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Long-term studies of macrozoobenthos in intertidal and shallow subtidal habitats near the island of Norderney (East Frisian coast, Germany)

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Abstract

Near the East Frisian island of Norderney two sites are investigated permanently in order to study long-term fluctuations of macrozoobenthos: one transect (since 1977) at the northern side in shallow subtidal waters and another one (since 1976) at the sheltered southern side in the intertidal area of the Wadden Sea. Since 1980 the investigations have been continued in the frame of COST-47, sedimentary intertidal programme (including the shallow subtidal habitats colonized by the *Macoma balthica* community).

The results up to 1984, respectively to 1985, are presented and the changes of abundance of the dominant species are discussed. Discussed are also the influences of water temperatures and sediment disturbances caused by wave action. There is evidence that the intertidal variety of the *Macoma balthica* community shows a greater stability than the subtidal variety.

Introduction

Although mankind has always experienced in nature the alternation of 'fat' and 'lean' years there were quite static ideas of the marine littoral benthos for a long time. Many former authors found that structures and densities of animal communities have changed over the years (e.g. Thamdrup, 1935; König, 1943; Jepsen, 1965). Also the population dynamics of selected animal species were the object of investigations at an early stage (e.g. Dales, 1951; Kristensen, 1958; Gibbs, 1968). However, the increasing pollution of the sea since the 1960's has channeled our stronger interest in the changes within a given time, which the littoral communities are subjected to. The first to undertake an approach to such a complex of questions in the area of the Wadden Sea were Hauser (1973), Beukema (1974), Beukema *et al.* (1978) and Essink (1978).

Long-term investigations were started on the East Frisian coast in 1976 (eulittoral) and 1977 (sublittoral). Since 1980 they have been continued within the scope of the COST programme.

The habitats which were investigated belong to the distribution area of the *Macoma balthica* community, which is characteristic for the North Sea littoral. In the intertidal area it forms the 'intertidal variety of the *Macoma* community', which is poor in species, while the sublittoral is inhabited by the 'subtidal variety of the *Macoma* community', the species richness of which is considerably higher.

The following report contains a first analysis and evaluation of the data and above all shows the development of the dominant species.

For the part of the work dealing with the intertidal bottom fauna we received financial support from the Federal Ministry of Research and Technology.

Area of investigation and methods

Intertidal and subtidal habitats near the East Frisian island of Norderney are the area of investigation. Norderney is a 'barrier' island between the Wadden Sea and the North Sea. As can be seen in

Fig. 1 the stations 1 to 4 lie south of the island on a transect in the intertidal area.

Since 1976 samples were taken in intervals of one month (till 1977), of two months (till 1980), and three months (from 1981 on). For each year only the data for January, April, July, and October will be presented in this paper. Station 2 is identical with a permanent plot which was already inves-

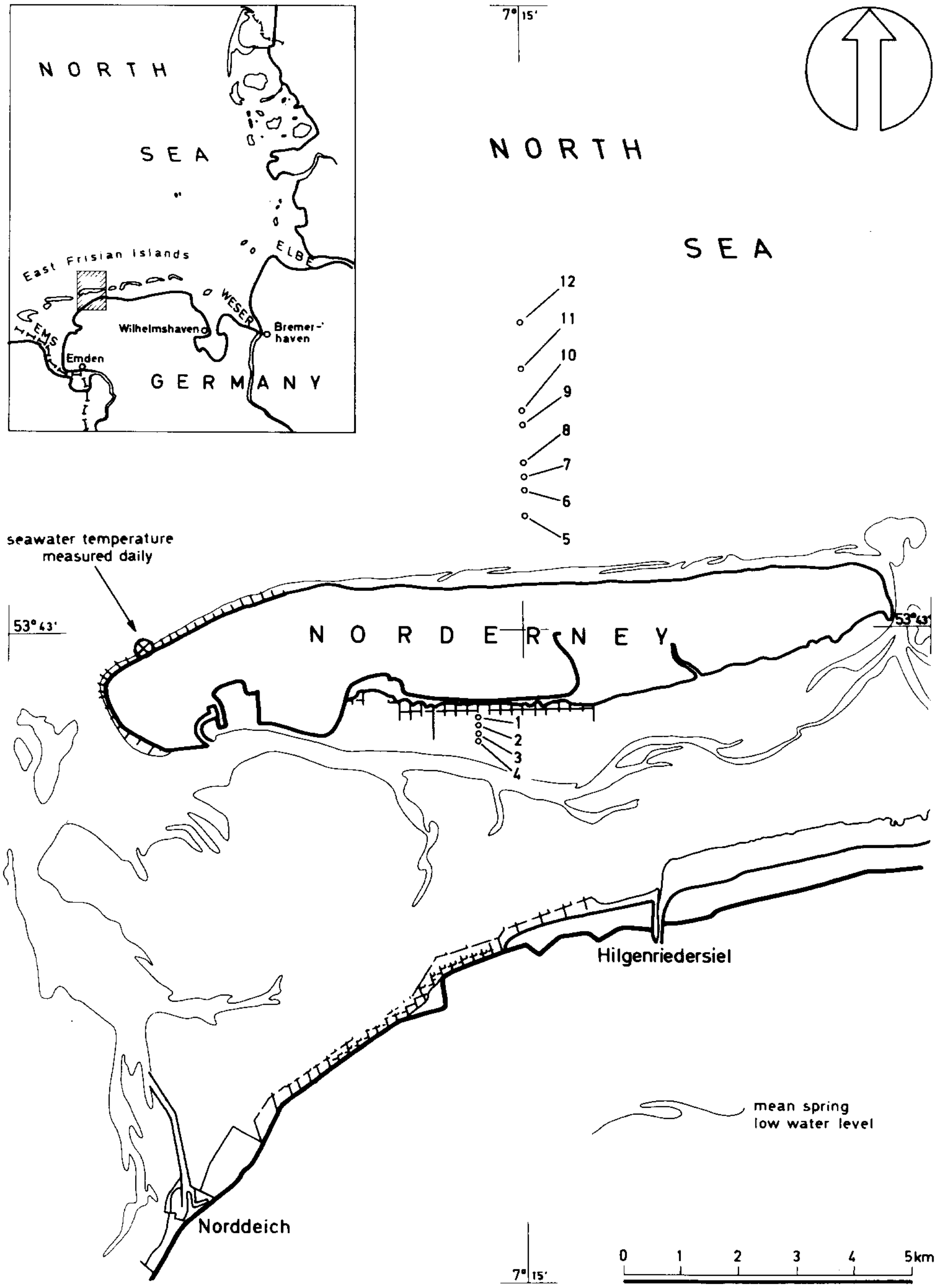

Fig. 1. Map of the investigation area with the intertidal stations 1–4 and the subtidal stations 5–12.

tigated by Hauser (1973) in 1970 till 1972.

At each station one sample of 0.125 m^2 was taken till 1977; from 1978 on 7 samples of 177 cm^2 were taken at each station. The bottom fauna was sieved with a 1 mm mesh aperture and then sorted out and counted in a live state. The biomass was determined as ash-free dry weight (ADW), at first according to Beukema (1974), from 1984 on with a reduced combustion temperature according to Lappalainen & Kangas (1975). Mollusc shells were separated from the flesh, apart from small gastropods (*Hydrobia, Littorina* juv.) and the spat of bivalves.

