Helgol Mar Res (2012) 66:63–75
DOI 10.1007/s10152-011-0247-2

ORIGINAL ARTICLE

The megaepifauna of the Dogger Bank (North Sea): species composition and faunal characteristics 1991–2008

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Received: 27 May 2010 / Revised: 20 January 2011 / Accepted: 27 January 2011 / Published online: 13 February 2011
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Abstract During a long-term study in the summer months of the years 1991–2008, 176 megaepifaunal species were recorded through a series of beam trawl surveys on a grid of fixed stations on the Dogger Bank (central North Sea). This paper gives a qualitative overview on species composition throughout the research period, determined from samples collected during 15 cruises. In recent years, a number of species with more oceanic distribution patterns (e.g. species from SW British coasts) has been collected. In spite of these newcomers, there was a slight decrease in total species numbers during the research period.

Keywords Beam trawl survey · Dogger Bank · Epibenthos · Megaepifauna · North Sea

Introduction

The Dogger Bank is a shallow sand bank in the central North Sea. The shortest distance from its edge to the British coast is around 60 n.m. (Türkay and Kröncke 2004). There are several reasons why the Dogger Bank provides an ideal platform for long-term research. For example, the sea floor is flat and covered by uniform sandy sediment, rarely interspersed with stones and gravel of glacial origin. This is supported by grain size analyses made in the years 1992 and 1994 (Wehrmann, unpublished data), revealing that the sand fraction never drops below 94% at stations above the 30-m depth contour. In addition, the flatness of this sand bank allows the monitoring of a large area with only slight depth and substrate variances. These relatively constant environmental conditions as well as the excellent background information about the ecology of the Dogger Bank (Kröncke and Knust 1995; Diesing 2009) facilitate the identification of other possible factors governing changes in benthic faunal composition. The first comprehensive bottom sampling in that area with an Agassiz-Trawl and a Petersen grab was undertaken by Davis (1923, 1925). The main target of those studies was to analyse the gut contents of fish caught by the Agassiz-Trawl, as the Dogger Bank was "known to be a comparatively rich feeding ground and one on which transplanted plaice thrive and grow at an exceptional rate" (Davis 1923). Petersen grab samples showed a dominance of the endobenthic bivalves *Spisula subtruncata* and *Mactra stultorum* and provided a good overview of the endobenthos, while no epibenthic data were collected at that time. In May 1950 and 1951, the Danish Commission for Fishery and Sea Investigations undertook additional endobenthic sampling on the Dogger Bank with the Van Veen and the Petersen grab (Ursin 1952). The published results were rediscussed by Birkett (1953), who recommended the Van Veen grab as the better tool for comparable bottom sampling. Afterwards, Ursin (1960) published a comprehensive paper based upon a comparatively large series of Van Veen grab samples, treating the echinoderm fauna of the central North Sea and covering a large part of the Dogger Bank. His work gives an insight into the complexity of the echinoderm fauna composition of the Dogger Bank for the years 1950–1954. Furthermore, Kirkegaard (1969)

Communicated by H.-D. Franke.

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published a study on the diversity of polychaetes of the central North Sea, using material from Ursin. A total of 61 polychaete species were identified in this study. Petersen (1977) focused on the bivalves of the central North Sea, using material from both Petersen and Van Veen grab samples. Kröncke (1988, 1990, 1992) re-sampled Ursin's stations from 1985 to 1987 and described temporal differences in the endobenthic community structure.

Subsequently, several studies of the epibenthos were performed covering the whole North Sea (Dyer et al. 1983; Frauenheim et al. 1989; Jennings et al. 1999; Zühlke et al. 2001; Callaway et al. 2002, 2007; Reiss et al. 2010). Rees et al. (1999) compared benthic in- and epifauna of an even larger research area, including parts of the North Sea, the English Channel, the Celtic and the Irish Sea in a period from 1992 to 1996. Because of the large research areas of the studies mentioned here, only few stations were located on the Dogger Bank. Due to the sparse coverage of the epibenthos in our research area and because of different sampling methods, there is little comparable information. In other studies (Künitzer 1990a, b; Neumann et al. 2008, 2009a, b; Frid et al. 2009), in- and/or epifauna were sampled on a narrower grid or highly localized, but outside the Dogger Bank area. Neumann et al. (2009b) reported on the development of epifaunal communities in the south-eastern part of the North Sea including the Dogger Bank tail end, examining material of several IBTS (International Bottom Trawl Survey) cruises. So, additional information about the epifauna of the Dogger Bank tail end of the late 20th and early twenty-first century is provided by that study.

The research on the infauna of the Dogger Bank continues until today (Wieking and Kröncke 2001, 2003, 2005), but the epifauna is covered only sparsely by the majority of the above studies. The focus of our work is the detailed monitoring of the epibenthos on a narrow grid in order to get an idea on the time scales of natural changes and such caused by direct or indirect anthropogenic influence.

Materials and methods

This paper deals with the qualitative results gathered on 15 epibenthos monitoring cruises on the Dogger Bank with RV Senckenberg in July/August of the years 1991–2008 (Table 1). The sampling grid consisted of 37 stations (Fig. 1), covering an area of approximately 17,000 km^2. Station 40 at the tail end of the bank was surveyed for 48 h during every cruise at 3-h intervals, whenever allowed by weather conditions, in order to get an idea on diurnal (daylight- and tidal current-induced) variability. Only the first sample each at station 40 is included in this study in order to retain comparability of cruises and stations. Due to interference with other projects, no monitoring cruises could take place in 1998, 2000 and 2007. The research cruise of the year 2005 was excluded from the species list (Table 2), because extremely bad weather conditions did not allow to sample all stations.

Table 1 Sampling periods for the years 1991–2008

Cruise year	Sampling period	Cruise year	Sampling period
1991	30.07 to 04.08	2001	19.07 to 25.07
1992	29.07 to 31.07	2002	26.07 to 31.07
1993	01.08 to 03.08	2003	30.07 to 06.08
1994	21.07 to 26.07	2004	04.08 to 08.08
1995	26.07 to 31.07	2005	03.08 to 06.08
1996	23.07 to 29.07	2006	19.07 to 25.07
1997	17.07 to 22.07	2008	30.07 to 04.08
1999	04.08 to 08.08		

The station grid was designed first by choosing 40 equally distributed stations, mainly within the 30-m depth contour. After first try-and-error trawls, the stations with seafloor conditions improper to trawling were skipped because of foul ground (1, 2 and 19). Furthermore, stations where underwater cables or pipelines were laid during the survey period had to be moved. The epibenthos survey was performed with a 2-m beam trawl, showing a minimum mesh size of 1 cm^2 in the cod end. The trawl was towed for one nautical mile at a speed of 2.2 knots. The catch was sieved using three different mesh sizes (10 mm, 5 mm and 300 µm). The megafauna (>1 cm) was separated from the fine fractions, which were preserved in 5% formaldehyde in sea water. Only the 1-cm fraction was quantified, because only animals with body sizes above 1 cm were systematically retained by the net. The 1-cm fraction was determined to species level and counted on board ship. Megafaunal components that were not identifiable on the spot and species of special scientific interest were preserved in 5% formaldehyde in sea water (rarely in EtOH 99%) for subsequent determination in the laboratory.

