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The macrofauna of a stony sand area in the German Bight (North Sea)

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ABSTRACT: The sublittoral macrofauna of the Steingrund, a stony area east-northeast of Helgoland, was investigated from May till October 1991 using a van Veen grab and a small dredge. The diverse endo- and epifauna of the sandy bottoms, pebbles and boulders of this Saalian end moraine comprised 289 taxa, whereby the polychaetes *Magelona papillicornis, Lanice conchilega* and *Spiophanes bombyx* dominated in terms of abundance. Species rare in the German Bight, such as the sponge *Leucandra fistulosa*, the sea urchin *Echinus esculentus*, and the sea anemone *Haliplanella lineata*, were also found. The two sample sets were processed separately with multivariate techniques, and differentiated on the basis of occurrence and numbers of the abundant species. The analysis of the grab samples revealed two types of the *Tellina-fabula*-community. These associations were differentiated by the presence of species of the coarse-sand-inhabiting *Goniadella-Spisula*-community and were related to the distribution of the grain size of the sediment. Likewise, two epifaunal assemblages were distinguished. Sandy bottoms were characterized by *Ophiura albida, Liocarcinus holsatus* and *Pagurus bernhardus*, while boulders and pebbles were covered by a varied sessile and mobile epifauna dominated by the sessile bryozoan *Flustra foliacea* and the mobile pantopode *Aechelia echinata*. Numerical density, biomass and annual production estimates are in the range of values determined for the macrobenthos of the German Bight, while annual P/B ratios mounted up to 5.

INTRODUCTION

The composition, structure and distribution of sublittoral macrobenthic communities in the German Bight were investigated by Blegvad (1922), Hagmeier (1925), Caspers (1939), Stripp (1969), Dörjes (1977), Salzwedel et al. (1985) and others. All of these surveys dealt with communities living in soft bottoms. However, little is known about the macrobenthic communities of the sublittoral, hard substrata in the southeastern North Sea (Caspers, 1950; Dörjes, 1977). The scarcity of these substrata in the German Bight (Fig. 1) is one reason for this; the difficulty in obtaining quantitative samples is another. The majority of these substrata are regarded as residues of the end moraines of Saalian and Weichselian stages of the Glacial Period (Pratje, 1951).

The structural heterogeneity and the physical resistence of these hard substrata impede a comprehensive quantitative sampling of sessile and mobile macrobenthos. Even Janke (1986), whose macrobenthic investigations were limited to the rocky intertidal zone of Helgoland, faced these problems. Lüning (1970) and de Kluijver (1991) used SCUBA diving as a suitable method, while the investigations of Caspers (1950) and Dörjes (1977) were based on grab samples.

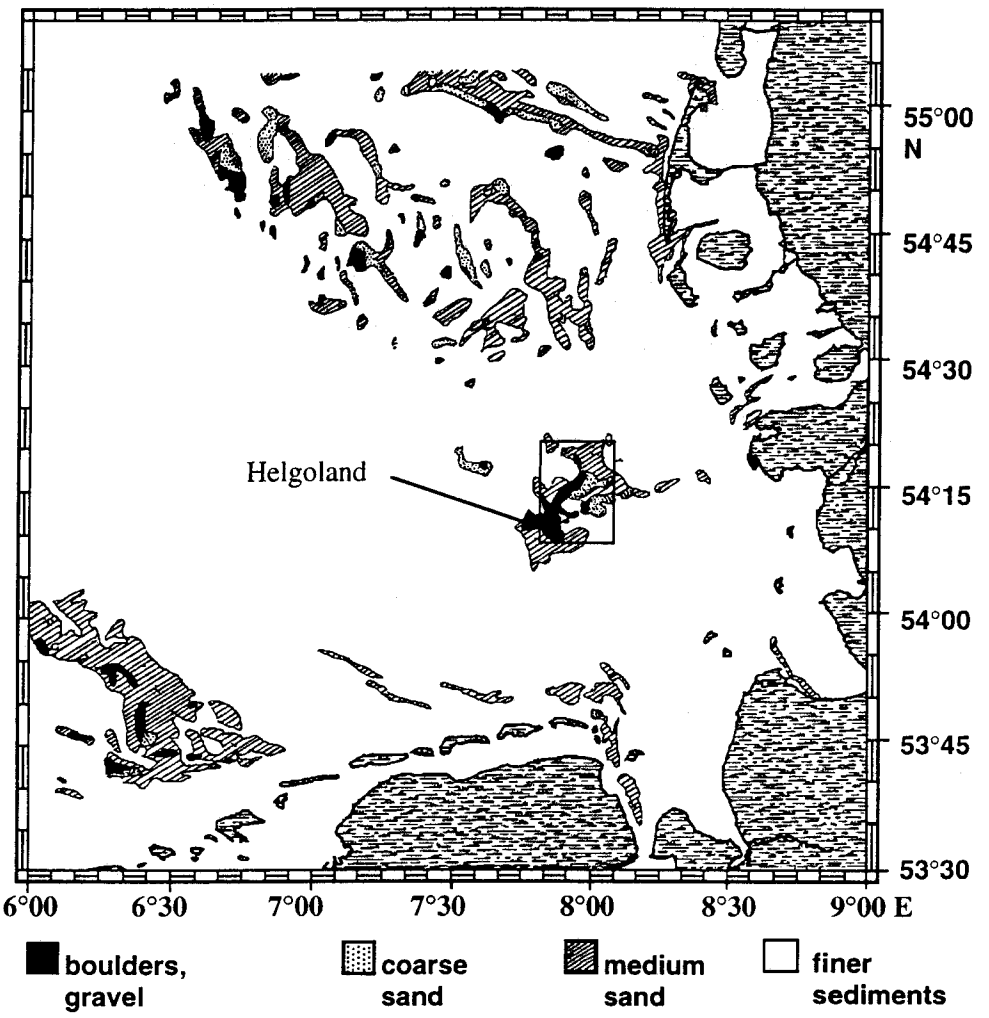

Fig. 1. Distribution of the sandy and rocky deposits in the German Bight with the area of investigation (framed) near Helgoland (after Figge, 1981)

This synecological study of the sessile and mobile macrobenthos at the Steingrund near Helgoland is based on an investigation of Kühne (1992), who combined two different sampling techniques (using van Veen grabs and a dredge).

MATERIAL AND METHODS

Area of investigation

The Steingrund, literally stony ground, is the remains of a Saalian end moraine, about 11 km east-northeast of Helgoland. The study area (Fig. 2) stretches from the

