-70 % wet weight at the sediment surface to about 36 % in 6-8 cm depth; for samples with a tube lawn values were about 5-10 % higher (Fig.1). In 5.5 cm sediment depth the porewater content of the samples without a lawn are starting to be larger than the values for the samples with lawns.

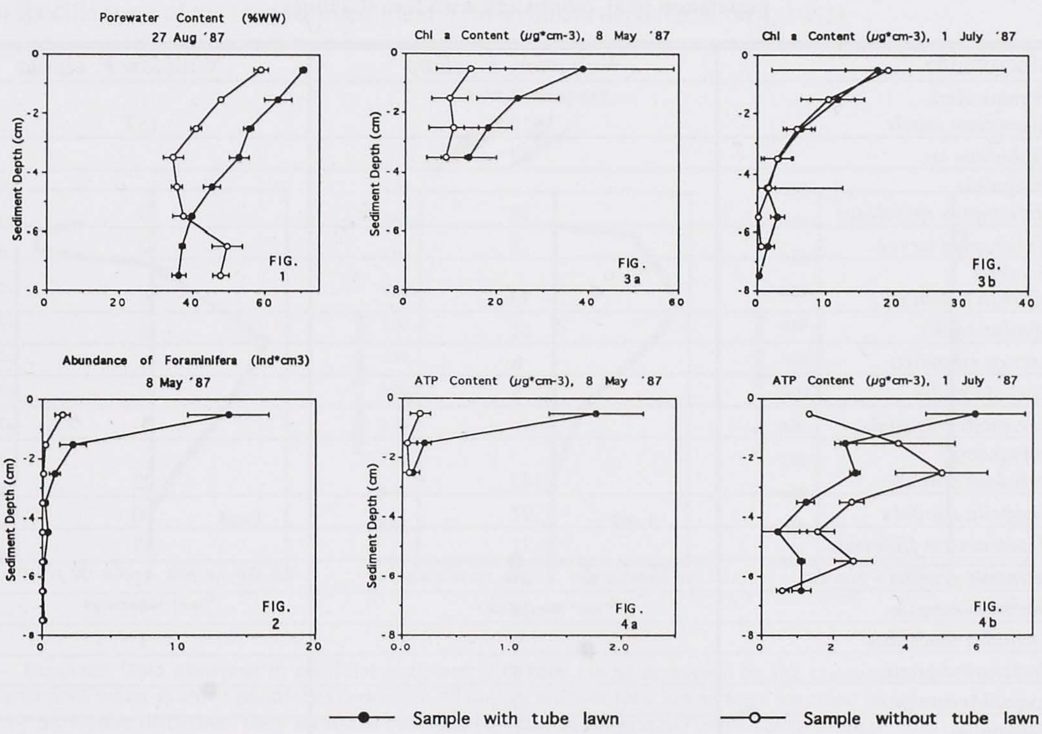

FIG. 1. — Porewater content (% of sediment wet weight (WW)) of the sediment on 27 August 1987. Mean values with standard deviations (bars) of three measurements per sediment depth layer. FIG. 2. — Abundance of foraminifera in the sediment on 8 May 1987. Mean values with standard deviations (bars) of five measurements per sediment depth layer (two measurements per depth layer below 5cm). FIG. 3. — Chlorophyll *a* content of the sediment. Mean values with standard deviations (bars) of five measurements per depth layer. (a) 8 May 1987, (b) 1 July 1987. FIG. 4. — ATP-content of the sediment. Mean values with standard deviations (bars) of five measurements per depth layer in a mixed sample. (a) 8 May 1987, (b) 1 July 1987.