All epibenthic animals above 1 cm in size found on the cruises are listed in Table 2. Some species in this list are semi-endobenthic or rarely even endobenthic, such as *Tubulanus superbus*. These species sometimes appeared in the catches as they occasionally come close to the sediment surface layer. Such species are dug out by the tickler chains and caught with the trawl. They are often difficult to assign to either an epi- or endobenthic lifestyle and were thus kept in the species list (similar to Callaway et al. 2007).

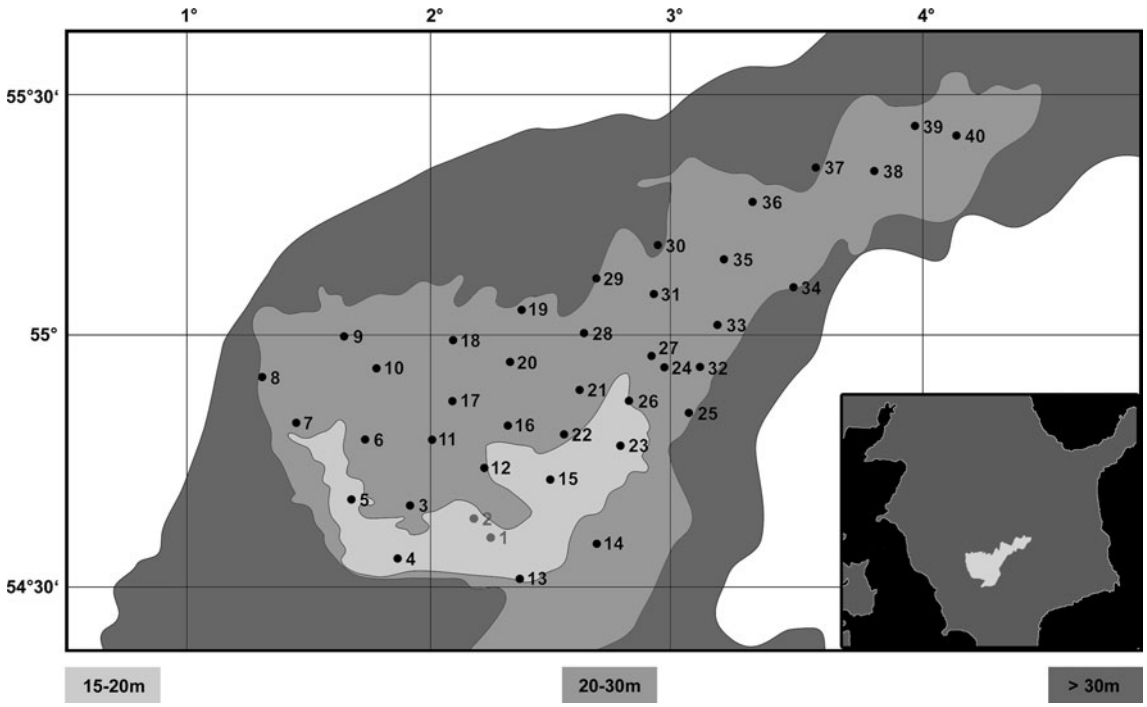

Fig. 1 Sampling sites on the Dogger Bank. *Bottom right* position of the Dogger Bank in the North Sea. With a few exceptions, all stations are above the 30-m depth line

Results

Species composition

Table 2 lists all megaepifaunal (>1 cm) species caught throughout the research period. A total of 176 species were recorded, with a mean of 64 species per cruise. The list includes Porifera (4 spp.), Cnidaria (25 spp.), Nemertini (1 sp.), Annelida (11 spp.), Arthropoda (30 spp.), Mollusca (40 spp.), Bryozoa (6 spp.), Echinodermata (14 spp.) and Chordata (45 spp.).

Twenty-one species (marked in grey in Table 2) appeared on all 14 cruises. They belong to the phyla Cnidaria (1 sp.), Annelida (1 sp.), Arthropoda (3 spp.), Mollusca (1 sp.), Bryozoa (2 spp.), Echinodermata (5 spp.) and Chordata (6 spp.).

The eight species with the highest MSPI (mean species presence index, see Table 2) are marked with bold lines. As a descriptive measure of variability (with no implication that the variation is random), we give the standard deviation.

Warm water species

Cruises since 2002 revealed the occurrences of some species with more southern/oceanic distribution patterns, but uncommon in the Dogger Bank area. These include (with the year of first appearance in our records), *Necora puber* (2002), *Luidia sarsi* and *Mullus surmuletus* (2003), *Trisopterus minutus* and *Zeus faber* (2004), *Atelecyclus rotundatus* (2006) and *Luidia ciliaris* (2008).

The species *N. puber* appeared only sporadic (2002, 2004, 2006) and in low abundances at the western part of the research area. One specimen of the echinoderm *L. sarsi* was found in 1993 at station 8. Then, the species disappeared until 2003, when 191 specimens were recorded, with a highest abundance on stations 17 and 18. Except in 2005, this species was found consistently, but on varying stations, more in the west than in the east of the Dogger Bank. The species *M. surmuletus* (red mullet) appeared only once at station 36; one specimen of *T. minutus* was detected at station 40, while *Z. faber* was also recorded with just one individual at station 36. The decapod *A. rotundatus* first appeared at the west of the Dogger Bank in 2006 (station 7), where it was detected again in 2008. In this year, it was also sampled at station 30 in the east. The starfish *L. ciliaris* appeared with two individuals at the western part of the research area at stations 9 and 11 in 2008.

Species richness

Figure 2 shows the total number of species per cruise (absolute species number). Additionally, the number of species per cruise divided by the number of stations sampled per cruise (smoothed species index) is shown. This

Table 2 Qualitative summary of (epi) benthic species found on the Dogger Bank with presence indices (number of stations where the species was recorded divided by the number of stations sampled during the respective cruise) for the sampling years 1991–2008

