The benthic macrofauna of the inner German Bight: Present and past *)

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Abstract

In July and August 1995, a macrobenthos survey in the sublittoral of the inner German Bight was carried out at 16 stations around the island of Helgoland. 44 single multibox cores provided the basis for analysis of the distribution of macrobenthic organisms and their abundance and biomass. In total 84 species and 3 taxonomic groups were identified. The mean abundance (5808 Ind. m^{-2}) and mean biomass (total wet weight · m^{-2}) of 668.5 g indicate a strong overall increase compared to previous investigations; in addition, changes in the composition of the fauna were revealed.

Kurzfassung

Das Makrobenthos der inneren Deutschen Bucht: Gegenwart und Vergangenheit

Im Juli und August 1995 wurde das Makrozoobenthos des Sublitorals der inneren Deutschen Bucht auf 16 Stationen im Umfeld der Insel Helgoland untersucht. Mit einem „multibox corer" wurden auf diesen Stationen insgesamt 44 Kerne gewonnen, von denen Abundanzen und Biomassen der Benthosorganismen bestimmt wurden. 84 Arten und 3 taxonomische Gruppen wurden unterschieden. Verglichen mit früheren Untersuchungen belegen 5808 Ind. m^{-2} und 668,5 g Feuchtgewicht · m^{-2} einen deutlichen Anstieg der Individuendichte und Biomasse; auch in der Zusammensetzung der Fauna wurden Unterschiede deutlich. Unsere Daten werden mit anderen Erhebungen verglichen, und mögliche Ursachen dieser Veränderungen werden diskutiert.

Resumen

La macrofauna bentónica de la Bahía Alemana interior: Presente y pasado

Durante los meses de julio y agosto de 1995, se realizó un muestreo del macrobentos en el sublitoral de la Bahía Alemana interior. Se muestrearon 16 estaciones en el área que circunda la isla de Helgoland. Un total de 44 cores, procedentes de un "multibox corer", se muestrearon en dichas estaciones, proporcionando la base para realizar el análisis de la distribución de los

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organismos macrobentónicos, así como de su abundancia y biomasa. Se identificaron un total de 84 especies y 3 grupos taxonómicos. La abundancia media (5808 Ind. m^{-2}) y la biomasa media (668,5 g, peso húmedo × m^{-2}), indican un fuerte incremento de ambos valores en comparación con resultados anteriores, así como cambios en la composición faunística. Los datos han sido comparados con resultados de investigaciones anteriores y se discuten las posibles causas de dichos cambios.

Introduction

The German Bight is one of the most intensively investigated areas of the North Sea. The first quantitative investigation of the distribution of benthic communities in the German Bight was that of Hagmeier in the early twenties (Hagmeier 1925). Especially during the seventies and early eighties comprehensive benthos studies tried to evaluate the effects of eutrophication and fishery activitites on the benthos (Dörjes 1968, 1977; Stripp 1969; Rachor *et al.* 1981; Salzwedel *et al.* 1985).

The latter publication was the most comprehensive work in the German Bight, covering an area of about 24 000 km² The mean macrobenthic biomass at the 66 stations under study was 116 g w.w. m^{-2}, the corresponding mean abundance was 2377 Ind. m^{-2}. By means of a clustering method five different bottom communities were identified: the *Nucula nitidosa*-, the *Amphiura filiformis* -, the *Tellina fabula* -, the *Spio filicornis* -, and the *Gonadiella-Spisula* association.

The present study covers an area of about 3000 km² around the island of Helgoland mainly within the *Nucula nitidosa* - and *Amphiura filiformis* associations after Salzwedel *et al.* (1985). Data obtained were compared with earlier data, *e.g.* Hagmeier (1925), Stripp (1966), Salzwedel *et al.* (1985), Büsselberg (1984) and with data from Bischoff (1996), also obtained in 1995, in order to analyse changes in the benthic regime of this sensitive area.

Materials and methods

Area of investigation

The German Bight covers an area of about 25 000 km² in the southeastern part of the North Sea. The water depth is generally less than 40 m, only the deep trench off Helgoland, the "Helgoländer Tiefe Rinne" (57 m) and the northwesterly running, funnel shaped pleistocene Elbe River valley reach greater depths. The complicated hydrographic structure of the German Bight, with its strong currents, stirrings, frontal systems and different water masses, all of which influence the distributio n of benthic and planktonic organisms, has been the subject of numerous studies (*e.g.* Goedecke 1968; Gerdes and Hesse 1993; Gerdes 1985; Budeus 1986; Krause *et al.* 1986). The sediment distribution has been described in detail by Figge (1981).

In August 1995, the benthic fauna of 16 stations in the inner German Bight was studied by means of a multibox corer (Figure1).