Significant differences between sediments with and without lawns were found for biomass parameters in the sediment. Chlorophyll *a* content at the surface of samples with a lawn was approx. 2.5 times higher than in the sediments without a lawn on 8 May 1987 (Fig. 3a). On 1 July both sediment types had similar mean concentrations in the surface layers (Fig. 3b). Likewise, mean ATP-concentrations in sediments with a tube lawn were 10 times higher in the surface layer (Fig. 4a). After subtraction of *Polydora*-ATP, the ATP-content in the sediments with a tube lawn was still 5.5 times higher. On 1 July the difference between the sediments was smaller, but the total ATP content had increased (Fig. 4b). The organic matter content was very similar in both sediment types on 1 July 1987, and surface values of 22-24 mg POM. cm^{-3} increased to about 28mg POM. cm^{-3} below 1 cm sediment depth.

The meiofauna analysis showed differences in diversities and abundances between the two sediment types. Representatives of the following groups were found: Nematoda, Harpacticida, Ostracoda, Halacarida, Turbellaria, Foraminifera, Tardigrada, larvae of Decapoda, Mollusca and Priapulida. In sediments with a tube lawn meiofauna was more diverse and 2 to 3 times more abundant than in the sediments without a lawn, i.e. 112.6 vs. 44.9 individuals. cm^{-3} in the upper cm of the sediment. Corresponding differences for nematodes (84 vs. 40 ind. cm^{-3} in 0-0.5 cm) and the foraminifer *Elphidium* sp. (approx. 13.6 vs. 1.5 ind. cm^{-3} in 0-0.5 cm) (Fig. 2) were especially large. Regarding macrofauna, mostly juvenile organisms were found, and diversity and abundance were greater in sediments with a moderate *Polydora* population (Tab.1). Besides *Polydora ciliata* the agglutinated foraminifer *Ammotium cassis* Parker was the most common species (3519 vs. 157 ind. 0.1 m^{-2} in sediments with and without a lawn, respectively). The foraminifera were located directly below or between *Polydora* tubes.

TABLE 1. — Macrofauna abundance (ind. 0.1 m^{-2}) in sediments with a moderate (less dense than a tube lawn) population of *P. ciliata* and with few *P. ciliata*.

Macrofauna	With many *P. ciliata*	With few *P. ciliata*
Foraminifera *Ammotium cassis*	3519	157
Elphidium sp.	42	
Priapulida *Halicryptus spinulosus*	18	3
Halicryptus larvae	3	2
Bivalvia *Mysella bidentata*	79	6
Mytilus edulis	11	2
Arctica islandica	6	1
Corbula gibba	5	
Cerastoderma edule		1
Polychaeta *Polydora ciliata*	1142	22
Capitella capitata	91	20
Heteromastus filiformis	71	37
Paraonis gracilis	54	51
Harmothoe sp.	18	5
Anaitides maculata	9	3
Pectinaria koreni	4	
Scoloplos armiger	3	
Nephtys sp.	1	
Eteone elongata	1	
Ostracoda	13	4
Malacostraca *Diastylis rathkei*	62	4
TOTAL	5152	318

Studies on fluid transport in artificial sediments showed slightly increased transport rates (0.1-0.2 mg bromide. cm^{-3} in addition to molecular diffusion) down to 6cm sediment depth in the samples with a tube lawn (Fig. 5). It was assumed that the samples without tube lawn represent the pure tracer input by molecular diffusion as all macrofauna was excluded before the experiments were started. The molecular diffusion coefficient (Ds = 5.0+/- 0.8. 10^{-6} cm. s^{-1}) is quite low compared to the coefficient in natural sediments in Kiel Bight (KITLAR, 1988).