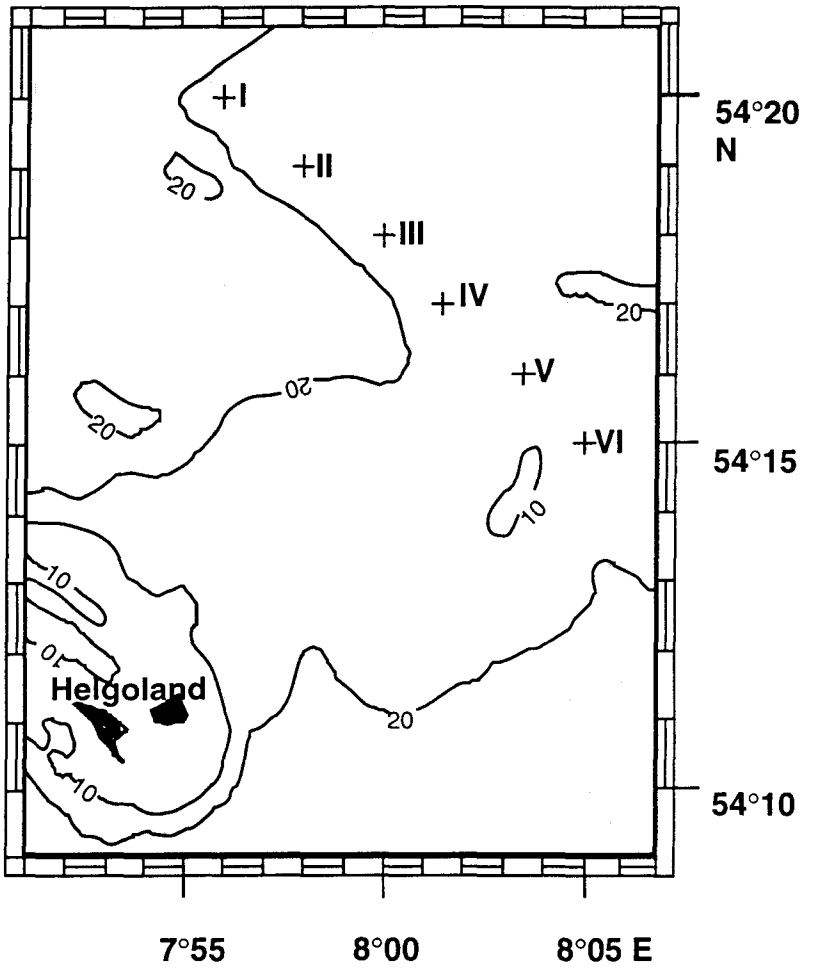

Fig. 2. Investigation area northeast of Helgoland, with the stations I to VI in the Steingrund

northwestern border of Steingrund to its highest parts at the buoy "Tonne Steingrund" (54° 14′ N, 8° 05.5′ E).

Water depths varied between 8 and 22 m, and water temperatures in the area are quite uniform, changing seasonally (2–19 °C). Variations in salinity, between 30 and 33 ‰, are caused by the fluctuating estuarine water inflow from the river Elbe. Nevertheless, this area can be considered as not heavily polluted. Strong tidal currents with a mean velocity of 0.6 kt allow almost saturated concentrations of dissolved oxygen of about 8–10 mg/l in the bottom waters.

The sediment consists mainly of medium to coarse sands, locally intermixed with boulders and pebbles (Schulz, 1983).

Sampling and sample treatment

The macrofauna of the Steingrund was investigated during three cruises with the RV "Victor Hensen" of the AWI Bremerhaven. Infauna samples were taken with a van Veen grab (0.1 m^2) at six stations (I–VI, Fig. 2) in May, August and October 1991. These samples were separately sieved on 1-mm screens and preserved in 5 % formalin buffered with hexamethylene-tetramine for further laboratory analysis.

In addition, 15 hauls were made with a small frame dredge (1 m width, 1 cm mesh size), each trawl covering an area of about 900 m^2. These samples were sorted and the fauna determined on board.

Moreover, supplementary information was gained from some larger grab samples and by visual observations during diving.

The animals were counted and identified to species level as far as possible. Total wet weights were measured separately for the following 5 groups: polychaetes, molluscs, crustaceans, echinoderms and all remaining taxa ("miscellaneous"). Larger animals, such as the heart urchin *Echinocardium cordatum*, were weighed individually. The wet weights were converted into ash-free dry weights using the comparably high conversion factors 0.2 for polychaetes, crustaceans and miscellaneous (0.1 for the tunicate *Molgula* sp.) and 0.07 for molluscs and echinoderms (Thorson, 1957; Rumohr et al., 1987; Atkins & Wacasey, 1976; cf. also Salzwedel et al., 1985).

Data processing

Simpson's diversity index (Simpson, 1949) and Heip's evenness (Heip, 1974) were calculated. K-dominance curves were drawn to compare diversities and dominances of different clusters (see Lambshead et al., 1983).

The van Veen grab and the dredge samples, 2 sample sets representing the different sampling techniques and the 3 sampling dates, were processed separately. These sample sets were subjected to analyses by three different multivariate techniques: (1) an agglomerative, hierarchical clustering method, using unweighted pair-groups method with arithmetic averages (UPGMA), (2) a divisive, hierarchical classification method, named the two-way indicator-species analysis (TWINSPAN), and (3) a correspondence analysis (CA; or reciprocal averaging). These techniques are described in detail by Hill (1979), ter Braak (1987) and Piepenburg (1988).

Bryozoans and hydroids as well as the anthozoan *Alcyonium digitatum* were omitted in these computer analyses. The classification and ordination of the dredge samples were based on the ranked data of 144 taxa.

Characterizing species were identified in order to describe and differentiate benthic associations according to the method of Salzwedel et al. (1985). A species is considered characteristic of a station group when it fulfills at least three of the following conditions:

- numerical dominance within the association is more than 5 %
- presence within the association is more than 66 %
- the number of individuals of the species concerned within the association divided by the total number of individuals of that species found in the whole study area (DAI) is more than 0.66 (66 %)
- the number of stations within the association at which the species occurred divided

by the total number of stations at which the species occurred (DAS) is more than 0.66 (66 %)

For the determination of epibenthic associations (rank data), the degree of association regarding individuals (DAI) was replaced by the degree of association regarding ranks (DAR).

RESULTS

Bottom deposits

The substrata of the area were very heterogeneous. They varied from boulders and stones (station I) to medium sand (station VI), and were locally intermixed with fine sand (station III). The general gradient in grain size from south to north is superimposed by a strong patchiness of stones and boulders. In some areas, pebbles and boulders were intermixed with small amounts of coarse sand. The hard substrata were covered by the bryozoans *Flustra foliacea* and *Alcyonidium* sp., the anthozoans *Alcyonium digitatum* and *Metridium senile* and other sedentary animals.

Species composition

In total, 289 different taxa were found, comprising 75 Crustacea, 73 Annelida, 50 Mollusca, 32 Coelenterata, 23 Chordata, 12 Echinodermata, 7 Bryozoa and 17 others (Table 1). Species that are rare in the German Bight (cf. "Red List": Rachor et al., 1995), for example the sponge *Leucandra fistulosa,* the anthozoan *Haliplanella lineata* and the edible sea urchin *Echinus esculentus,* were also found. In addition, a few individuals of the rare flatfishes *Arnoglossus laterna* (station group 2) and *Phrynorhombus laterna* (station group 1) were collected by the dredges. According to Fricke (1987), they accidentally migrate from the north into the German Bight.

Station groups and associations

Multivariate analyses of grab and dredge samples, comprising only the "non-colonial" taxa, produced two station groups (Figs 3,4,5): group 1 including stations I and II and group 2 all other stations (III to VI).

This clustering was consistent in both sample sets (grabs and dredges) on all sampling dates (May, August and October). It is correlated with the composition of the sediment, in that group 2 comprises the sites with medium to coarse sands, and station group 1 those with boulders and pebbles.

The position of sample IIIMa in the ordination plot (Fig. 6) suggests that this sample shares characteristic species of both clusters. Depending on the multivariate technique used, this sample is classified either in group 1 or 2.

The macrofauna of the two station groups differ in the composition, number, abundance and biomass of the species (Fig. 7), and are subsequently taken as specific associations.

