

Senckenberg am Meer 498

## Decadal Changes in Macrofauna Communities on the Dogger Bank Caused by Large-Scale Climate Variability

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With 9 Text-Figures and 9 Tables

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### Abstract

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In order to investigate, whether the rise in the North Atlantic Oscillation (NAO) index and the connected change in the hydroclimatic regime of the North Sea since 1988 caused changes in offshore macrobenthic communities, 28 stations on the Dogger Bank (Central North Sea) were revisited in May 1996-98, which were previously sampled in May 1985-87. Compared to the 80s, abundances of southern and interface-feeding species increased in the 90s on top and in the southern parts of the bank, whereas abundances of northern species decreased. Along the northern slope of the Dogger Bank abundances and total number of species, which prefer coarser sediment, increased in the 90s as well as diversity of feeding types and total number of northern species, whereas abundances of species preferring fine sand and interface-feeding species decreased. The results are discussed in relation to changes in temperature, primary production and the current regime of the central as well as the entire North Sea, which in turn are connected to the NAO.

### Introduction

The North Sea area is subject to comparatively large natural fluctuations because of continental and atmospheric influences (OTTO et al. 1990). The dominant signal of interannual variability in the atmospheric circulation of this area is the North Atlantic Oscillation (NAO). The NAO index is defined as the difference between the normalized sea level pressure anomalies during wintertime at Lisbon, Portugal and Stykkisholmur, Iceland. It influences the position and strength of weather systems as

they cross the North Atlantic, which in turn determine precipitation (HURREL 1995), sea surface temperature (PLANQUE & TAYLOR 1998) the direction and flow of marine currents, the height of waves and the stability of the water column (REID et al. 1998a). A high index is associated with strong and a low one with weak westerly winds. Consequently, during high NAO winters the moderating influence of the ocean results in unusually warmer winter temperatures in Europe (HURREL 1995).

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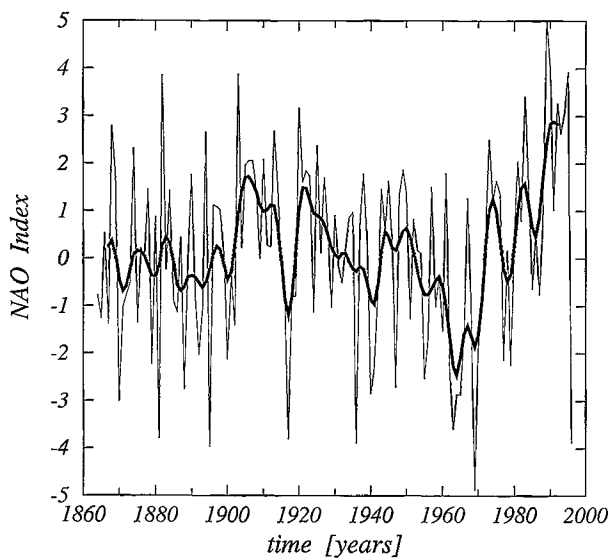


Fig. 1. North Atlantic Oscillation index (NAOI) for winter, modified after HURREL (1995). – Thick line: low-pass filtered time series.

BECKER & PAULY (1996) and DIPPNER (1998) have shown that in nearly all areas of the North Sea the sea-surface temperature (SST) anomalies are correlated with the NAO-Index. PLANQUE (1996) showed that 54% of the Gulf Stream index variability, which is often discussed in connection with changes in the North Sea ecosystem (TAYLOR 1995), could be predicted from the NAO-Index integrated over a 3-year period. Furthermore, the flow between the North Atlantic and the North Sea is strongly connected to the NAO-Index (PLANQUE & TAYLOR 1998; REID et al. 1998a; STEPHENS et al. 1998).

After a period of mainly negative values between 1960 and 1972 the NAO-Index increased to the highest consistently positive values of this century after 1987 (Fig. 1). After 1987 a number of investigations showed marked changes in plankton and fish populations of the North Sea (REID et al. 2001). They stated that these changes signalled the beginning of a regime shift in the North Sea ecosystem.

In contrast to several investigations identifying strong relationships between the NAO-Index and changes in plankton and fish dynamics (e.g. EHRICH & STRANSKY 2001), there are only few investigations connecting climate and benthos.

KRÖNCKE et al. (1998) showed that macrofauna abundance, species number and biomass off the island of Norderney in the 2<sup>nd</sup> quarter of the year correlated with the North Atlantic Oscillation Index. The mediator between the NAO and benthos was probably the sea-surface temperature (SST) in late winter and early spring. Macrofaunal communities were severely affected by cold winters. Mild meteorological conditions connected with a rising NAO-Index resulted in an increase in total biomass since 1989.

Changes in benthic biomass at the Northumberland Coast were correlated with the intensity of inflow of Atlantic water masses into that area (AUSTEN et al. 1991;

BUCHANAN 1993). Strong connections between the inflow of North Atlantic Water to the North Sea and the NAO-Index (PLANQUE & TAYLOR 1998) suggest a possible relationship to the Northumberland benthos.

TUNBERG & NELSON (1998) and HAGBERG & TUNBERG (2000) proposed that climatological links affecting surface primary production resulted in bottom-up control of benthic population changes off the west coast of Sweden. The NAO-Index was positively correlated with Skagerrak deep-water temperature and negatively correlated with stream flow from western Sweden. Stream flow was correlated with benthic abundance and biomass at stations down to 100 m depths, but negatively correlated with bottom water oxygen content.

All these long-term series as well as older investigations, which serve as a basis for long-term comparisons are mainly restricted to small-scale studies in coastal areas. To investigate whether the rise in the NAO and the connected regime shift in the North Sea since 1988 caused changes in offshore macrobenthic communities we revisited 28 stations in the Dogger Bank area in May 1996-98 after the regime shift, which were sampled previously by KRÖNCKE (1990, 1991, 1992) in 1985-87 before the regime shift. The Dogger Bank is a special ecological region (KRÖNCKE & KNUST 1995) characterized by its low depth, sandy sediments (in mainly muddy surroundings), the occurrence of fronts (BO PEDERSEN 1994; NIELSEN et al. 1993), subsurface phytoplankton blooms (RIEGMAN et al. 1990; NIELSEN et al. 1993;

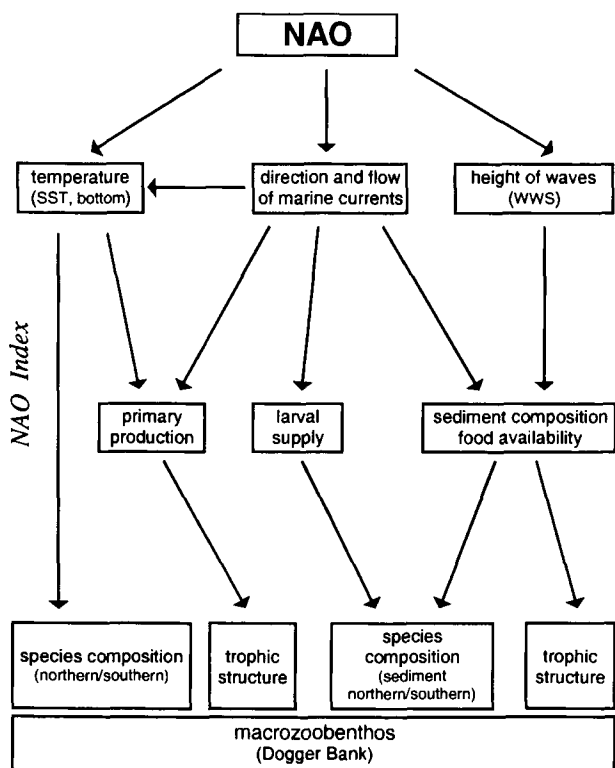


Fig. 2. Postulated links between the North Atlantic Oscillation and the macrofauna of the Dogger Bank. – SST = sea surface temperature; WWS = west wind stress.

RICHARDSON et al. 1998) and primary production occurring throughout the year (BROCKMANN & WEGNER 1985; RICHARDSON & OLSEN 1987; BROCKMANN et al. 1990). In the Dogger Bank area southern water masses from the English Channel and northern water masses from the North Atlantic and northern North Sea meet and mix (OTTO et al. 1990; NIELSEN et al. 1993).

Due to its importance for fisheries in former years, the Dogger Bank was the aim of intensive investigations since the beginning of the 20<sup>th</sup> century. First investigations were carried out by DAVIS (1923; 1925) in 1921-24.

In 1950-54 the echinoderm, polychaete and bivalve fauna of the Dogger Bank area were investigated intensively by URSIN (1960), KIRKEGAARD (1969) and PETERSEN (1977), partly because there were plans of transplanting plaice from the west coast of Jutland to the Dogger Bank. At approximately the same time, BIRKETT sampled the western part of the Dogger Bank (in KRÖNCKE 1991).