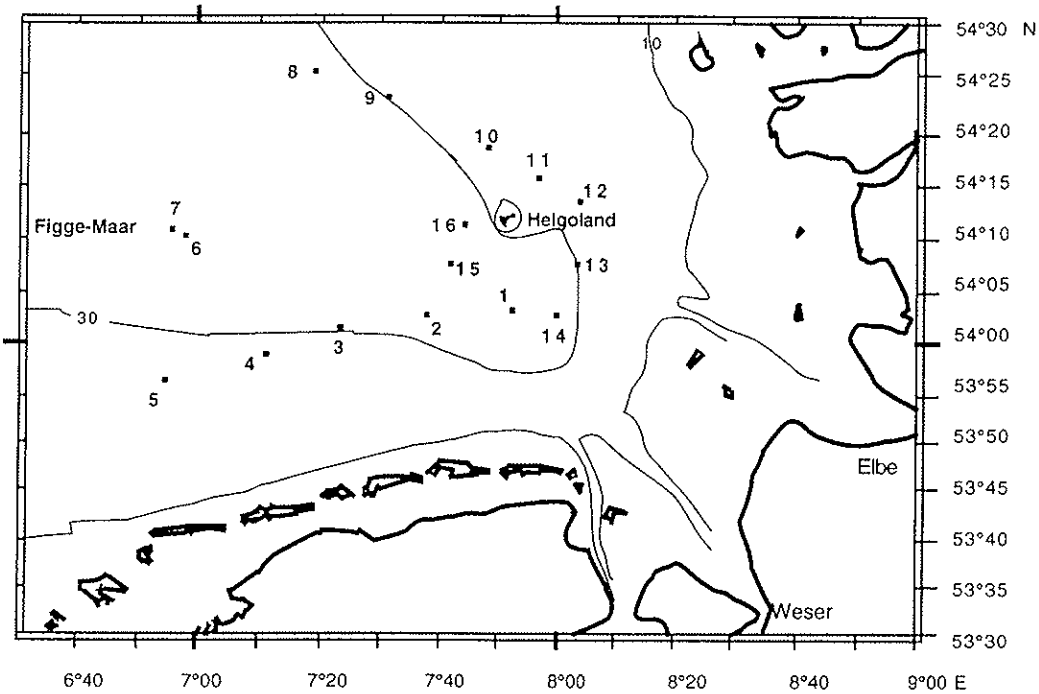

Figure 1: Study area in the German Bight; August 1995

Tab. 1: Station list and data

Station No.	Longitude (N)	Latitude (E)	Water depth (m)	No. of cores	Penetration depth (cm)
1	54°03,2'	07°52,8'	39	4	24–37
2	54°02,8'	07°37,9'	37	6	25–30
3	54°01,5'	07°24,8'	32	2	15–19
4	53°58,8'	07°11,2'	29	3	13–18
5	53°57,1'	06°54,2'	27	3	12–15
6	54°10,1'	06°58,3'	46	2	44–45
7	54°10,2'	06°57,9'	46	3	45
8	54°25,8'	07°18,4'	31	3	13–15
9	54°22,5'	07°31,9'	27	3	10–14
10	54°19,1'	07°44,5'	24	2	15
11	54°15,8'	07°57,1'	21	2	15 and 18
12	54°14,1'	08°06,7'	15	2	20
13	54°08,0'	08°07,2'	23	3	38–40
14	54°03,6'	08°00,5'	29	2	35
15	54°06,4'	07°41,8'	39	3	37–42
16	54°12,4'	07°41,0'	40	1	25

The study area roughly covers 3000 km² around the island of Helgoland. Most of the stations were situated within the *Amphiura filiformis* - and in the *Nucula nitidosa* association and some in the *Goniadella-Spisula* association as described by Salzwedel *et al.* (1985).

Sampling and sample treatment

The multibox corer is a multiple corer, providing simultaneously (depending on the type of sediment) up to nine samples per deployment over a sampling area of 3 m²; each core covers an area of 12 x 20 cm and penetrates the sediment to a maximum depth of 45 cm (Gerdes 1990).

The number of cores obtained per station varied between 4 and 9. For the analysis of the macrofauna between 1 and 6 cores per station were used (Table 1), whereas the rest of the cores provided the basis for other studies to be published elsewhere.

The biological samples were sieved through 0.5 mm mesh size and preserved in 4 % hexamethylene-tetramine buffered formalin prior to sorting in the laboratory. The organisms were mainly identified to species level and 4 taxonomic groups; biomass was determined in terms of gramm total wet weight per square meter.

In order to identify groups of stations, the "Bray Curtis Similarity" of abundance values (Ind. m^{-2}) was used with the software package PRIMER (Clarke and Warwick 1994). For the clustering procedure and the calculation of the Shannon-Wiener diversity index

Table 2: Sediment fractions at the 16 sampling stations in the German Bight; August 1995

Station No.	Gravel (%)	Sand (%)	Silt (%)	Clay (%)
1	0.2	69.8	20.7	9.3
2	0.1	85.8	10.1	4
3	0.1	89.5	7.9	2.4
4	0.4	97.3	1.8	0.5
5	0.4	98.1	1.2	0.3
6	0.1	53.2	35.8	11
7	0.1	57.1	31.6	11
8	0.1	98.9	0.8	0.2
9	0.4	98.2	0.8	0.4
10	0.3	98.7	0.7	0.2
11	7.2	91.5	0.9	0.4
12	0	99	0.8	0.2
13	4.1	46.8	42.6	6.5
14	3.4	45.9	38.8	11.8
15	0	89.6	5.6	4.7
16	0.3	94.8	2.9	2.1

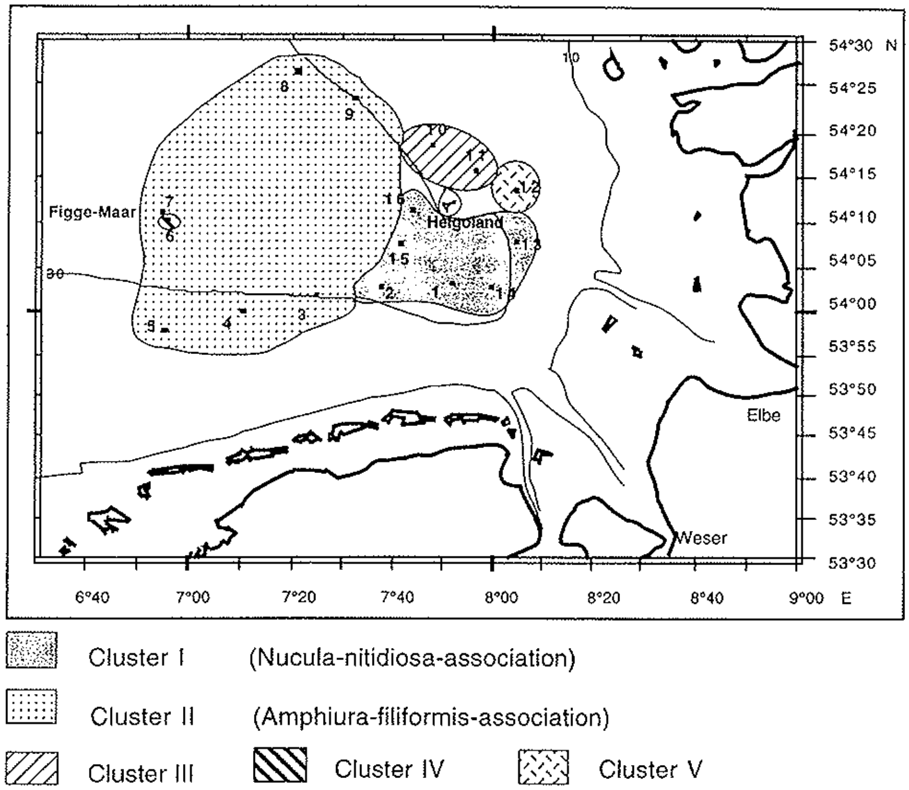

Figure 2: Areas of benthic associations achieved by clustering of 16 stations in the German Bight; August 1995; Bray-Curtis Index of abundance values of macrozoobenthos

(H′) and Pielou′s evenness index (J′), all species and taxonomic groups were considered; colonial hydrozoans were considered as one animal.

