



A century of North Sea epibenthos and trawling: comparison between 1902–1912, 1982–1985 and 2000

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ABSTRACT: The effects of towed fishing gear on benthic fauna are under intense scrutiny and evidence is growing that trawling may significantly affect benthic communities in the North Sea. Most studies explore the current fauna or compare today's situation with that of 2 or 3 decades ago, when North Sea-wide information on benthos and fishing became available. However, in the North Sea, extensive mechanised trawling began more than a century ago. This study compared historical and recent records in order to explore potential long-term links between changes in the epibenthos and fishing. Based on reconstructed species lists from museum specimens, we compared epibenthos data from 1902 to 1912 with those from 1982 to 1985 and 2000. We analysed changes in average taxonomic distinctness (AvTD), a biodiversity indicator, and changes in biogeographical species distributions. Landings data were collated for round- and flatfish caught in the northern, central and southern North Sea from 1906 to 2000 as proxies for total otter and beam trawl effort, respectively. These indicate that the southern and much of the central North Sea were fished intensively throughout the 20th century, whilst the northern North Sea was less exploited, especially in earlier decades; exploitation intensified markedly from the 1960s onwards. For epibenthos, the mean AvTD decreased significantly from the 1980s to 2000, when it was below expected values in 4 ICES rectangles, 3 of these located in heavily trawled areas. Biogeographical changes from the beginning to the end of the century occurred in 27 of 48 taxa. In 14 taxa, spatial presence was reduced by 50 % or more, most notably in the southern and central North Sea; often these were long-lived, slow-growing species with vulnerable shells or tests. By contrast, 12 taxa doubled their spatial presence throughout the North Sea. Most biogeographical changes had happened by the 1980s. Given that other important environmental changes, including eutrophication and climate change, have gained importance mainly from the 1980s onwards, we have concluded that the changes in epibenthos observed since the beginning of the 20th century have resulted primarily from intensified fisheries.

KEY WORDS: North Sea · Epibenthos · Historic data · Fishing impact · Taxonomic distinctness · Biogeography

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INTRODUCTION

Since the beginning of the 20th century, the benthic fauna of the North Sea has been subjected to a range of anthropogenic impacts, including fisheries, eutrophication, climate change, and oil and gas extraction (Daan et al. 1996). Among the most conspicuous changes is the dramatic increase in levels of demersal

trawling. Until the late 19th century, there had only been wooden sailing trawlers, operating a single small beam trawl relatively close to shore. From the 1890s onwards, a large fleet of steam-powered otter trawlers developed in Britain, and other European nations were soon to follow. From the 1900s until the 1960s, many hundreds of steam otter trawlers, gradually increasing in vessel size and capacity, roamed the entire North

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Sea (Engelhard 2005). Thereafter they were replaced by more advanced, more powerful, and increasingly sophisticated diesel trawlers. The 1960s also saw the introduction of modern heavy twin-beam trawling, and the use of these powerful vessels has increased steadily since then, especially in the southern and central North Sea (Jennings et al. 1999b).

Thus, it is reasonable to hypothesise that a century of trawling has had significant impacts on the benthic fauna, given the susceptibility of epibenthic species to trawled gear and short-term, localised effects of trawling disturbance on benthic communities (Bergman & Hup 1992, Lindeboom & de Groot 1998, Hiddink et al. 2006).

But to what extent has the North Sea benthos changed over the course of a century? Estimating long-term, large-scale changes of the faunal communities requires knowledge of the undisturbed situation as a reference point. However, it seems impossible to reconstruct a picture of the 'pristine' North Sea ecosystem; historical data are sparse, and at the time the value of faunal records for the years and decades to come was not anticipated.