During April/May 1985-87 part of URSIN's stations were revisited by KRÖNCKE (1990, 1991, 1992). The long-term comparison of the macrofauna communities on the Dogger Bank revealed an increase in opportunistic species and a 8-fold increase in biomass. The extensive *Spisula* patches and *Mactra* patches described by DAVIS (1923, 1925) and to a lesser extent by PETERSEN (1977) and BIRKETT (KRÖNCKE 1991) disappeared. The observed changes were discussed as a result of an increasing eutrophication and pollution of the central North Sea.

The aim of the present comparison was to investigate long-term changes in the macrofauna communities of the Dogger Bank and identify to what extent these changes are linked to the rise in NAO and the connected regime shift in the North Sea. Based on known relationships between the NAO and hydroclimatic parameters we postulated the following links between the NAO and the macrobenthos of the Dogger Bank (Fig. 2):

- Temperature itself will influence the distribution of northern and southern species.
- The flow of marine currents determines the transport of larvae to the different communities and therefore the species composition of the communities.
- Primary production is influenced by temperature and the direction and flow of marine currents (e.g. via the transport of nutrients). The amount of primary production reaching the benthic system strongly influences the trophic structure of the communities in question.
- Current velocities and the height of waves influence the sediment composition, which reflects food availability. Consequently changes in both factors will affect species composition with regard to sediment preference and the trophic structure of the benthic communities of the Dogger Bank.

Changes in species abundance and distribution were analysed with regard to the functional groups we expected to be affected.

## Material and Methods

28 stations were located on the Dogger Bank, a shallow area situated in the Central North Sea, approximately 300 km in extent. The depth of the area of investigation ranged from 18 m at the shallow station on top of the bank towards 68 m in the deeper southern part and 47 m in the northern part (Fig. 3, Tab. 1).

The station grid and the sampling procedure were identical to those employed by KRÖNCKE in 1985-87. All samples were taken in May. Two samples were taken at each station with the same 0.2 m<sup>2</sup> van-Veen-grab weighing 150 kg and washed over the same sieves with 1 mm mesh size. Material retained was preserved in 4% buffered formalin. In the laboratory the samples were stained with Bengal rose prior to sorting. The organisms were sorted, identified to the lowest possible taxon and counted.

One additional grab sample was taken at each station to analyse the silt content and the TOC of the sediment. The silt fraction was separated by wet sieving over 63 µm mesh size.

Surface sediment samples taken for TOC analyses were frozen at -20°C. After freeze-drying the samples were pulverised. An aliquot of 10 mg was analysed using a Heraeus CHNS-Analyser (vario el). Prior to analysis, the samples were kept in a desiccator with concentrated HCl underneath to eliminate the carbonate.

Species abundance data are standardised to a total number per m<sup>2</sup> at each site. The species number is given as total number per both samples (0.4 m<sup>2</sup>). The PRIMER (Plymouth Routines In Multivariate Ecological Research) software package was used for statistical analyses. To compare the benthic communities between different years and stations, multi-dimensional scaling (MDS) analyses were performed. The data were transformed using double square roots. Similarities were calculated using the Bray-Curtis coefficient (BRAY & CURTIS 1957). Significance testing for differences between communities in the 80s and 90s was performed using the ANOSIM randomisation test (CLARKE & GREEN 1988). Discriminating species contributing most to the differences between the communities in both time periods were identified using the SIMPER (similarity percentage) tool.

If species were not identified as two different species in the 80s (e.g. *Nephtys hombergii* and *N. assimilis*, *Mage-lona johnstoni* and *M. filiformis*) they are grouped on the higher taxonomic level. *M. johnstoni* is one of two co-existing species, which were formerly referred to *Mage-lona mirabilis* (FIEGE et al. 2000).

The classification for the species distribution, sediment preference and feeding type were taken from HARTMANN-

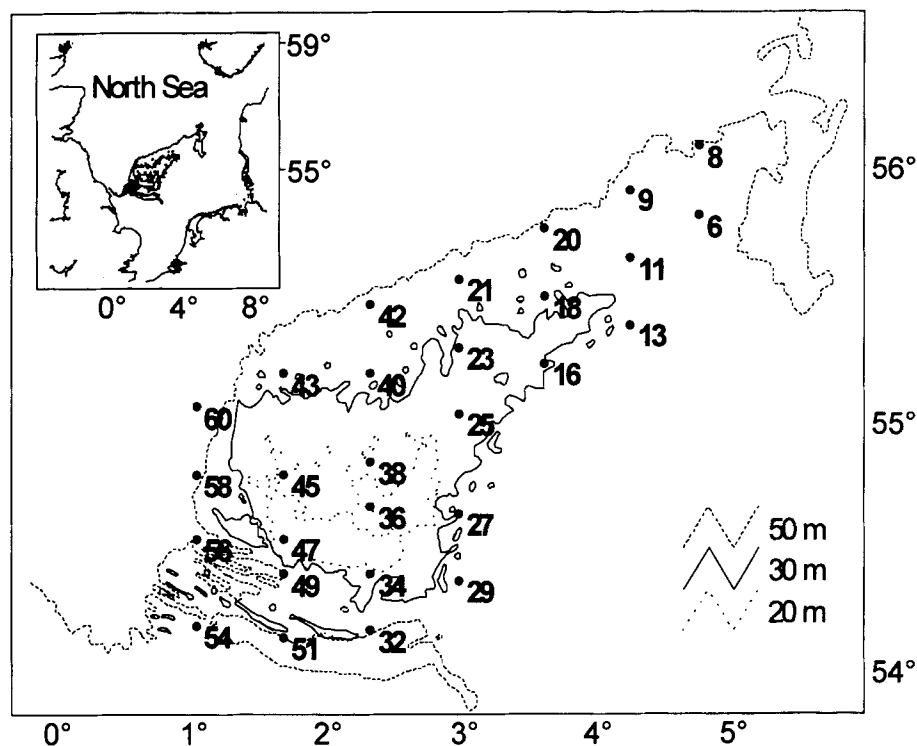


Fig. 3. Area of investigation with sampling locations.

station	Lat.	Long.	depth [m]	85	86	87	96	97	98
6	55°48'N	04°51'E	34	x	x	x	x		x
8	56°04'N	04°51'E	43	x	x	x	x	x	x
9	55°54'N	04°20'E	43			x	x	x	x
11	55°38'N	04°20'E	32			x	x	x	x
13	55°22'N	04°20'E	42			x	x	x	x
16	55°13'N	03°40'E	32	x	x	x	x	x	x
18	55°29'N	03°40'E	31	x	x	x	x	x	x
20	55°45'N	03°40'E	47	x	x	x	x	x	x
21	55°33'N	03°00'E	40			x	x	x	x
23	55°17'N	03°00'E	29			x	x	x	x
25	55°01'N	03°00'E	23			x	x	x	x
27	54°37'N	03°00'E	33			x	x	x	x
29	54°21'N	03°00'E	39			x	x	x	x
32	54°09'N	02°20'E	51			x	x	x	x
34	54°23'N	02°20'E	27	x		x	x	x	x
36	54°39'N	02°20'E	18	x	x	x	x	x	x
38	54°50'N	02°20'E	27	x	x	x	x	x	
40	55°11'N	02°20'E	32		x	x		x	
42	55°27'N	02°20'E	44		x	x	x	x	x
43	55°11'N	01°40'E	36			x	x	x	x
45	54°47'N	01°40'E	23			x	x	x	x
47	54°31'N	01°40'E	18			x	x	x	x
49	54°23'N	01°40'E	48		x	x	x	x	x
51	54°07'N	01°40'E	68		x		x		x
54	54°10'N	01°00'E	45		x		x	x	x
56	54°31'N	01°00'E	55		x	x		x	x
58	54°47'N	01°00'E	50			x	x	x	x
60	55°03'N	01°00'E	61			x		x	x

Table 1. Geographical positions and depth of the sample sites.

SCHRÖDER (1996), KÜNITZER et al. (1992), LINCOLN (1979) and HAYWARD & RYLAND (1990) and references therein. Species that clean their food off sand grains were separated from subsurface deposit feeders and classified as sandlickers. Since Anthozoa and *Corymorpha nutans* are known to feed mainly on pelagic copepods and Harpacticoids swimming in the water column at night, these species were separated from suspension feeders as hyperbenthos predators.

A few species, such as *Ophelia borealis*, are known to occur on a variety of sediments, but occur preferably on fine sand on the Dogger Bank (KIRKEGAARD 1969, KÜNITZER et al. 1992). For their classification we used the information available for the Dogger Bank area.

The classification of southern and northern species is based on their distribution in the North Sea instead of their zoogeographical distribution, since classification differs among groups and authors.

## Results

### Sediment

In both periods a classification of the sediments was carried out with an analysis of the silt content, but size fraction analysis was undertaken only in 1987. In the 80s the sediments of the Dogger Bank proper were characterised as fine sands with varying amounts of dead shells, whereas the sediments of the deeper parts were said to be muddy fine sands. The spatial pattern of the silt content of the sediment was very similar in the 80s and the 90s (Tab. 2). The shallow part of the Dogger Bank showed the lowest values (station 45 and 47: 0.09%) and the silt content increased towards the deeper sites. Maximum values were reached in the Outer Silver Pit (station 32: 8.09%; station 51: 13%), whereas the highest value of the northern station was 1.97% (station 42). There is no clear trend, but compared to 1987 there seemed to be an increase in silt content in the 90s especially in the deeper southern parts. Most shallow and northern stations showed higher values in 1996 but decreased again in 1997 and 1998.