DISCUSSION

CHARACTERISTICS OF *POLYDORA CILIATA* JOHNSTON. — *Polydora ciliata* Johnston (body length < 30 mm) is a cosmopolitan polychaete (RAMBERG & SCHRAM, 1983) which expresses typical opportunistic life patterns especially in disturbed environments (PEARSON & ROSENBERG, 1978; RUMOHR, 1980) and reproduces nearly the whole year round with pelagic larvae (RAMBERG & SCHRAM, 1983). It is able to increase very rapidly forming spionid tube lawns. One reason for the concentrated settlement of spionid larvae next to adult individuals may be the chemosensory recognition of conspecific tubes or of chemical analogs of the tube cement (JENSEN, 1991). Video sequences from the present study site showed that *Polydora* tube lawns covered an area of 10 to 20m^2. Within these lawns were tubeless zones of 0.8 to 1 m^2 area, reasons for this colonization pattern are unknown. *P. ciliata* builds an approx. 5-cm long U-shaped tube which protrudes out of the sediment. The polychaetes either filter feed on suspended particles in the bottom water or deposit feed on sediment when the current falls below acertain speed (DAUER *et al.*, 1981; TAGHON *et al.*, 1980). Filter feeding can be important for maintenance of water quality within moderately polluted systems (DAVIES *et al.*, 1989). Filter feeding by pelagic spionid larvae can influence phytoplankton stocks (WATRAS *et al.*, 1985) via selectivity during feeding. The fecal pellets are stored in specific parts of the tube between 1 and 3 cm sediment depth (SCHÄFER, 1962).

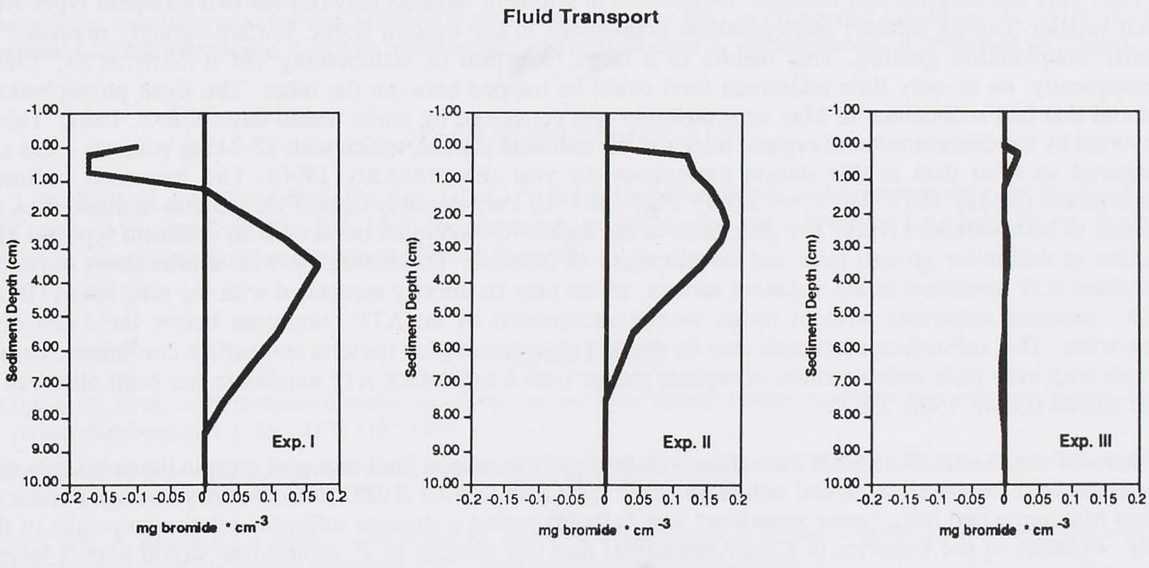

FIG. 5. — Biogenic fluid transport in artificial sediment with tube lawns measured by the concentration of bromide in the sediment pore water in three parallel experiments. (Samples without tube lawns were assumed to represent the pure tracer input by molecular diffusion. They served as base line (0-value in the graphs) in the calculations).

EFFECT ON SEDIMENTS. — Decreased relative sediment stability and higher water content are associated with burrowing, tube building, defecation and irrigation of the tubes by *P. ciliata* populations. The expected differences in grain size (FÉRAL, 1989; LUCKENBACH *et al.*, 1988) between the sediments with and without a tube lawn were not evident and could be caused by the sample treatment, as samples were treated with hydrogen peroxide to destroy organic aggregates. Redox profiles will be discussed later.