For the classification of the sediments, the total grain size fraction was separated by wet sieving into 2 fractions (> 63 µm = sand and gravel fraction, < 63 µm = silt and clay fraction). The first fraction was further separated by dry sieving into gravel (> 2 mm) and sand (63 µm to 2 mm) and the latter into silt (2 µm to 63 µm) and clay (< 2 µm).

Results

Sediment analyses

With the exception of the rocky island of Helgoland, bottom sediments in the German Bight mainly consist of sand, mud and mixtures of both; in certain places (*e.g.* stations 11, 13, 14) gravel and even boulders are also found. Sand is the dominant fraction at most of the stations, although locally, especially in the area of mud south and southeast of Helgoland (stations1, 2, 13, 14) and in the artificial Figge Maar crater (stations 6, 7), higher proportions of silt and clay occur (Table 2).

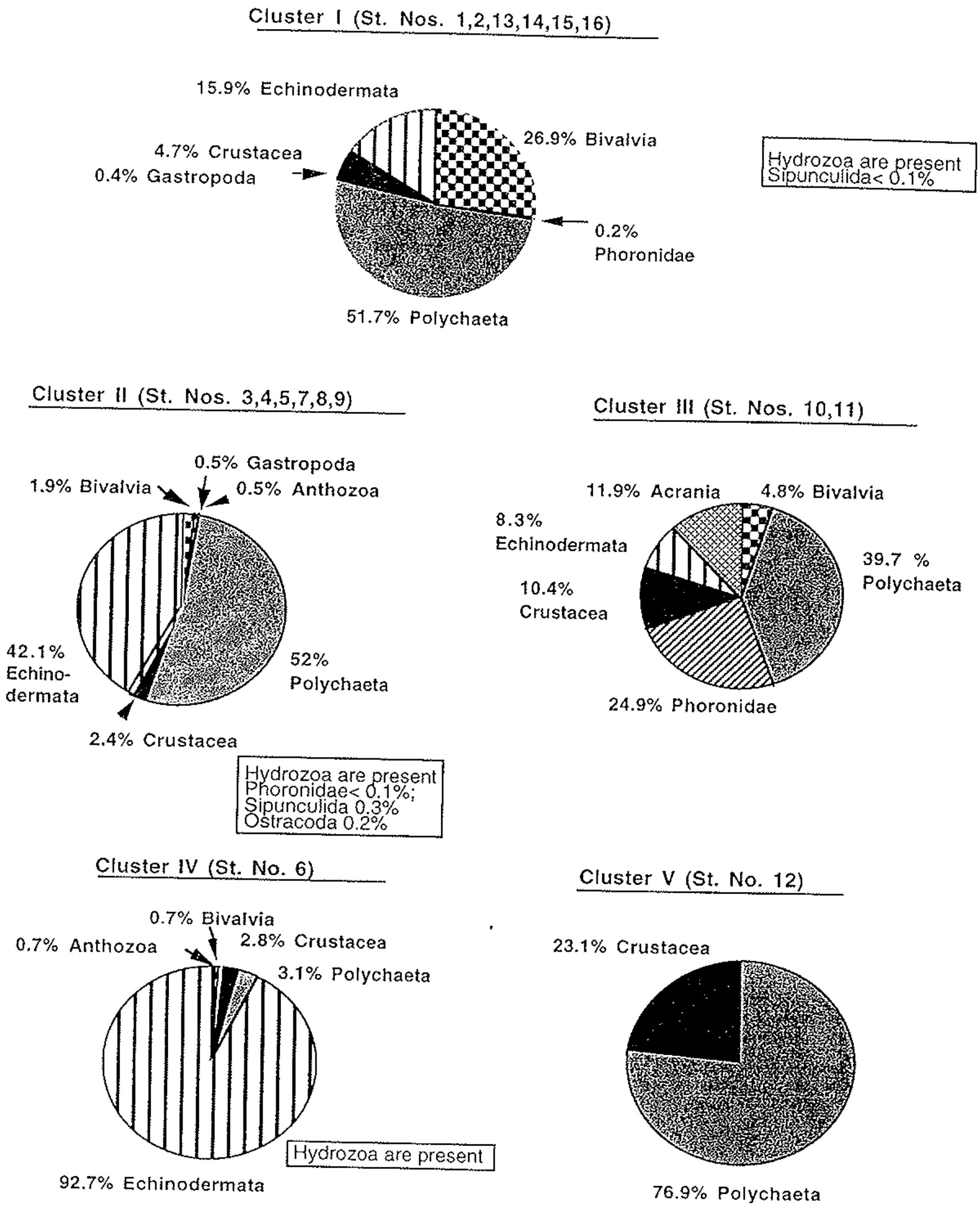

Figure 3: Composition of the macrozoobenthos in the different benthic associations in the German Bight on the basis of abundance data; August 1995

Distribution of macrozoobenthos

Altogether, 84 species were identified: 12 bivalves, 9 gastropods, 36 polychaetes, 18 crustaceans, 6 echinoderms, *Phoronis* spp. and some rare, only locally occurring species such as *Branchiostoma lanceolatum* and *Golfingia* sp.; species of the groups Anthozoa, Hydrozoa and Ostracoda were taken as one taxon each (Annex). The number of species per station varied between 11 (station 11) and 39 (station 2). Abundance values were found to vary from 273 Ind. m^{-2} to a maximum of 11739 Ind. m^{-2} at station 13. Biomass values varied from 15.6 (station 12) to 2478.9 g w.w. m^{-2} at station 13. The mean abundance over the whole area was 5808 Ind. m^{-2}, and the corresponding biomass value was 668.5 g w.w. m^{-2}.

At some stations large numbers of recently settled juveniles contributed considerably to high abundance values. Examples were *Echinocardium cordatum*, making up 70 % of all benthic organisms at station 3, *Amphiura filiformis*, which accounted for 81 % of the benthos at station 6 and *Lanice conchilega* with 77 % at station 5 (see also chapter "Discussion" and Annex).