The following abiotic parameters were investigated: sea-level for calculating the inundation time, grain size distribution of the sediment, organic matter as loss on ignition, water content, salinity of the interstital water, and depth of the oxidized layer. The weather station on Norderney put data on water temperature at our disposal, which were measured once per day at the northern edge of the island (see Fig. 1). Data on ice formation were also received from the weather station and completed by our own observations. At the sublittoral stations 5 to 12 a first survey was carried out in 1970, the results of which have been published by Dörjes (1976). Since 1977 samples were taken in monthly intervals. Due to rough seas and ice-drift there have been some gaps. The Van Veen grab with a sampling area of 0.2 m^2 was used. At each station only 1 sample was taken. The bottom fauna was sieved with 0.63 mm mesh aperture and fixed in formaldehyde. The biomass was not determined. Sedimentological data (grain size distribution) have been placed at our disposal by an investigation of Reineck (1976) which is running parallel to ours.

Results

Environmental conditions

The characteristic water temperatures for the area vary (according to monthly averages of long-term measurements on the seaward side) between a maximum of 18.5 °C in July/August and a minimum of 2.0 °C in January/February. The deviations from the average which have appeared between 1976 and 1985 can be seen in Fig. 2. Above average temperatures prevailed in the hot summers of 1976, 1982, and 1983. The cold winters of 1978/79, 1981/82 and 1984/85 are distinguished by ice-drift and a long-lasting ice-cover in the intertidal area.

According to long-term measurements monthly averages of salinity at the south side of Norderney fluctuate between 31‰ (in July) and 28‰ (in January). Altogether the deviations extend from 34‰ to 21‰. The lower values show the influence of the Ems estuary which lies to the west. In the seaward area salinities are higher and more constant and they generally don't drop below 30‰.

The mean tidal amplitude at Norderney is 2.4 m. As the intertidal stations lie on a transect with decreasing level the inundation time increases from ca. 35% at Station 1 to ca. 55% at station 4.

The sediments of the intertidal stations can be classified as sand between fine and medium sand with an average medium value of about 200 μm, a small portion (up to 4%) of silt (< 63 μm), an average loss on ignition of 1 – 2% and an average water content of 20 – 30%. The sediment composition is very constant. Since the investigations of 1970 to 1972 (Hauser, 1973) the grain size distribution shows practically no changes (Fig. 3).

The oxidized layer is rather thin, only 0.5 to 3.0 cm deep in summer and autumn, and 0.5 to 8.0 cm deep in winter and spring. This fact can be explained by the sheltered position of the habitat.

The sublittoral stations are situated in water of 5 m (station 5) to 14 m depth (station 12). The sediments consist of fine sand and medium sand (Fig. 3).

Composition of the bottom fauna

In the intertidal stations 35 species occurred (18 annelids, 9 molluscs, 7 crustaceans, and 1 insect), not including several unidentified nemertines (Table 1). The species which were already found in 1970 – 1972 by Hauser (1973) at station 2 are marked with an asterisk. The most constant members of the community are also dominant ones with respect to density and/or biomass. *Nereis diversicolor, Scoloplos armiger, Heteromastus filiformis, Cerastoderma edule, Macoma balthica, Tubificoides benedeni*, and in a less frequent occurrence, *Pygospio elegans* and *Hydrobia ulvae* belong to the most dominant species in numbers (Fig. 4b). Dominant species according to weight are

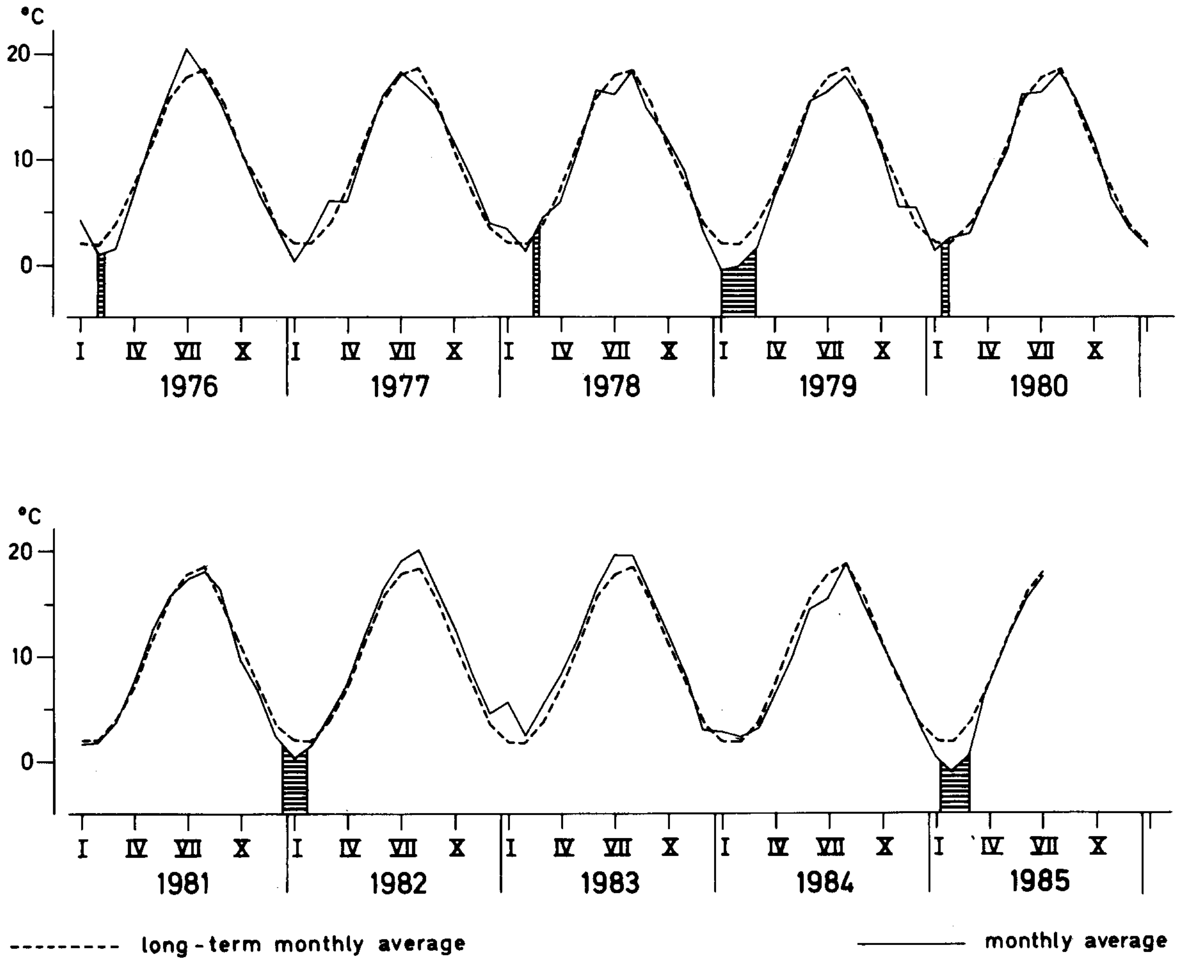

Fig. 2. Mean water temperature measured at the seaward side of the island (monthly means of 1971–1984) and deviations in the period 1976–1984. Hatched: ice-cover on tidal flats.