For some parts of the North Sea, historical infauna data are available and Frid et al. (2000) compared grab samples taken in 5 ICES rectangles before 1925 and after 1978. They found changes in the benthic community composition in 3 of the rectangles, concurrent with the mechanization of the fishing fleet. Quantitative benthos data for the entire North Sea were not recorded before the late 1970s; systematic benthos surveys were carried out from 1982 to 1987 and in 1996, 1999 and 2000 (Dyer et al. 1983, Frauenheim et al. 1989, Dann & Harding 1992, Künitzer et al. 1992, Jennings et al. 1999a, Zühlke et al. 2001, Callaway et al. 2002). However, Stein et al. (1990) reconstructed epibenthos records from historical specimens at the Zoological Museum in Kiel, Germany, which had been collected over the years 1902 to 1912 at a wide range of locations throughout the North Sea. To our knowledge this is the earliest large-scale record of the North Sea epibenthos. Although hampered by a lack of detailed information about sampling methods, these data may be crucial in providing a picture of the state of the benthic fauna only a decade or so after the onset of steam-trawling in the North Sea.

This paper has the following objectives: (1) to compare the North Sea epibenthos from 1902 to 1912, 1982 to 1985, and 2000, accounting as best as possible for inconsistencies in survey methods; (2) to provide baseline information on historical levels of demersal fishing during and comparisons between these 3 widely different periods of time; (3) to view any changes in epibenthos between the start and end of the 20th century in the light of fisheries and other possible factors, including climate change and eutrophication.

MATERIALS AND METHODS

Levels of fishing. Comparing long-term changes in fishing effort with changes in the benthos requires long-term and spatially detailed data on total international trawling effort in the North Sea. Unfortunately, no such data exist. In most countries, systematic collection of effort data started only a few decades ago, although some early data are available (e.g. for England). Furthermore, countries may use different units for quantifying effort, such as number of hours fished, number of arrivals or days absent from port. Within countries, effort units may vary by period. Apart from the availability of data, using long-term trends in fishing effort as a measure of disturbance on the sea floor affecting epibenthos is problematic due to technological creep: 1 h fishing for a 1920s sailing trawler is incomparable with the same unit for a modern diesel trawler.

Given the complications with data on effort per se, this paper uses, as a proxy for total international bottom fishing effort in the North Sea, the total international landings by fishing region (northern, central and southern) for the 3 main roundfish and 4 flatfish species as listed in official fisheries statistics. Caution is required when interpreting landings data as an indicator for bottom fishing effort, as landings vary with effort as well as with stock size. Combining a range of species partly accounts for this, but not if species vary in synchrony, such as was the case for several roundfish species during the 1960s 'gadoid outburst' (Hislop 1996). However, while stock fluctuations may go up and down, resulting in noise when interpreting long-term landings data for effort, fishing efficiency will generally only improve over time. The latter would result in bias if, for example, hours fished were used. Roundfish species include cod *Gadus morhua*, haddock *Melanogrammus aeglefinus* and whiting *Merlangius merlangus*, and flatfish include plaice *Pleuronectes platessa*, sole *Solea solea*, turbot *Scophthalmus maximus* and brill *Scophthalmus rhombus*. Taken together, these 7 species comprise about 80 to 84% of the total groundfish landings. The combined catch-per-unit effort for these species is about evenly distributed over the North Sea, although flatfish tend to be more abundant in the southern and roundfish in the northern North Sea. Time-series covering most of the century were compiled for the total roundfish and flatfish landings. They were analysed separately for the ICES (International Council for the Exploration of the Sea) divisions IVa, IVb, and IVc representing the northern, central and southern North Sea (Fig. 1). In order to account for differences in area between the ICES divisions, time-series are also provided for the landings per unit area ($t\ km^{-2}$). Combined, these