EFFECT ON BIOMASS IN THE SEDIMENT. — Differences in total biomass parameters between sediment types can be attributed to behavior and life history of *Polydora ciliata*. The 2.5-fold higher concentration of chlorophyll *a* in the samples with a *Polydora* lawn at the beginning of May may result from active suspension feeding and passive trapping of sedimenting algae by tubes protruding out of the sediment (ALLER & ALLER, 1986; BAILEY-

BROCK, 1984; CAREY, 1983). Laminar current is reduced to about 20 to 30 % on the lee side of tubes (CAREY, 1983), which accordingly, increases sedimentation rates (BUHR, 1979; WARNER, 1979). Samples with tube lawns contained approx. 50 µg chl *a* . cm^{-3} more than the ones without lawns. Expressed as organic carbon (C_{org} : chl *a* = approx. 40 : 1, BANSE, 1974) this additional amount of organic carbon corresponds to sedimentation during a regular spring phytoplankton bloom in this region (SMETACEK, 1980). In addition large amounts of benthic fecal pellets and flocculant detritus were trapped between the tubes. This highly concentrated organic material represented an ideal food source for other fauna. A study by YAP (1991) showed increased numbers of benthic organisms in response to greater food supply. Results of the ATP measurements and meio- and macrofauna analyses are hence not surprising. The higher meiofauna diversity and abundances down to 9 cm sediment depth in the samples with a *Polydora* lawn were presumably a result of increased amount of organic matter (ALONGI, 1985), enlarged substrate surface for meiofaunal and bacterial colonization on oxygenated tubes (BELL & COEN, 1982; BELL, 1985), and of the deep-reaching bioturbation of the more diverse and abundant macrofauna in these sediments. Large standard deviations in meiofauna abundances and diversities might be caused by patchiness in sedimented material induced by minor differences in water current and bottom topography (ECKMAN & THISTLE, 1991). Nematodes and foraminifera seemed to be best adapted to these fast-changing environmental conditions (LINKE & LUTZE, 1993). MOODLEY (1990) found for the southern North Sea that living benthic foraminifers (including *Elphidium* sp.) were enriched in areas with large amounts of organic carbon. The populations increased with rising temperature and increasing input of organic carbon. Enriched foraminifer densities were not restricted to the surface sediment but also extended into deeper sediment layers. The fact that the macrofauna was mainly comprised of juvenile organisms might be an indicator of a recent oxygen deficiency situation which had killed the benthos.

On 1 July the situation had changed. Differences in sediment biomass between the two sediment types were much smaller. During summer phytoplankton populations in the western Baltic Sea are strongly regulated by intense zooplankton grazing. This results in a large reduction of sedimenting chl *a* (SMETACEK, 1980). Consequently, no or only little additional food could be trapped between the tubes. The fresh phytoplankton material that had sedimented in May very probably was consumed by fauna within days (GRAF, 1987). This is supported by the concentration of organic matter at the sediment surface, which with 22-24 mg POM. cm^{-3} was low compared to POM data at this station throughout the year (EVERSBERG, 1990). The increased sediment temperatures (8 May 1987: 3.4 °C vs. 1 July 1987 : 6.4 °C) very possibly caused the general increase in ATP-biomass in both sediment types. The difference in the degree of food input between both sediment types in May resulted in dissimilar growth rates and development of biomass. The sediments with a tube lawn showed a significant ATP maximum at the sediment surface, which may be directly associated with the tube lawns (BELL, 1985), whereas sediments without lawns were characterized by an ATP maximum below the 1-cm deep chemocline. This subsurface maximum may be due to chemoautotrophic bacteria and sulfate consumers. During periods with very little sedimentation of organic matter such a subsurface ATP maximum has been observed in other studies (GRAF, 1986, 1987).