Station groups – associations

The cluster procedure based on the abundance values of all taxonomic groups and species led to the identification of 5 clusters (Figure 2). The 6 stations 1, 2, 13, 14, 15 and 16 of Cluster I represent the *Nucula nitidosa* assosciation *sensu* Salzwedel *et al.* (1985). Species with highest abundance and presence values in this association were *Lanice conchilega* (1967 Ind. m^{-2}; 83 % presence), *Nucula nitidosa* (800 Ind. m^{-2}; 83 %), *Amphiura filiformis* (590 Ind. m^{-2}; 100 %), *Scalibregma inflatum* (553 Ind. m^{-2}; 100 %), *Montacuta ferruginosa* 477 Ind. m^{-2}; (67 %), *Ophiura albida* (421 Ind.; 100 %), *Glycinde nordmanni* (385 Ind. m^{-2}; 100 %), *Abra alba* (242 Ind. m^{-2}; 67 %), *Pariambus typicus* (146 Ind. m^{-2}; 83 %), and *Owenia fusiformis* (101 Ind. m^{-2}; 50 %).

In this association a mean density of 6678 Ind. m^{-2} was found; the corresponding biomass was 1077.8 g w.w. m^{-2}. Diversity was 2.6, evenness 0.6. *Echinocardium cordatum* was the dominant species in Cluster II, represented by stations 3, 4, 5, 7, 8 and 9. This cluster is equivalent to the *Amphiura filiformis* association *sensu* Salzwedel *et al.* (1985). The most abundant and evenly distributed species were *E. cordatum* (2650 Ind. m^{-2}; 100 % presence), *Magelona minuta* (2583 Ind. m^{-2}; 100 %), *Lanice conchilega* (322 Ind. m^{-2}; 67 %), *Ophiura albida* (152 Ind. m^{-2}; 67 %), and *Glycinde nordmanni* (113 Ind. m^{-2}; 100 %). The mean abundance (6880 Ind. m^{-2}) was slightly higher than in the *Nucula nitidosa* association, the corresponding mean biomass was 609.4 g w.w. m^{-2}. The diversity was 2.3, evenness 0.6.

Station 6 created a single station cluster within the *Amphiura filiformis* association. This station is situated in a 46 m deep crater and is characterized by an extremely high abundance of juvenile *Amphiura filiformis*. Together with juvenile *E. cordatum*, which was also quite abundant at this location, this brittle star contributed nearly 92 % to the macrobenthos in the crater. Consequently the mean abundance (6023 Ind. m^{-2}) was high and the biomass (76.5 g w.w. m^{-2}) appeared low, as do diversity (0.8) and evenness (0.3).

Stations 10 and 11 northwest of Helgoland are combined in one cluster with rather low mean abundance (2623 Ind. m^{-2}) and biomass (241.4 g w.w. m^{-2}). This cluster is characterized by the occurrence of *Phoronida* spp. and *Branchiostoma lanceolatum* (Figure 3).

Station 12 represents another single station cluster north of the island of Helgoland. This coarse sand station is characterized by having the lowest mean abundance (315 Ind. m^{-2}) and the lowest mean biomass (15.6 g w.w. m^{-2}) of all the stations.

The composition of the major macrobenthic taxa within the five clusters is shown in more detail in Figure 3.

Changes in the macrobenthic fauna

Abundance/biomass and species composition data from the *Nucula nitidosa*- and the *Amphiura filiformis* associations were compared with corresponding data from 4 earlier and 1 concurrent survey. The mean abundance and biomass data provide the basis for the analysis of covariance (ANOVA) and subsequent Games-Howell *post hoc* test for testing the significance of the noted differences between the 6 surveys.

The Stripp (1969) data are from 15 stations in the *Nucula nitidosa* association (*Abra alba* ass. sensu Stripp), sampled between March and October 1966, and from 7 stations in the *Amphiura filiformis* association (*Echinocardium cordatum/Amphiura filiformis* association sensu Stripp), sampled in October/November 1966. From July to October 1975 Salzwedel *et al.* (1985) took samples from 7 stations in the *Nucula nitidosa* association and from 11 stations in the *Amphiura filiformis* association. Based on data obtained in April 1984, Büsselberg (1984) distinguished between an *Amphiura filiformis* association in the outer northwestern part of the German Bight and two *Amphiura filiformis* associations in the inner German Bight, one influenced by *Nucula nitidosa* - and another by *Tellina fabula* association elements. For comparison we have taken the data from 10 stations (Büsselberg 1984; Annexy) of the two latter associations, because they cover exactly the area of the *Amphiura filiformis* association, as found *e.g.* by Salzwedel *et al.* (1985) and the present study. From the Bischoff (1996) survey 10 stations from the *Nucula nitidosa* association (Cluster A1 *sensu* Bischoff) and 8 from the *Amphiura filiformis* association (Cluster B *sensu* Bischoff) are considered; the first data are from June and October, the latter from September 1995.

In the *Nucula nitidosa* association the lowest mean abundance reported so far is that of Hagmeier (1925) from the early twenties. The other data show a clear trend of increasing overall abundance, even though the differences between Salzwedel *et al.* and our data and Bischoff and our data are not significant at this high level, probably due to the high standard deviations (Table 3). The overall density we obtained for this association differs from that of Bischoff (1996), although also obtained in the same year and in a comparable season. This was due to the high occurrence of juvenile *Owenia fusiformis* (19510 Ind. m^{-2}) at Bischoff's station 417; without this outstanding abundance the overall organism density would decrease to a value of 8700 Ind. m^{-2}, which is in the same order of magnitude as that obtained by us. On the basis of biomass our results differ significantly

Table 3: Differences between group means of abundance and biomass (log N transferred) of 2 associations in the German Bight. * = significantly different; – = test not possible; n.s. = not signifcantly different

Data from: **1)** Hagmeier (1925, Tabs. 4 and 8), no statistics; **2)** Stripp (1969, Tabs. 15 and 18); **3)** Salzwedel et al. (1985, Tabs. A3 and A4); **4)** Büsselberg (1984, Tab.5: St. Nos. 4, 21–24, 26–28, 30, 31); **5)** Thatje and Gerdes, present data; **6)** Bischoff (1996, Tables I1 and I3).

One-way analysis of variance (ANOVA, significant difference: p = ≤ 0.001) and subsequent Games-Howell post-hoc test; α = 0.05.