Arenicola marina, Nereis diversicolor, Scoloplos armiger, Heteromastus filiformis, Cerastoderma edule, and *Macoma balthica* (Fig. 4c).

The sublittoral bottom fauna at stations 5 to 12 is almost three times as rich in species (Table 2). The nemertines excluded, 103 species were found, which are distributed among the various taxonomic groups as follows: 36 polychaetes, 32 crustaceans, 24 molluscs, 5 echinoderms, 2 coelenterates, 2 pisces, 1 phoronid, and 1 pantopod. In the sublittoral there is also a restricted number of species which appear regularly and create dense populations. These are *Magelona papillicornis, Macoma balthica, Scoloplos armiger, Nephtys hombergi* and – less frequent and abundant – *Lanice conchilega, Bathyporeia pelagica, Spio filicornis, Urothoe grimaldii var. poseidonis,* and *Pectinaria koreni.* There are 23 species which occur commonly in the intertidal and in the subtidal habitats (Tab. 1, 2).

Changes in abundance and biomass of dominant intertidal species

Figures 4, 5 and 6 demonstrate the periodic seasonal changes for a number of species in abundance and biomass. This seasonal variation generally shows a maximum in summer or autumn and a minimum in late winter or early spring, often in

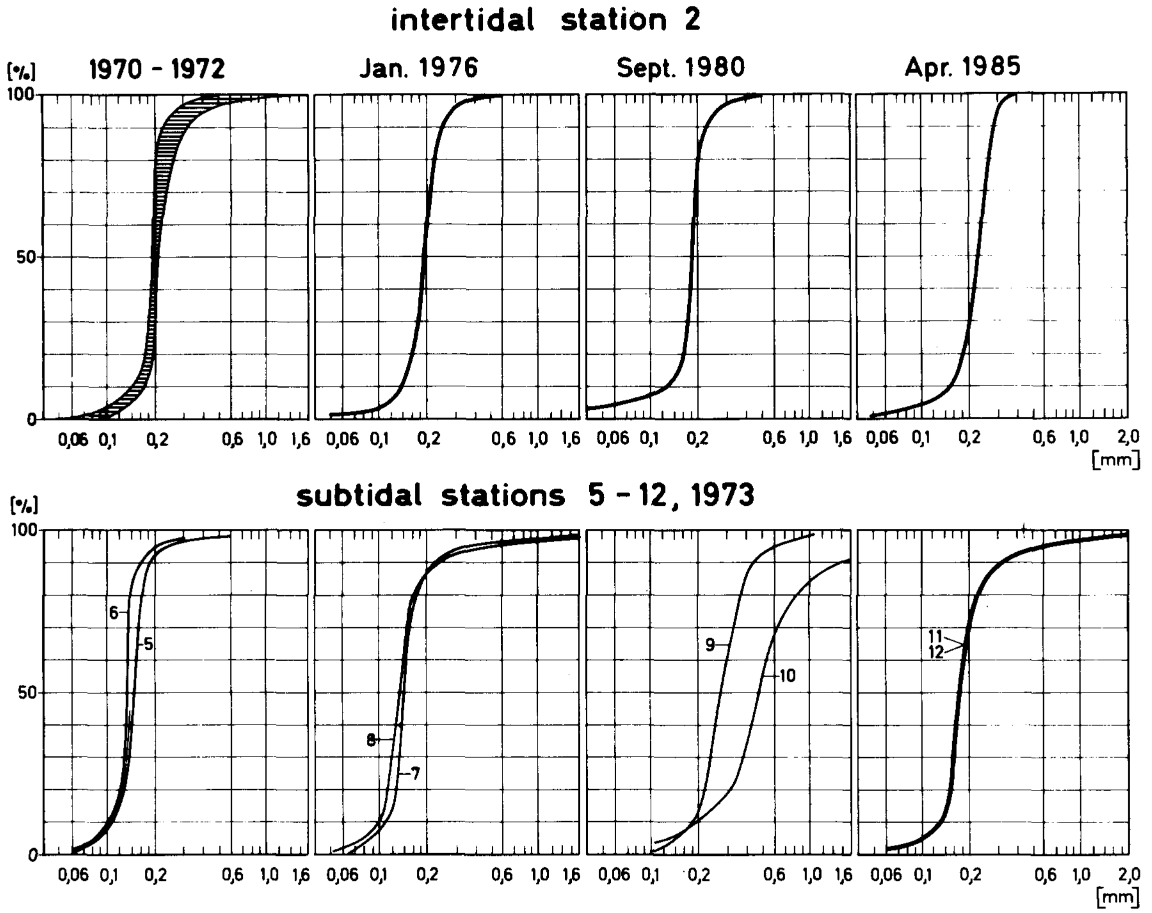

Fig. 3. Above: grain size distribution at station 2. Conditions found by Hauser (1973) compared with later investigations. Below: grain size distribution at station 5–12 in 1973.

April. The total maximum densities amount to 15000–40000 individuals · m^{-2}. At the time of the minimum densities, there are still about 4000–10000 specimens · m^{-2} present.

The maximum values of the total biomass are about 50 to 80 g ADW · m^{-2}, in some years even 150 g and more. The minima lies in general at 20 and 30 g, measured against the maximum weight one fifth to one third.

Figure 4b shows the share of 8 dominant species in the total population density. Figure 4c shows how the total biomass is distributed among the 6 species which are dominant in weight. With respect to the different species the following can be said.

The lugworm *Arenicola marina,* with maximal densities of 40 to 60, is not dominant in numbers (Fig. 5). However, it is significant with respect to weight (10–20% of the total biomass). It has survived the severe winters 1978/79 and 1984/85 with surprisingly high densities (25–35 animals · m^{-2}). Relatively low numbers and biomass values were found in the years 1982–1984.

The ragworm *Nereis diversicolor* has a weak dominance by numbers but a great constancy. Its contribution to the total biomass remains mostly under 10% (Fig. 5).

Scoloplos armiger is a very typical inhabitant of the biotope that was investigated, with densities of mostly more than 600 animals · m^{-2}. The biomass contributes to the total weight with a maximum of 10% (Fig. 5). The mass production of egg capsules in every spring (March/April), which cover the bottom surface, is spectacular. In April 1976 a weight of 0.7 g ADW was determined for an aver-

Table 1. Species found at the intertidal stations 1 – 4 from 1976 to 1985. With asterisk: Species already found by Hauser (1973) at station 2. Underlined: Species common to the intertidal and subtidal transect.