IMPACT ON FLUID TRANSPORT RATES. — Only slightly increased fluid transport rates in the sediments with tube lawns were observed. In natural sediments of the same area KITLAR (1988) found that *Nephtys* sp., *Pectinaria koreni* Malmgren and *Halicryptus spinulosus* Von Seibold exerted a stronger influence relative to results of this study. Because of the behavior (e.g. tube irrigation) and life strategy of *P. ciliata* one would expect largely increased transport rates for fluids. In addition the surface for diffusion processes is largely increased by a dense colonization by U-shaped tubes (FOSTER-SMITH, 1978). ALLER (1983), on the other hand found that tight tubes which are coated by organic material hinder the exchange of anions because of their negatively charged tube walls. This might lead to low fluid-transport rates. This could also explain why there were no significant changes in the redox potential of the sediment. It seems that these U-shaped *P. ciliata* tubes represent a nearly closed system which allows only a minor exchange between the sediment surface and deeper sediment layers.

ECOLOGICAL IMPLICATIONS

This study indicates that dense *P. ciliata* tube lawns can significantly improve the environmental conditions for other benthic species by loosening the sediment texture, increasing fluid transport into the sediment, increasing the concentration of easily degradable POM and enriching the diversity and abundance of benthic fauna. Therefore, in areas with disturbed sediments dense assemblages of this spionid polychaete are important as reconditioners of the sea bottom. As the conditions in certain areas of the sea floor worsen from year to year, e.g. due to eutrophication, oxygen deficiency and trawl-fishing, animals such as *P. ciliata* become important for the re-establishment of a benthic community.

SUMMARY

This study addresses the influence of *Polydora ciliata* on sediment properties, associated fauna and transport processes through the sediment surface. The investigation area was a 19 m deep station in Kiel Bight (western Baltic). Samples were taken from sediments with and without *Polydora* tube lawns with a box corer and grab during 10 cruises between May and November 1987. Each lawn was approximately 10 to 20 m^2 within which tubeless zones were present. Sediments were analyzed for redox potential, shear strength, grain sizes, porewater, particulate organic matter, chlorophyll *a*, living biomass as ATP and composition of macro- and meiofauna. In addition, experimental studies on defaunated sediments were conducted to address transport of fluids.

Relative to sediments without tube lawns the sediment stability in samples with a lawn was greater, and porewater content was lower. After sedimentation of the phytoplankton bloom in May, chlorophyll *a* and ATP concentrations were about 2.5 and 10 times higher in the sediment surface of the samples with a lawn compared with those without, respectively. In sediments with lawns, diversity and abundance of meiofauna and macrofauna were greater. Only slightly increased fluid transport rates through the sediment surface in the presence of tube lawns was observed.

The enhanced accumulation of organic matter by dense *Polydora* assemblages is a result of both the filter-feeding activity of the polychaetes and of the trapping effect of the tube. This additional food source and increased tube-related substrate area for colonization significantly improve the environmental conditions for other benthic organisms. Therefore, dense *P. ciliata* assemblages can be important as reconditioners of disturbed sediments.

ACKNOWLEDGMENTS

I thank Dr. G. GRAF and Prof. Dr. S.A. GERLACH for critical discussions and support during the field work for this study. Also thanks to Dr. T.T. NOJI for comments on the manuscript and on the language. Dr. G. BIANCHI helped in translating the abstract into the French language.

REFERENCES

ALLER, R.C., 1978. — Experimental studies of changes produced by deposit feeders on pore water, sediment and overlaying water chemistry. *Am. J. Sci.*, **217** : 1185-1234.

ALLER, R.C., 1983. — The importance of the diffusive permeability of animal burrow linings in determining marine sediment chemistry. *J. mar. Res.*, **41** : 299-322.

ALLER, J.Y. & ALLER, R.C., 1986. — Evidence for localized enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic. *Deep-Sea Res.*, **33** : 755-790.

ALONGI, D.M., 1985. — Microbes, meiofauna, and bacterial productivity on tubes constructed by the polychaete *Capitella capitata*. *Mar. Ecol. Progr. Ser.*, **23** : 207-208.

ATTERBERG, A., 1905. — Die rationelle Klassifikation der Sande und Kiese. *Chem. Ztg.*, **29** : 195-198.