	Abundance values (Mean ± S.D.)						Biomass values (Mean ± S.D.)					
							***Nucula nitidosa* Association**					
	1)	2)	3)	4)	5)	6)	1)	2)	3)	4)	5)	6)
	700	1757	3832	–	6678	11487	105.4	193.3	172.3	–	1077.8	467.4
	–	± 983	± 2224	–	± 3840	10846	–	–	± 64.9	–	± 898.5	± 462.2
1)	/						/					
2)	–	/					–	/				
3)	–	*	/				–	–	/			
4)	–	–	–	/			–	–	–	/		
5)	–	*	n.s.	–	/		–	–	*	–	/	
6)	–	*	*	–	n.s.	/	–	–	n.s.	–	n.s.	/
							***Amphiura filiformis* Association**					
	1)	2)	3)	4)	5)	6)	1)	2)	3)	4)	5)	6)
	1770	4874	2185	1651	6880	26872	123.4	127.4	108.3	332.8	609.4	172.3
	–	± 862	± 1420	± 862	± 3303	± 14271	–	–	± 40.5	–	± 539.0	± 63.8
1)	/						/					
2)	–	/					–	/				
3)	–	*	/				–	–	/			
4)	–	*	n.s.	/			–	–	–	/		
5)	–	n.s.	*	*	/		–	–	*	–	/	
6)	–	*	*	*	*	/	–	–	*	–	*	/

from those of Salzwedel *et al.*, indicating a drastic increase in overall biomass in this association, whereas no significant difference was found in comparison with the lower biomass value of Bischoff (1996). Between 1966 and 1975 biomass levels appear relatively constant and we proposed that they all differ significantly compared to the high biomass we discovered. However, we could not prove this statistically, because only the pooled association means and not the station means are available, as is also the case for the *Amphiura filiformis* association data of Stripp (1969), Büsselberg (1984) and Hagmeier (1925).

Stripp (1969), Thatje and Gerdes (present data) and especially Bischoff (1996) obtained significantly higher values for mean organism densities in the *Amphiura filiformis* asso-

Tab.4: Dominant species (Abundance > 100 Ind.m^{-2}) in the *Nucula nitidosa*- and *Amphiura filiformis*-associations, German Bight; changes from 1923 till 1995; modified after Rachor, 1990

[1] Data of Hagmeier (1925): *Nuclula nitidosa* association: Table 4; *Amphiura filiformis* association: Table 8; [2] Data of Stripp (1969): *Nucula nitidosa* association: Table 15; *Amphiura filiformis* association: Table 18; [3] Data of Salzwedel et al.(1985): calculated from Tables A3 and A4; [4] Data of Büsselberg (1984): considered are Stations 4, 21, 22, 23, 24, 26, 27, 28, 30, 31, i.e. *Amphiura filiformis* association, partly influenced by elements of the *Nucula nitidosa* association; [5] Data of our investigation; [6] Data of Bischoff (1996)

1923/24 [1]	1966 [2]		1975 [3]		1984 [4]		1995 [5]		1995 [6]	
Abundance	Abundance	Presence	Abundance	Presence	Abundance	Presence	Abundance	Presence	Abundance	Presence
					Nucula nitidosa Association					
N. nitidosa (506)	N. nitidosa (431)	100 %	N. nitidosa (1254)	100 %			L. conchilega (1967)	83 %	O. fusiformis (3923)	100 %
	D. rathkei (351)	93 %	S. bombyx (324)	71 %			N. nitidosa (800)	83 %	M. bidentata (1388)	100 %
			O. albida (262)	71 %			A. filiformis (590)	100 %	S. inflatum (1070)	100 %
			M. bidentata (232)	100 %			S. inflatum (553)	100 %	N. nitidosa (977)	100 %
			N. hombergii (168)	100 %			M. ferruginosa (477)	100 %	A. alba (412)	100 %
			Phoronis spp. (158)	57 %			O. albida (421)	67 %	Phoronis spp (477)	100 %
			O. texturata (151)	100 %			G. nordmanni (385)	100 %	P. minuta (464)	100 %
			S. armiger (123)	71 %			A. alba (242)	67 %	O. albida (247)	100 %
			A. alba (104)	100 %			P. typicus (146)	83 %	A. filiformis (244)	100 %
					Amphiura filiformis Association					
A. filiformis (281)	Phoronis spp. (1796)	100 %	Ophiura juv. (648)	100 %	Phoronis spp. (287)	100 %	E. cordatum (2650)	100 %	Phoronis spp. (16522)	100 %
S. inflatum (247)	O. fusiformis (633)	100 %	A. filiformis (297)	100 %	O. albida (209)	100 %	M. minuta (2583)	100 %	O. fusiformis (3034)	100 %
	O. albida (478)	100 %	V. striatula (157)	91 %	S. inflatum (196)	60 %	L. conchilega (322)	67 %	M. papillicornis (1681)	100 %
	A. brevicornis (201)	100 %	P. minuta (135)	100 %	S. bombyx (141)	100 %	O. albida (152)	67 %	S. bombyx (1206)	100 %
	N. nitidosa (174)	86 %	M. bidentata (115)	100 %			G. nordmanni (113)	100 %	A. filiformis (1010)	100 %
	A. nitida (109)	86 %							Nemertini spp. (782)	100 %
	G. maculata (109)	100 %							M. minuta (461)	100 %
									E. cordatum (250)	100 %
									C. pellucidus (157)	100 %

ciation compared to the 1975 and 1984 surveys of Salzwedel *et al.* and Büsselberg. The latter two surveys do not differ significantly from each other, as neither do the mean densities from Stripp andThatje and Gerdes, although the mean abundance in the present study is considerably higher. The outstandingly high mean abundance found by Bischoff (1996) differs significantly from all other abundance data considered here. *Phoronis* sp., which occurred at some stations in extraordinarily dense patches (up to 38500 Ind. m^{-2}), contributed to 62 % of this high overall density. The only biomass values in this association, which could be treated statistically, were those of Salzwedel *et al.*, Thatje and Gerdes and Bischoff. The highest biomass resulted from our survey, being significantly higher than that of Salzwedel *et al.* The corresponding biomass found at the same time by Bischoff (1996), however, was significantly lower than ours. The biomass from the survey of Stripp (1969) is similar to that of Salzwedel *et al.*, however, the biomass found by Büsselberg (1984) some years later is about 3 times higher.

In order to assess the differences noted between the data sets it is necessary to consider aspects such as sampling techniques, sampling treatments and the different seasons in which the surveys were performed; this will be done in detail in the discussion.