Phylum	Genus/Species	1991	1992	1993	1994	1995	1996	1997	1999	2001	2002	2003	2004	2006	2008	MSPI	SD
Po	*Halichondria panicea* (Pallas, 1766)		0.03				0.03		0.05	0.05		0.08		0.11	0.05	0.029	0.03
Po	*Suberites ficus* (Johnston, 1842)											0.03				0.002	0
Po	*Suberites virgultosus (*Johnston, 1842)					0.03			0.03							0.004	0
Po	*Sycon ciliatum* (Fabricius, 1780)								0.03							0.002	0
Cn	*Abietinaria abietina* (Linnaeus, 1758)			0.04	0.11	0.05	0.03	0.03	0.05	0.24		0.08				0.045	0.07
Cn	*Alcyonium digitatum Linnaeus, 1758*	*0.08*	*0.11*	*0.25*	*0.11*	*0.16*	*0.11*	*0.11*	*0.16*	*0.43*	*0.14*	*0.35*	*0.32*	*0.14*	*0.11*	*0.184*	*0.10*
Cn	*Bougainvillia muscus* (Van Beneden, 1844)			0.04												0.003	0
Cn	*Calliactis parasitica* (Couch, 1838)									0.08						0.006	0
Cn	*Calycella syringa* (Linnaeus, 1758)				0.05			0.05								0.008	0
Cn	*Clytia hemisphaerica* (Linnaeus, 1767)			0.13	0.05	0.11		0.03	0.03	0.08	0.03	0.05	0.03			0.038	0.04
Cn	*Diphasia attenuata* (Hincks, 1866)									0.03						0.002	0
Cn	*Epizoanthus incrustatus* (Düben & Koren)	0.03	0.03	0.04	0.03			0.03	0.05		0.03	0.03			0.03	0.020	0.01
Cn	*Eudendrium capillare* Alder, 1856			0.04												0.003	0
Cn	*Eudendrium rameum* (Pallas, 1766)				0.08	0.03			0.03				0.03			0.012	0.02
Cn	*Filellum serpens* (Hassall, 1848)			0.04		0.03										0.005	0.00
Cn	*Halecium beanii* (Johnston, 1838)			0.04	0.03	0.03	0.03	0.05	0.05		0.03	0.05	0.03			0.024	0.01
Cn	*Halecium halecium* (Linnaeus, 1758)			0.08	0.19	0.03	0.03	0.03	0.08			0.03				0.033	0.05
Cn	*Hydractinia carnea* M. Sars, 1846				0.03											0.002	0
Cn	*Hydractinia echinata* Fleming, 1823											0.11				0.008	0
Cn	*Hydrallmania falcata* (Linnaeus, 1758)			0.08	0.11	0.14	0.05	0.03	0.05	0.16	0.14	0.05	0.03			0.060	0.05
Cn	*Kirchenpaueria pinnata* (Linnaeus, 1758)							0.03		0.03						0.004	0
Cn	*Laomedea flexuosa* Alder, 1857				0.16	0.16			0.03	0.05			0.03			0.031	0.06
Cn	*Nemertesia antennina* (Linnaeus, 1758)			0.08	0.08			0.05	0.03			0.08				0.023	0.02
Cn	*Obelia geniculata* (Linnaeus, 1758)			0.04	0.16					0.03			0.03			0.018	0.06
Cn	*Obelia longissima* (Pallas, 1766)					0.03			0.27		0.08					0.027	0.10
Cn	*Parerythropodium coralloides* (Pallas, 1766)														0.03	0.002	0
Cn	*Podocoryna borealis* (Mayer, 1900)			0.04												0.003	0
Cn	*Sertularella polyzonias* (Linnaeus, 1758)				0.03	0.03		0.05		0.08		0.03				0.015	0.02
Cn	*Sertularia cupressina* Liinaeus, 1758			0.13	0.38	0.16	0.03	0.30	0.11	0.35	0.14	0.16	0.05		0.05	0.132	0.12
Ne	*Tubulanus superbus* (Kölliker, 1845)		0.03													0.002	0
An	*Aphrodita aculeata Linnaeus, 1758*	*0.30*	*0.24*	*0.04*	*0.19*	*0.19*	*0.57*	*0.35*	*0.16*	*0.27*	*0.11*	*0.16*	*0.08*	*0.11*	*0.03*	*0.200*	*0.14*
An	*Branchiomma bombyx* (Dalyell, 1853)												0.03			0.002	0
An	*Eunoe nodosa* (M. Sars, 1861)				0.03											0.002	0
An	*Gattyana cirrhosa* (Pallas, 1766)				0.03			0.03								0.004	0
An	*Glycera gigantea* Quatrefages, 1866											0.03				0.002	0

Table 2 continued

Phylum	Genus/Species	1991	1992	1993	1994	1995	1996	1997	1999	2001	2002	2003	2004	2006	2008	MSPI	SD
An	*Glycera lapidum* Quatrefages, 1865										0.03					0.002	0
An	*Neanthes fucata* (Savigny, 1818)		0.08			0.05		0.05	0.03			0.08	0.11			0.029	0.03
An	*Owenia fusiformis* Delle Chiaje, 1842					0.03						0.03				0.004	0
An	*Pectinaria (Lagis) koreni* (Malmgren, 1866)				0.05											0.004	0
An	*Pomatoceros triqueter* (Linnaeus, 1758)											0.05			0.03	0.006	0.01
An	*Terebellides stroemii* M.Sars, 1835											0.03				0.002	0
Ar	*Anapagurus laevis* (Bell, 1845)										0.03	0.05				0.006	0.01
Ar	*Atelecyclus rotundatus* (Olivi, 1792)													0.03	0.05	0.006	0.01
Ar	*Balanus crenatus* Bruguiére, 1789													0.05		0.004	0
Ar	*Cancer pagurus Linnaeus, 1758*	*0.16*	*0.08*	*0.13*	*0.11*	*0.05*	*0.11*	*0.11*	*0.19*	*0.14*	*0.11*	*0.08*	*0.22*	*0.14*	*0.14*	*0.125*	*0.04*
Ar	*Corystes cassivelaunus* (Pennant, 1777)	0.78		0.29	0.62	0.57	0.78	0.62	0.89	0.84	0.30	0.86	0.78	0.59	0.78	0.623	0.19
Ar	*Crangon allmanni* Kinahan, 1857						0.03	0.03								0.004	0
Ar	*Ebalia cranchii* Leach, 1817				0.22	0.03	0.19	0.05	0.14			0.19	0.03			0.060	0.08
Ar	*Ebalia tumefacta* (Montagu, 1808)				0.43	0.16	0.22	0.24	0.22	0.03		0.38	0.03	0.03		0.124	0.14
Ar	*Galathea intermedia* Lilljeborg, 1851											0.03				0.002	0
Ar	*Hyas coarctatus* Leach, 1815	0.03	0.08	0.04	0.11	0.03	0.05	0.11	0.11	0.03	0.03		0.03	0.03	0.03	0.049	0.03
Ar	*Inachus dorsettensis* (Pennant, 1777)				0.03							0.03				0.004	0
Ar	*Inachus phalangium* (Fabricius, 1775)								0.03			0.03	0.03			0.006	0
Ar	*Liocarcinus depurator* (Linnaeus, 1758)								0.03		0.03	0.08	0.11	0.19	0.27	0.050	0.09
Ar	***Liocarcinus holsatus (Fabricius, 1798)***	***1.00***	***0.92***	***0.92***	***1.00***	***1.00***	***1.00***	***0.97***	***1.00***	***0.95***	***0.86***	***1.00***	***0.97***	***0.97***	***0.95***	***0.965***	***0.04***
Ar	*Liocarcinus marmoreus* (Leach, 1814)	0.03		0.04	0.03				0.14	0.03	0.05	0.11	0.03	0.03		0.034	0.04
Ar	*Liocarcinus pusillus* (Leach, 1815)	0.08		0.13	0.05	0.05			0.11			0.30	0.05			0.055	0.08
Ar	*Macropodia rostrata* Linnaeus, 1761	0.03		0.13	0.19	0.03	0.11	0.11	0.14	0.08		0.41	0.16	0.08	0.11	0.111	0.10
Ar	*Necora puber* (Linnaeus, 1767)										0.03		0.03	0.03		0.006	0
Ar	***Pagurus bernhardus (Linnaeus, 1758)***	***0.97***	***0.97***	***1.00***	***1.00***	***0.97***	***0.97***	***0.95***	***1.00***	***1.00***	***0.97***	***1.00***	***1.00***	***1.00***	***1.00***	***0.986***	***0.02***
Ar	*Pagurus cuanensis* Bell, 1845										0.03	0.05			0.03	0.008	0.01
Ar	*Pandalina brevirostris* (Rathke, 1843)											0.03				0.002	0
Ar	*Pandalus montagui* Leach. 1815											0.03	0.03	0.03		0.006	0
Ar	*Philocheras bispinosus* (Hailstone, 1835)				0.03											0.002	0
Ar	*Philocheras trispinosus* (Hailstone, 1835)				0.14		0.03	0.14				0.05	0.03			0.027	0.05
Ar	*Pilumnus hirtellus* (Linnaeus, 1761)													0.03		0.002	0
Ar	*Pinnotheres pisum* (Linnaeus, 1767)							0.03						0.05		0.006	0.01
Ar	*Pisidia longicornis* (Linnaeus, 1767)							0.03	0.05							0.006	0.01
Ar	*Processa modica modica* Will.& Roch., 1979				0.05	0.05	0.03	0.03	0.03							0.014	0.01
Ar	*Semibalanus balanoides* (Linnaeus, 1758)													0.03		0.002	0