Table 1. List of species found in the Steingrund (* indicates "Red List" species; see text)

Species	Species	Species
CHORDATA	ECHINOIDEA	*Hippomedon denticulatus* (Bate)
VERTEBRATA	*Echinocardium cordatum* (Pennant)	*Jassa falcata* (Mont.)
Agonus cataphractus (Linné)	*Echinocyamus pusillus* (O. F. Müller)*	*Lembos websteri* Bate
Ammodytes aff. *tobianus* L.	*Echinus esculentus* L.*	*Megaluropus agilis* Hoek
Arnoglossus laterna (Walbaum)	*Psammechinus miliaris* (Gmelin)*	*Metopa alderi* (Bate)
Buglossidium luteum (Risso)	BRYOZOA	*Microprotopus maculatus* Norman
Callionymus juv.	*Alcyonidium* aff. *gelatinosum* (L.)	*Orochomene nana* (Kröyer)
Callionymus reticulatus Valenciennes	*Bugula* aff. *flabellata* (Thoms.)	*Parapleustes bicuspis (Kröyer)*
Ctenolabrus rupestris (L.)	*Conopeum reticulum* (L.)	*Perioculodes longimanus* (Bate & Westwood)
Gadus morhua L.	*Crisia eburnea* (L.)	*Photis longicaudata* (Bate & Westwood)
Gobiidae indet. spp.	*Electra pilosa* (L.)	*Photis reinhardi* Kröyer
Hyperoplus lanceolatus (Le Sauvage)	*Flustra foliacea* (L.)	*Phoxocephalus holbolli* (Kröyer)*
Limanda limanda (L.)	*Scrupocellaria* sp.	*Pontocratus arenarius* (Bate)
Liparis aff. *liparis* (L.)	CRUSTACEA	*Stenula rubrovittata* (Sars)
Merlangius merlangus (L.)	AMPHIPODA	*Synchelidium haplocheles* (Sars)
Microstomus kitt (Walbaum)	*Ampelisca brevicornis* (Costa)	*Urothoe poseidonis* Reibisch
Myoxocephalus scorpius (L.)	*Ampelisca diadema* (Costa)	ISOPODA
Pholis gunnellus (L.)	*Ampelisca spinipes* Boeck	*Janira maculosa* Leach*
Phrynorhombus norvegicus (Günther)	*Ampelisca* sp.	CUMACEA
Platichthys flesus (L.)	*Ampelisca tenuicornis* Lilljeborg	*Bodotria scorpioides* (Mont.)
Pleuronectes platessa L.	*Amphilochus* sp.	*Diastyloides biplicata* (Sars)
Solea solea Quensel	Amphipoda juv.	*Diastylis bradyi* Norman
Syngnathus acus L.	*Amphithoe rubricata* (Montagu)	*Diastylis cornuta* (Boeck)
Trachurus trachurus (L.)	*Aora typica* Kröyer	*Iphinoe trispinosa* (Goods.)
ACRANIA	*Argissa hamatipes* (Norman)	*Lamprops fasciata* Sars
Branchiostoma lanceolatum Pallas	*Atylus falcatus* Metzger	*Pseudocuma similis* G. O. Sars
ECHINODERMATA	*Atylus swammerdami* (Milne-Edwards)	DECAPODA
ASTEROIDEA	*Bathyporeia elegans* Watkin	Brachyura larvae
Asterias rubens L.	*Bathyporeia guilliamsoniana* (Bate)	*Cancer pagurus* L.*
OPHIUROIDEA	*Bathyporeia gracilis* Sars	*Corystes cassivelaunus* (Pennant)
Acrocnida brachiata (Montagu)*	*Bathyporeia pelagica* (Bate)	*Crangon allmanni* Kinshan
Amphipholis squamata Delle Chiaje*	*Caprella linearis* (L.)*	*Crangon crangon* (L.)
Amphiura filiformis (O. F. Müller)*	*Corophium crassicorne* Bruzelius	*Crangon* juv.
Ophiothrix fragilis (Abildgaard)*	*Corophium sextonae* Crawford	*Eualus pusiolus* (Kröyer)
Ophiura albida Forbes	*Corophium* juv.	*Galathea intermedia* Lilljeborg
Ophiura ophiura (L.)	*Gammaropsis maculata* (Johnston)	*Galathea strigosa* (L.)*
Ophiuridae juv.	*Gammaropsis nitida* (Stimpson)	*Hyas araneus* (L.)
		Liocarcinus holsatus (Fabrizius)

Table 1 (continued)

Species	Species	Species
DECAPODA	*Eteone longa (Fabricius)*	*Sabellaria spinulosa* Leuckart*
Liocarcinus pusillus (Leach)*	*Eteone* sp.	*Scalibregma inflatum* (Rathke)
Macropodia rostrata (L.)	*Eulalia bilineata* (Johnston)	*Scolelepis (S.) bonnieri* (Mesnil)
Maja squinado (Herbst)	*Eulalia viridis* (L.)	*Scoloplos armiger* (O. F. Müller)
Pagurus bernhardus (L.)	*Eumida sanguinea* (Oersted)	*Sphaerodorum flavum* (Rathke)
Pandalina brevirostris (Rathke)*	*Eusyllis blomstrandi* Malmgren	*Spio armata* (Thulin)
Pandalus montagui Leach	*Flabelligera affinis* M. Sars	*Spio filicornis* (Müller)
Pilumnus hirtellus (L.)	*Gattyana cirrosa* (Pallas)	*Spio goniocephala* Thulin
Pinnotheres pisum (L.)*	*Glycera capitata* Oersted*	*Spiophanes bombyx* (Claparede)
Pisidia longicornis (L.)*	*Glycera rouxii* Audouin & Milne-Edw.*	*Sthenelais limicola* (Ehlers)
Thia scutellata (Fabricius)*	*Glycinde nordmanni* (Malmgren)	*Syllides longocirrata* Oersted
Thoralus aff. *cranchii* (Leach)	*Goniada maculata* Oersted	*Syllis gracilis* Grube
CIRRIPEDIA	*Goniadella bobretzkii* (Annenkova)	*Thelepus cincinnatus* (Fabricius)
Balanus balanoides (L.)	*Harmothoe (H.) impar* (Johnston)	*Travisia forbesi* Johnston
Balanus sp.	*Lanice conchilega* (Pallas)	Polychaeta indet spp.
Verruca stroemia (O. F. Müller)	*Lepidonotus squamatus* (L.)*	MOLLUSCA
COPEPODA	*Magelona alleni* Wilson*	CEPHALOPODA
Copepoda indet spp.	*Magelona papillicornis* F. Müller	Decabrachia spp.
Harpacticoidea indet spp.	*Nephtys caeca* (Fabricius)	LAMELLIBRANCHIATA
ANNELIDA	*Nephtys cirrosa* Ehlers	*Abra alba* (Wood)
HIRUDINEA	*Nephtys hombergi* Savigny	*Abra nitida* (Müller)*
Calobdella nodulifera Malm	*Nepthys longosetosa* Oersted	*Angulus donacinus* (L.)
OLIGOCHAETA	*Nereis pelagica* L.*	*Arctica islandica* (L.)*
Oligochaeta indet. spp.	*Nicolea zostericola* (Oersted)	*Astarte triangularis* (Montagu)
POLYCHAETA	*Ophelia limacina* (Rathke)	*Cardium edule* L.
Ampharete finmarchica (M. Sars)	*Ophelina acuminata* Oersted	*Cochlodesma praetenue* (Pulteney)
Anaitides groenlandica (Oersted)	*Orbinia (O.) sertulata* (Savigny)	*Corbula gibba* (Olivi)*
Anaitides aff. *maculata* (L.)	*Owenia fusiformis* Chiaje	*Cultellus pellucidus* (Pennant)
Anaitides mucosa (Oerstedt)	*Pectinaria koreni* Malmgren	*Donax vittatus* (da Costa)
Anaitides subulifera Eliason	*Pholöe minuta* (Fabricius)	*Dosinia exoleta* (L.)
Aonides paucibranchiata Southern	Phyllodocidae juv.	*Ensis siliqua* L.
Autolytus prolifer (Müller)	*Pisione remota* (Southern)	*Ensis* sp.
Capitella capitata (Fabricius)	*Poecilochaetus serpens* Allen	*Hiatella rugosa* (L.)
Chaetozone setosa Malmgren	*Polycirrus medusa* Grube	*Mactra corallina* Montagu
Chone infundibuliformis Kröyer	*Polycirrus* sp.	*Modiolus* aff. *barbatus* (L.)
Cossura longocirrata Webster & Benedict	*Polydora antennata* Claparede	*Modiolus modiolus* L.*
Eteone barbata (Malmgren)	*Polydora caeca* (Oersted)	*Montacuta bidentata* (Montagu)
Eteone flava (Fabricius)	*Polydora pulchra* (Carazzi)	*Montacuta ferruginosa* (Montagu)
	Polygordius spec.	*Mya arenaria* L.
	Pomatoceros triqueter (L.)	*Nucula nitidosa* Winckworth
	Protodorvillea kefersteini (McIntosh)	