Long-term changes in species composition are generally difficult to assess. However, comparison of species composition from both, our and Bischoff's surveys with that of the former investigations shows evidence of the increasing dominance of small polychaetes, such as *Owenia fusiformis*, *Scalibregma inflatum*, and *Magelona papillicornis* and *M. minuta* in both associations (Table 4). The same holds true for *Phoronis* sp., which reached extraordinary densities in September 1995 in the *Amphiura filiformis* association (Bischoff 1996), and also for the subsurface dwelling sea urchin *Echinocardium cordatum*, which contributed considerably to the increased overall abundance/biomass in this association. On the other hand, bivalves such as *Arctica islandica*, *Venus striatula* and *Cultellus pellucidus*, all occurring quite regularily during the Salzwedel *et al.* (1985) investigation, were not present at all in our samples and occurred only very seldom, with the exception of *C. pellucidus*, in the material collected by Bischoff (1996). Other bivalves like *Abra alba* and *Nucula nitidosa* show a more constant distribution over the time span considered.

Discussion

Comparability of methods

This paper compares macrofauna data from several investigations, performed with different sampling and sieving gears and during different seasons. For our investigation, a multibox corer was deployed in the German Bight for the first time in order to get reliable quantitative samples for the evaluation of benthic orgainsm density, biomass and composition. This gear, described in more detail by Gerdes (1990), allows the economical multiple sampling of the often patchily distributed macrobenthos. Although a total of 91 single samples were collected from 16 stations, only 44 of these were used for biological analyses, thus covering an average of 0.066 m^{-2} of study area per station. This area is less than the areas studied by the other authors, some of which (Hagmeier 1925; Stripp 1969; Bischoff 1996) used several van Veen grabs (0.1 or 0.2 m^2) per station, or a combination of this grab and a Reineck corer (0.017 m^2; Salzwedel *et al.* 1985; Büsselberg 1984). Thus the areas investigated varied between 0.2 m^2 (Stripp 1969) to maximum of 1 m^2 per station Hagmeier (1925). However, our replicate samples provide a data set containing 2.8 estimates from an area of 3 m^2 at each station. Taking into account the patchy distribution of organisms such as *Phoronis* sp., the multibox corer probably provides more reliable figures of the actual abundance than a single corer. However, the lower numbers of species in our samples (57 species in the *Amphiura filformis* association and 62 in the *Nucula nitidosa* association), may be due to the smaller overall area sampled per station as well as the limited number of stations. Due to the weight of the multibox corer we achieved much greater penetration into the sediment (on average 26 cm) compared to the other studies. Also due to its open construction our samples may be regarded as being only minimally disturbed, a point for which grabs and corers are often criticized (*eg.* Wigley 1967; McIntyre 1971).

In the subsequent treatment of the samples, we used 0.5 mm mesh size for sieving the organisms, thus making our results comparable to those of Salzwedel *et al.* (1985), Büsselberg (1984) and Bischoff (1996). However, Hagmeier (1925) and Stripp (1969) used 1 mm sieves, which probably caused underestimation of smaller forms as well as young recruits.

Since abundance/biomass of most species may undergo strong seasonal and even yearly fluctuations, the actual sampling time has to be taken into consideration. In the North Sea, winter and spring are commonly assumed to be seasons of low organism density and biomass, both of which increase in summer, with biomass reaching its maximum towards autumn (Stripp 1969a; Arntz 1971). With the exception of Büsselberg (1984), who performed his study in April 1984, all other studies were performed during summer and autumn. Therefore, his relatively low abundance value in the *Amphiura filiformis* association (Table 4) may be explained by this fact, whereas the respective biomass supports the observed trend towards a general increase in biomass over time.

The associations obtained on the basis of our data

As our main interest is in long-term changes in the *Nucula nitidosa* - and the *Amphiura filiformis* associations, the results obtained from clustering will only be briefly discussed, in order to allow a better assessment of the observed changes. The cluster procedure identified 6 stations as belonging to each of the above mentioned associations, the former of which is tied to the mud area south and southeast of Helgoland and the latter to silty fine sand sediments west of Helgoland in the pleistocene Elbe valley. The boundaries between the associations seem to be quite stable over time (Salzwedel *et al.* 1985), although an area of transitional character between the *Amphiura filiformis* - and the *Nucula nitidosa* associations is sometimes mentioned (Stripp 1969; Bischoff 1996). We appointed our Cluster I-stations to the *Nucula nitidosa* association for the following reasons:

1. Five of the dominant species, as defined by Salzwedel *et al.* (1985), were also dominant (abundance > 100 Ind. m^{-2}) in our survey.

2. With the exception of station 16, the characteristic species *Nucula nitidosa* occurred regularly in high numbers (Table 4), making it the second most abundant species in this association.

3. The mean biomass (1077.6 g m^{-2}) was very high compared to that of the *Amphiura filiformis* association (609.4 g m^{-2}).

Stations 13 and 14 with their high biomasses contributed specially to the high mean in the *Nucula nitidosa* association. Although quite diverse, a few species, such as *N. nitidosa* and the polychaetes *Aphrodite aculeata* and especially *L. conchilega* made up 90 % of the outstandingly high biomass (2478.9 g m^{-2}) at station 13, and at station 14, *L. conchilega* made up 89.4 % of the total biomass (1894.6 g m^{-2}).

In the *Amphiura filiformis* association, *Echinocardium cordatum* and the polychaetes *Glycinde nordmanni* and *L. conchilega* were among the dominant species in our samples; they were also regarded as dominant by Salzwedel *et al.* (1985). Interestingly, the characteristic brittle star *Amphiura filiformis* occurred in even higher numbers in the *Nucula nitidosa* association (590 Ind. m^{-2}) than in the *Amphiura filiformis* association, where the mean abundance (85 Ind. m^{-2}) was rather low.

The patchy occurrence of juveniles of *E. cordatum* and *A. filiformis* is an indication that our survey took place shortly after a recruitment event. station 6, within the *Amphiura filiformis* association, was separated from the surrounding stations because of the dominance of recruits of these two echinoderm species, especially of *A. filiformis*. The high proportions of silt and clay (Table 2) found on the crater's bottom indicate, too, that this crater acts as a sediment trap by concentrating seston and meroplanktonic larvae.

Stations 10 and 11 north of Helgoland were appointed to the *Goniadella Spisula* association, which shows a rather heterogeneous distribution in the German Bight, restricted to coarser sediments (Salzwedel *et al.* 1985). Low abundance and species numbers coincide with the findings of Salzwedel *et al.* (1985). The biomass was low in our samples, whereas Salzwedel reported the highest biomass of all associations due to big individuals of the genus *Spisula* which, however, were scarce in our samples. We found the acrania *B. lanceolatum* contributed most to abundance (23.8 %) and biomass (19.4 %).