Table 2 continued

Phylum	Genus/Species	1991	1992	1993	1994	1995	1996	1997	1999	2001	2002	2003	2004	2006	2008	MSPI	SD
Ar	*Upogebia deltaura* (Leach, 1815)											0.03				0.002	0
Mo	*Acanthocardia echinata* (Linnaeus, 1758)						0.03			0.05					0.03	0.008	0.01
Mo	*Acanthodoris pilosa* (Abildgaard in Müller, 1789)		0.03													0.002	0
Mo	*Acteon tornatilis* (Linnaeus, 1758)				0.03											0.002	0
Mo	*Aequipecten opercularis* (Linnaeus, 1758)	0.14	0.24	0.17	0.16	0.22	0.11	0.03	0.11	0.30			0.35		0.14	0.139	0.09
Mo	*Alloteuthis media* (Linnaeus, 1758)		0.03													0.002	0
Mo	*Alloteuthis subulata* (Lamarck, 1798)		0.05	0.08		0.08				0.11					0.03	0.025	0.03
Mo	*Aporrhais pespelecani* (Linnaeus, 1758)	0.08			0.16	0.05	0.03		0.11	0.03			0.08	0.05	0.22	0.058	0.06
Mo	*Arctica islandica* (Linnaeus, 1767)	0.05	0.03		0.03			0.03								0.010	0.01
Mo	*Astarte montagui* (Dillwyn, 1817)				0.03											0.002	0
Mo	*Barnea candida* (Linnaeus, 1758)									0.03						0.002	0
Mo	*Buccinum undatum Linnaeus, 1758*	*0.46*	*0.24*	*0.42*	*0.35*	*0.16*	*0.22*	*0.16*	*0.46*	*0.49*	*0.38*	*0.51*	*0.11*	*0.32*	*0.27*	*0.325*	*0.13*
Mo	*Chamelea striatula* (da Costa, 1778)				0.03		0.03								0.03	0.006	0
Mo	*Colus gracilis* (da Costa, 1778)	0.14	0.03		0.03	0.03				0.03						0.017	0.04
Mo	*Donax vittatus* (da Costa, 1778)	0.14	0.05	0.04	0.14	0.03		0.05	0.03	0.03				0.03		0.038	0.04
Mo	*Dosinia exoleta* (Linnaeus, 1758)		0.03													0.002	0
Mo	*Eledone moschata* (Lamarck, 1798)			0.04												0.003	0
Mo	*Ensis arcuatus* (Jeffreys, 1865)	0.03													0.05	0.006	0.01
Mo	*Ensis ensis* (Linnaeus, 1758)	0.08	0.05		0.14	0.03		0.14	0.05	0.03			0.05		0.03	0.042	0.04
Mo	*Ensis siliqua* (Linnaeus, 1758)	0.05	0.22	0.04	0.08	0.03	0.03	0.03	0.05	0.03				0.03	0.03	0.044	0.05
Mo	*Euspira catena* (da Costa, 1778)	0.49	0.41	0.29	0.84	0.68	0.54	0.78	0.54	0.78	0.05		0.62		0.43	0.461	0.22
Mo	*Euspira montagui* (Forbes, 1838)		0.11													0.008	0
Mo	*Euspira pulchella* (Risso, 1826)									0.03						0.002	0
Mo	*Gari fervensis* (Gmelin, 1791)	0.08			0.38	0.03	0.03	0.08	0.05	0.08		0.03	0.08	0.14	0.08	0.075	0.09
Mo	*Gari tellinella* (Lamarck, 1818)								0.03							0.002	0
Mo	*Gibbula tumida* (Montagu, 1803)	0.03			0.03	0.03	0.03									0.008	0
Mo	*Hiatella arctica* (Linné, 1758)	0.03				0.03										0.004	0
Mo	*Laevicardium crassum* (Gmelin, 1791)			0.04					0.03							0.005	0.00
Mo	*Lutraria lutraria* (Linnaeus, 1758)						0.03									0.002	0
Mo	*Mactra stultorum* (Linnaeus, 1758)	0.43	0.32	0.13	0.30	0.30	0.08	0.11	0.11	0.05			0.16	0.14	0.11	0.160	0.11
Mo	*Modiolarca subpicta* (Cantraine, 1835)													0.05		0.004	0
Mo	*Mytilus edulis* Linnaeus, 1758							0.03							0.03	0.004	0
Mo	*Neptunea antiqua* (Linnaeus, 1758)	0.16	0.05	0.04	0.05	0.03	0.05	0.03	0.03	0.03		0.05				0.038	0.04
Mo	*Pecten maximus* (Linnaeus, 1758)	0.03	0.03													0.004	0
Mo	*Scaphander lignarius* (Linnaeus, 1758)				0.03		0.03									0.004	0