Station No.	1	2	3	4
Nemertini				
Several unidentified species				
Annelida				
**Anaitides mucosa*	+	+	+	+
**Arenicola marina*	+	+	+	+
**Capitella capitata*	+	+	+	+
**Eteone longa*	+	+	+	+
**Harmothoe sarsi*	+	+	+	+
**Heteromastus filiformis*	+	+	+	+
**Lanice conchilega*	+	+	+	+
Lumbricullus lineatus	+	+	+	+
**Magelona papillicornis*		+		
**Nephtys hombergii*	+	+	+	+
**Nereis diversicolor*	+	+	+	+
**Paranais litoralis*	+			
Polydora ligni	+	+	+	+
**Pygospio elegans*	+	+	+	+
Scolelepsis foliosa			+	+
**Scoloplos armiger*	+	+	+	+
**Tharyx marioni*	+	+	+	+
**Tubificoides benedeni*	+	+	+	+
Mollusca				
**Cerastoderma edule*	+	+	+	+
Ensis directus	+	+		+
**Hydrobia ulvae*	+	+	+	+
**Littorina littorea*	+	+	+	+
**Macoma balthica*	+	+	+	+
**Mya arenaria*	+	+	+	+
**Mytilus edulis*		+	+	+
**Retusa obtusa*	+	+		
Scrobicularia plana		+	+	+
Crustacea				
**Bathyporeia sarsi*	+	+	+	+
**Carcinus maenas*	+	+	+	+
**Corophium cf. volutator*	+	+	+	+
**Crangon crangon*	+	+	+	+
**Gammarus* sp.	+	+	+	+
Jaera albifrons		+	+	+
**Urothoe grimaldii var. poseidonis*	+	+	+	
Insecta				
Chironomidae (larvae)			+	
Number of species	29	32	31	30

age of 152 capsules · m^{-2}; compared with the coincident weight of the population of 1.3 g ADW · m^{-2} it is a remarkable amount. The high loss of substance due to spawning results to minimal values of the biomass after the spawning time in only a few years (1979, 1981, 1983).

Heteromastus filiformis (Fig. 5) is generally considered to be a species which preferably colonizes muddy, anaerobic sediments. It kept to this rule at the time of Hauser's (1973) investigation and did not exceed densities of 100 individuals · m^{-2} at station 2. In our period of investigation the densities exceed 1000 · m^{-2} for the first time in 1976, and till 1980 rise above 7000 specimens · m^{-2}. After occurrence of relatively low densities in 1981 and 1982 very high densities occur again in 1983. From 1984 on there seems to be an indication of a decline.

In respect of the seasonal fluctuations it is remarkable that maximal and submaximal densities often coincide with the minimum temperature in January, as in 1977, 1978, 1980, 1983 and 1984. The biomass increased to values of 9 g ADW and more after 1980 and contributed 10 to 20% to the total biomass.

Cerastoderma edule is in principle a constant species of the habitat with densities which mostly amount to several hundreds, often 1000 individuals · m^{-2} (Fig. 6). It was temporarily wiped out due to ice-drift in the severe winters of 1978/79 and 1984/85, and was strongly decimated in winters with only short-term ice formation (1975/76, 1979/80, and 1981/82). A new population was established at the deserted spots only due to spatfall. Strong spatfalls led to densities of 8000 to 20000 animals · m^{-2} in the summers of 1976, 1981, and 1984.

The significance of *Cerastoderma* for the total biomass of the habitat is outstanding. 20 to 40 g ADW · m^{-2} are predominant values, the maxima can exceed 100 g. The share of the total biomass amounts to 40 – 60% over several years. After severe winters the biomass was temporarily reduced to zero, as in 1978/79. After that the biomass improved till 1981 to a level of 10 g · m^{-2}.

The population of *Macoma balthica* shows an extraordinary constant minimum density of 100 to 300 individuals · m^{-2} (Fig. 6). Spatfalls of significant size resulted in the summer 1979 after 2 hard winters and also in 1976, 1981 and 1984 after moderate or mild winters. The maximum of 1979 amounted to almost 8000 individuals · m^{-2}. The biomass shows minima of 1 to 3 g ADW · m^{-2} in late winter or early spring. The maxima, which mostly result in July, reach values of 4 to 14 g

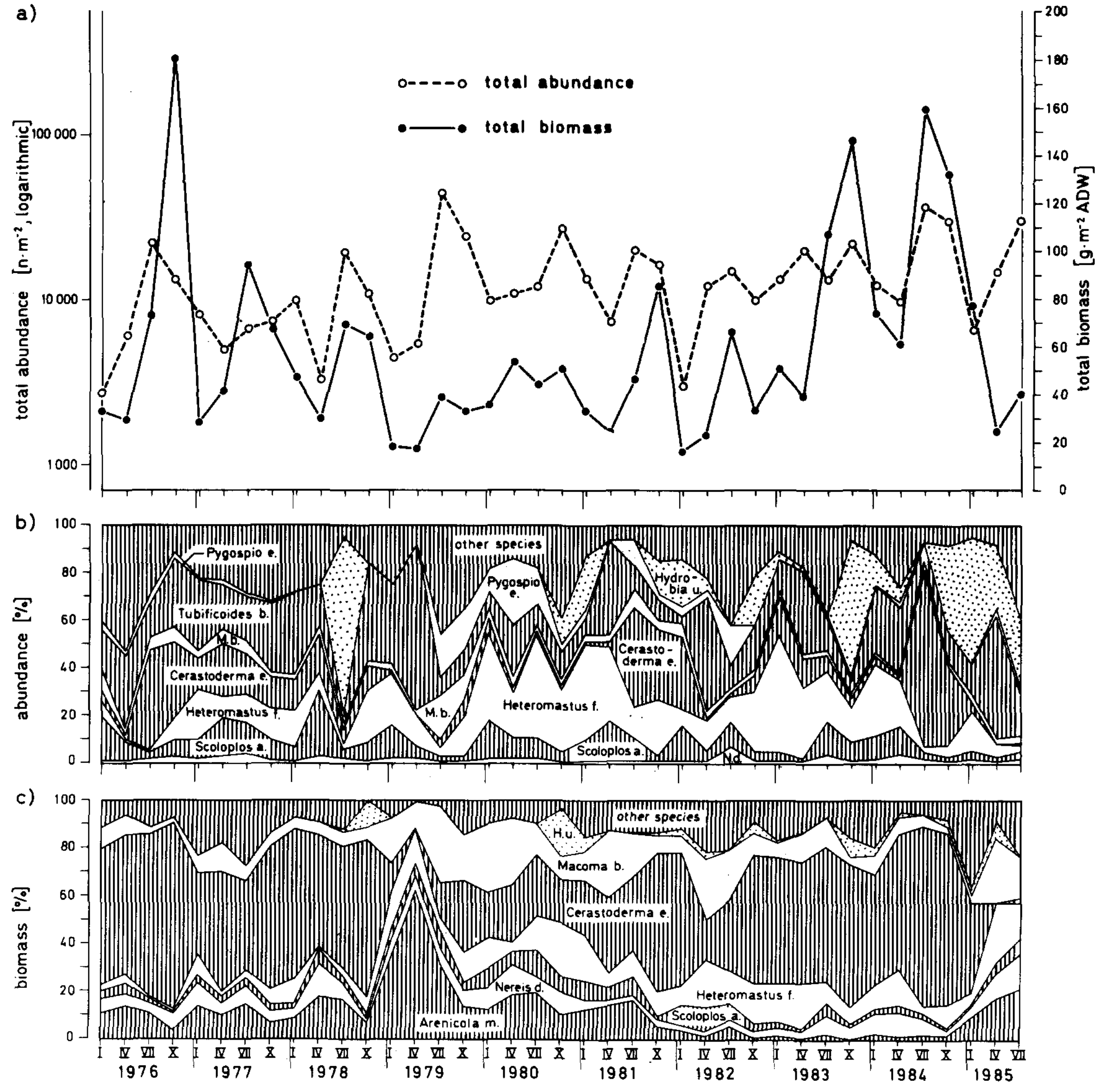

Fig. 4. Intertidal macrobenthos. a) Variations in total abundance (number of individuals) and total biomass (ash-free dry weight). b) Share of dominant species in total abundance. c) Share of dominant species in total biomass. a, b, c: means of the stations 1–4 are demonstrated. N.d.: *Nereis diversicolor*; M.b.: *Macoma balthica*; H.u.: *Hydrobia ulvae*.