Long-term changes and possible reasons

Whereas the boundaries of the benthic associations in the German Bight seem to be relatively stable, thus indicating no fundamental changes in the distribution patterns, the organism densities/biomasses as well as the species composition reveal changes, as already noted some years ago by Salzwedel *et al.* (1985) and Rachor (1990). These findings, however, are not specific to the German Bight, they rather seem to be typical for sublittoral benthic communities throughout the North Sea and elsewhere. Kröncke (1995) presented a short review of recent articles dealing with such long-term changes in the North Sea benthos south of latitude 58° N.

To assess long-term changes in benthic communities correlated to changing environmental conditions (due to eutrophication or pollution) is very difficult. Yet many monitoring programmes are only done over relatively short periods of time. Gray and Christie (1983) described long-term changes in several pelagic and benthic species, following hydrographic cycles with amplitudes of up to 10 years and even more. This can make the prediction of long-term effects on the benthos caused by pollutants an unattainable goal.

Nevertheless, there exists a great deal of literature from coastal regions, where changes in benthic communities due to eutrophication or pollution have been proven (for references see Kröncke 1995). Interestingly, the symptoms in affected communities look very much the same everywhere, thus indicating that the observed changes cannot be explained by natural factors alone.

There is typically

1. an overall increase in organism density and biomass:

This phenomenon is often assumed to be positively correlated to enhanced primary production, due to enrichment of the water with nutrients (cf. Josefson *et al.*1993 and further citations therein). The long-term data series on nutrients and phytoplankton standing stocks in the German Bight, published by the Biologische Anstalt Helgoland, clearly document an increase in phosphate up until 1982 and a continuing increase in nitrate, accompanied by an increase in phytoplankton biomass 3 to 4 times (Radach and Berg 1986; Hickel *et al.* 1993). Our increased abundance and biomass values fit nicely into this scheme, indicating a pronounced response by the benthic communities to increased eutrophication and, hence, organic enrichment of the bottom sediments.

2. a change in the species composition

The high dominance of forms such as *Phoronis* sp. and especially small polychaetes described above is another indication that productive food conditions have developed in the inner German Bight. The predominance of small and adaptive species is favoured by this, while long-lived species seem to become less important. This may explain why almost 50 % of the common bivalves found by Salzwedel *et al.* (1985) were not present in our samples. At least some of them should have occurred, even taking into account the different sampling techniques. Comparable shifts in the community structure are also reported for other areas (cf. Rosenberg *et al.* 1987; Duineveld *et al.* 1987), thus making this shift in the benthic community structure due to harmful changes of the environment a widespread fact. The 1995 data from Thatje and Gerdes and Bischoff also suggest that densities of the echinoderms *E. cordatum* and particularly *A. filiformis* have increased. The latter was also shown to be more abundant in other eutrophicated areas, e.g. the Skagerrak/Kattegat area (Josefson *et al.* 1993) or the northeastern Skagerrak and Oslo Fjord (Rosenberg *et al.* 1987). According to Duineveld *et al.* (1987), *A. filiformis* shows increased densities all over the shallower parts of the southern North Sea, but has remained stable in the deeper, northern parts.

We assume the different surveys performed in the German Bight since the early twenties provide a reasonable data base for the evaluation of changes in the benthic regime. A lot of work has done in between to evaluate effects of short-term disturbances, such as severe winters, locally occurring oxygen deficiencies or the impact of fisheries on the benthos. All this is shown to cause an impoverishment of the benthos in terms of decreases in biomass/abundance, as well as reduced species numbers (cf. Ziegelmeier 1964; Dethlefsen and Westernhagen 1983; Bergmann and van Santbrink 1994). The recovery in biomass of affected stocks takes place within about 2 years, the re-establishment of the faunal composition is even quicker (Niermann *et al.* 1990). Such short-term oscillations and seasonal (natural) fluctuations generally overlie long-term changes. Macrobenthic communities in temperate European shallow waters are characterized by such oscillations, *i.e.* they hardly reach a stable climax situation, rather they oscillate irregularly between immature succession stages (Buchanan *et al.* 1974). The two surveys from 1995, with pronounced differences in abundance and biomass may present one example of unbalanced community stages. Performed after a long period without any superimposed disturbances like severe winters or anaerobic conditions, the results of these surveys clearly emphasize the changes, which however, were already proposed to take place 10 years ago in association with anthropogenic changes in the environment.