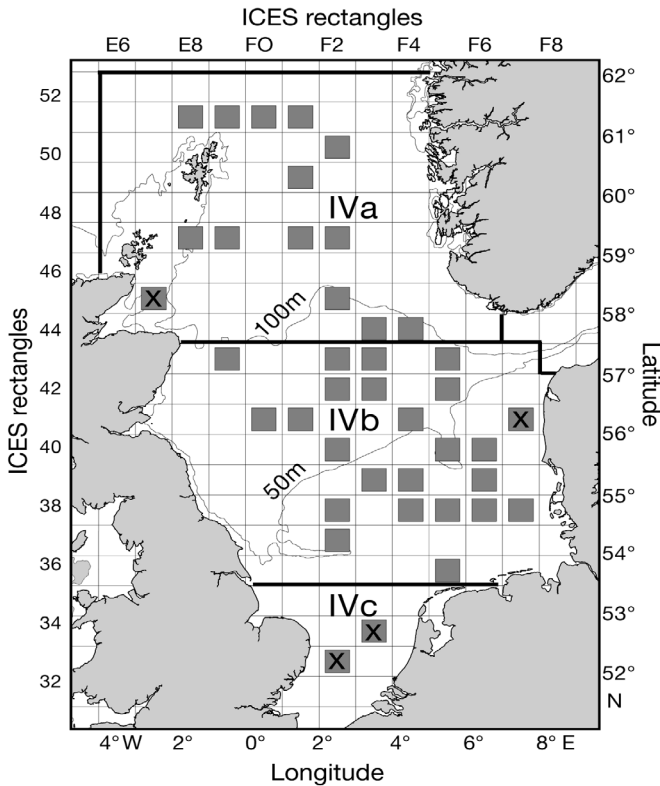


Fig. 1. ICES rectangles sampled in all 3 surveys (■). ICES sub-areas IVa, b and c indicated; X: ICES rectangles with low 'average taxonomic distinctness' in 2000 (see Fig. 7)

figures provide insight into long-term changes in the relative levels of fishing in the different parts of the North Sea.

Landings data by division were collated for the periods from 1906 to 1912 and from 1947 to 2000; for 1913 to 1946 only global data for the entire North Sea were available. These data were collated from the *Bulletin Statistique des Pêches Maritimes* and *ICES Fisheries Statistics* (ICES, Copenhagen), which include landings data for the entire North Sea from 1902 onwards and landings by division from 1947 onwards. For 1906 to 1912, landings data by division were compiled for Britain only, where at the time about 72 to 84% of the entire North Sea demersal catch was landed. English data were based on *Sea Fisheries Annual Reports for England and Wales* (Board of Agriculture and Fisheries, London), attributing landings to 19 areas that can be identified within

divisions IVa, IVb and IVc. Scottish data were from *Scottish Sea Fisheries Annual Reports* (Fishery Board for Scotland, Edinburgh), where North Sea landings into districts south of Aberdeen were attributed to division IVb, and landings into Aberdeen and further north were attributed to division IVa (cf. Graham 1934).

For other countries, if data were lacking for the earlier years for the division where landings were caught, some assumptions were made if it was considered realistic to do so (Table 1). For example, all North Sea landings into Belgium from 1906 to 1912 were assumed to have derived from the southern division IVc. These assumptions are likely to have only marginally influenced our results. Firstly, in most years the majority of demersal landings could be safely attributed to divisions based on existing data. Secondly, especially in the earlier years, most vessels would have operated relatively close to the port of landing, given that vessels had less motive power and limited capability to conserve the catch.

Epibenthos surveys. In order to assess long-term changes in the epibenthic fauna of the North Sea, 3 epibenthos surveys between 1902 and 2000 were compared. Here we define epibenthos as animals sampled by trawled sampling equipment such as dredges and beam trawls. Some of the recorded species live in the upper layers of the sea floor sediment or migrate

Table 1. Overview of years where landings data were only available for the global North Sea (ICES sub-area IV) but not for separate divisions (ICES divisions IVa, IVb and IVc: respectively, northern, central and southern North Sea); including the fraction of the global annual North Sea catch that these cases represented. Assumptions pertain to the division where these landings would have been caught