ADW · m^{-2}. Correspondingly the share of the total weight fluctuates between 5 and 25%.

Of the other dominant species *Tubificoides benedeni* is the only one which is continuously present in densities of 600–5000 individuals · m^{-2} (20 to 40% of the total abundance). Its contribution to the biomass is insignificant (< 3%).

Members of the community with a strongly irregular occurrence are *Pygospio elegans* and *Hydrobia ulvae.* In the short term *Hydrobia* can become a predominant species as happened in July 1978, January 1982, and October 1983 to April 1984 (Fig. 4b) and then it can be of great significance for the biomass (Fig. 4c).

Changes in the abundance of dominant subtidal species

Only very few species are really abundant in the foreshore and the upper sublittoral. Some of them

Table 2. Species found at the subtidal stations 5 – 12 from 1977 to 1984. + rare; + + medium frequent; + + + frequent. Underlined: Species common to the intertidal and subtidal transect.

Station No.	5	6	7	8	9	10	11	12
Water depth (m)	5	6	7	8	9	10	12	14
Nemertini								
Several unidentified species	+	+	+	+	+	+	+	+
Annelida								
Anaitides groenlandica	+	+	+	+	+	+	+	+
Anaitides mucosa	+	+	+	+	+	+	+	(+)+
Capitella capitata	+	+	+	+	+	+	+	+
Eteone lactea			+		+	+	+	+
Eteone longa	+	+	+	+	+	+	+	+
Eulalia viridis	+	+	+	(+)+	+ +	+	+	+ +
Eumida sanguinea			+					
Goniada maculata	+	+	+	+	+	+	+	+
Harmothoe longisetis		+						
Harmothoe lunulata	+	+	+	+	+	+	+	+
Harmothoe sp.	+	+	+	+	+		+	+
Heteromastus filiformis	+	+	+		+			+
Lanice conchilega	+	+	+ +	+ +	+ + +	+ +	+ +	+ +
Magelona papillicornis	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +
Microphthalmus similis						+		
Nephtys hombergi	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +
Nereis succinea	+	+					+	+
Nereis virens				+	+			
Ophelia limacina	+	+	+	+	+	+ +	+	+
Owenia fusiformis		+	+					
Pectinaria koreni	+ +	+ +	+ +	+ +	+	+	+	+
Pholoe minuta	+	+	+	+	+		+	+
Pisione remota						+		
Polydora caeca							+	
Polydora ligni	+		+					
Polydora pulchra				+	+			
Pygospio elegans			+					
Scalibregma inflatum								+
Scolelepis bonnieri	+	+	+	+	+	+	+	+
Scolelepis foliosa						+		
Scoloplos armiger	+ +	+ +	+ +	+ +	+ +	+ +	+ + +	+ + +
Sphaerodorum flavum						+	+	
Sigalion mathildae				+				
Spio filicornis	+ +	(+)+	+ +	+ +	+	+	+	+
Spiophanes bombyx	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +
Tharyx marioni		+	+	+	+	+	+	+
Mollusca								
Abra alba	+	+	+	+	+		+	+
Abra nitida								+
Abra prismatica					+			
Angulus fabula	+	+	+ +	+ +	(+)+	+	+ + +	+ +
Angulus tenuis		+				+		+
Astarte triangularis	+	+		+	+	+	+	+
Cerastoderma edule	+	+	+					+
Donax vittatus	+	+	+	+	+	+	+	+
Ensis directus	+	+	+	+	+	+	+	+
Hydrobia ulvae	+			+				+
Lunatia nitida		+			+			+
Lunatia sp.			+	+		+	+	
Macoma balthica	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ +	+ +

Table 2. Continued.

Station No.	5	6	7	8	9	10	11	12
Water depth (m)	5	6	7	8	9	10	12	14
Mactra corallina	+			+	+		+	+
Montacuta ferruginosa	+	(+)+	+	+	+	+	+	+
Mya arenaria	+		+		+		+	+
Mya truncata								+
Mysella bidentata	+	+	+	+	+	+	+	+
Mytilus edulis	+	+	+	+	+	+	+	+
Retusa obtusa	+							
Spisula elliptica				+	+		+	+
Spisula solida	+	+	+	+	+	+	+	+
Spisula subtruncata					+		+	+
Venus gellina					+			
Crustacea								
Ampelisca sp.							+	+
Bathyporeia gracilis							+	
Bathyporeia pelagica	++	++	++	++	++	+	++	++
Bodotria scorpioides							+	+
Caprella linearis				+	+	+	+	+
Carcinus maenas					+	+		
Corophium cf. volutator	+		+		+			+
Corystes cassivelaunus				+				
Crangon crangon	+	+	+	+	+	+	+	+
Cumopsis goodsiri	+	+	+	(+)+	++	+	+	++
Diastylis bradyi	+	+	+	+	+	+	+	++
Eurydice pulchra	+	+	+	+	+	+	+	+
Gammaridea sp. I	+	+	+	+	+	+	+	+
Gammaridea sp. II	++	+	+	(+)+	++	++	(+)+	+
Gammaridea sp. III	+	+	+	+	+	+	+	+
Gammaridea sp. IV	+	+	+	+	+	+	+	+
Gammaridea sp. V		+	+	+	+		+	+
Gammaridea sp. VI			+		+		+	
Gastrosaccus sanctus						+		
Gastrosaccus spinifer		+	+	+	+	+	+	+
Hyas araneus					+			
Idothea linearis	+					+		
Iphinoe trispinosa		+	+	+	+	+	+	+
Isopoda sp.						+		
Lamprops fasciata	+	+	+	+	+	+	+	+
Liocarcinus holsatus	+	+	+	+	+	+	+	+
Mesopodopsis slabberi	+	+	+	+		+	+	+
Pagurus bernhardus	+		+	+	+	+	+	+
Paramysis kervillei	+	+	+	+	+	+	+	+
Pinnotheres pisum	+				+			
Processa canaliculata		+						+
Urothoe grimaldii var. poseidonis	+	+	+	(+)+	++	+	++	++
Echinodermata								
Amphiura filiformis						+		
Asterias rubens	+	+	+	+	+	+	+	+
Echinocardium cordatum	+	+	+	+	+	+	+	+
Ophiura albida	+	+	+	+	+	+	+	+
Ophiura texturata							+	
Coelenterata								
Edwardsia cf. danica								+
Sagartia troglodytes					+			

Table 2. Continued.

Station No.	5	6	7	8	9	10	11	12
Water depth (m)	5	6	7	8	9	10	12	14
Pisces								
Hyperoplus lanceolatus		+		+		+	+	+
Pomatoschistes minutus							+	
Phoronida								
Phoronis mülleri					+	+		
Pantopoda								
Nymphon sp.								+
Number of species	58	59	61	61	69	62	68	73

are *Macoma balthica, Scoloplos armiger, Nephtys hombergi* and *Magelona papillicornis,* the annual cycles of which (mean values of stations 5–12) are shown in Fig. 7. The first two species do also occur abundantly in the tidal flat habitat. Therefore comparisons of fluctuations and dynamic processes of these species are possible.