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Annex: Raw data

Taxon	MG 1	MG 2	MG 3	MG 4	MG 5	MG 6	MG 7	MG 8	MG 9	MG 10	MG 11	MG 12	MG 13	MG 14	MG 15	MG 16
Hydrozoa	p	p	p	p	0	p	p	0	0	0	0	0	0	p	p	p
Anthozoa	0	21	63	28	42	42	0	0	42	0	0	0	0	0	0	0
Abra alba	446	111	63	14	42	0	111	97	97	21	42	0	415	478	0	0
Astarte triangularis	0	0	0	0	0	0	0	0	0	21	125	0	0	0	0	0
Corbula gibba	21	0	0	0	0	0	14	0	0	0	0	0	125	312	42	42
Ensis ensis	0	0	0	0	0	0	0	0	0	0	0	0	42	21	0	0
Montacuta ferruginosa	799	104	0	0	0	0	0	0	14	0	0	0	0	146	1812	0
Mysella bidentata	177	104	0	0	0	0	0	0	0	0	0	0	0	0	14	0
Mya truncata	0	0	0	0	0	0	0	0	0	0	0	0	180	0	0	0
Nucula nitidosa	94	83	125	0	0	0	0	42	0	0	0	0	1245	3362	14	0
Nucula nucleus	21	0	0	0	0	0	0	0	0	0	0	0	125	249	0	0
Spisula subtruncata	0	35	84	0	55	42	0	0	0	42	0	0	0	0	0	0
Thyasira flexuosa	63	56	0	0	0	0	0	0	0	0	0	0	0	0	28	0
Venus gallina	0	7	0	0	0	0	0	0	28	0	0	0	0	0	14	0
Brachistomia rissoides	0	0	0	0	0	0	0	0	0	0	0	0	0	42	0	0
Cingula vitrea	31	35	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cylichna cylindracea	0	7	0	0	0	21	0	0	0	0	0	0	0	0	0	0
Eulima alba	0	0	0	0	0	21	0	0	0	0	0	0	0	0	0	0
Eulimella commutata	0	0	0	0	28	0	0	0	0	0	0	0	0	0	0	0
Hydrobia ulvae	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0
Lunatia nitida	11	0	21	14	28	0	42	14	14	0	0	0	14	21	0	0
Lunatia montagui	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0
Turritella communis	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0
Aphrodite aculeata	0	0	0	0	0	0	0	0	0	0	0	0	0	21	0	0
Anaitides subulifera	0	0	0	28	0	0	0	0	0	0	0	0	0	0	0	125
Autolytes prolifer	0	7	0	0	14	0	0	0	0	0	0	0	0	0	0	0
Capitella capitata	42	0	0	0	28	0	0	0	0	0	0	0	0	104	0	125
Chaetozone setosa	0	0	0	0	55	0	0	0	0	0	0	42	0	0	0	0
Eteone flava	0	0	0	0	0	0	0	0	0	0	0	21	0	0	0	0
Eteone longa	0	0	0	0	0	0	0	0	0	0	0	21	0	0	0	0
Exogone hebes	0	0	0	0	0	0	0	0	0	0	0	0	55	0	0	0
Glycera capitata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	125
Glycera convoluta	0	0	0	0	0	21	0	0	0	0	0	0	0	0	14	0
Glycinde nordmanni	333	105	62	194	166	21	97	55	101	0	104	21	125	166	916	666
Harmothoe lunulata	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	83
Harmothoe nodosa	0	0	0	0	42	0	0	0	0	0	0	0	0	0	0	0
Hesionura augeneri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	42	0
Heteromastus filiformis	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lanice conchilega	104	720	63	55	291	0	0	0	1522	831	0	21	7885	2968	0	125
Magelona minuta	83	21	1831	2424	7644	63	153	888	2556	0	0	0	0	0	14	42
Magelona papillicornis	0	76	458	139	0	0	0	0	0	0	0	0	0	0	0	0
Notomastus latericeus	0	0	0	0	28	0	0	0	0	0	0	0	42	0	0	0
Nephtys caeca	0	0	0	49	28	0	14	0	55	0	0	0	0	42	0	0
Nephtys cirrosa	0	0	0	0	0	0	0	0	0	21	0	21	0	0	0	0
Nephtys hombergii	114	35	62	475	153	0	0	97	0	0	0	21	69	125	55	125
Nereis virens	0	7	0	0	28	0	0	0	0	0	21	0	0	0	0	0

Annex: Raw data (continued)

Taxon	MG 1	MG 2	MG 3	MG 4	MG 5	MG 6	MG 7	MG 8	MG 9	MG 10	MG 11	MG 12	MG 13	MG 14	MG 15	MG 16
Nereis longissima	31	14	21	69	0	0	28	42	55	0	62	21	42	0	42	83
Ophelina acuminata	0	0	0	0	0	0	0	0	0	0	0	0	125	0	0	0
Owenia fusiformis	62	0	21	125	0	0	0	153	0	479	271	0	0	250	0	291
Pholoe minuta	10	21	146	69	347	42	14	0	55	0	0	21	319	0	0	42
Pectinaria auricoma	10	28	0	0	0	0	14	0	0	42	0	0	0	83	0	0
Pectinaria koreni	0	0	0	0	0	42	0	0	0	104	104	0	28	0	0	42
Poecilochaetus serpens	0	0	0	0	42	0	14	0	0	0	0	0	0	0	0	0
Polydora antennata	0	0	0	0	0	0	28	0	0	0	0	0	0	0	0	0
Polydora pulchra	10	7	0	28	0	0	0	0	0	42	0	0	0	0	0	0
Polydora quadrilobata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	42
Scalibregma inflatum	114	14	0	83	42	0	0	0	0	0	0	0	236	458	1706	791
Scoloplos armiger	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0
Spiophanes bombyx	0	69	0	208	0	0	0	0	0	0	0	0	0	0	0	0
Phoronis spp.	0	0	21	0	0	0	0	0	0	1308	0	0	28	0	56	0
Golfingia spp.	0	14	21	0	0	0	0	0	125	0	0	0	0	0	0	0
Ostracoda spp.	0	0	0	0	28	0	0	69	0	0	0	0	0	0	0	0
Ampelisca brevicornis	21	21	0	125	0	0	0	55	14	21	21	0	42	42	14	0
Aora gracilis	0	14	0	0	0	0	0	0	14	21	0	0	0	0	14	0
Argissa hamatipes	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corophium lacustre	0	0	0	0	97	0	0	0	0	0	0	0	0	0	0	0
Corophium volutator	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
Pariambus typicus	11	215	83	56	55	167	14	97	42	84	21	0	69	0	498	83
Bodotria scorpoides	0	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0
Cumopsis longipes	0	0	0	0	0	0	28	0	0	0	0	0	0	0	28	0
Eudorella truncatula	11	7	21	0	0	0	0	0	0	0	0	0	0	0	55	0
Pseudocuma longicornis	0	7	21	28	14	0	0	0	0	0	83	21	0	21	0	0
Pseudocuma similis	0	21	0	0	0	0	0	0	0	0	63	0	0	0	0	0
Pagurus cuanensis	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0
Anapagurus laevis	11	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liocarcinus spp.	32	0	0	14	14	0	69	0	15.	84	21	42	70	0	28	42
Callianassa spp.	83	42	21	14	0	0	0	0	14	0	0	0	14	0	83	83
Corystes cassivelaunus	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
Galathea spp.	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
Crangon crangon	83	21	0	14	0	0	0	28	0	42	63	0	28	0	0	42
Amphipholis squamata	0	0	0	0	0	0	0	0	42	0	0	0	14	0	69	0
Amphiura filiformis	696	90	63	0	14	4856	332	56	42	0	166	0	69	208	2394	83
Ophiura albida	478	153	0	42	0	0	83	55	733	250	0	0	263	748	291	540
Ophiura ophiura	0	0	0	0	0	0	0	0	0	0	0	0	56	125	14	0
Ophiura affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0
Echinocardium cordatum	11	76	7595	595	609	685	6223	125	752	21	0	0	0	0	0	0
Branchiostoma lanceolatum	0	0	0	0	0	0	0	0	0	0	623	0	0	0	0	0
Abundance (Ind. m^{-2})	4044	2397	10887	4890	9948	6023	7306	1915	6332	3455	1790	273	11739	9992	8271	3622
No. of species	33	39	24	26	28	13	20	18	21	18	15	11	28	23	27	22
Biomass (g w.w. m^{-2})	407.4	880.2	183.9	816.6	206.4	76.5	1595.4	544.1	309.8	382.8	99.9	15.6	2478.9	1894.6	452.1	352.5