Country	Period	% of total landings	Assumption
Belgium	1906–1912	1	All caught in IVc
Denmark	1906–1912	3	All caught in IVb
	1961–1973	24	All caught in IVb, except haddock: half in IVa, half in IVb
France	1950–1951	8	All caught in IVc
	1964–1966	7	All caught in IVa
Germany	1906–1912	7	All caught in IVb
	1947–1960	4	All caught in IVb
Netherlands	1906–1912	8	Caught half in IVb, half in IVc
	1947–1957	11	Caught half in IVb, half in IVc
Norway	1906–1912	3	All caught in IVa
	1947–1950	2	All caught in IVa
	1954–1960	2	All caught in IVa
	1965–1972	1	All caught in IVa
Sweden	1947–1948	4	Not attributed to division
	1950–1957	3	Not attributed to division
	1962–1977	2	Not attributed to division
	1980–1993	<0.5	Not attributed to division
USSR	1955–1973	5	Not attributed to division

between the sediment and the surface and could strictly be classified as infauna. We included those species in this study if it could reasonably be assumed that they were sampled representatively.

Survey 1, 1902 to 1912: North Sea epibenthos data from 1902 to 1912 were available from preserved material at the Zoological Museum of Kiel and published after the reconstruction of sample protocols by Stein et al. (1990). The material was collected during surveys by the 'Deutsche wissenschaftliche Kommission für die internationale Meeresforschung' and the 'Biologische Anstalt Helgoland.' For details about the history of the surveys, preserved museum specimens, and construction of the database see Stein et al. (1990) and Rumohr & Kujawski (2000).

Faunal information of 261 samples from 182 stations was available from 51° N in the southern North Sea to 62° N north of the Shetland Islands. Cruises took place in February, May, August and November. No quantitative information (i.e. number of individuals per species per haul) was available for either sessile or free-living species.

Information about the sampling equipment and sample processing was limited, although state-of-the-art methods were used at the time. Various types of dredges and trawls were used, including Austern-dredge (oyster dredge), botanische Dredge (naturalists' dredge), grosse Dredge (large dredge), Kurre (trawl), grosse Kurre (large trawl), Granatkurre (shrimp trawl), Helgoländer Trawl, neues Helgoländer Trawl (the new Helgoland trawl), Agassiz Trawl, Petersen Trawl, 50-Fuß-Trawl (50-foot trawl), Scheerbrutnetz or Eiernetz. No information was available about the duration of trawls and net mesh sizes. This set of data is referred to as 'Survey 1'.

Survey 2, 1982 to 1985: During the English groundfish surveys from 1982 to 1985, epibenthos samples were taken with a 2 m beam trawl (1982) and a 1.5 m Agassiz trawl (1982 to 1985) (Dann & Harding 1992). Trawl duration varied between 5 and 22 min. Information about mesh sizes and sample treatment is not available. In total, 162 stations were sampled in the southern, central and northern North Sea. Quantitative data for free-living species are available for all stations, but not for the sessile fauna. This set of data is referred to as 'Survey 2'.

Survey 3, 2000: In the framework of a European Union project about biodiversity in the North Sea, 270 stations were sampled for epibenthos in 2000 during the English, German, Dutch, Norwegian and Danish groundfish surveys. A 2 m steel beam trawl (Jennings et al. 1999a) was towed for 5 min and the samples were washed through sieves with 5 mm mesh. Animals in the samples were identified to species level and counted. Quantitative data are available for all free-

living fauna and presence–absence data for sessile species. Further detail about the study is given in Callaway et al. (2002). These data are referred to as 'Survey 3'.

Collating data from the 3 surveys. It was uncertain whether the museum samples from 1902 to 1912 contained the complete suite of animals that at the time had been sampled by the gear. That is, the absence of a species in the museum samples may not necessarily mean that it was absent from the original sample, but may be the result of it not being retained in the museum's collections. Aggregating the material from 10 yr assured the most comprehensive species list, but it is still potentially incomplete. Hence, species absent from the period 1902 to 1912 but present from 1982 to 1985 and 2000 may or may not have colonised an area, which was considered in the data analyses. The taxonomic determinations for Survey 1 were made or confirmed by a contemporary specialist.