Table 1 (continued)

Species	Species	Species
LAMELLIBRANCHIATA	*Nassarius incrassatus* (Ström)*	*Laomedea* sp.
Spisula solida L.*	*Polycera quadrilineata* (Müller)	*Metridium senile* L.*
Spisula subtruncata da Costa*	*Tritonia plebeia* Johnston	*Perigonium cirratus* Hartlaub
Tellina fabula Gronovius	*Tritonia* sp.	*Plumularia setacea* (L.)
Tellina tenuis da Costa*	COELENTERATA	Polymorpha spp.
Thracia villosiuscula (Macgillivray)	ACNIDARIA	*Sagartia troglodytes* Price
Venerupis pullastra (Montagu)*	*Pleurobrachia pileus* Müller	Scyphozoa indet. spp.
Venus striatula da Costa	Ctenophora indet spp.	*Sertularella rugosa* (L.)
	CNIDARIA	*Sertularia cupressina* L.*
GASTROPODA	*Abietinaria abietina* (L.)	*Sertularia tenera* G. O. Sars
Acanthodoris pilosa (Müller)	*Alcyonium digitatum* L.*	*Tealia felina* L.
Aeolidia papillosa (L.)*	Anthozoa sp.	*Tubularia* spp.
Antiopella sp.	*Calicella syringa* (L.)	
Buccinum undatum L.*	*Campanularia* aff. *johnstoni* Adler	MISCELLANEOUS
Coryphella spp.	*Cerianthus lloydii* Gosse	*Molgula* sp.*
Cuthona concinna (Alder & Hancock)	*Corymorpha* sp.*	Chaetognatha indet spp.
Cuthona gymnota	*Diphasia rosacea* (L.)	*Aechelia echinata* Hodge*
Dendronotus frondosus (Ascanius)	*Edwardsia* sp.	*Nymphon rubrum* Hodge*
Doris sp.	*Eudendrium* sp.*	*Golfingia* sp.
Doto coronata (Gmelin)	*Halecium halecinum* (L.)	Sipunculidae indet spp.
Eubranchus exiguus (Alder & Hancock)	*Haliplanella lineata* (Verrill)*	*Phoronis* sp.
Eubranchus sp.	*Hydractinia echinata* Fleming	*Cryptocelis alba*
Gibbula cineraria L.	*Hydrallmania falcata* (L.)*	Polycladidae indet spp.
Hydrobia ulvae Pennant	*Laomedea conferta* Hartlaub	Nemertines indet. spp.
Limacia clavigera (Müller)	*Laomedea dichotoma* (L.)	*Oncholaimus* sp.
Lunatia catena da Costa	*Laomedea geniculata* (L.)	Nematodes indet spp.
Lunatia nitida Donovan	*Laomedea neglecta* Alder	*Cliona lobata* Hancock
	Laomedea pelagica (van Breemen)	*Cliona* sp.*
		Leucandra fistulosa (Johnston)*
		Porifera indet sp.

Grab samples

All the grab samples showed some similarities in species composition, but, according to the station clusters, also distinct differences. The main average structural association data are presented in Tables 2 and 3 and in Figure 7.

Station group 1

The association structure of the fauna of stations I and II is related to their substrate and habitat heterogeneity, created by the intermixture of coarse sand with boulders and pebbles. Accordingly, the total species number of 116 was larger than in the other station group. 18 of all identified species (Table 1) were solely found in the grab samples of station group 1. Among them, only *Scalibregma inflatum, Protodorvillea kefersteini, Corophium sextonae* and *Doris* sp. occurred in more than two samples and are therefore

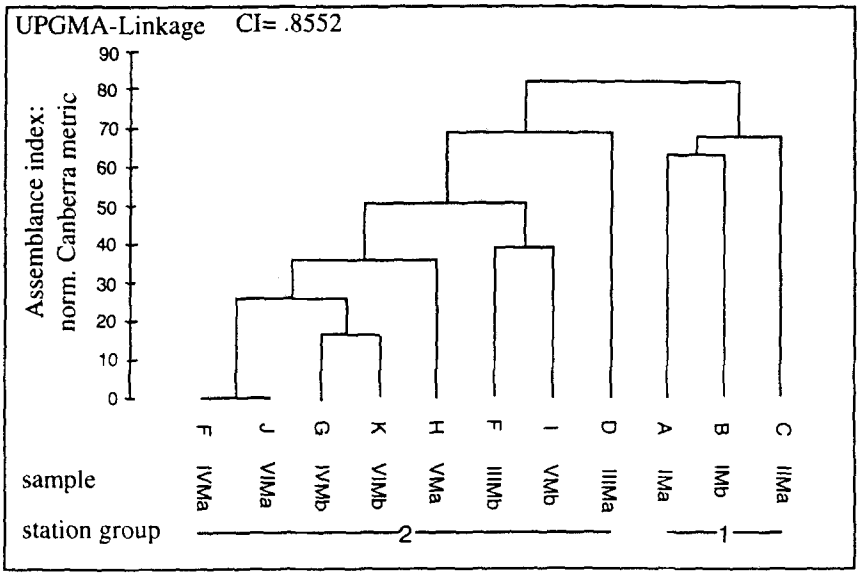

Fig. 3. Dendrogram of the hierarchical classification (COMM-Program) of the grab samples of May (Ma, Mb = single grabs, obtained at the different locations indicated by the numbers I–VI)

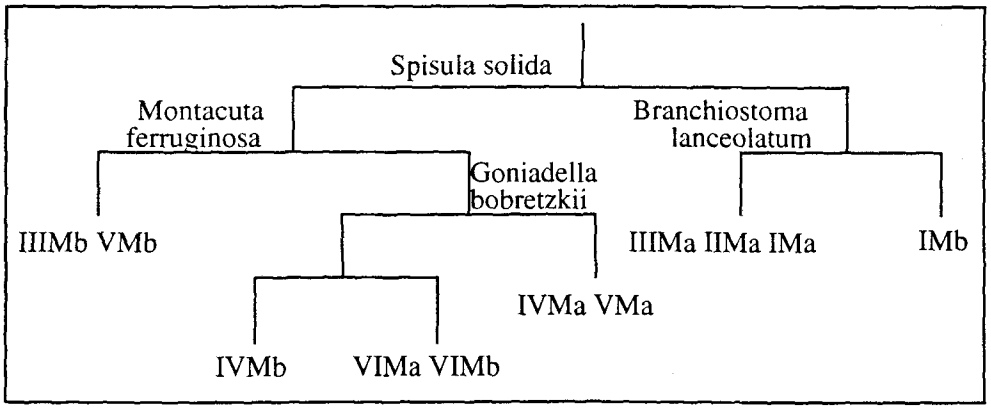

Fig. 4. Dendrogram of the divisive classification (TWINSPAN) of the May subsamples (grab). The main divisions are marked by an "indicator species" and its group affiliation (site of occurrence). For further explanations, see Fig. 3

considered as specific for this association. Epibenthic species such as the polycladid *Cryptocelis alba*, the crustaceans *Pilumnus hirtellus* and *Thia scutellata*, the balanid *Verruca stroemia*, the sponge *Cliona* sp. and the brittle star *Ophiotrix fragilis* were also found only in this association. Fifteen species of bryozoans (e.g. *Flustra foliacea*) and hydroids (e.g. *Sertularella rugosa*) were present.