Table 2 continued

Phylum	Genus/Species	1991	1992	1993	1994	1995	1996	1997	1999	2001	2002	2003	2004	2006	2008	MSPI	SD
Mo	*Sepiola atlantica* d'Orbigny, 1839			0.04												0.003	0
Mo	*Sepiola aurantiaca* Jatta, 1896		0.03													0.002	0
Mo	*Spisula elliptica* (Brown, 1827)														0.03	0.002	0
Mo	*Spisula solida* (Linne, 1758)				0.03											0.002	0
Mo	*Spisula subtruncata* (da Costa, 1778)			0.04	0.03		0.03									0.007	0.00
Mo	*Zirfaea crispata* (Linnaeus, 1767)														0.05	0.004	0
Br	*Alcyonidium diaphanum (Hudson, 1778)*	*0.46*	*0.57*	*0.38*	*0.30*	*0.27*	*0.08*	*0.03*	*0.22*	*0.19*	*0.38*	*0.51*	*0.32*	*0.05*	*0.65*	*0.314*	*0.18*
Br	*Bugula angustiloba* (Lamarck, 1816)													0.08		0.006	0
Br	*Electra pilosa* (Linnaeus, 1767)	0.03	0.03											0.16	0.41	0.044	0.16
Br	*Flustra foliacea (Linnaeus, 1758)*	*0.41*	*0.03*	*0.17*	*0.05*	*0.08*	*0.08*	*0.11*	*0.11*	*0.24*	*0.03*	*0.03*	*0.32*	*0.30*	*0.43*	*0.170*	*0.14*
Br	*Membranipora membranacea* (Linnaeus, 1767)														0.03	0.002	0
Br	*Securiflustra securifrons* (Pallas, 1766)		0.03													0.002	0
Ec	*Acrocnida brachiata* (Montagu, 1804)					0.03		0.03				0.03				0.006	0
Ec	***Asterias rubens Linnaeus, 1758***	***1.00***	***0.97***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***0.92***	***1.00***	***1.00***	***1.00***	***1.00***	***0.992***	***0.02***
Ec	***Astropecten irregularis (Pennant, 1777)***	***0.81***	***0.84***	***0.83***	***0.95***	***0.95***	***0.97***	***0.95***	***1.00***	***1.00***	***0.92***	***1.00***	***1.00***	***0.97***	***0.97***	***0.940***	***0.06***
Ec	*Echinocardium cordatum (Pennant, 1777)*	*0.32*	*0.11*	*0.08*	*0.35*	*0.14*	*0.11*	*0.14*	*0.24*	*0.32*	*0.24*	*0.14*	*0.14*	*0.59*	*0.54*	*0.247*	*0.15*
Ec	*Echinus esculentus* Linnaeus, 1758		0.03													0.002	0
Ec	*Leptasterias muelleri* (M. Sars, 1846)							0.08								0.006	0
Ec	*Luidia ciliaris* (Philippi, 1837)														0.03	0.002	0
Ec	*Luidia sarsi* (Düben & Koren in Düben, 1845)											0.16	0.22	0.16	0.19	0.052	0.02
Ec	*Ophiocten sericeum* (Forbes, 1852)	0.03														0.002	0
Ec	*Ophiothrix fragilis (Abildgaard in O.F. Müler, 1789)*	*0.03*	*0.11*	*0.08*	*0.08*	*0.14*	*0.19*	*0.14*	*0.22*	*0.14*	*0.08*	*0.38*	*0.19*	*0.27*	*0.08*	*0.151*	*0.09*
Ec	*Ophiura albida* Forbes, 1839	0.73	0.19		0.62	0.54	0.62	0.62	0.68	0.86	0.41	0.78	0.22	0.51	0.14	0.494	0.22
Ec	*Ophiura ophiura (Linnaeus, 1758)*	*0.76*	*0.30*	*0.33*	*0.76*	*0.76*	*0.51*	*0.84*	*0.97*	*0.81*	*0.22*	*0.76*	*0.30*	*0.54*	*0.65*	*0.607*	*0.23*
Ec	*Ophiura sarsii* Lütken, 1855	0.03	0.03													0.004	0
Ec	***Psammechinus miliaris (P.L.S. Müller, 1771)***	***0.95***	***0.81***	***0.96***	***0.95***	***0.95***	***0.92***	***0.86***	***0.92***	***0.92***	***0.54***	***1.00***	***0.73***	***0.84***	***0.41***	***0.839***	***0.17***
Ch	*Agonus cataphractus (Linnaeus, 1758)*	*0.24*	*0.11*	*0.17*	*0.14*	*0.16*	*0.05*	*0.14*	*0.05*	*0.19*	*0.03*	*0.19*	*0.14*	*0.19*	*0.05*	*0.132*	*0.06*
Ch	*Ammodytes marinus* Raitt, 1934	0.22	0.03	0.21	0.05		0.27	0.03								0.057	0.10
Ch	*Ammodytes tobianus* Linnaeus, 1758					0.08				0.03					0.03	0.010	0.02
Ch	*Aplidium elegans* (Giard, 1872)									0.03		0.03				0.004	0
Ch	***Arnoglossus laterna (Walbaum, 1792)***	***0.89***	***0.86***	***1.00***	***0.97***	***0.95***	***0.86***	***0.86***	***0.97***	***0.97***	***1.00***	***1.00***	***0.97***	***1.00***	***1.00***	***0.952***	***0.05***
Ch	*Ascidiella scabra* (Müller, 1776)			0.75	0.54	0.57	0.08	0.22	0.11	0.59	0.35	0.54	0.22	0.27	0.30	0.324	0.20
Ch	*Botryllus schlosseri* (Pallas, 1766)							0.08		0.08	0.03	0.03		0.08		0.021	0.02
Ch	***Buglossidium luteum (Risso,1810)***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.000***	***0***
Ch	*Callionymus lyra Linnaeus, 1758*	*0.76*	*0.27*	*0.13*	*0.32*	*0.46*	*0.59*	*0.32*	*0.78*	*0.68*	*0.38*	*0.68*	*0.68*	*0.54*	*0.32*	*0.493*	*0.20*