The TOC content of the <63 µm fraction was analysed in 1996 and 1997 only. Highest TOC contents were found in the eastern part of the Dogger Bank, but decreased towards the deeper southern parts characterised by muddy fine sands (Tab. 2).

### Macrofauna

Based on the abundance data of the macrofauna four different communities (Fig. 4) were identified in the 90s using cluster and ordination techniques. The dominant species of these communities are given in Tab. 3. The station on top of the Dogger Bank (Bank community) were inhabited by a *Bathyporeia-Fabulina* association, dominated by amphipods on the shallow fine-sand station (*Bathyporeia elegans*: 207 ind./m<sup>2</sup>, *Bathyporeia guilliamsoniana*: 152 ind./m<sup>2</sup>). At the southern slope the abundance of *Fabulina fabula* (67 ind./m<sup>2</sup>), *Amphiura brachi-*

Table 2. Sediment characteristics of the sample sites during 1987 and 1996-98. - TOC is given in % of the fine fraction (<63 µm).

station	sediment silt content [%]				TOC [%]	
	87	96	97	98	96	97
6		0.41	0.35	0.23	3.98	
8	0.16	0.12	1.21	0.11	3.25	
9	0.09	0.67	0.66	0.51	3.65	
11		0.26	0.33	0.27	4.09	4.65
13		1.46	1.13	2.58	4.03	
16	0.23	0.98	0.82	0.6	4.13	
18	0.21	0.24	0.28	0.2	2.71	3.85
20	0.54	1	0.81	0.76	3.4	2.94
21	0.21	1.07	0.24	0.35	2.45	3.1
23		0.33	0.38	0.25	3.52	3.27
25		0.58	0.32	0.14	3.01	2.64
27		2.37	1.59	2.59	2.85	2.37
29		3.79	3.93	5.01	2.38	2.25
32		6.07	6.42	8.09	2.23	2.04
34		1.76	0.91	1.7	4.07	2.61
36		0.43	0.29	0.21	3.31	2.86
38		0.34	0.44		3.76	
40			0.51			2.54
42	0.27	1.97	0.47	0.79	2.16	2.54
43	0.09	0.48	0.24	0.12	3.15	2.34
45	0.11	0.39	0.15	0.09	3.06	3.75
47	0.1	0.63	0.13	0.09	2.24	4.12
49		4.62	7.1	6.36	2.23	1.96
51		11.07		13.58	1.9	
54		1.71	3.17	0.9	3.1	3.02
56			0.74	1.46		3.57
58		6.55	3.79	3.34	2.76	2.31
60	0.82		3.89	2.86		2.25

Table 3. Characteristic species for the different communities found on the Dogger Bank in 1996-98. - Species are ordered in decreasing contribution to similarity, as indicated by SIMPER.

Bank Community	ind./m <sup>2</sup>	Southern Community	ind./m <sup>2</sup>	Western Community	ind./m <sup>2</sup>	Northeastern Community	ind./m <sup>2</sup>
<i>Spiophanes bombyx</i>	320	<i>Amphiura filiformis</i>	640	<i>Amphiura filiformis</i>	541	<i>Scoloplos armiger</i>	70
<i>Bathyporeia elegans</i>	207	<i>Mysella bidentata</i>	127	<i>Spiophanes bombyx</i>	179	<i>Spiophanes bombyx</i>	138
<i>Bathyporeia guilliamsoniana</i>	152	<i>Spiophanes bombyx</i>	300	<i>Pholoe baltica</i>	39	<i>Bathyporeia elegans</i>	90
<i>Fabulina fabula</i>	67	<i>Pholoe baltica</i>	66	<i>Mysella bidentata</i>	50	<i>Cerianthus lloydii</i>	74
<i>Magelona johnstoni</i>	52	<i>Magelona johnstoni</i>	38	<i>Diplocirrus glaucus</i>	28	<i>Polinices pulchellus</i>	16
<i>Polinices pulchellus</i>	40	<i>Polinices pulchellus</i>	13	<i>Phaxas pellucidus</i>	11	<i>Edwardsia</i> spp.	25
<i>Amphiura brachiata</i>	43	<i>Nucula nitidosa</i>	61	<i>Phoronis mülleri</i>	12	<i>Chaetozone</i> sp F group	12
<i>Urothoe poseidonis</i>	20	<i>Echinocardium cordatum</i>	10	<i>Edwardsia</i> spp.	10	<i>Perioculodes longimanus</i>	15
<i>Perioculodes longimanus</i>	22	<i>Phaxas pellucidus</i>	11	<i>Nucula nitidosa</i>	50	<i>Dosinia</i> spp.	13
<i>Owenia fusiformis</i>	22	<i>Bathyporeia tenuipes</i>	11	<i>Echinocardium cordatum</i>	5	<i>Nephtys assimilis</i>	10
<b>Mean total abundance</b>	<b>1292</b>	<b>Mean total abundance</b>	<b>1668</b>	<b>Mean total abundance</b>	<b>1489</b>	<b>Mean total abundance</b>	<b>886</b>
<b>Mean species number/0.4m<sup>2</sup></b>	<b>44</b>	<b>Mean species number/0.4m<sup>2</sup></b>	<b>48</b>	<b>Mean species number/0.4m<sup>2</sup></b>	<b>51</b>	<b>Mean species number/0.4m<sup>2</sup></b>	<b>53</b>

Table 4. ANOSIM results for the comparison between the periods 1985-87 and 1996-98 ( $\sqrt{N}$  transformed abundance data).

	Bank Community	Southern Community	Northeastern Community	Western Community
R	0.692	0.33	0.465	0.307
p	0	0.1	0	0.3

ata (43 ind./m<sup>2</sup>) and polychaetes (*Spiophanes bombyx*: 320 ind./m<sup>2</sup>; *Owenia fusiformis*: 22 ind./m<sup>2</sup>) increased. This community changed towards a southern *Amphiura* association (KÜNITZER et al. 1992) in the deeper southern parts on muddy sands (southern community). This association was characterised by *Amphiura filiformis* (640 ind./m<sup>2</sup>), *Mysella bidentata* (127 ind./m<sup>2</sup>), *Pholoe baltica* (66 ind./m<sup>2</sup>) and *Nucula nitidosa* (61 ind./m<sup>2</sup>). *Magelona johnstoni* as well as *Polinices pulchellus* belonged to the dominant species in both communities.

Though very similar in the dominant species (*A. filiformis*: 541 ind./m<sup>2</sup>; *S. bombyx*: 179 ind./m<sup>2</sup>; *P. baltica*: 39 ind./m<sup>2</sup>; *M. bidentata*: 50 ind./m<sup>2</sup>), the *Amphiura* association in the south-western part (western community) was characterised by an increasing number of species described from the northern part of the North Sea. These species were found in low abundances (*Leptopentacta elongata*, *Brissopsis lyrifera*) or in higher numbers at single station only (*Golfingia* spp., *Lumbrineris tetraura*).

The community in the northern and north-eastern part (north-eastern community) was a transitional community between the *Bathyporeia-Fabulina* association on top of the bank and the *Amphiura* association described for the central North Sea by DUINEVELD et al. (1987) and KÜNITZER (1990), but *Amphiura filiformis* was restricted to the deepest northern stations. In this area we found high species numbers and lowest total abundance and

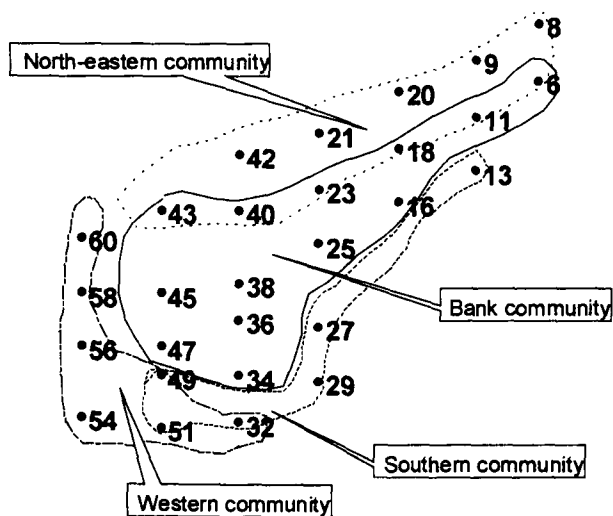


Fig. 4. Spatial distribution of benthic communities on the Dogger Bank during the period 1996-1998.

consequently highest diversity. Most abundant species were *Scoloplos armiger* (70 ind./m<sup>2</sup>), *Spiophanes bombyx* (138 ind./m<sup>2</sup>) and *Bathyporeia elegans* (90 ind./m<sup>2</sup>).

For the following analyses, stations were grouped based on these results. Intermediate stations between different communities were considered in both communities.