Magelona papillicornis is the most abundant species in the upper sublittoral. In certain years densities of more than 2000 specimens · m^{-2} are reached. In contrast to the winter minima the overall low population densities in 1977 to 1979 as well as 1981 are difficult to explain. Maxima occur only in 1980, 1982, and 1983.

Nephtys hombergi is represented in the upper sublittoral in much lower numbers than *Magelona papillicornis.* The highest numbers with more than 100 specimens·m^{-2} are reached in summer or early autumn. In 1977, 1978 as well as in 1980 and 1981 no distinct maxima are developed.

After *Magelona papillicornis* the polychaete *Scoloplos armiger* is the second common species in the foreshore and the upper sublittoral with distinct maxima in summer and distinct minima during winter times. An exception of this cycle occurred in 1983 probably due to a low spatfall. Generally for *Scoloplos armiger* a decreasing trend in the number of individuals can be determined since 1978.

In the early years of investigation *Macoma balthica, Nephtys hombergi,* and *Magelona papillicornis* show low densities, and recruitment is failing or rather low. Since 1979 (*Nephtys*) respectively 1980 (*Macoma, Magelona*) recruitment in these species is more successful and their abundance is raised to higher levels.

Discussion

The investigation of permanent sampling stations in the East Frisian intertidal and shallow subtidal area resulted in two habitats which are rather different in species richness and community structure. The intertidal bottom fauna is distinguished by great constancy, in spite of the seemingly unstable environment. It is on the whole poor in species (35), and only a small group of species is significant for the formation of the stock (total abundance, total biomass). This is a general feature of the intertidal macrofauna of the Wadden Sea as described by Hauser (1973), Beukema (1974, 1981), Meyer & Michaelis (1980), Obert (1982), and others. In the habitat investigated here, the basic pattern of composition is formed by 8 species and has maintained itself unchanged from 1976 to 1985. Of course, there have been certain alternations in the order of precedence.

In contrast to the eulittoral, constancy of species composition in the sublittoral is considerably less pronounced. Many of the great number of species (103) only have a sporadic appearance. Others, like *Pectinaria koreni* and *Donax vittatus,* develop large populations in certain years but in other years they are unimportant in quantitative respect, or disappear completely. Possibly instability of the substrate is a controlling factor. Also in the sublittoral the number of species which occur regularly is restricted. However, with exception of *Magelona papillicornis,* they cannot be called abundant or dominant in the same sence as the dominating species of the eulittoral. The abundance of *Macoma balthica* and *Scoloplos armiger,* for instance, is one

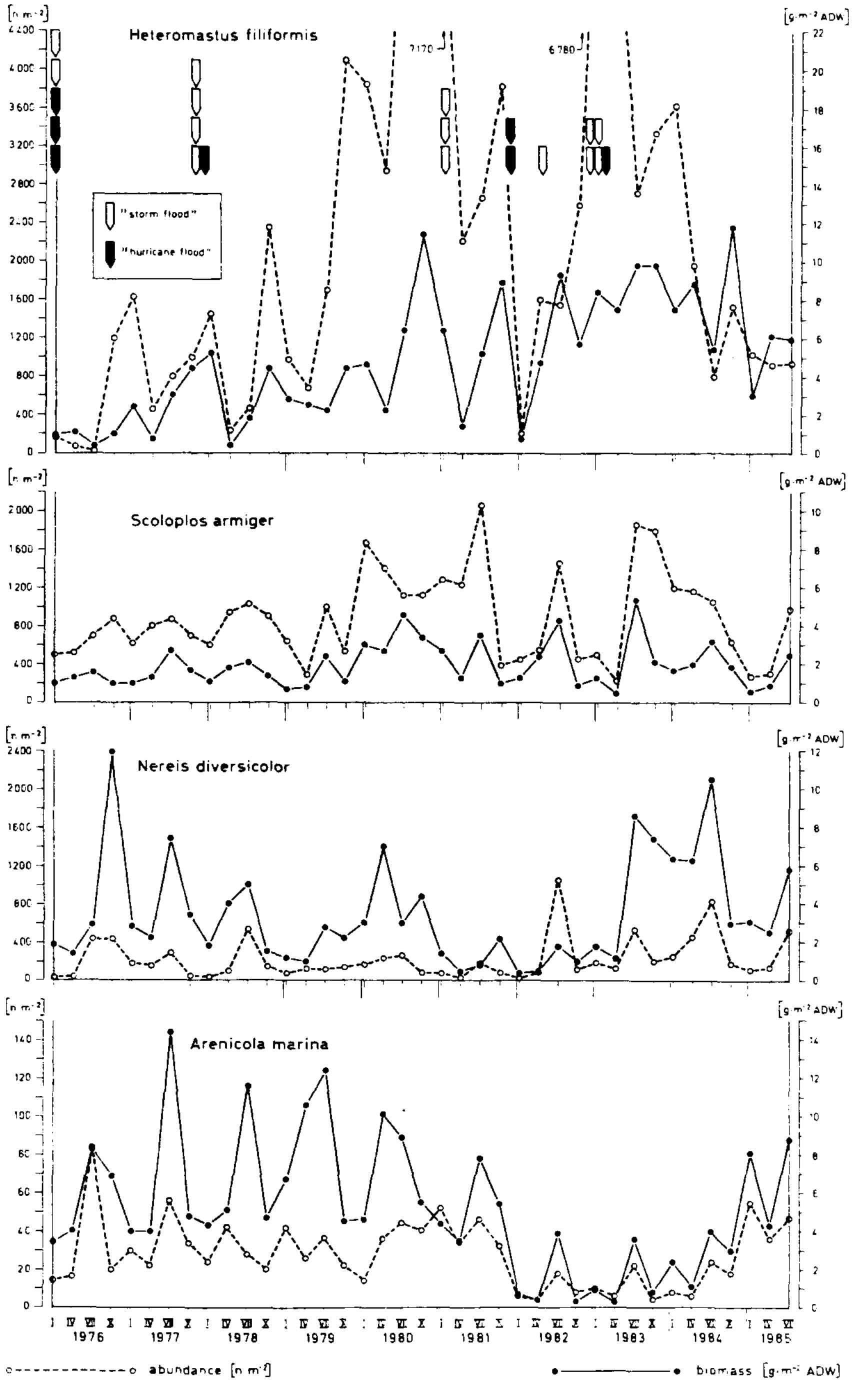

Fig. 5. Intertidal macrobenthos. Variations in abundance and biomass (means of stations 1–4) of dominant species (polychaetes). Each arrow indicates one 'storm flood' respectively 'hurricane flood'. Several storm surges occurring within a short time are represented by arrows standing above each other.