Table 2 continued

Phylum	Genus/Species	1991	1992	1993	1994	1995	1996	1997	1999	2001	2002	2003	2004	2006	2008	MSPI	SD
Ch	*Callionymus maculatus* Rafinesque, 1810	0.22	0.11	0.04		0.03			0.08	0.08		0.03	0.35	0.14		0.076	0.10
Ch	*Callionymus reticulatus* Valenciennes, 1837			0.13	0.03	0.03	0.08									0.019	0.04
Ch	*Chelidonichthys lucerna* (Linnaeus, 1758)	0.03	0.27	0.17	0.22	0.35			0.11	0.03						0.083	0.11
Ch	*Clupea harengus* Linnaeus, 1758			0.04			0.03									0.005	0.00
Ch	*Cyclopterus lumpus* Linnaeus, 1758												0.03			0.002	0
Ch	*Diplecogaster bimaculata* (Bonnaterre, 1788)	0.03		0.04												0.005	0.00
Ch	*Echiichthys vipera (Cuvier, 1829)*	*0.65*	*0.51*	*0.79*	*0.70*	*0.73*	*0.70*	*0.73*	*0.81*	*0.68*	*0.70*	*0.68*	*0.73*	*0.73*	*0.41*	*0.682*	*0.10*
Ch	*Enchelyopus cimbrius* (Linnaeus. 1766)				0.03											0.002	0
Ch	*Entelurus aequoreus* (Linnaeus, 1758)	0.03	0.03			0.05							0.03	0.19		0.023	0.06
Ch	*Eutrigla gurnardus (Linnaeus, 1758)*	*0.38*	*0.14*	*0.17*	*0.16*	*0.22*	*0.65*	*0.32*	*0.54*	*0.54*	*0.41*	*0.43*	*0.41*	*0.08*	*0.19*	*0.330*	*0.17*
Ch	*Gadus morhua* Linnaeus, 1758			0.04	0.03		0.22	0.08								0.026	0.08
Ch	*Gymnammodytes semisquamatus* (Jourdain, 1879)	0.03		0.04	0.03	0.03					0.08				0.03	0.016	0.02
Ch	*Hippoglossoides platessoides* (Fabricius, 1780)									0.03						0.002	0
Ch	*Hyperoplus lanceolatus* (Le Sauvage, 1824)	0.03		0.04	0.05	0.11	0.03		0.05	0.14		0.08	0.03		0.03	0.042	0.04
Ch	***Limanda limanda (Linnaeus, 1758)***	***1.00***	***0.95***	***0.96***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***1.00***	***0.95***	***0.989***	***0.02***
Ch	*Liparis liparis* (Linnaeus, 1766)			0.04												0.003	0
Ch	*Lophius piscatorius* Linnaeus, 1758					0.05						0.03			0.03	0.008	0.01
Ch	*Melanogrammus aeglefinus* (Linnaeus, 1758)						0.03			0.03						0.004	0
Ch	*Merlangius merlangus* (Linnaeus, 1758)	0.24	0.49	0.33	0.14	0.35	0.43	0.30	0.19	0.16	0.03	0.03	0.11		0.11	0.207	0.14
Ch	*Merluccius merluccius* (Linnaeus, 1758)								0.03							0.002	0
Ch	*Microstomus kitt* (Walbaum, 1792)			0.04	0.05	0.08	0.05	0.19	0.16	0.19	0.27	0.43	0.41	0.38	0.73	0.213	0.20
Ch	*Molgula occulta* Kupffer, 1875				0.27							0.14				0.029	0.07
Ch	*Mullus surmuletus* Linnaeus, 1758											0.03				0.03	0
Ch	*Myoxocephalus scorpius* (Linnaeus, 1758)						0.03					0.03		0.08		0.010	0.02
Ch	*Pleuronectes platessa* Linnaeus, 1758	0.11	0.11		0.11	0.11	0.14	0.14	0.16	0.24	0.32	0.57	0.41	0.38	0.68	0.247	0.18
Ch	*Pomatoschistus lozanoi* (de Buen, 1923)	0.54	0.03													0.041	0.26
Ch	*Pomatoschistus microps* (Krøyer, 1838)		0.03		0.03								0.03			0.006	0
Ch	*Pomatoschistus minutus* (Pallas,1770)	0.41	0.27	0.38	0.76	0.70	0.86							0.11		0.249	0.26
Ch	*Pomatoschistus pictus* (Malm, 1865)			0.04												0.003	0
Ch	*Raja clavata* Linnaeus, 1758	0.08	0.03													0.008	0.03
Ch	*Scomber scombrus* Linnaeus, 1758					0.03										0.002	0
Ch	*Solea solea* (Linnaeus, 1758)	0.08	0.08	0.08	0.08		0.03		0.03		0.03	0.05		0.08		0.039	0.02
Ch	*Sprattus sprattus* (Linnaeus, 1758)		0.03													0.002	0
Ch	*Syngnathus acus* Linnaeus, 1758	0.03														0.002	0
Ch	*Syngnathus rostellatus* Nilsson, 1855	0.14	0.03	0.04	0.14	0.19							0.24	0.05		0.059	0.08

Table 2 continued

Phylum	Genus/Species		1991	1992	1993	1994	1995	1996	1997	1999	2001	2002	2003	2004	2006	2008	MSPI	SD
Ch	*Trisopterus minutus* (Linnaeus, 1758)													0.03			0.002	0
Ch	*Zeus faber* Linnaeus, 1758													0.03			0.002	0
	Taxa found per Cruise		61	60	68	84	72	62	64	68	64	44	71	62	55	59	64	8.80
	Stations per cruise		37	37	24	37	37	37	37	37	37	37	37	37	37	37		

Phylum abbreviations (column 1): *Po*, porifera, *Cn* cnidaria, *Ne* nemertini, *An* annelida, *Ar* arthropoda, *Mo* mollusca, *Br* bryozoa, *Ec* echinodermata, *Ch* chordata. *MSPI* mean species presence indices, with standard deviation (*SD*). The 21 species recorded on all cruises are lined with italics. The 8 species with the highest mean species presence index are enclosed by bold italics

buffers variations in species numbers caused by differences in the number of stations sampled per cruise (relevant for the years 1993 and 2005). Although both curves have a slightly negative slope, only the smoothed species index shows a significant decrease ($P = 0.04$) over the sampling period in a linear regression.

Species discovery curve

The species discovery curve (Fig. 3) was fitted to the cumulative number of species encountered in the study area since the first survey in 1991, representing the sampling effort in time. It is related to, but not identical with, a classical species–area curve.

Discussion

Species composition and associated dynamics

The species with the highest mean species presence index (MSPI) at the Dogger Bank was the Yellow Sole *Buglossidium luteum*, which appeared on all stations and cruises. The species reached the highest abundance in nearly all catches, hence supporting its MSPI ranking. *Buglossidium luteum* is reported to be common on sandy grounds, in shallow areas inshore and offshore (Hayward and Ryland 1998), feeding on a wide range of benthic organisms, mainly crustaceans (copepods, amphipods, cumaceans), bivalves and polychaetes. The Dogger Bank therefore appears to provide ideal conditions of life.

The second-highest MSPI is that of *Asterias rubens*, the most abundant echinoderm on the Dogger Bank during the sampling period. Like *B. luteum* and *Limanda limanda*, it was detected on almost all stations on all cruises.

The animal with the third-highest MSPI is the Dab *Limanda limanda*, also being a typical representative of the Dogger Bank fauna, as adults live mainly on sandy bottoms, from a depth of a few metres to about 100 m. The species feeds predominantly on crustaceans and small fish (Murua and Saborido-Rey 2003). It is characteristic of and widespread throughout the Dogger Bank, but much less abundant compared with *B. luteum*. At the beginning of the study, many dab specimens showed dermal abscesses, maybe caused by ectoparasitic copepods (Newell et al. 1979) or water pollution (Lang et al. 2003; Dethlefsen et al. 2001), but in recent times, the abscess rate has dropped to nearly zero.

The species ranking fourth in MSPI is the common hermit crab *Pagurus bernhardus*. It was found on almost all stations of all cruises, often in high abundance. It mainly feeds as scavenger (Ramsay et al. 1997), but also on small organisms (Orton 1927), taking advantage of the discards of commercial fisheries (Ramsay et al. 1997).