For Survey 2 there were suspicions that not all epibenthic species were caught with the Agassiz trawl or that some species had been misidentified. Several species were recorded regularly in Surveys 1 and 3, but never in Survey 2 (e.g. *Phaxas pellucidus*, *Amphiura* spp., *Pagurus pubescens*) despite other benthos studies in the 1980s reporting their presence (Künitzer et al. 1992, Rumohr & Kujawski 2000). Species potentially missed or misidentified during Survey 2 are marked in Table 2. The 2 m beam trawl used in Survey 3, although not necessarily sampling the complete suite of epibenthic species present at a station, is currently the most refined equipment for epibenthic surveys, and samples may be assumed to provide a reliable indicator of the community composition.

Most of the species recorded for the period from 1902 to 1912 belonged to the group of free-living epibenthos, while sessile groups such as bryozoans, hydrozoans and sponges were not recorded at all. It is very unlikely that these groups were absent in nature and so for comparability the databases of Surveys 2 and 3 were shortened to the spectrum of species in Survey 1, namely free-living epibenthos and some sessile species such as ascidians and sessile bivalves.

In order to allow spatial comparisons of species' presence, the sampling stations of each survey were grouped according to ICES rectangles of 0.5° latitude by 1° longitude. At North Sea latitudes these rectangles measure approximately 30 × 30 nautical miles. The 3 surveys had 40 ICES rectangles in common (Fig. 1), of which 14 were located in the northern North Sea in ICES sub-area IVa, 24 in area IVb and 2 in IVc. Sub-areas IVb and IVc were pooled to represent the southern-central North Sea. Most of the 40 common ICES rectangles were sampled once or twice in each survey. For rectangles sampled more

than twice, 2 randomly selected samples were entered into the analyses.

Analysis of benthos data. The different sampling methods of the 3 surveys precluded calculating most indices commonly used in benthic community analyses, such as species richness, Hill's indices or the Bray-Curtis coefficient. These indices are dependent on sampling effort and should only be applied to surveys with standardised sampling methods. Instead, biogeographical changes were analysed to ascertain changes in the distribution of individual species, and the taxonomic distinctness to assess an aspect of biodiversity.

Biogeography. Biogeographical changes were analysed based on the presence or absence of species in the 40 ICES rectangles sampled in each of the 3 surveys. The following categories were defined:

(1) Decreasing spatial presence: the number of rectangles where a species was recorded at least halved from Survey 1 to Survey 2 or 3. Only species recorded in at least 5 rectangles in Survey 1 were considered in order to reduce the risk of allocating a species to this category on the basis of individual accidental recordings.

(2) Increasing spatial presence: the number of rectangles where a species was recorded at least doubled from Survey 1 to Survey 2 or 3. Given some uncertainty about whether the absence of a species from a rectangle in Survey 1 was either real or due to loss of data over time (see above), it seemed prudent to only consider species with 100% or more increase in spatial presence. Even then, this category has to be regarded with caution.

(3) Unchanged spatial presence: the number of rectangles where a species was recorded changed by less than 20% from Survey 1 to Survey 3.

Taxonomic distinctness. In contrast to other diversity indices, the mean values of the average taxonomic distinctness (AvTD, denoted by Δ^+) and the variation in taxonomic distinctness (VarTD, denoted by Λ^+) are independent from sampling effort and sample size (Clarke & Warwick 1998, 2001). Both indices are calculated from information on presence or absence of taxa and are suitable for comparing surveys with different and uncontrolled degrees of sampling effort, assuming that the same faunal groups are compared and comparable taxonomic accuracy is applied (Clarke & Warwick 1998).

AvTD is the mean taxonomic path length through the taxonomic tree connecting every pair of species in a list, and is a measure of the average degree to which individuals in an assemblage are related to each other. VarTD is the variance of the pairwise path lengths between species, and reflects the evenness or unevenness of the taxonomic tree in a species list.