BAILEY-BROCK, J.H., 1984. — Ecology of the tube-building polychaete *Diopatra leuckarti* Kinberg, 1865 (Onuphidae) in Hawai : Community structure, and sediment stabilizing properties. *Zool. J. Linn. Soc.*, **80** : 191-199.

BANSE, K., 1974. — On the interpretation of data for the carbon-to-nitrogen ratio of phytoplankton. *Limnol. Oceanogr.*, **19** : 695-699.

BUHR, K.-J., 1979. — Eine Massensiedlung von *Lanice conchilega* (Polychaeta: Terebellidae) im Weser-Ästuar. *Veröff. Inst. Meeresforsch. Bremerhaven*, **17** : 101-149.

BELL, S.S., 1985. — Habitat complexity of polychaete tube-caps: Influence of architecture on dynamics of a meioepibenthic assemblage. *J. Mar. Res.*, **43** : 647-671.

BELL, S.S. & COEN, L.D., 1982. — Investigations on epibenthic meiofauna. 1. Abundances on and repopulation of the tube-caps of *Diopatra cuprea* (Polychaeta: Onuphidae) in a subtropical system. *Mar. Biol.*, **67** : 303-309.

CAREY, D.A., 1983. — Particle resuspension in the benthic boundary layer induced by flow around polychaete tubes. *Can. J. Fish. Aquat. Sci.*, **40** : 301-308.

DAUER, D.M., MAYBURY, C.A. & EWING, R.M., 1981. — Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *J. exp. mar. Biol. Ecol.*, **54** : 21-38.

DAVIES, B.R., STUART, V. & DE VILLIERS, M., 1989. — The filtration activity of a serpulid polychaete population (*Ficopomatus enigmaticus* (Fauvel)) and its effects on water quality in a coastal marina. *Estuar. Coast. Shelf Sci.*, **29** : 613-620.

DICKE, M., 1986. — Vertikale Austauschkoefficienten und Porenwasserfluß an der Sediment/Wasser-Grenzfläche. *Ber. Inst. für Meereskunde an der CAU Kiel*, **155**.

ECKMAN, J.E., NOWELL, A.R.M. & JUMARS, P.A., 1981. — Sediment destabilization by animal tubes. *J. mar. Res.*, **39** (2) : 361-374.

ECKMAN, J.E. & THISTLE, D., 1991. — Effects of flow about a biologically produced structure on harpacticoid copepods in San Diego Trough. *Deep-Sea Res.*, **38** : 1397-1416.

EKMAN, S., 1947. — Über die Festigkeit der marinen Sedimente als Faktor der Tierverbreitung, ein Beitrag zur Associationsanalyse. *Zool. Bidrag, Uppsala*, **25** : 1-20.

EVERSBERG, U., 1990. — Abbau und Akkumulation von organischer Substanz in den Sedimenten der Kieler Bucht. *Ber. Inst. für Meeresforsch.*, Univ. Kiel, **193**, 1-98.

FAGER, E.W., 1964. — Marine sediments: effects of a tube-building polychaete. *Science*, **143** : 356-359.

FÉRAL, P., 1989. — Biosedimentological implications of the polychaete *Lanice conchilega* (Pallas) on the intertidal zone of two Norman sandy shores (France). *Bull. Soc. Geol. Fr.* (8 Sér.), **5** (6) : 1193-1200.

FOSTER-SMITH, R.L., 1978. - An analysis of water flow in tube-living animals. *J. exp. mar. Biol. Ecol.*, **34** : 79-95.

FRITHSEN, J.B. & DOERING, P.H., 1986. — Active enhancement of particle removal from the water column by tentaculate benthic polychaetes. *Ophelia*, **25** 169-182.

GRAF, G., 1986. — Winter inversion of biomass and activity profile in a marine sediment. *Mar. Ecol. Progr. Ser.*, **33** : 231-235.

GRAF, G., 1987. — Benthic energy flow during a simulated autumn bloom sedimentation. *Mar. Ecol. Prog. Ser.*, **39** : 23-29.