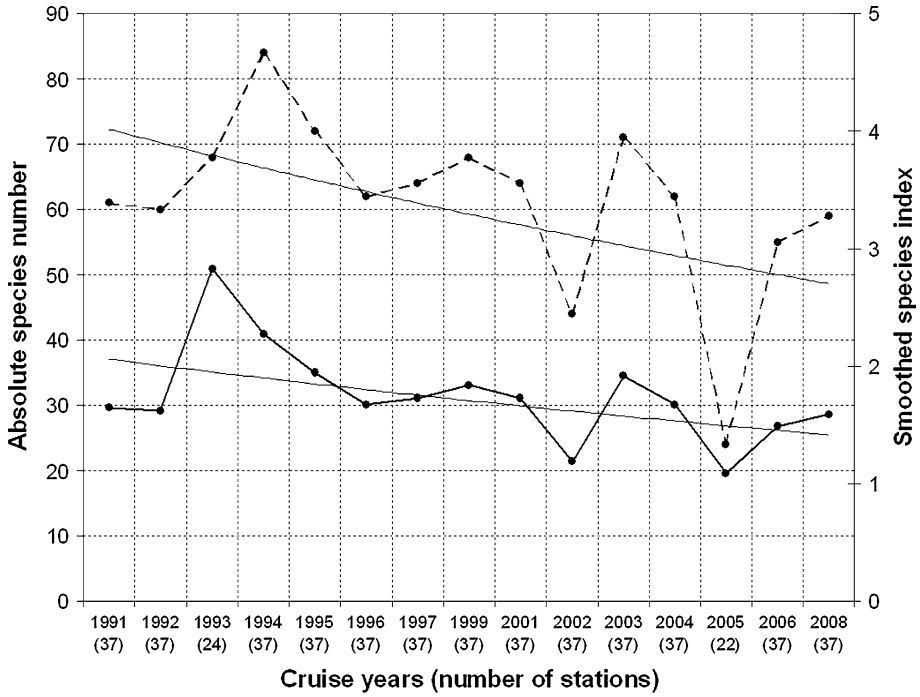

Fig. 2 Species richness. The upper curve (*broken line*) shows the total number of species determined per cruise (*left y-axis*). The lower, *solid line* (*smoothed species curve*) was constructed by dividing the total number of species by the number of stations sampled per cruise and is non-dimensional by itself (*right y-axis*). The two *thin lines* are the exponential curve fits

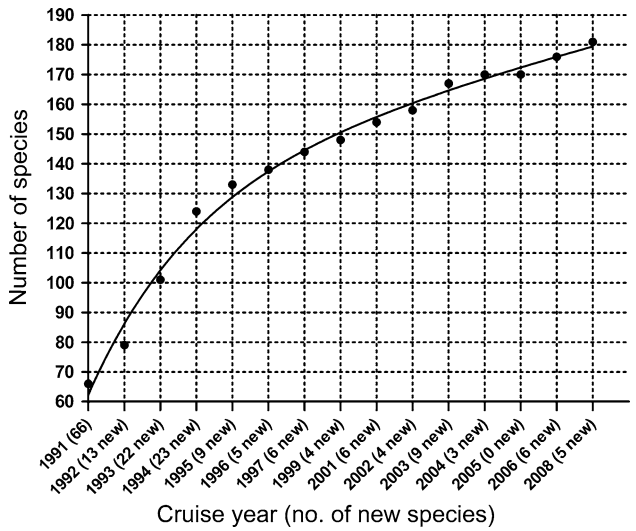

Fig. 3 Species discovery curve. The *y*-value for 1991 represents the number of species detected during this first cruise. The values for the subsequent cruise years were calculated as the number for the previous cruise year *plus* the number of species newly detected on the respective cruise

The fifth-ranking species in MSPI is the swimming crab *Liocarcinus holsatus*, which occurred on almost all stations on all cruises. It mainly appeared subtidally down to 50 m (personal observations), but is also reported to occur occasionally in depths of more than 200 m (d'Udekem d'Acoz 1999). This omnivorous crab was often found in high abundance throughout the Dogger Bank.

The scaldfish *Arnoglossus laterna* is ranked sixth in MSPI. It also appeared on nearly all stations on all cruises. Out of all fish species in the catches, it generally showed the highest abundance next to *B. luteum*. The habitat conditions do not seem to be optimal for this flatfish, which lives on mixed or muddy bottoms and feeds on small fish and invertebrates (Nielsen 1986).

The species with MSPI rank seven is the starfish *Astropecten irregularis*. In terms of echinoderm abundance, it takes rank two after *Asterias rubens*. Its occurrence frequency was relatively constant over time. It was found on slightly fewer stations in the beginning of the research period in 1991. This species prefers sandy bottoms, where it tends to bury (Mortensen 1927).

The sea urchin *Psammechinus miliaris* was found consistently on almost all stations until the year 2001. From 2001 to 2002, its SPI dropped from 0.92 to 0.54. This decrease coincided with a general decrease in species richness (Fig. 2) for unknown reasons. Then, the overall SPI rose again to a maximum of 1.0 (2003), again followed by a decrease to 0.4 in 2008. A population shift may be in progress, but further information could only be provided by integrating data on occurrences and abundances of this species. Generally, *P. miliaris* occurs in a diverse range of habitats, frequently at high densities, particularly in shallow and littoral locations, but mass occurrences are often limited to unique microbiotopes (alike assemblages of *Ophiothrix fragilis* on the sponge *Halichondria panicea*). Its omnivorous behaviour is well documented (Otero-Villanueva et al. 2004). The grazing activity of *P. miliaris* is likely to have a profound impact on the biodiversity and distribution of subtidal and intertidal encrusting invertebrates, but little is known on the extent to

which *P. miliaris* regulates these community structures. The species occurs mainly in the southern and eastern part of the North Sea, including the Dogger Bank, the German and Danish Wadden Sea and the southern German Bight. Its main bathymetric distribution ranges from the littoral to approximately 100 m, and it is relatively tolerant of low temperatures (Kelly and Cook 2001).

The species mentioned above are the most common and, as confirmed by our ongoing investigations, are also the most abundant component of the epifauna of the Dogger Bank. Our long-term studies show that the species with a MSPI between 0.8 and 0.15 are part of the common Dogger Bank fauna, but are generally not dominant. The animals with an MSPI around or lower than 0.12 are detected less frequently, but they represent the majority of the species list. Furthermore, a small number of secondary species (e.g. *Raja clavata*) is often limited to a distinct area of the Dogger Bank, some of them only appearing in deeper waters (at or slightly below 30 m), in the eastern part of the sand bank. Others such as *Microstomus kitt* occur predominantly in shallow, gravelly areas in the western part of the bank. The majority of the secondary species of the Dogger Bank cannot be correlated with a distinct area.

Warm water species

The appearance of temperate oceanic species new to the Dogger Bank is in line with the recorded increase in North Sea surface temperatures (Loewe et al. 2006). This is further supported by the fact that in some temperate species that have always been present, the regular appearance in recent catches has significantly increased, e. g. *Echiichthys vipera* (Türkay and Kröncke 2004).

The velvet swimming crab *N. puber* is known from the south-west coast of Norway, the western coast of Great Britain, as well as from the Dutch and German coastal areas (Christiansen 1969; Clark 1986). A detailed distribution map of *Necora puber* from Belgium and the Netherlands is available in Adema (1991).