In this study, AvTD was significantly negatively correlated with VarTD ($r = -0.858$, $n = 117$). Therefore

VarTD did not yield additional independent information and further analyses were carried out for AvTD only. One of the 40 common ICES rectangles was excluded from this analysis because only a single species was recorded in Survey 2.

In order to test for the independence of AvTD from sampling effort, AvTD was correlated with species richness, an index dependent on sampling gear and effort. The indices were unrelated ($r = -0.037$, $n = 117$), which was taken as evidence that AvTD was an appropriate diversity index to calculate for this study with partly uncertain sampling effort.

A randomisation test was carried out to detect differences in the taxonomic distinctness for any observed set of species from the expected value derived from a master species list with all species of all 3 surveys (Clarke & Warwick 1998). From the master species list, expected AvTD values were calculated by randomly selecting subsets of the master list and a 95% probability funnel was constructed. We then compared AvTD values of the actual surveys with expected values and assessed whether observed values were outside the confidence borders of expected values. The test is not assumed to be as sensitive as tests using diversity measures calculated from abundance data obtained from a standardised sampling design. However, for the comparisons of studies with partly unknown sampling effort, there is little choice and only certain aspects of diversity such as taxonomic distinctness can validly be compared. The master species list for the 3 surveys consisted of 188 species (4 Polychaeta, 1 Octocorallia, 59 Crustacea, 78 Mollusca, 40 Echinodermata and 6 Ascidiacea).

Stepwise regression was applied in order to investigate a possible relationship between AvTD and environmental factors. ICES supplied data for bottom water temperature and salinity for the period from 1905 to 1912, which was used as an approximate match for Survey 1. For Survey 2 (1982 to 1985) and Survey 3 (2000), data provided by ICES covered only a small part of the North Sea and were considered insufficient for the analyses. However, ICES data for 1998 to 1999 were used in the analysis as a proxy for the year 2000. Mean summer (June to September) and winter (December to March) temperature and salinity were calculated per ICES rectangle. For the stepwise regression measures, the following factors were included in the analysis: mean annual temperature, mean summer temperature, mean winter temperature, the difference between summer and winter temperature, mean annual salinity, mean summer salinity, mean winter salinity, difference between summer and winter salinity, water depth, longitude and latitude. All factors were examined for normality and autocorrelation among variables.

RESULTS

Levels of fishing

Throughout the 20th century, high landings of demersal fish species were taken from the North Sea (Fig. 2). Already in 1906, roundfish and flatfish landings amounted to 250 000 and 50 000 t, respectively, remaining at these levels for a number of decades. Exceptions were significant reductions during both World Wars, when fishing effort was strongly reduced as a direct consequence of war.

Roundfish landings rose steeply after 1962, and in most years from the mid-1960s to mid-1980s they were about twice as high as in the first half of the century. Particularly high catches occurred in 1969 and 1970 coinciding with the 'gadoid outburst'. From the mid-1980s onwards, however, a decline to current low levels commenced.

Flatfish landings from 1945 to 1960 were considerably higher than before World War II (WWII). A second increase occurred during the 1960s, and flatfish landings from the 1960s to the 1980s were about 2 to 3 times higher compared to pre-war levels. They declined during the last decade of the century.

Landings differed between the northern, central and southern ICES divisions of the North Sea (respectively, IVa, IVb and IVc). From 1906 to 1912, roundfish landings per unit area (Fig. 3a) were similar in the northern and southern North Sea, but about twice as high in the central North Sea. From 1947 to 2000, roundfish landings per unit area showed long-term fluctuations but were generally similar in the 3 divisions, in spite of highest roundfish abundance in the northern and lowest in the southern North Sea.