The characterizing species was the polychaete *Anaitides mucosa*. Together with

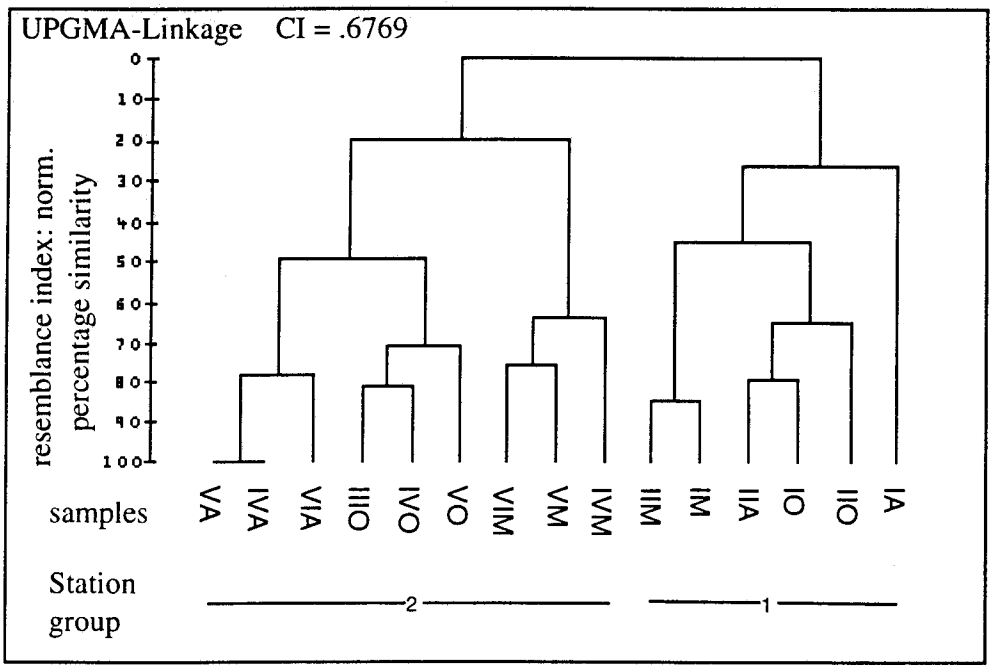

Fig. 5. Dendrogram of the hierarchical classification (COMM-Program) of the dredge subsamples (May = M, August = A, October = O). The data were not transformed. For further explanations, see Fig. 3

Lanice conchilega it contributed 38.8 % to the total number of individuals found in this association (Table 3).

The mean numbers of individuals and the mean biomass (ash-free dry weights) are much lower than in group 2 (Fig. 7). In spite of this, the highest number of individuals and the maximum species numbers in single samples were found in group 1. Especially in August, extreme densities of *Lanice conchilega* (6620 ind./m^2) and *Anaitides mucosa* (7100 ind./m^2) were recorded. Altogether, the polychaetes dominated with regard to numerical abundance and the number of species.

Station group 2

108 species were found in the medium to coarse sands at stations III to VI; and, according to Simpson's index, the association of group 2 was less diverse than that of group 1 (Table 2).

The association is characterized by the polychaetes *Magelona papillicornis, Spiophanes bombyx, Nephtys cirrosa,* and the bivalve *Spisula solida. M. papillicornis* and *S. bombyx* accounted for more than 60 % of all individuals found (Table 3). 16 species, for example the bivalves *Astarte triangularis, Montacuta ferruginosa, Thracia villosciusculus* and *Ensis siliqua,* the amphipod *Bathyporeia guilliamsoniana* and the polychaete *Anaitides subulifera* were specific for this association.

The echinoderms *Acrocnida brachiata, Amphiura filiformis* and *Echinocyamus pusil-*

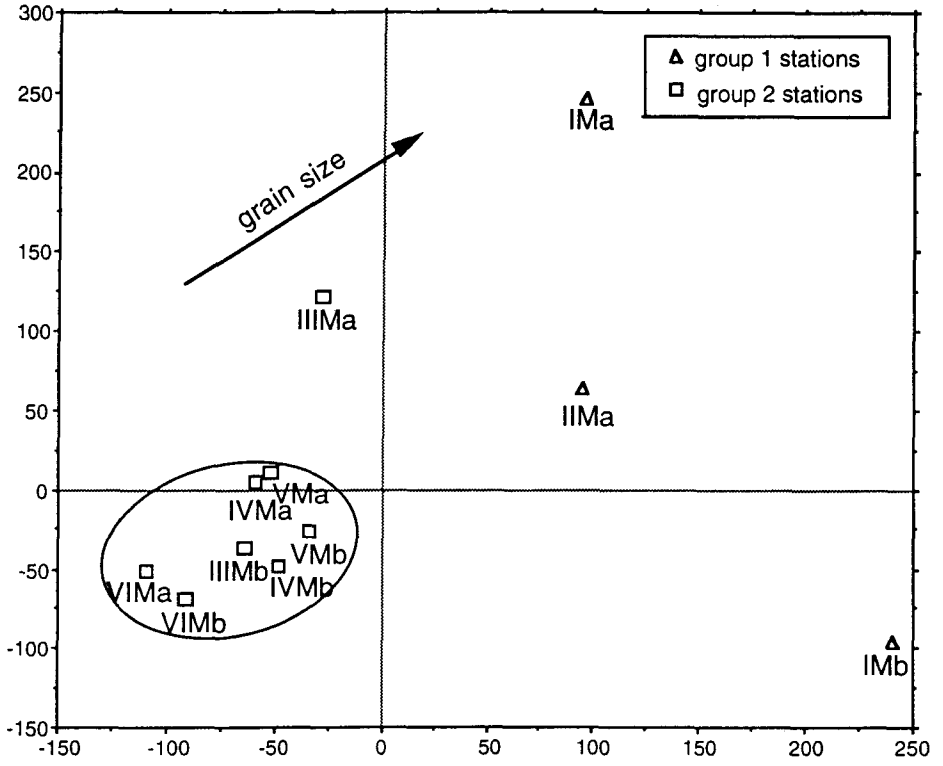

Fig. 6. Canonical community ordination (CANOCO) of the May subsamples (grabs) correlated to the grain size increasing towards sample IMa. For further explanations, see Fig. 3

lus, the crustaceans *Pontocrates arenarius, Jassa falcata, Synchelidium haplocheles* and *Pandalina brevirostris* and the polychaetes *Chaetozone setosa, Flabelligera affinis* and *Poecilochaetus serpens* occurred, in low numbers, only in this association. A few epibenthic species like the nudibranch *Eubranchus exiguus* and the echinoderm *Ophiura ophiura* were also found.

While mean numbers of species were almost equal, numerical abundances and mean biomasses were generally higher than in association 1, except in August (Fig. 7). The overall maximum biomass (182.4 g/m^2) was found at station IV in August.

Dredge samples

The ranked data of the dredge samples did not allow the same analytical treatment as the abundance data of the grab samples. Nevertheless, these macrofauna samples were divided into the same two station groups as the grab samples, with two different associations (Fig. 5) according to their species composition.