To analyse changes in the trophic structure of the different communities of the Dogger Bank, we compared the abundance of feeding types. Since the structure is rather stable in the 80s and 90s, except for the western community, the results for the years 1987 and 1998 are given as example for both periods.

#### Bank Community (*Bathyporeia-Fabulina* Association)

Mean total abundance as well as species number per station remained rather similar, at around 1250 ind./m<sup>2</sup> and 42 species/0.4 m<sup>2</sup> in all years (Fig. 5A). In 1996 the lowest total abundance was observed (958 ind./m<sup>2</sup>).

Table 5. Discriminating species of the Bank community between the periods 1985-87 and 1996-98. – Species are ordered in decreasing contribution to dissimilarity, as indicated by SIMPER (S = southern; N = northern; F = fine; C = coarser).

species	average abundance		distribution	sediment
	1985-87	1996-98		
<i>Lanice conchilega</i>	1	26	S	
<i>Megaluropus agilis</i>	1	13	S	
<i>Nephtys caeca</i>	11	0	N	
<i>Echinocyamus pusillus</i>	1	10	S	C
<i>Amphiura brachiata</i>	7	43	S	F
<i>Spiophanes bombyx</i>	110	319		F
<i>Ophiura</i> spp. juveniles	18	1		
<i>Siphonocoetes kroyeranus</i>	36	7	N	
<i>Perioculodes longimanus</i>	5	22		
<i>Abra prismatica</i>	9	5	N	
<i>Ensis ensis</i>	2	7	S	
<i>Donax vittatus</i>	13	7	S	
<i>Bathyporeia elegans</i>	406	207		F
<i>Nephtys cirrosa</i>	70	21		C
<i>Phoronis mülleri</i>	15	9		

As indicated by ANOSIM there was a significant difference between the communities in the 80s and the 90s (Tab. 4).

The ordination of the MDS (Fig. 6A) shows a clear separation of the stations in the 80s and those in the 90s. As a subgroup of the 90s the 1996 samples showed highest similarity to the communities in 1985-87, though clearly separated from the 80s.

The separation of the communities in 1985-87 and 1996-98 is mainly due to an increase in abundance of southern species and a decrease in abundance of northern species (Tab. 5).

In 1985-87 the amphipod *Megaluropus agilis* occurred only on the shallow stations in low abundances (mean: 1 ind./m<sup>2</sup>), but in 1996-98 it increased in abundance (mean: 13 ind./m<sup>2</sup>; max.: 50 ind./m<sup>2</sup>), spread over the whole Dogger Bank and occurred even in the deeper areas (Fig. 8A). The brittle star *Amphiura brachiata* (80s: 7 ind./m<sup>2</sup>; 90s: 43 ind./m<sup>2</sup>) increased especially at the southern slopes and the eastern shallower part of the bank (Fig. 8B). Higher numbers of *Lanice conchilega* (80s: 1 ind./m<sup>2</sup>; 90s: 43 ind./m<sup>2</sup>) were the result of an increase in juveniles especially since 1997 at the more northerly sites of this community. Within the *Bathyporeia-Fabulina* community the sea urchin *Echinocyamus pusillus* (80s: 1 ind./m<sup>2</sup>; 90s: 10 ind./m<sup>2</sup>) increased only in the eastern part (Fig. 8F).

With regard to the trophic structure there was an obvious increase in interface-feeding species (*Spiophanes bombyx*, Fig. 8D; *Amphiura brachiata*, Fig. 8B) in the 90s. In contrast this community was dominated by sandlicking species (*Bathyporeia elegans*, *B. guilliamsoniana*) in the 80s (Fig. 7).

#### Southern Community (*Amphiura* Association)

In the southern *Amphiura* community (Fig. 5B) total abundance is higher than in the *Bathyporeia-Fabulina* community. Mean abundance per year ranged between 2008 ind./m<sup>2</sup> and 1207 ind./m<sup>2</sup>. Lowest values were found in 1986 (1233 ind./m<sup>2</sup>) and in 1996 (1207 ind./m<sup>2</sup>). In the 90s, mean species number per station was higher and increased from 44 species/0.4 m<sup>2</sup> in 1996 to 53 species/0.4 m<sup>2</sup> in 1998, whereas especially in 1985 and 1986 mean species numbers were very low (37 species/0.4 m<sup>2</sup> and 34 species/0.4 m<sup>2</sup>, respectively).

Table 6. Discriminating species of the Southern community between the periods 1985-87 and 1996-98. - Species are ordered in decreasing contribution to dissimilarity, as indicated by SIMPER (S = southern; N = northern; F = fine; C = coarser).

species	average abundance		distribution	sediment
	1985-87	1996-98		
<i>Abra prismatica</i>	62	7	N	
<i>Spiophanes bombyx</i>	83	300		F
<i>Abra alba</i>	0	20	S	F
<i>Phoronis mülleri</i>	105	11		F
<i>Fabulina fabula</i>	17	46	S	F
<i>Edwardsia</i> spp.	56	5		
<i>Nephtys assimilis/hombergii</i>	23	7		
<i>Thyasira flexuosa</i>	61	16		F
<i>Ophiura</i> spp. juveniles	41	3		
<i>Harpinia antennaria</i>	1	7		F
<i>Nuculoma tenuis</i>	70	6	N	
<i>Bathyporeia tenuipes</i>	6	10		
<i>Diplocirrus glaucus</i>	35	29		
<i>Nucula nitidosa</i>	56	61	S	F
<i>Amphiura brachiata</i>	12	20	S	

The results obtained from the multivariate analyses were similar to those for the Bank community. There was a significant difference between the communities in the 80s and the 90s (Tab. 4).

Also the ordination of the MDS shows a clear separation of the station in both periods (Fig. 6B). Like the Bank community, the community in 1996 showed a higher similarity to the communities in 1985-87 than those in 1997-98.

As indicated by SIMPER, the separation of the communities in 1985-87 and 1996-98 was mainly due to an increase in abundance of southern species and a decrease in abundance of northern species (Tab. 6). But discriminating species differed from those of the Bank community.

The northern *Abra prismatica* (80s: 62 ind./m<sup>2</sup>; 90s: 7 ind./m<sup>2</sup>) was partly replaced by the southern *Abra alba* (80s: 0 ind./m<sup>2</sup>; 90s: 20 ind./m<sup>2</sup>), which was not found in 1985-87. The northern *Nuculoma tenuis* decreased from 70 ind./m<sup>2</sup> in the 80s to 6 ind./m<sup>2</sup>, whereas abundances of the southern *Nucula nitidosa* remained nearly constant at around 60 ind./m<sup>2</sup> (Tab. 6). Though not indicated as a discriminating species the southern polychaete *Ophiodromus flexuosus* was found at the deeper station with a maximum abundance of 33 ind./m<sup>2</sup>, but there is no single record in 1985-87 (Fig. 8C).

Like on top of the Dogger Bank interface-feeding species (e.g. *Spiophanes bombyx*) increased in abundance in the 90s compared with the 80s, especially at site 13 (Fig. 8D).

#### North-Eastern Community (Transitional Association)

In the north-eastern part (Fig. 5C) the maximum mean total abundance was found in 1987 (1810 ind./m<sup>2</sup>). In general, lowest mean total abundances in the Dogger Bank area, except from the very shallow station 45 and 47 on top of the bank, were found in this community (Tab. 3). But even if the mean species number was rather low in the 80s, especially in 1985-86 (36 and 40 species/0.4 m<sup>2</sup> respectively), the species numbers showed the highest values in this part of the Dogger Bank in the 90s (1996: 48 species/0.4 m<sup>2</sup>, 1997 and 1998: 56 species/0.4 m<sup>2</sup>).

As mentioned for the other two communities a significant difference was found between the 80s and 90s (Tab. 4, Fig. 6C). However, in contrast to those communities, northern and southern species partially increased as well as decreased (Tab. 7), but the total number of northern species in this area definitely increased. This increase is mainly due to an increase in rather rare species (Tab. 8).