No other observations of *Necora puber* from the central North Sea and the Dogger Bank can be found in the published literature.

Nevertheless, the predominantly sandy bottom of the Dogger Bank may explain why *L. sarsi* has not achieved a higher spatial coverage or abundance in the research area. The species has been reported from "all round the British Isles, but rare in the English Channel and southern North Sea" (Southward and Campbell 2006), on muddy sand grounds. Frauenheim et al. (1989) compared summer and winter catches, detecting *L. sarsi* only in summer. Reiss et al. (2010), defined the species as characteristic of the northern North Sea. It was also detected in the IBTS cruises in 1999 (Zühlke et al. 2001). The species seems to be less abundant in the southern North Sea, and there have been no reports from the Dogger Bank so far.

The red mullet *Mullus surmuletus* and the poor cod *Trisopterus minutus* were classified as "southern" species by Corten (1996). Additionally, *M. surmuletus* was reported occasionally before 1995 and more regularly thereafter from the IBTS Fishing Area 4B (central North Sea) by Beare et al. (2004). According to this study, also *T. minutus* was found at low abundance, but more regularly than *M. surmuletus,* on the IBTS surveys before 1995, and then showed a remarkable increase in abundance in the late 1990s.

Regarding *Zeus faber*, one specimen has already been detected on the Dogger Bank on a cruise in 1996 at 55°18′N 3°12′E (information from the homepage of the Zoologisk Museum København 2010). The detection of *Z. faber* coincides with its increase in abundance in the southern North Sea in the late 20th and early twenty-first century, detected in the IBTS database, reported by Beare et al. (2004).

Concerning *Atelecyclus rotundatus*, these are the first published records for the Dogger Bank. The species is reported from the southern coast of Norway and the west coast of Great Britain (Christiansen 1969). Clark (1986) describes the species' distribution over the northern part of the North Sea, following the course of the Gulf Stream and parts of the south-western North Sea adjacent to the English Channel, while the central North Sea with the Dogger Bank area remains blank. Adema (1991) reviewed the state of knowledge about the distribution of *A. rotundatus*. Some records in the IBTS (International Bottom Trawl Survey) database of ICES (International Council for the Exploration of the Sea) are reported by Zühlke et al. (2001) without giving the exact sampling location. Records from the Dutch coast since 2005 are summarized in Vanhaelen (2009). Additional information on the distribution of *A. rotundatus* and *N. puber* is available in d'Udekem d'Acoz (1999).

The starfish *Luidia ciliaris* was not known to occur in this area of the North Sea. Sparse information is available on its distribution. An occurrence map is available at the online-portal MarLIN (Avant 2008), showing the species' distribution along the west coast of Great Britain, all around the Irish coast and around the coasts of the Shetlands and Orkneys. This is supported by Southward and Campbell (2006) who also mentioned the species to occur "close to the northeast coast of the British Isles as far south as Yorkshire". In Hayward and Ryland (1998), the species is described as "common on all British coasts except southern North Sea".

Species richness

In 1993, an unusually high number of taxa was detected in comparison with the relatively small number of sampled

stations (Fig. 2). The highest absolute number of taxa was recorded in 1994. In 2002 and 2005, the relatively low absolute taxon numbers are also reflected in the smoothed species curve, which seeks to compensate for variable sample numbers (as in 2005).

The fitted curves show a general decrease in species numbers during our investigation period. After an initial rise in the taxon numbers from 1991 to 1994, a noticeable decrease in the absolute number of identified taxa per cruise occurred from 1995 to 1996, down to a level comparable to the ones of 1991 and 1992. A slight increase in 1997 and 1999 was followed by a slight decrease in 2001 and then a larger one due to the absence of 20 species from 2001 to 2002. In 2003, the species numbers rose again to 71, reaching the highest level since 1996, re-entering a downward trend in 2004. The large reduction in species number in 2005 needs to be treated with some caution, even though supported by the smoothed species curve. Due to bad weather conditions, only 22 stations could be sampled. In 2006 and 2008, the species number increased again, but not to the levels previously encountered.

Species occurrence and sampling efficiency

In all years, except 2005, some new taxa (i.e.taxa recorded for the first time during our Dogger Bank investigation such as *Anapagurus laevis* and *Pagurus cuanensis* in 2002) were detected (Fig. 3). The species discovery curve indicates a rapid increase in newly discovered taxa in the first four cruises until 1994. Then, in 1995, this rate dropped by approximately 50% and halved again in 1996, indicating that the sampling technique needs to be repeated over at least five annual cruises to get an acceptable overview on the taxon number within the research area.

From 1996 to 2002, the discovery rate remained relatively constant between four and six new records per cruise. In 2003, the rate of new taxa doubled again in comparison with the rate of 2002. When compared with the species richness curve in Fig. 2, the total taxon number was also comparatively high. In 2004, only three additional taxa were detected; the cause for this decrease remains unclear. In 2005, the detection rate dropped to zero. This may be due to the sampling of only 22 stations caused by bad weather conditions. The rates of 2006 and 2008 are again comparable with the ones of 1996 to 2001.

The species discovery curve (Fig. 3) indicates that approximately three subsequent cruises using a comparable monitoring technique and research area/station grid seem to be necessary to record more than 50% of the estimated entire epibenthic bottom fauna. The species discovery curve, however, does not reveal whether newly detected species were already present in the area before but merely remained undetected or whether they are recent invaders. It was anticipated that the curve shows an asymptotic curve fit, reaching a plateau phase in the last segment, but that is not exactly the case. The species discovery curve does not level out in spite of the high number of samples, which means that there is still an evident increase in species numbers. This is in accordance with the results of Neumann et al. (2008), who stated that even after 60–67 replicates, the accumulation curves did not reach a plateau phase. In spite of slight differences in the sampling methods and area of individual samples, our curve shows basically the same characteristic. Due to the twofold longer period of our sampling, we are not sure whether the whole dataset can be treated as taken from the same unit. The species richness curve (Fig. 2) shows through the decrease in total species numbers that the species composition in the individual years was not constant, which is further supported by the increase in more oceanic warm water elements during recent years. This suggests that the open end of the species discovery curve might be due to changes in the local species composition in the context of environmental changes, rather than to a random addition of species.

Acknowledgments We thank the Biodiversity and Climate Research Centre (BiK-F) in Frankfurt am Main, Germany for funding our work and data analysis. We also thank the crew (the old sea dogs as well as the newcomers) of the Research Vessel Senckenberg, who always gave their best for our cruises to succeed. Several colleagues of the Senckenberg Research Institute in Frankfurt am Main helped us in the identification of material of a number of animal groups: Dr. D. Fiege with the identification of annelids, Dr. J. Scholtz with the Bryozoa, Dr. D. Janussen with the Porifera and Dr. R. Janssen with some difficult groups of Mollusca. We gratefully acknowledge their input. Dr. A. Wehrmann from the Senckenberg branch at Wilhelmshaven undertook sediment grain size analyses for us. We are grateful to him for allowing us to use these valuable data.

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