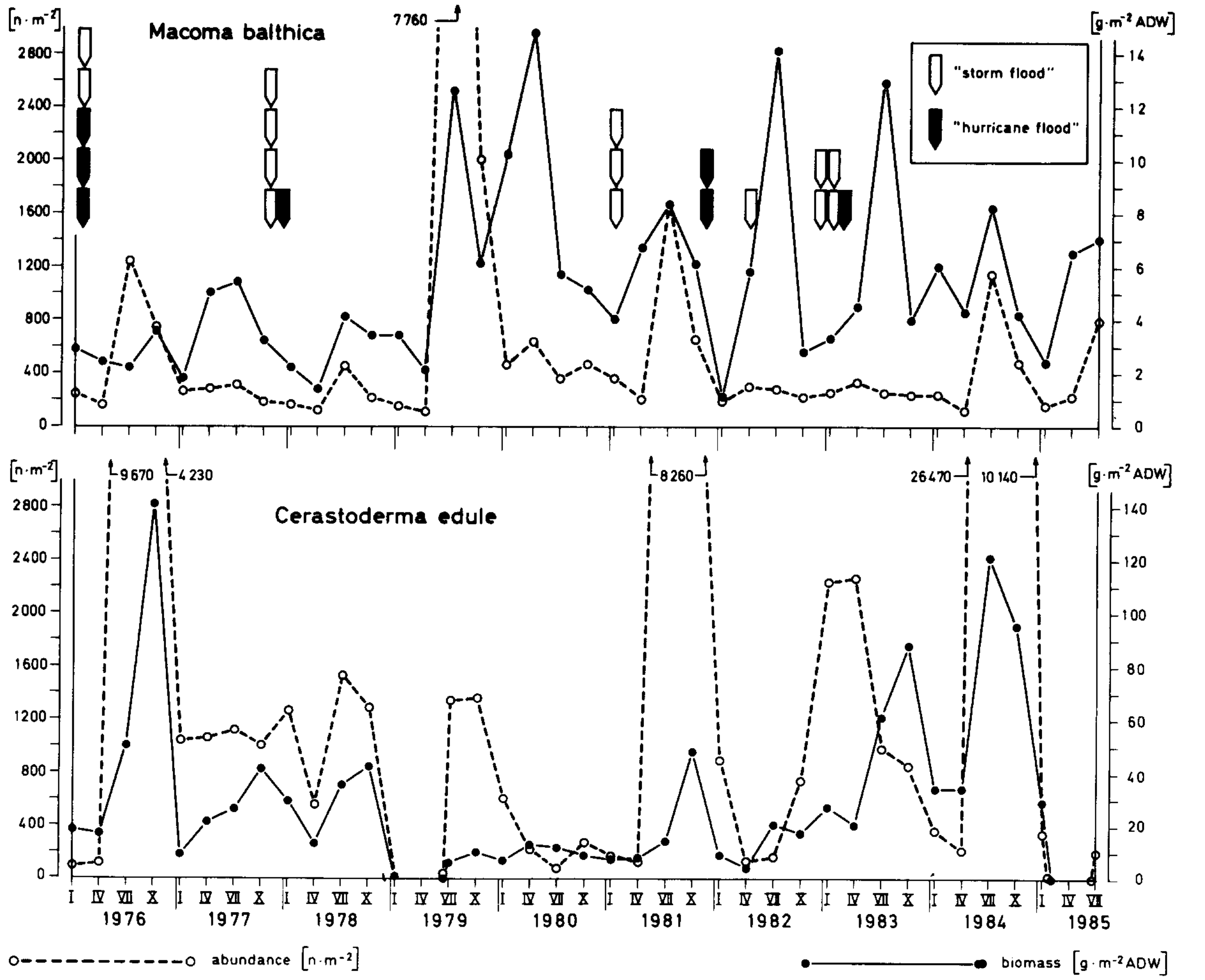

Fig. 6. Intertidal macrobenthos. Variations in abundance and biomass (means of stations 1–4) of dominant species (bivalves). Each arrow indicates one 'storm flood' respectively 'hurricane flood'. Several storm surges occurring within a short time are represented by arrows standing above each other.

order of magnitude lower in the sublittoral than in the intertidal area.

In the variation of abundance and biomass the seasonal fluctuations are the most obvious ones, as well in the individual species as in the whole communities. The underlying processes are (Beukema 1974): from spring to summer and autumn a net increase due to settlement of larvae, to immigration and to growth of the individuals; from autumn to winter and spring a net loss due to the predominance of mortality, migration and the losses of weight of the individuals. In bivalves it is considered to be the rule, that particularly successful spatfalls follow directly after severe winters (literature reviewed by Beukema, 1982). In the present investigation that applies only to one of the cases observed: *Macoma* had a rich spatfall in 1979 in the intertidal, but not in the subtidal stations. High spatfalls of *Cerastoderma* in the intertidal area were preceded either by moderate (1976) or by mild, ice-free winters (1981, 1984).

Referring to the total biomass of the intertidal habitat, the highest summer values (50–180 g ADW · m^{-2}) and the lowest winter values (15–60 g ADW · m^{-2}) are above the average, certainly due to the dense cockle population. By comparison, the

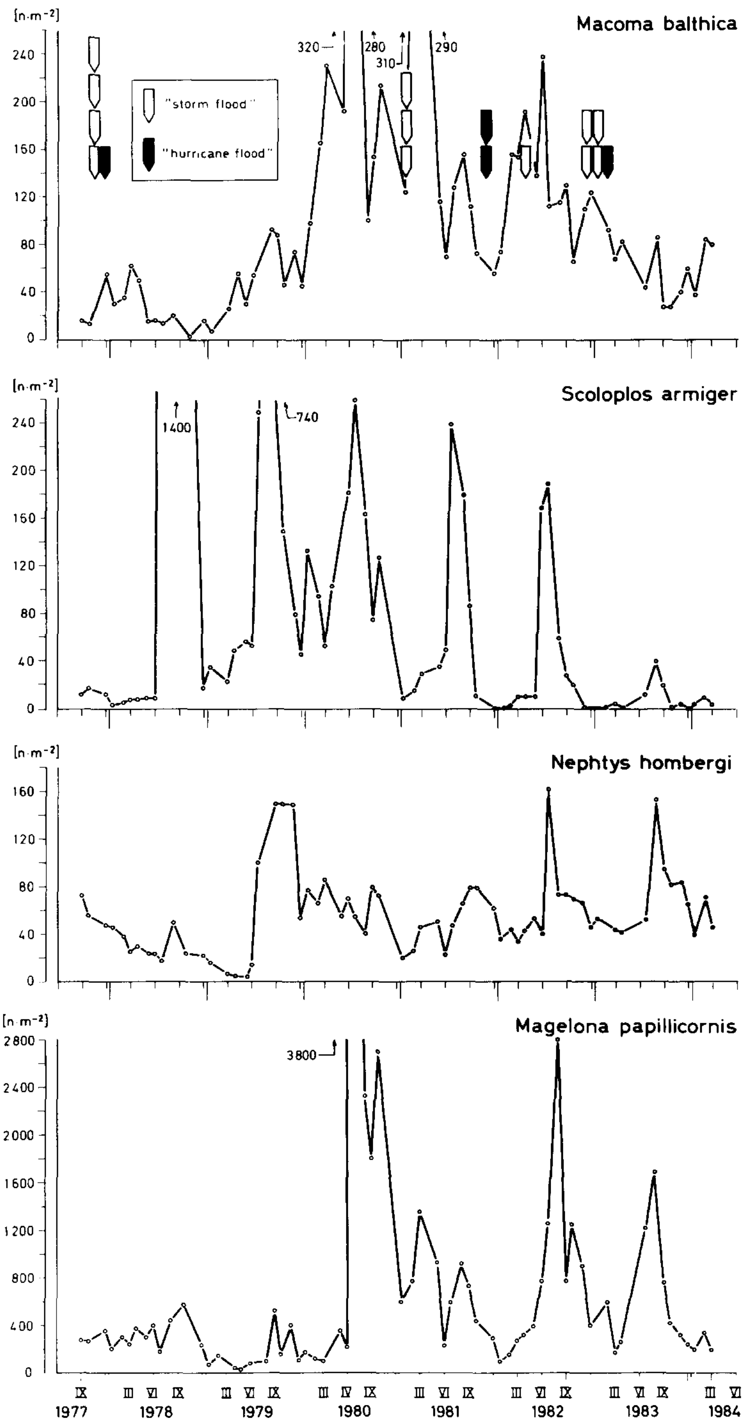

Fig. 7. Subtidal macrobenthos. Development of abundance (means of stations 5–12) of dominant species. Each arrow indicates one 'storm flood' respectively 'hurricane flood'. Several storm surges occurring within a short time are represented by arrows standing above each other.