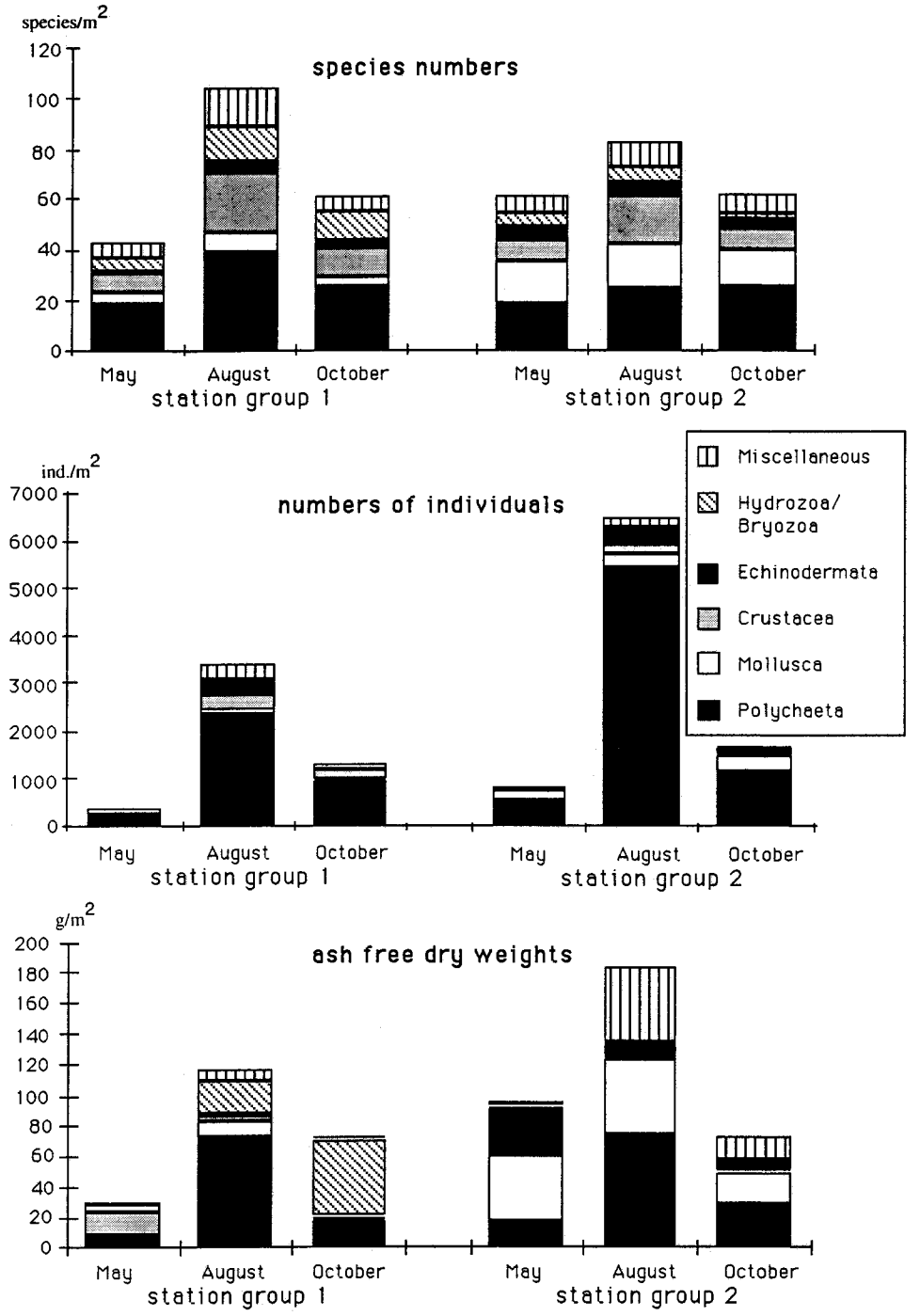

Fig. 7. Numbers of species and individuals and biomass (ash-free dry weight) of the grab samples

Table 2. Species numbers, diversity, evenness and the names of the dominant species for each station group, sample set and date

	Station group	Species number	Spec. number (90 % of indiv.)	Dominant species	Simpson's index	Heip's evenness
van Veen grab						
May	1	39	20	*Aonides paucibranchiata*	0.92	0.493
	2	56	23	*Aonides paucibranchiata*	0.92	0.356
August	1	92	26	*Lanice conchilega*	0.837	0.18
	2	77	12	*Magelona papillicornis*	0.661	0.077
October	1	50	21	*Anaitides mucosa*	0.854	0.264
	2	60	14	*Magelona papillicornis*	0.705	0.126
Dredge						
May	1	43	35	*Eusyllis blomstrandi*	0.964	0.784
	2	28	23	*Ophiura albida*	0.933	0.696
August	1	41	36	*Aora typica*	0.969	0.894
	2	63	47	*Liocarcinus holsatus*	0.977	0.802
October	1	59	47	*Eusyllis blomstrandi*	0.975	0.812
	2	46	36	*Ophiura albida*	0.961	0.725

Station group 1

The macrozoobenthos association of this station group is more diverse than that of group 2 (see Table 2 and Fig. 9), with the exception of the August samples. 65 % of the 124 epibenthic species found in all the dredge samples are present in this association, 16 species being restricted to it. 17 were also found in the grab samples of this station group.

The mean number of species in this association was larger than in association 2. The summation of the ranks (classes of abundance) shows the same trend. The crustaceans dominated by the numbers of species and individuals. The pantopode *Aechelia echinata* and the polychaete *Eusyllis blomstrandi* were identified as the characteristic species (Table 4). However, they were not restricted to this station group, as were the polychaete *Pomatocerus triqueter* and the crustacean *Pandalus montagui*. Although the bryozoan *Flustra foliacea* was present in several dredges (seen also during diving) and is to be regarded typical for the area, a quantification and ranking was not possible and, accordingly, no further analytical treatment.

Station group 2

The ophiurid *Ophiura albida*, the bivalve *Spisula solida* and the crustacean *Liocarcinus holsatus* were the characteristic species.

14 species of 91 in total were restricted to this association; but, only the sandeel *Ammodytes tobianus* belonged to the 20 dominants (Table 4). The bivalves *Angulus donacinus*, *Astarte triangularis* and *Thracia villosciusculus*, the other sandeel *Hyperoplus lanceolatus* and the polychaete *Nephtys longosetosa* were typical, but of very low incidence. *Spisula solida*, the hermit crab *Pagurus bernhardus*, and *Ophiura albida* had a presence of 100 %, but they were not restricted to the association.

Table 3. List of the 20 dominant species found in the grab samples from the two station groups. * Characterizing species; ** typical species (presence 100 %); POL = Polychaeta; CHO = Chordata; CRU = Crustacea; VER = Vertebrata; ECH = Echinodermata; ANT = Anthozoa; MOL = Mollusca

VanVeen STATION GROUP 1	Class.	Number of indiv. [ind./m^2]	Dominance [%]	Presence [%]	DAS [%]	DAI [%]
Lanice conchilega	POL	593	27.96	53.85	28.00	70.54
*Anaitides mucosa**	POL	230	10.84	69.23	45.00	72.57
Aonides paucibranchiata	POL	172	8.09	76.92	35.71	53.22
Ophiuridae juv.	ECH	115	5.44	61.54	29.63	38.86
Aora typica	CRU	77	3.63	53.85	87.50	99.01
Pectinaria koreni	POL	62	2.90	38.46	55.56	85.11
*Gattyana cirrosa***	POL	55	2.57	46.15	100.00	100.00
Glycera capitata	POL	45	2.14	53.85	70.00	81.94
Sabellaria spinulosa	POL	42	1.96	38.46	83.33	94.74
Cerianthus lloydi	ANT	41	1.92	46.15	54.55	82.81
Liocarcinus holsatus	CRU	38	1.81	38.46	50.00	78.13
Eumida sanguinea	POL	37	1.74	38.46	41.67	30.97
Nemertines		37	1.74	69.23	40.91	53.93
Goniadella bobretzkii	POL	27	1.27	76.92	50.00	17.07
Pomatoceros triqueter	POL	26	1.23	23.08	75.00	87.18
Anthozoa sp.	ANT	26	1.23	38.46	55.56	82.93
Scoloplos armiger	POL	24	1.12	46.15	40.00	65.96
Mya arenaria	MOL	22	1.02	38.46	83.33	96.55
Abra alba	MOL	20	0.94	38.46	41.67	59.09
*Protodorvillea kefersteini***	POL	20	0.94	46.15	100.00	100.00
STATION GROUP 2						
*Magelona papillicornis**	POL	1546	51.34	70.83	99.65	73.91
*Spiophanes bombyx**	POL	286	9.49	87.50	99.28	84.00
Lanice conchilega	POL	134	4.46	75.00	29.46	72.00
Ophiuridae juv.	ECH	98	3.27	79.17	61.14	70.37
Tellina fabula	MOL	97	3.21	58.33	99.15	93.33
*Astarte triangularis***	MOL	87	2.88	37.50	100.00	100.00
Aonides paucibranchiata	POL	82	2.71	75.00	46.78	64.29
Goniadella bobretzkii	POL	71	2.35	41.67	82.93	50.00
*Nephtys cirrosa**	POL	59	1.95	95.83	88.68	82.14
Anaitides mucosa	POL	47	1.56	45.83	27.43	55.00
Echinocardium cordatum	ECH	46	1.54	54.17	83.46	72.22
Eumida sanguinea	POL	45	1.48	29.17	69.03	58.33
Euphausidae	CRU	35	1.16	45.83	93.33	78.57
Spio filicornis	POL	32	1.05	54.17	98.70	92.86
Edwardsia sp.	ANT	29	0.95	41.67	84.15	62.50
Ophelia limacina	POL	28	0.94	62.50	73.12	71.43
*Spisula solida**	MOL	20	0.65	70.83	94.00	85.00
Nemertines		17	0.57	54.17	46.07	59.09
Branchiostoma lanceolatus	CHO	15	0.48	37.50	61.40	56.25
Donax vittatus	MOL	14	0.46	41.67	94.29	90.91