The landings of flatfish per unit area were far higher in the southern and central North Sea than in the north (Fig. 3b), which is deeper and has lower flatfish abundance. In all 3 divisions, flatfish landings per unit area generally increased from 1906 to 1912 until about 1990. However, the land-

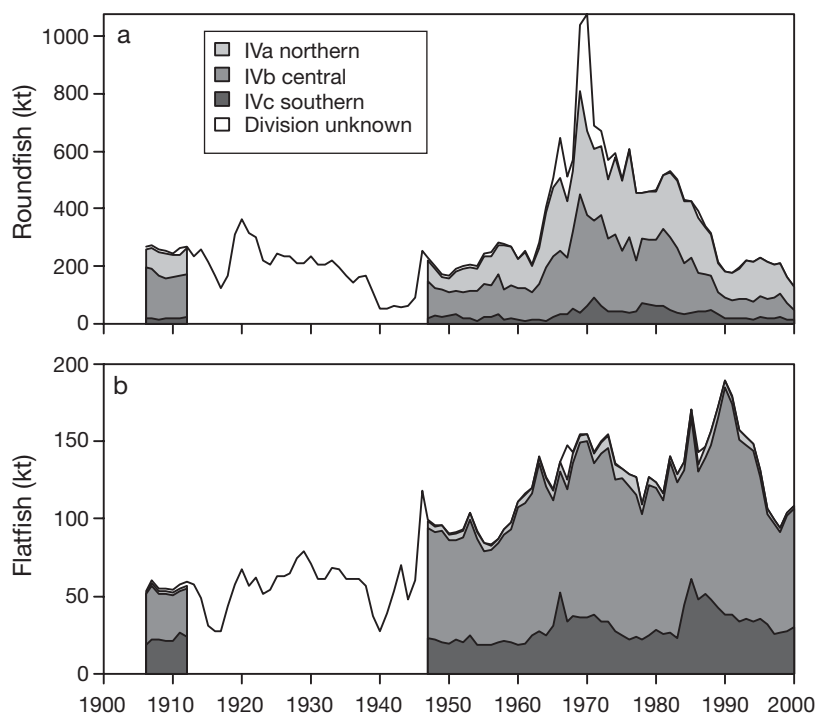


Fig. 2. Long-term changes in landings of (a) roundfish and (b) flatfish from the northern, central and southern North Sea throughout the 20th century

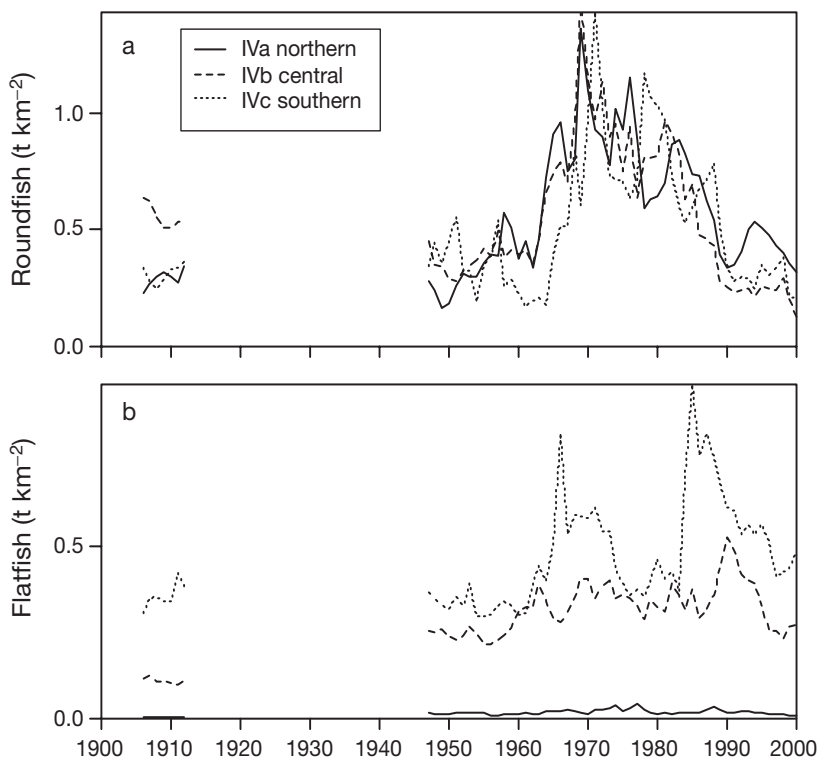


Fig. 3. Long-term changes in landings per area of (a) roundfish and (b) flatfish for the northern, central and southern North Sea throughout the 20th century (no data by ICES division for 1913 to 1946)