JEFFREY, S.W. & HUMPHREY, G.F., 1975. — New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanz.*, **167** : 191-197.

JENSEN, P., 1983. — Meiofaunal abundance and vertical zonation in a sublittoral soft bottom, with a test of the Haps corer. *Mar. Biol.*, **74** : 319-326.

JENSEN, R.A., 1991. — Bioadhesion and morphogenesis in a marine polychaete. *In*: M.-F. THOMPSON, R. SAROJINI & R. NAGABHUSHANAM (eds), *Bioactive compounds from the marine organisms with emphasis on the Indian Ocean. An Indo-United States Symposium*: 179-183.

JØRGENSEN, B.B. & FENCHEL, T., 1974. — The sulfur cycle of a marine sediment model system. *Mar. Biol.*, **24** : 189-201.

KITLAR, J., 1988. — *Leistungen verschiedener Benthostiere beim Wasseraustausch an der Grenzfläche zwischen Meer und Meeresboden.* Master's Thesis, Univ. Kiel, 68 pp.

KITLAR, J., 1991. - Der Einfluß der Bioturbation auf den Transport gelöster Stoffe im Porenwasser. *Ber. Inst. Meereskunde,* Univ. Kiel, 210, 1-99.

KÖLMEL, R., 1979. — *Ökosysteme im Wechsel zur Anaerobiose. Zoobenthos und Abbau in zeitweise anoxischen Biotopen der Kieler Bucht.* PhD. Thesis, Univ. Kiel, 304 pp.

KREMLING, K., 1983. — Determination of the major constituents. *In*: GRAßHOFF, K., ERHARDT, M. & KREMLING, K. (eds.). *Methods of Seawater Analysis.* Verlag Chemie, Weinheim, 2 edition : 260-262.

LINKE, P. & LUTZE, G.F., 1993. — Microhabitat preferences of benthic foraminifera - a static concept or a dynamic adaptation to optimize food acquisition? *Mar. Micropal.*, **20** : 215-234.

LUCKENBACH, M.W., HUGGETT, D.V. & ZOBRIST, E.C., 1988. — Sediment transport, biotic modifications and selection of grain size in a surface deposit-feeder. *Estuaries*, **11** : 134-139.

MCCALL, P.L. & TEVESZ, M.J.S., 1982. — *Topics in geobiology, volume 2. Animal-sediment relations. The biogenic alteration of sediments.* Plenum Press, New York. 329 pp.

MOODLEY, L., 1990. — Southern North Sea seafloor and subsurface distribution of living benthic foraminifera. *Neth. J. Sea Res.*, **27** : 57-71.

NOJI, C.I.-M. & NOJI, T.T., 1991. — Tube lawns of spionid polychaetes and their significance for recolonization of disturbed benthic substrates: a review. *Meeresforsch.*, **33** : 235-246.

NOWELL, A.R.M. & CHURCH, M., 1979. — Turbulent flow in a depth-limited boundary layer. *J. Geophys. Res.*, **84** : 4816-4824.

OLAFSSON, E., MOORE, C.G. & BETT, B.J., 1990. — The impact of *Melinna palmata* Grube, a tube-building polychaete, on meiofaunal community structure in a soft-bottom subtidal habitat. *Estuar. coast. Shelf Sci.*, **31** : 883-893.

PAMATMAT, M.M., GRAF, G., BENGTSSON, W. & NOVAK, C.S., 1981. — Heat production, ATP concentration and electron transport activity of marine sediments. *Mar. Ecol. Progr. Ser.*, **4** : 135-143.

PEARSON, T.H., ROSENBERG, R., 1978. — Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. mar. Biol. Ann. Rev.*, **16** : 229-311.

POWILLEIT, M., 1988. — *Die Bioturbationsleistung des Priapuliden Halicryptus spinulosus in der Kieler Bucht.* Master's Thesis, Univ. Kiel, 67 pp.