The most striking difference between 1985-87 and 1996-98 was the decrease in species, which are said to prefer fine-sands, such as *Spiophanes bombyx* (80s: 308 ind./m<sup>2</sup>; 90s: 138 ind./m<sup>2</sup>), *Eudorellopsis deformis* (80s: 34 ind./m<sup>2</sup>, 90s: 6 ind./m<sup>2</sup>) and *Ophelia borealis* (80s: 87 ind./m<sup>2</sup>; 90s: 9 ind./m<sup>2</sup>). *Ophelia borealis* belonged to the dominant species in this community in the 80s, but it decreased dramatically (Fig. 8E). In contrast, species, which occur on coarser and unstable sediment, increased

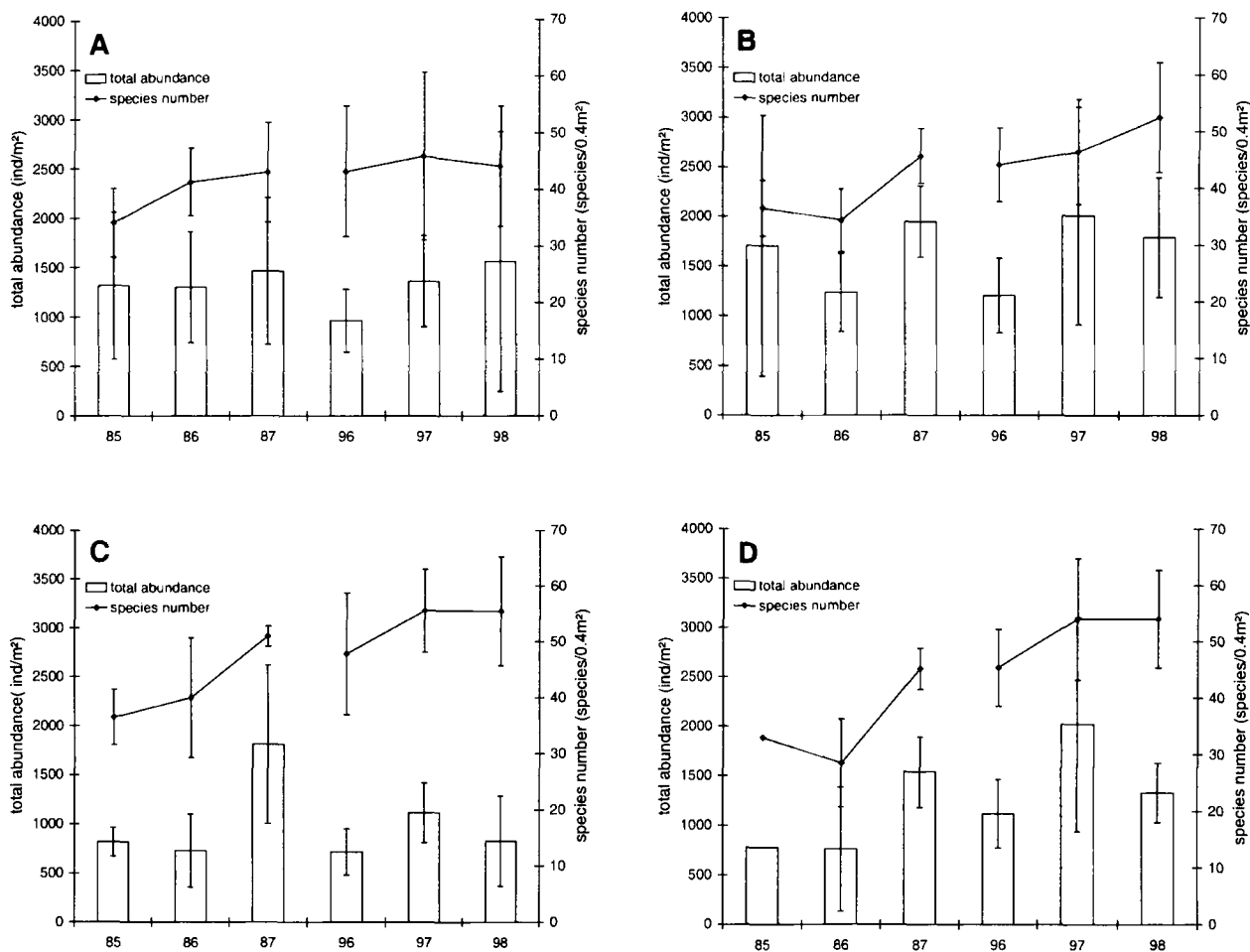


Fig. 5. Changes in mean total abundance and mean species number during the periods 1985-87 and 1996-98 in the (A) Bank community, (B) Southern community, (C) North-eastern community and (D) Western community.

Table 7. Discriminating species of the North-eastern community between the periods 1985-87 and 1996-98. – Species are ordered in decreasing contribution to dissimilarity, as indicated by SIMPER (S = southern; N = northern; F = fine; C = coarser).

species	average abundance		distribution	sediment
	1985-87	1996-98		
<i>Cerianthus lloydii</i>	1	74	N	C
<i>Ophiura albida</i>	20	1	S	F
<i>Spiophanes bombyx</i>	308	138		F
<i>Ophelia limacina</i>	87	9		F
<i>Eudorellopsis deformis</i>	34	6	N	F
<i>Phoronis mülleri</i>	19	30		F
<i>Ophiura</i> spp. juveniles	51	18		
<i>Abra prismatica</i>	44	27	N	
<i>Amphiura filiformis</i>	32	15		F
<i>Arctica islandica</i>	7	1		
<i>Travisia forbesii</i>	15	1	N	
<i>Echinocyamus pusillus</i>	4	20	S	C
<i>Perioculodes longimanus</i>	3	15		
<i>Urothoe poseidonis</i>	10	8	S	F
<i>Bathyporeia guilliamsoniana</i>	10	3	S	F

Table 8. Discriminating species of the Western community between the periods 1985-87 and 1996-98. – Species are ordered in decreasing contribution to dissimilarity, as indicated by SIMPER (S = southern; N = northern; F = fine; C = coarser).

species	average abundance		distribution	sediment
	1985-87	1996-98		
<i>Mysella bidentata</i>	117	50		F
<i>Ophiura</i> spp. juveniles	39	1		
<i>Amphiura filiformis</i>	410	541		F
<i>Nucula nitidosa</i>	20	50	S	F
<i>Spiophanes bombyx</i>	31	179		F
<i>Harpinia antennaria</i>	0	9		F
<i>Eudorellopsis deformis</i>	28	9	N	F
<i>Nuculoma tenuis</i>	33	13	N	F
<i>Abra prismatica</i>	16	5	N	
<i>Echinocyamus pusillus</i>	14	52	S	C
<i>Diplocirrus glaucus</i>	27	28		F
<i>Nephtys hombergii</i>	7	9		
<i>Polinices pulchellus</i>	2	10		
<i>Phaxas pellucidus</i>	7	11		
<i>Bathyporeia elegans</i>	3	25		F



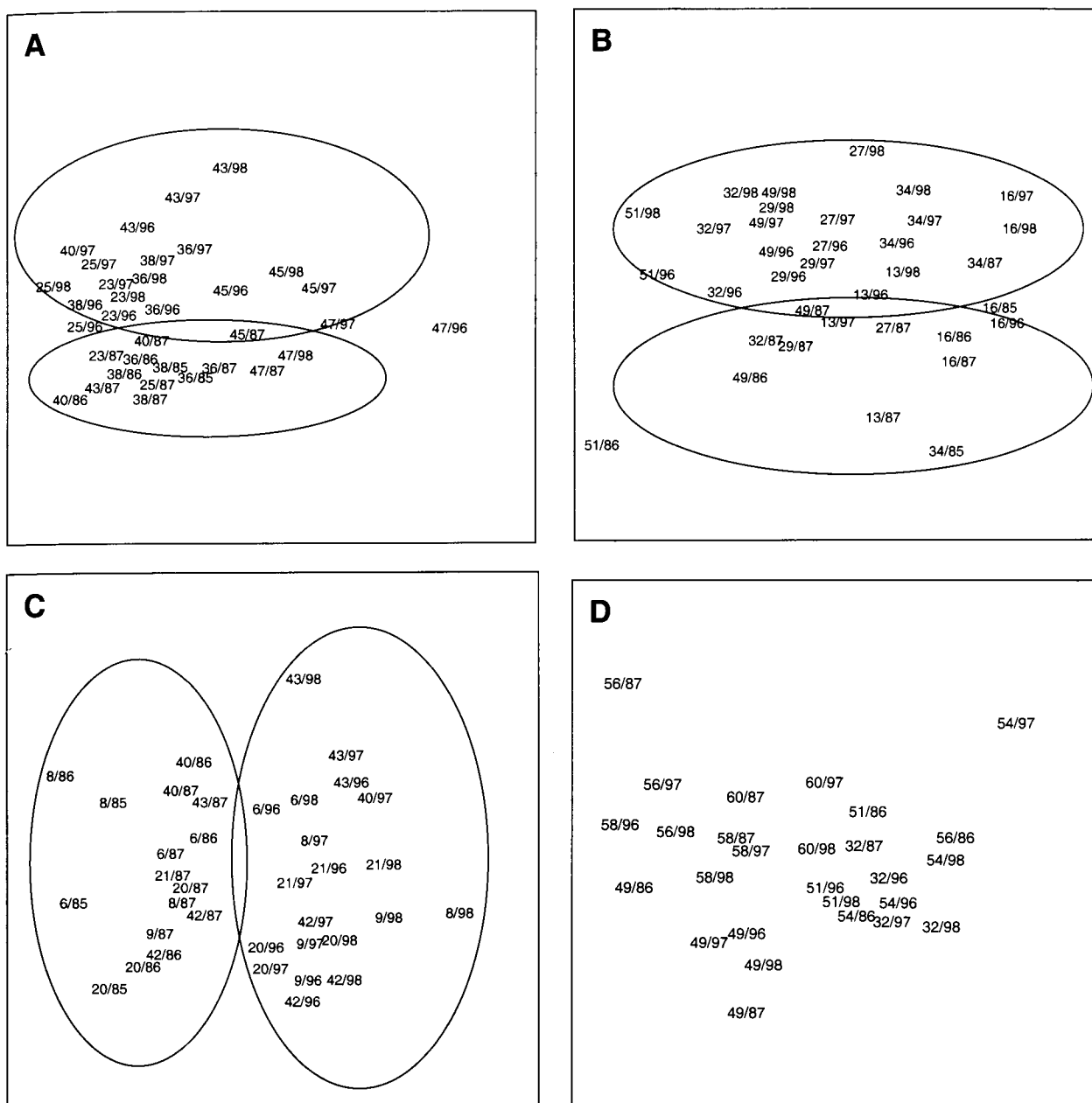


Fig. 6. MDS ordination of  $\sqrt{V}$  transformed abundance data from the (A) Bank community (stress: 0.17), (B) Southern community (stress: 0.14), (C) North-eastern community (stress: 0.14) and (D) Western community (stress: 0.19) during the periods 1985-87 and 1996-98.