Some comments on algae

Only drifting material of the red algae *Delesseria sanguinea, Chorda filum* and brown algae of the genus *Laminaria* were found in the dredges and in some grabs; but,

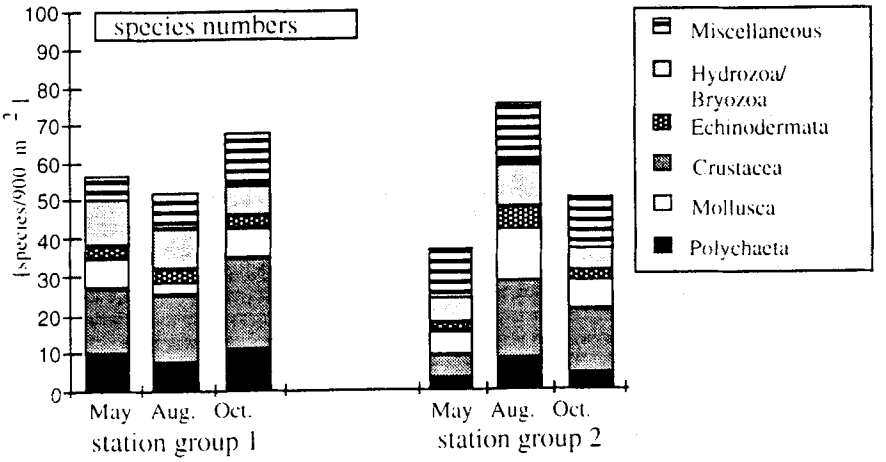

Fig. 8. Number of species in the two station groups based on all dredge sample sets (May, August, October)

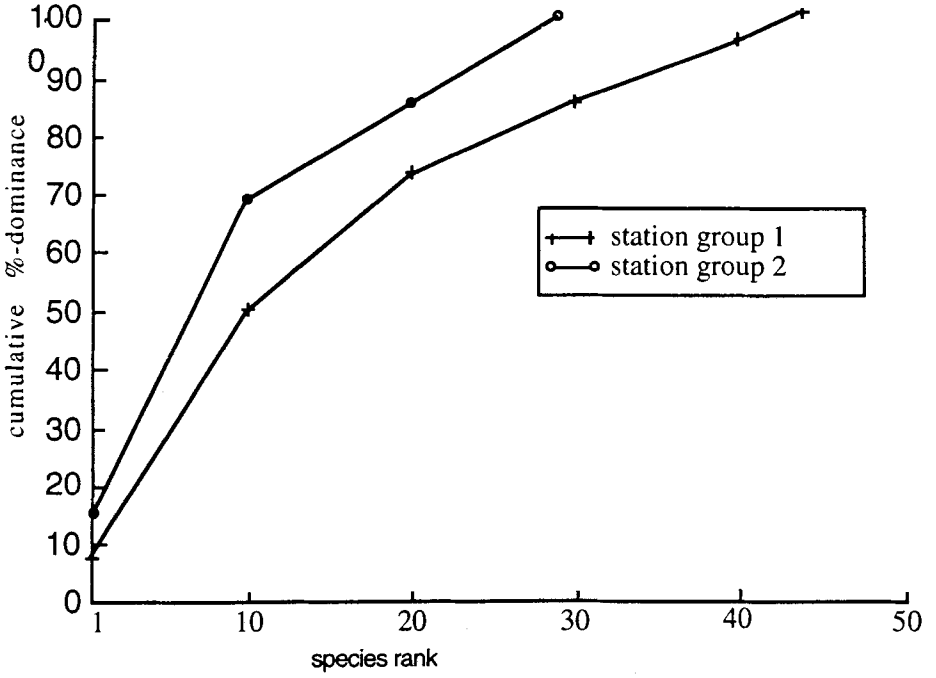

Fig. 9. Comparison of the k-dominance curves of the two station groups (dredge samples in May)

Table 4. List of the 20 dominant species found in the dredge samples from the two station groups. Other explanations: see Table 3; VER = Vertebrata (fish)

Dredge STATION GROUP 1	Class.	Dominance [%]	Presence [%]	DAS [%]	DAR [%]
*Eusyllis blomstrandi**	POL	6.55	100.00	90.00	75.00
Asterias rubens	ECH	4.36	83.33	66.67	55.56
Metridium senile	ANT	4.36	66.67	85.71	66.67
Crangon allmanni	CRU	3.64	83.33	45.45	45.45
Aora typica	CRU	3.27	66.67	42.86	44.44
*Aechelia echinata**	CRU	2.55	83.33	87.50	83.33
Corophium sextonae	CRU	2.55	66.67	77.78	66.67
Cancer pagurus	CRU	2.18	66.67	75.00	66.67
Hyas araneus	CRU	2.18	66.67	50.00	40.00
Pisidia longicornis	CRU	2.18	50.00	75.00	75.00
*Pomatoceros triqueter***	CRU	2.18	50.00	100.00	100.00
Pagurus bernhardus	CRU	1.82	66.67	27.78	30.77
*Pandalus montagui***	CRU	1.82	66.67	100.00	100.00
Modiolus modiolus	MOL	1.82	50.00	55.56	75.00
Spisula solida	MOL	1.82	33.33	21.74	18.18
Ophiura albida	ECH	1.82	66.67	16.67	30.77
Nematodes	NET	1.82	33.33	83.33	66.67
Gobiidae	VER	1.45	50.00	23.53	33.33
Myoxocephalus scorpius	VER	1.45	50.00	80.00	75.00
Crangon crangon	CRU	1.45	33.33	26.67	28.57
STATION GROUP 2					
*Ophiura albida**	ECH	7.40	100.00	83.33	69.23
*Spisula solida**	MOL	5.33	100.00	78.26	81.82
Gobiidae	VER	3.85	66.67	76.47	66.67
Pagurus bernhardus	CRU	3.85	100.00	72.22	69.23
Aora typica	CRU	3.55	55.56	57.14	55.56
Crangon allmanni	CRU	3.55	66.67	54.55	54.55
*Liocarcinus holsatus**	CRU	3.55	77.78	75.00	77.78
Crangon crangon	CRU	3.25	55.56	73.33	71.43
Callionymus reticulatus	VER	2.66	66.67	75.00	75.00
Anthozoa spp.	ANT	2.66	55.56	69.23	62.50
Lunatia nitida	MOL	2.37	55.56	80.00	71.43
Balanus spp.	CRU	2.07	33.33	77.78	60.00
Ophiura ophiura	ECH	2.07	66.67	77.78	85.71
*Ammodytes tobianus***	VER	1.78	44.44	100.00	100.00
Hyas araneus	CRU	1.78	66.67	50.00	60.00
Asterias rubens	ECH	1.78	44.44	33.33	44.44
Ophiuridae juv.	ECH	1.78	33.33	85.71	75.00
Anaitides mucosa	POL	1.78	44.44	66.67	66.67
Eumida sanguinea	POL	1.78	33.33	85.71	75.00
Buglossidium luteum	VER	1.48	44.44	71.43	80.00

no seaweeds were found growing on stones at the shallowest sites of the Steingrund during diving. Only some small patches of crustose red algae were found on collected boulders; they were not identified.