flats near the island Borkum, west of Norderney, revealed a mean summer biomass of 36 g ADW $\cdot$ m^{-2} (Obert, 1982) and from the western Dutch Wadden Sea winter values varying from 14 to 24 g ADW $\cdot$ m^{-2} were reported (Beukema, 1981). In the shallow subtidal area biomass has not been measured. Informations from similar habitats in the southern North Sea are not available.

Except the more or less regular seasonal variations there are single extreme situations which cause the most drastic changes. In the case of temperature the benthic community experiences great shocks due to severe winters, as has often been described for the eulittoral as well as the sublittoral (Smidt, 1944; Ziegelmeier, 1964; Hauser, 1973; Beukema, 1979; Dörjes, 1980; and others). In the time of investigation there are two of such winters with an iceing-up of the intertidal flats over a longer period, namely in 1978/79 and in 1984/85. In the intertidal *Scoloplos, Nereis,* and *Macoma* had to sustain slight losses, but hardly affected was the predominant species in the habitat, the cockle. The same about this species has been reported by numerous other authors (e.g. Kristensen,1958; Hauser, 1973; Essink, 1978; Beukema, 1979; Dörjes, 1980; Madsen, 1984). The cockle, which was previously the second in numbers and the first according to biomass, disappeared in 1979 and 1985 until the new spatfall in the summer.

Concerning the sublittoral, it would seem that severe winters cause greater damage to the fauna than in the eulittoral. This was the case in the winter 1978/79. The abundance of *Nephtys* and *Magelona* dropped close to zero, while *Macoma* and *Scoloplos* were less clearly affected. From the species represented in Table 2 a great part disappeared and the regeneration of the whole community required a number of years. According to Ziegelmeier (1964, 1978), Rachor & Gerlach (1978), and Dörjes (1980) large parts of the benthos were destroyed in the winters of 1962/63 and 1978/79 in depths of up to 30 m. A new colonization of completely different structure follows and former conditions are only reestablished if the development is undisturbed over several years (Rachor & Gerlach 1978).

The other factor leading to irregular and drastic changes in the benthic communities is wave action caused by strong gales. In the period of our investigations some series of 'storm floods' and 'hurricane floods' (according to the classification used in Germany) have occurred at times which can be seen in Figs 5, 6, and 7. In the intertidal bottom fauna they have caused noticeable declines in the development of *Heteromastus* and *Macoma* during the winters 1975/76, 1977/78 and especially after the 'hurricane floods' of November 1981 (Fig. 5, 6). *Arenicola* only reacted upon these last events (November 1981) with a serious decrease. There followed a period of almost three years with very low densities, but that may also be attributed to other reasons. Slight effects can be supposed in *Cerastoderma* (Fig. 6) while *Scoloplos* and *Nereis* seem to be able to withstand the short-term effects of heavy wave action without suffering greater losses (Fig. 5).

Total abundance and biomass are reduced to values belonging to the lowest of the whole investigation period (Fig. 4). Therefore, it may be concluded, that exceptionally strong gales, like in the winters 1975/76 and 1981/82, have similar effects as low temperatures in severe winters, like 1978/79 and 1984/85.

There is evidence, that great damage has also been done to the sublittoral bottom fauna by gales, probably because sediments are strongly disturbed and reworked by wave action. *Macoma, Scoloplos,* and *Magelona* show deep depressions in their abundance especially after the two 'hurricane floods' in November 1981. An exception is given by *Nephtys,* probably due to its ability of quick movement in the sediment.

As in the case of the severe winter 1978/79, also after the storms of November 1981 the total number of species was reduced considerably and did not recover completely until 1984, the present state of the evaluation.

The significance of the wave action factor for the spatial distribution of benthic animals has already been pointed out earlier by Muus (1967) and Wolff (1973). Therefore, equally strong influences by this factor must be accepted in the temporal demension. As far as the Wadden Sea fauna is concerned, questions have rarely been asked in this direction. In the case of the cockle the observation was made that it is susceptible to erosion, is swept out of the bottom by wave action, and is transported down to the channels by currents (Schäfer, 1962; Ohde, 1981).

A study focussing directly on this subject was carried out by Madsen (1984) in the Danish Wadden Sea, using the opportunity of the severe storm flood in November 1981. He found a reduction of total abundance and biomass of 20–25%. Compared to Norderney, there were partly similar, partly different reactions of the individual species. Madsen concludes, that on the whole the losses of macrofauna caused by gales may be relatively small in the Danish area. The sublittoral communities of the southern North Sea are known to be rather sensitive to the influence of storms. Rachor & Gerlach (1978) assume that the seasonal decline of the bottom fauna is not only caused by low temperature and a lack of food, but also by increased intensity of wave action. In addition, they consider strong storms to be a frequent cause of destruction of the sublittoral bottom fauna in depths of up to 30 m. For example, Rachor (1980) described the devastating effects of heavy gales in January 1976 on a mud bottom community in the German Bight.

At the attempt of interpreting the fluctuations of individual species and the whole community, biotic interactions remained largely unconsidered, as this investigation was restricted to the endobenthic sector of the ecosystem. Neither the changing food supply can be referred to as explanation, nor the predation pressure, due to shrimps, crabs, fishes and birds, the outstanding significance of which for the structure, density and biomass of the intertidal fauna has been shown by Reise (1977a, b, 1985), de Vlas (1979), and Smit (1980). Some observations could be made on parasitic infestation of intertidal bivalves. Infection by trematode larvae resulted in mortality of *Macoma* and *Cerastoderma* in certain years (Michaelis 1981). During the summer months animals were found which had left the bottom and lay weakened, dying or dead on the surface. However, the losses did not cause obvious declines of the populations.

As far as long-term changes are concerned, only in one species a clear trend of a recently deviating development can be recognized: the intertidal population of *Heteromastus filiformis* started in 1977 to spread out from its traditional muddy habitat to sandy sediments and establish itself there as a dominant species (Fig. 5). It would appear to be a widespread phenomenon, since 1978 a multiplication of density was determined near Texel in the Dutch Wadden Sea (Cadée, 1979) and this species was distributed over a large area and in great densities in 1981 on sandy flats of the Ems estuary (Obert, 1982). With regard to the other species and to the whole community the range of seasonal and annual fluctuations is too wide as to distinguish long-term changes after the period of ten, respectively seven years of investigation. However, it may be finally mentioned, that Beukema and Cadée (in press) recently could prove benthos responses to eutrophication in the western Dutch Wadden Sea. During 1970–1984 they found in half of the common species an increase in numbers and biomass and a doubling of the total biomass.

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