Northern species	'Coarse sediment' species
<i>Aricidea cerrutii</i>	<i>Corymorpha nutans</i>
<i>Aricidea simonae</i>	<i>Pisione remota</i>
<i>Ampharete falcata</i>	<i>Phoxocephalus holbolli</i>
<i>Montacuta substriata</i>	<i>Sphaerosyllis bulbosa</i>
<i>Spiophanes kröyeri</i>	
<i>Petalosarsia declivis</i>	
	<i>Protodorvillea kefersteini</i>
	<i>Aonides paucibranchiata</i>
	<i>Ophiura affinis</i>

Table 9. List of rare species, which were found predominantly in 1996-98. – The last three species belong to both groups.

in abundance (e.g. *Echinocyamus pusillus* (80s: 4 ind./m<sup>2</sup>; 90s: 20 ind./m<sup>2</sup>) and *Cerianthus lloydii* (80s: 1 ind./m<sup>2</sup>; 90s: 74 ind./m<sup>2</sup>)) in the 90s. *Echinocyamus pusillus* increased at those stations where *Ophelia borealis* decreased (Fig. 8F). Both coexisted in high abundances in the 90s only at station 54 in the south-western part of the bank.

The increase in rare northern species was paralleled by an increase in the 90s of 'coarse sediment species' (Tab. 8).

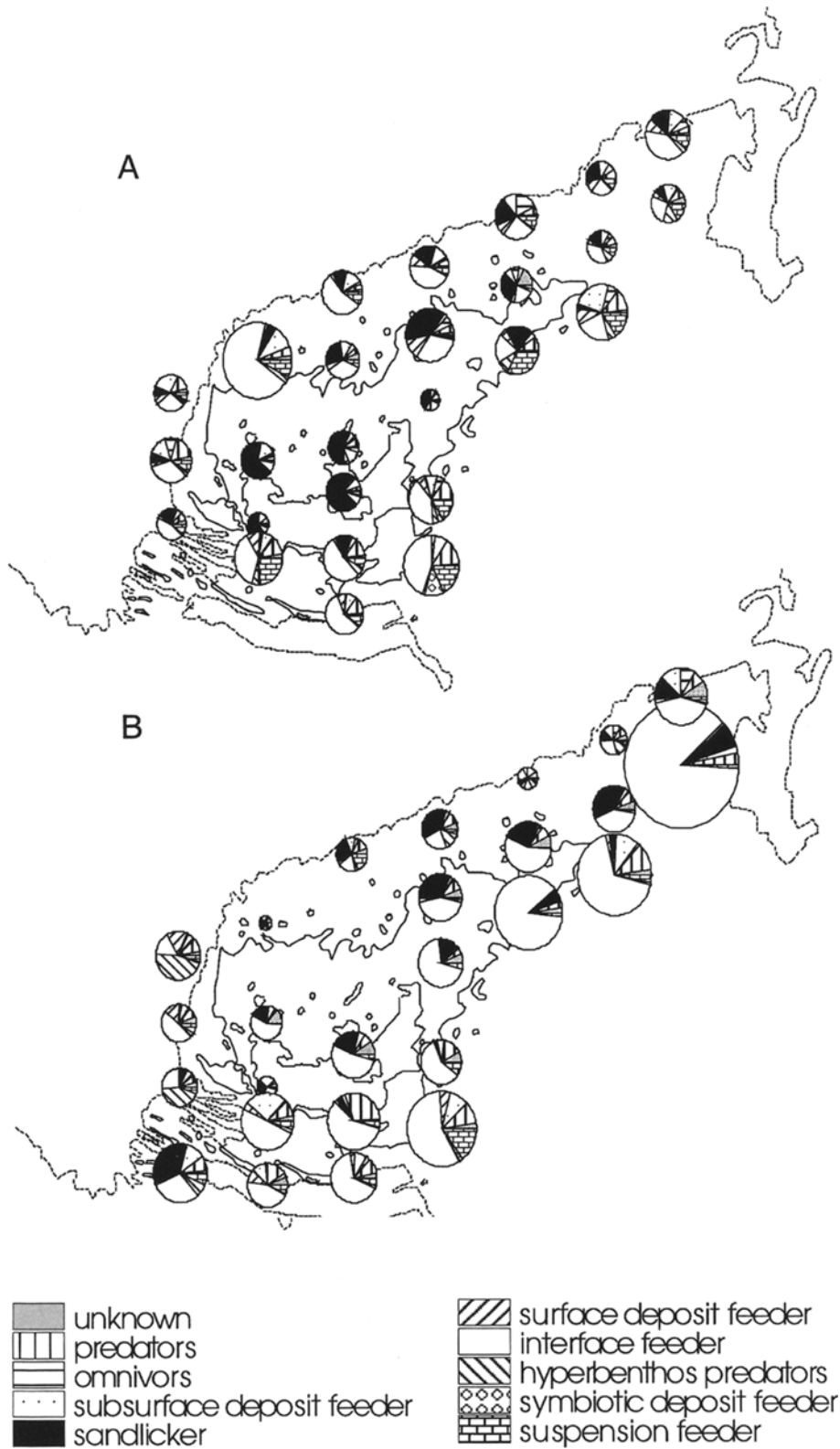


Fig. 7. Trophic structure (represented by the abundance of feeding types) of the Dogger Bank benthic communities in (A) May 1987 and (B) May 1998.