RAMBERG, J.P. & SCHRAM, T.A., 1983. — A systematic review of the Oslofjord species of *Polydora* Bosc and *Pseudopolydora* Czerniavsky, with some new biological and ecological data. (Polychaeta: Spionidae). *Sarsia*.

REICHARDT, W.T., 1986. — Polychaete tube walls as zonated microhabitats for marine bacteria. *Actes Colloq. IFREMER*, **3** : 415-425.

RHOADS, D.C., MCCALL, P.L., YINGST, J.Y., 1978. — Disturbance and production on the estuarine seafloor. *Am. Sci.*, **66** : 577-586.

RHOADS, D.C., 1974. — Organism-sediment relations on the muddy sea floor. *Oceanogr. mar. Biol. Annu. Rev.*, **12** : 263-300.

RUMOHR, H., 1980. — *Der "Benthosgarten" in der Kieler Bucht - Experimente zur Bodentierökologie*. Reports SFB 95, Univ. Kiel, Vol. 55. 179 pp.

SCHÄFER, W., 1962. — *Aktuo-Paläontologie nach Studien in der Nordsee.* Kramer Verlag, 666 pp.

SCHMAGER, C., 1988. — *Einfluss rasenbildender Spioniden auf den Stoffaustausch am Meeresboden.* Master's thesis, Univ. Kiel, 64 pp.

SHEPHARD, P.E., 1954. — Nomenclature based on sand-silt-clay ratios. *J. Sedimen. Petrol.*, **24** : 151-158.

SMETACEK, V., 1980. — Annual cycle of sedimentation in relation to plankton ecology in Western Kiel Bight. *Ophelia*, suppl., **1** : 65-76.

TAGHON, G.L., NOWELL, A.R. & JUMARS, P.A., 1980. — Induction of suspension feeding in spionid polychaetes by high particulate fluxes. *Science*, **210** : 562-564.

TRUEBLOOD, D.D., 1991. — Spatial and temporal effects of terebellid polychaete tubes on soft-bottom community structure in Phosphorescent Bay, Puerto Rico. *J. exp. mar. Biol. Ecol.*, **149** : 139-159.

VOGEL, S., 1981. — *Life in moving fluids. The physical biology of flow.* Willard Grant Press, Boston, 352 pp.

WARNER, G.F., 1979. — Aggregation in echinoderms. *In*: G. LARWOOD & B.R. ROSEN (eds), *Systematics Association Special Volume No. 11, Biology and Systematics of colonial organisms.* Academic Press, London & New York : 375-396.

WATRAS, C.J., GARCON, V.C., OLSON, R.J., CHRISHOLM, S.W. & ANDERSON, D.M., 1985. — The effect of zooplankton grazing on estuarine blooms of the toxic dinoflagellate *Gonyaulax tamarensis*. *J. Plankt. Res.*, **7** : 891-908.

WEIGELT, M., 1991. — Short- and long-term changes in the benthic community of the deeper parts of Kiel Bay (Western Baltic) due to oxygen depletion and eutrophication. *Meeresforsch.*, **33** : 197-224.

WEINBERG, J.R. & WHITLATCH, R.B., 1983. — Enhanced growth of a filter-feeding bivalve by a deposit-feeding polychaete by means of nutrient regeneration. *J. mar. Sci.*, **41** : 557-569.

WEINBERG, J.R., 1984. — Interactions between functional groups in soft-substrate : do species differences matter? *J. exp. mar. Biol. Ecol.*, **80** : 11-28.

WHITLATCH, R.B. & ZAJAK, R.N., 1985. — Biotic interactions among estuarine infaunal opportunistic species. *Mar. Ecol. Progr. Ser.*, **21** : 299-311.

WOODIN, S.A., 1981. — Disturbance and community structure in a shallow water sand flat. *Ecology*, **62** : 1052-1066.

YAP, H.T., 1991. — Benthic energy dynamics in a southern Baltic ecosystem. *Mar. Biol.*, **108** : 477-484.