The red alga *Audouinella membranacea* was detected in hydroids from the shallow

areas of the Steingrund. According to Kornmann & Sahling (1977), it lives in the chitinous walls of hydroids (e.g. *Sertularella* sp.).

DISCUSSION

Two main station groups (habitats) were differentiated applying multivariate techniques at the Steingrund, and each of them had a typical endofaunal association based on the van Veen grab samples as well as a distinct epifaunal association yielded by the dredge samples.

Up to five different soft-bottom macrofauna communities have been described for the German Bight (Hagmeier, 1925; Stripp, 1969; Salzwedel et al., 1985). The latter distinguished two different sand communities: the *Tellina-fabula*-community in fine sands and the *Goniadella-Spisula*-community in coarse sands. Very heterogeneous coarse sand sediments characterize the area of investigation (Steingrund) and its vicinity (Helgoländer Austernbank and Amphioxussand).

Following Salzwedel et al., the associations found in the grabs of both station groups are modifications of a *Tellina-fabula*-community. They have some additional and transitional stage characters: Association 1 was characterized by a large proportion of epibenthic decapods, nudibranchs, hydroids and bryozoans. Characteristic species of the *Tellina-fabula*-community were present (e.g. the polychaete *Spiophanes bombyx*), as well as typical species of the *Goniadella-Spisula*-community, such as *Protodorvillea kefersteini*. Therefore, this association is regarded as a *Tellina-fabula*-community, with some features of the *Goniadella-Spisula*-community and strong influences of a rock epifauna.

The presence of the bivalve *Abra alba*, an inhabitant of mud, silty sand and soft muddy gravel bottoms (Tebble, 1966), as well as species like the polychaete *Pomatocerus triqueter*, which is mainly found on hard substrata (Hartmann-Schröder, 1971), indicate the variability of the fauna and the sediment within this station group.

The influence of the *Goniadella-Spisula*-community was much stronger in the association of station group 2. *Tellina fabula*, which is characteristic for the *Tellina-fabula*-community, occurred together with *Spisula solida* and *Goniadella bobretzkii*, which are characteristic for the *Goniadella-Spisula*-community.

These two endofaunal associations differ greatly from the other soft-bottom communities described by Hagmeier (1925), Stripp (1969) and Salzwedel et al. (1985), and also partly from the sand-inhabiting "Venus-gallina-community" of the first two authors.

The two epifaunal associations, defined by dredge sampling, were totally different in their species composition. The association of stations I and II inhabits a field of boulders and pebbles that stretches from Helgoland to the northeast (see Fig. 1). The typical epibenthic species *Eusyllis blomstrandi* and *Aechelia echinata* were identified as characteristic. Other mobile species found, like *Cancer pagurus, Pilumnus hirtellus, Echinus esculentus* and *Pholis gunnellus*, were also regarded as typical of hard bottoms (Frauenheim et al., 1989). The main predators in this animal-dominated zone seem to be crustaceans and echinoderms, which is also true of other waters (Canadian: Logan, 1988).

In addition, the sessile epibenthic species *Alcyonium digitatum, Flustra foliacea* and *Metridium senile* were found in large numbers at both stations and also in the shallower parts of the Steingrund (during diving). Especially *Alcyonium* and *Flustra* are regarded typical of the hard substrata around Helgoland (de Kluijver, 1991).

In a comprehensive view, this Steingrund epifaunal association is to be characterized by *Flustra foliacea* and *Aechelia echinata*. But, it is not yet known whether these two species are generally typical for stony grounds in the southern North Sea, while there is some resemblance in species composition to the hard-bottom communities of the shallow sublittoral zone of the inner Hebrides (Mitchell et al., 1983).

Little is known about the densities and biomass of the macrofauna of stony sand areas in our waters. It was shown in this paper (Fig. 7) that the abundances in the Steingrund area are within the variability of the *Tellina-fabula-* and *Goniadella-Spisula-*communities as described by Salzwedel et al. (1985). Biomass figures (of October, the same sampling time as in Salzwedel et al.) are comparable with those of the *Tellina-fabula*-community, but – in station group 1 – not with those of the *Goniadella-Spisula-*community (about 3.7 g AFDW in October 1991 compared with 13 g in 1975). The epifauna, as a main component of the community, is not sufficiently included in these figures. Nevertheless, by comparing the minimal biomass values obtained in May with the maxima of August, an idea about the ("minimum") production (g AFDW m^{-2}) can be formed by subtraction:

Group 1: Aug.–May: 23.7–4.7 g = 19 g ; P/B_M = 5.0; (P/B = 1.8)

Group 2: Aug.–May: 19.2–8.6 g =10.6 g; P/B_M = 2.2; (P/B = 0.9)

P/B_M ratios (based on May biomass) are high, while (annual) production and P/B (based on average biomass) are within the variability known from the German Bight and other temperate waters (Warwick et al., 1978; Salzwedel, 1980).

The epifaunal association of station group 2 was typical of a sandy bottom community dominated by *Lunatia catena*. *Ophiura albida* and *Liocarcinus holsatus* were identified as the characterizing species. However, they were found in both station groups. Thus, the association of station group 2 is well differentiated only by the endobenthic bivalve *Spisula solida*. The occurrences of *Hyas araneus, Pilumnus hirtellus, Ophiura albida, Corystes cassivelaunus, Arnoglossus laterna* and *Solea solea* emphasized that this association is typical for the southern North Sea (Frauenheim et al., 1989).

The patchiness of the sediments is reflected by the spatial distribution of the benthos. A correlation between the benthos and the sediment was already proposed by Petersen (1913) and discussed many times (Davis, 1925; Jones, 1950; Künitzer et al., 1992). Nevertheless, the mean number of macro-infaunal species decreased towards station I and II, where boulders and gravel were intermixed with very coarse sands. On the other hand, the number of epifaunal species increased towards these stations.

The species composition of the neighbouring Helgoländer Austernbank (Caspers, 1950) and the Tiefe Rinne south of Helgoland (Caspers, 1939; Berberich, 1989) are not so similar (50–62 % of the species found there were also found at the Steingrund) as the species composition of the Borkum-Riffgrund (75 %, see Dörjes, 1977), another stony area in the German Bight north of the island of Borkum.

It must be mentioned that several of the species found in the Steingrund area are rare in the German Bight according to the "Red List" of Rachor et al. (1995), e.g. the sponge *Leucandra fistulosa*, the sea anemone *Haliplanella lineata*, the leather coral *Alcyonium digitatum*, and the edible sea urchin *Echinus esculentus* and about 40 other invertebrates, indicated in Table 1. This rarity can be explained by the scarcity of suitable hard substrates in the southeastern North Sea, the poor knowledge of their fauna, but also by the shelter provided by boulders especially from bottom trawling. As an example, the sea

urchin *Echinus esculentus* was probably more common early in this century, even on soft bottoms in the German Bight and the open North Sea (Gerdes, 1976; Stein et al., 1990).

More extensive synecological studies of stony grounds within the North Sea are required, using a combination of different sampling methods including imaging and diving, before a general description can be worked out.

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