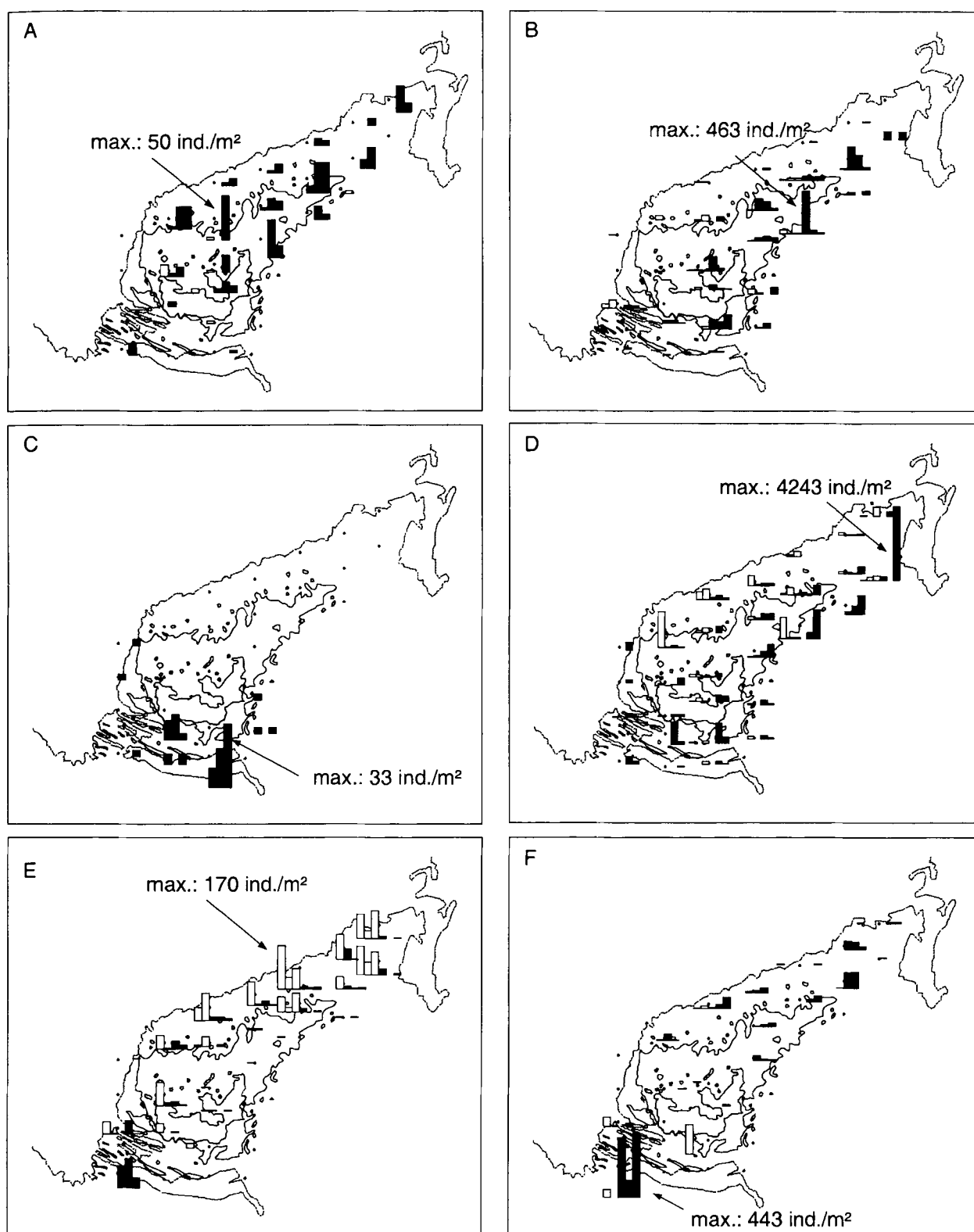


Fig. 8. Spatial distribution and abundance of (A) *Megaluropus agilis*, (B) *Amphiura brachiata*, (C) *Ophiodromus flexuosus*, (D) *Spiophanes bombyx*, (E) *Ophelia borealis* and (F) *Echinocyamus pusillus* on the Dogger Bank in 1985-87 (white columns) and 1996-98 (black columns).

These changes also resulted in striking differences in the trophic structure of this community between the 80s and the 90s (Fig. 7). Abundance of interface-feeding species as well as total abundance decreased. Hyperbenthic predators like *Cerianthus lloydii* in 1996 and *Corymorpha nutans* in 1998 showed higher abundances. In general, the diversity of feeding types was higher in 1996-98 compared to 1985-87, due to the increase in rare species and the lack of dominance of a single feeding type.

#### Western Community (Transitional *Amphiura* Association)

In the western community (Fig. 5D) low mean abundances were recorded in 1985 and 1986. In the 90s, mean abundances were highest in 1997 (2020 ind./m<sup>2</sup>). The changes in mean species numbers were similar to those observed for the north-eastern community. Values in 1985 and 1986 were very low (33 species/0.4 m<sup>2</sup>; 29 species/0.4 m<sup>2</sup>), increased in 1987 (45 species/0.4 m<sup>2</sup>) and highest

mean species numbers were recorded in 1997-98 (56 species/0.4 m<sup>2</sup>).

The results obtained by the ANOSIM and the ordination of the MDS differ completely from those of the other communities (Tab. 4, Fig. 6D). There was no clear separation of the communities in the 80s and in the 90s, because spatial variability was higher than temporal variability. Only the intermediate stations, which were more similar to the southern community, showed a relatively clear separation between the 80s and 90s. But in contrast to the other communities these differences were mainly caused by a shift in abundance of the dominant species (Tab. 3 and 9).

Since spatial variability was very high in this community, it was also very difficult to analyse changes in the trophic structure of the community. The deep station 32, 49 and 51 seemed to be rather similar in both periods (Fig. 7). Only at the westerly station the hyperbenthos predator *Corymorpha nutans* occurred in very high abundances in 1998 and made up to 50% of total abundances in contrast to 1985-87 (Fig. 7).

## Discussion

This long-term comparison showed significant differences in the macrofaunal community structure on the Dogger Bank between the years 1985-87 and 1996-98. Since we used exactly the same grab and sieves and calibrated our taxonomy, these differences do not result from methodological artefacts or from differences in taxonomic determination.

#### Changes in Species Composition of the Bank and Southern Community

The increase in southern species and a decrease in northern species constitute the major difference in the *Bathyporeia-Fabulina* and the southern *Amphiura* community between the 80s and the present study in the 90s. This shift indicates an increase in bottom temperatures in these areas of the Dogger Bank (Fig. 2). Several southern species like *Megaluropus agilis* and *Amphiura brachiata* reach their northern distributional limits at the Dogger Bank (URSIN 1960; LINCOLN 1979), probably because they require higher temperatures for biological processes such as reproduction and development. In contrast northern species are affected by higher temperatures because they are adapted to relatively constant low temperatures (KÜNITZER et al. 1992).

In the 80s several southern species occurred in the shallow western part only. This area was the only area that reached higher temperatures in summer (OTTO et al. 1990). Since the shallow stations are located in the homothermal part of the central North Sea, the SST is similar to the bottom temperature, which influences the macrobenthos. However, even bottom temperatures in the seasonally stratified southern and eastern part of the Dogger Bank seem to have increased. This is indicated by

the spreading of southern species like *M. agilis* (Fig. 8A) to the deeper eastern and southern parts of the bank as well as the decrease of northern species in these areas.

Station inhabited by the north-eastern community are located in a transitional area between the stratified water masses of the central North Sea and the well mixed water masses on top of the Dogger Bank, which might be the main reason for the different results compared to the more southerly communities.

As URSIN (1960) already emphasized, the distribution pattern of species is complicated by the fact that some patterns cannot be explained by temperature only, but are additionally influenced by different water masses. However, because of strong differences between the northern and southern part of the Dogger Bank in absolute temperature and seasonal variability of temperature, we expect little differences in temperature to result in strong changes in macrobenthic communities.

Our results are in accordance with several other observations in the North Sea. Winter SST is known to have increased in correlation with the NAO index (DIPPNER 1998). Higher surface temperatures were measured after 1987 especially in spring and summer months (REID et al. in press). As a result of higher temperatures, Lusitanian and Channel plankton species (which were never recorded before) were observed in the German Bight since the beginning of the 90s (GREVE et al. 1996).

#### Changes in Trophic Structure of the Bank and Southern Community

Striking differences were observed in the trophic structure of the central and southern Dogger Bank, where

interface-feeding species increased markedly in abundance. The Dogger Bank is a highly dynamic area, where periods of sedimentation and resuspension alternate, but no net deposition occurs (PULS 1987). Under these conditions, interface-feeding species, which can switch between suspension- and surface-deposit-feeding, will mainly profit from an increase in primary production and higher food supply to the benthic boundary layer (DAUWE et al. 1998; ROSENBERG 1995). For that reason we suppose that the strong increase in interface-feeding species indicates an increase in primary production connected to the NAO. Recent results of the Continuous Plankton Recorder (CPR) survey showed a stepwise increase of phytoplankton season length and abundance in the central North Sea after the mid-80s (REID et al. 1998b). PLANQUE & TAYLOR (1998) suggested that in years with early onset of stratification, there is a greater chance of mixing events early in the year providing extra nutrients for phytoplankton growth if nutrients have become depleted by an already developing bloom. The onset of stratification depends on temperature and the mixing on wind stress. Both in turn are positively correlated to the NAO.

To what extent the decrease in sandlicking species is related to the NAO cannot be estimated. It might be caused by interaction between the different trophic groups. On the other hand this group is mainly represented by a single genus (*Bathyporeia*). Therefore, observed changes could be the effect of interspecific competition or of differences in interannual cycles of the different species.

### Changes in Species Composition of the North-Eastern Community

The main difference between the 80s and 90s within the north-eastern community was the increase in species preferring coarse sediments and the decrease of species occurring on fine sands in this area. *Ophelia borealis*, *Spiophanes bombyx* and *Bathyporeia elegans* were described to occur on fine sands (KÜNITZER et al. 1992). KIRKEGAARD (1969) reported that even in the 50s *O. borealis* was one of the dominant species on the Dogger Bank occurring on fine sand. Our observations are supported by the results of the Dutch monitoring program (HOLTMANN et al. 1999). They showed an increase in median grain size on the Dogger Bank since 1986. The observed shift in species composition indicates a change in sediment composition towards coarser sediments, caused by an increase in current velocities along the northern slope and in the northeastern part of the Dogger Bank (Fig. 2).

In our opinion it is unlikely, that our results are mainly related to an increase in west wind stress or the height of waves, since the above-mentioned changes were restricted to the deeper northeastern part only. If this were the case, we would have also expected similar changes at the southern slope of the bank. In the shallow parts higher bottom stress might favour the development of a low diversity *Donax* association, which is typical for high-energy environments like the South-West Patch (own observations). But in contrast, species number and abundance increased in the 90s at the shallow stations, especially in the central and eastern part of the Bank

(Fig. 7). BROWN et al. (1999) observed seasonal jet-like circulations ( $7.5 \text{ cm sec}^{-1}$ ) at the northern slope of the Dogger Bank. The occurrence of these jets depends on the onset of thermal stratification and the flow is expected to intensify with increasing density contrast. These processes are connected to temperature, which in turn is correlated to the NAO. Furthermore, models showed an increasing current velocity at the Dogger Bank in March during the last two decades and in February during the last decade. These changes are the result of stronger southwesterly winds in both months (SIEGISMUND & SCHRUM 2001).

### Changes in Trophic Structure of the North-Eastern Community

There is only little evidence for causal animal sediment relationships, but sediment composition reflects the food availability (SNELGROVE & BUTMAN 1994), which influences trophic structure (DAUWE et al. 1998). Therefore, the shift in species composition of the north-eastern community should be discussed in the context of changes in the trophic structure of this community. Higher current velocities result in low sedimentation rates. Compared to 1987, decreasing food supply could explain the decrease in total abundance and especially the decrease in interface-feeding species.

Alternatively, this trophic structure is very similar to those reported from more refractory environments in the central and northern North Sea (ROSENBERG et al. 1996; DAUWE et al. 1998). They found high diversities of feeding types and an exceptionally high numerical contribution of predators. Predatory behaviour is a possible mechanism to fulfil the nutritional needs in refractory sediment (DAUWE et al. 1998). Interestingly, hyperbenthos predators such as *Corymorpha nutans* and *Cerianthus lloydii* increased in abundance in the western part and along the northern slope of the Dogger Bank. These species show predatory behaviour, which is in contrast to typical suspension feeders that feed on phytoplankton and detritus. Therefore, we believe that the increase in hyperbenthos predators was a result of a decrease in food quantity and quality, caused by a stronger or different inflow of northern water masses (SVENDSEN & MAGNUSSON 1992; SVENDSEN et al. 1995; IVERSEN et al. 1998).

### The Importance of Winter and Summer Temperatures

Our results support the idea that summer temperature is an important factor with regard to distribution and variability of Dogger Bank macrofauna, which has already been stressed by URSIN (1960), KIRKEGAARD (1969) and PETERSEN (1977). They showed, that in many cases species distribution followed specific summer isotherms. These observations are in contrast to several investigations in the Wadden Sea and coastal areas, which indicated that cold and mild winters are important determinants of changes in macrofaunal communities (BEUKEMA 1990; 1992; BEUKEMA et al. 1996; REISE 1993; KRÖNCKE et al. 1998).

Since the winter of 1995/96 was very cold (low NAO), we can roughly estimate the effects of cold

winters on offshore macrobenthic communities. Whereas in coastal areas and in the Wadden Sea macrofauna communities were strongly affected by cold temperatures, there was only a slight decrease in total abundance in the Dogger Bank area in 1996 (Fig. 5 A-D). Higher similarity of the 1996 samples to those of the 80s indicated a short-term reverse of long-term changes. But communities on the Dogger Bank still showed generally high diversity indicating that winter did not favour the survival of dominant species. At a sublittoral benthic station off Northumberland cold winters favoured the survival in the dominant species at the expense of the lesser-ranked species due to reduced primary production resulting in low diversity (BUCHANAN & MOORE 1986).

These differences in functioning of benthic systems were caused by the fact that absolute temperatures are more important than relative temperatures (BEUKEMA et al. 1996). Temperatures experienced during an unusually cold winter on the Dogger Bank are similar to a mild winter in coastal areas. But as already mentioned before, summer temperatures on the Dogger Bank might be lethal for northern species, respectively they do not reach values necessary for biological processes in southern species.

### Antropogenic influences

Fisheries impact, which is a major factor contributing to long-term changes in the southern North Sea (LINDEBOOM & DE GROOT 1998), seems to be of minor importance for the observed changes. Fisheries effort decreases towards the central North Sea and is known to be patchily distributed (JENNINGS et al. 1999; RIJNSDORP et al. 1998). This was confirmed by our mapping of different communities on the Dogger Bank with Side Scan Sonar in May and July 1998. We found few trawl tracks (resulting mainly from otter boards) only at the borders of the bank, especially at the Tail End. On the bank itself only few tracks were detected. This means fishery might be a structuring factor with regard to small-scale distribution, but the changes we found are obvious on the whole bank. Furthermore, communities were influenced by fisheries impact already in the 80s. Therefore, we conclude that fisheries cannot explain observed large-scale and decadal changes between 1985-87 and 1996-98, in contrast to the decrease of the extensive *Spisula* patches since the 20s.

Eutrophication and pollution have been discussed in connection with changes in macrofauna communities of the Dogger Bank by KRÖNCKE (1992). There are possible synergistic effects of climate, eutrophication and pollution, such as a possible climate driven transport of nutrient and contaminant rich coastal water masses into different areas (where for example light limitation becomes unimportant). BROWN et al. (1999) suggested the seasonal jet like circulation as a possible direct pathway for British coastal waters (and pollutants) to the central North Sea. Therefore, anthropogenic effects can only be perceived as a departure from a natural NAO variability baseline, which demands a prior understanding of factors and processes connecting NAO and macrofauna of the Dogger Bank.

### Hydrographic Scenarios

The observed decadal changes in macrobenthic communities of the Dogger Bank between 1985-87 and 1996-98 can be explained by factors and processes, which in turn are correlated with the NAO. Accordingly, we suggest that these changes are caused by the recent rise of the NAO and connected changes in the hydroclimatic regime of the North Sea since 1989.

Our investigation showed that changes on the Dogger Bank go beyond the simple replacement of northern species by taxonomically or morphologically similar southern species. There are also changes in the trophic structure of the communities, which in turn might affect functional aspects such as nutrient cycling.

Because of strong gradients, resulting in a variety of different environmental conditions, the Dogger Bank is a

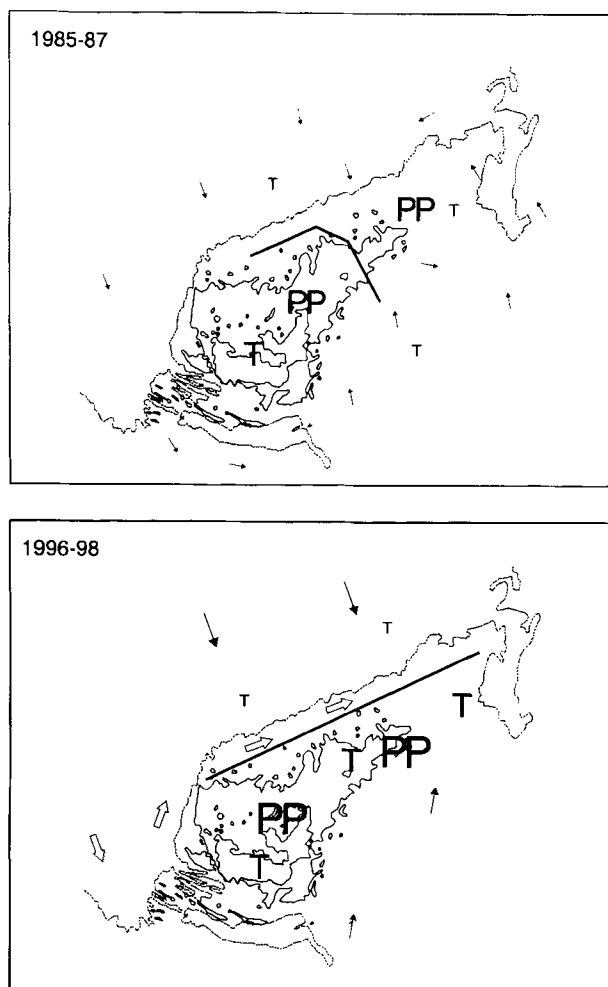


Fig. 9. Hypothetical hydrographic situation on the Dogger Bank during the periods 1985-87 and 1996-98 assessed by biological data. – The straight black lines show the separation of northern and southern species in the Dogger Bank area during both periods. The size of the letters PP and T indicates the relative values of both parameters primary production (PP) and temperature (T).

suitable area to investigate factors and processes linking climate and biology as well as the effects of long-term changes in climate forcing. For example the question arises as to what the possible effect of bottom fronts and subsurface plankton blooms (which occur around the Dogger Bank) may be on the macrofauna and, to what extent these are influenced by the NAO. Unfortunately, there is only a little hydrographical evidence for specific changes in the Dogger Bank area, but based on our biological data we suppose two different hydrographic situations in 1985-87 (low NAO) and 1996-98 (high NAO) in the Dogger Bank area (Fig. 9), which were recently confirmed by models of STEGISMUND (2001).

In the 80s only the shallow areas in the western part of the Dogger Bank showed higher temperatures. Though higher than in the surrounding deeper parts of the North Sea only a moderate amount of primary production reached the benthic system. Northern and southern water masses were broadly mixed in the Dogger Bank area.

In the 90s temperatures as well as primary production increased especially in the southern and eastern part. Along the northern slope two contrasting processes occurred. The increase in bottom temperature was lessened by an increasing or different inflow of cold-water masses from the central and northern North Sea in the 90s. Finally, stronger currents occurred between the well-

mixed water masses on top of the bank and the seasonally stratified water masses in the north.

To what extent these changes are a response to global warming we cannot estimate, but possible relationships between the rise in NAO and global warming were already discussed (REID et al. 1998a, b).

Finally, we believe that this investigation has stressed again the need to assess the occurrence of variation in functional groups and rare species, since the dominant and widespread species do not necessarily react to changes. This holds true especially for those communities characterised by high diversity. For this case species have to be grouped to functional groups to achieve reliable results, but necessary deeper knowledge of the biology and distribution of many of the species is still lacking even for the North Sea.

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