ings per unit area in the southern North Sea were already at high levels (approaching those of the 1990s) from 1906 to 1912, when those in the central North Sea were still comparatively low. In the central North Sea, flatfish landings per unit area tripled (and in some cases quadrupled) from the beginning of the century to the 1990s.

Spatial presence of epibenthos

In the 40 ICES rectangles sampled in all 3 surveys, 80 species were recorded in Survey 1, 66 in Survey 2 and 145 in Survey 3. Altogether, 48 species occurred in each survey in enough ICES rectangles, allowing meaningful analyses of their biogeography. From the beginning to the end of the 20th century, biogeographical changes were found for 27 epibenthic taxa (Figs. 4–6, Table 2).

It should be noted that the number of ICES rectangles in Table 2 and the number of marked positions in Figs. 4–6 do not tally since Table 2 only takes into account stations that were positioned in the 40 rectangles sampled during all 3 surveys (Fig. 1), while the maps (Figs. 4–6) show the original data of each survey in order to comprehensively visualize the available information.

Species with decreasing spatial presence

The presence of 14 species and one genus belonging to 6 classes and subclasses was reduced by 50% or more in Survey 2 or 3 compared with Survey 1 (Table 2, Fig. 4). Already by 1982 to 1985 (Survey 2) the presence of the bivalves *Arctica islandica* and *Aequipecten opercularis* and the echinoderms *Brissopsis lyrifera*, *Ophiothrix fragilis* and *Henricia sanguinolenta* was more than halved in comparison with the number of ICES rectangles in which they were sampled at the beginning of the century. Eight other species were absent in Survey 2 while present in Survey 1, but it is suspected that at least some of these species may have been overlooked during Survey 2 (Table 2). In 2000, *Modiolus modiolus* and *Spatangus purpureus* were found in even fewer rectangles than in 1982 to 1985, while the presence of *O. fragilis* more than doubled in this period of time (Table 2).

Decreases in spatial presence were more pronounced in the central and southern North Sea than in the north. In the northern North Sea the presence of 4 species decreased, while in the central and southern North Sea the presence of 17 taxa was reduced (Table 2).

The presence of *Arctica islandica*, *Aequipecten opercularis*, *Phaxas pellucidus* and *Leptasterias muel-*

leri remained unchanged in the north, while it was halved in the central and southern North Sea. For 2 taxa, *Ascidella* spp. and *Galathea* spp., the spatial presence was halved in the central and southern areas while it more than doubled in the north.

Species with increasing spatial presence

The spatial presence of 12 taxa belonging to 6 classes more than doubled from the beginning to the end of the last century (Table 2). Eight of the 12 taxa had increased their presence by the 1980s (e.g. *Aphrodita aculeata*, *Psammechinus miliaris*, *Echinocardium cordatum*, *Ophiura ophiura* and *Corystes cassivelaunus*) (3 are shown in Fig. 5). Only *A. aculeata* further doubled its presence between Surveys 2 and 3. The presence of the other species increased marginally or even decreased again, as for *Echinocardium cordatum* (Table 2).

Thirteen taxa increased in the north and 11 in the central and southern North Sea. *Psammechinus miliaris*, *Corystes cassivelaunus*, *Liocarcinus depurator* and *Aporrhais* spp. increased their presence in the central and southern areas but not in the north. The reverse, increased presence in the north but not in the central and southern areas, was found for *Ophiura albida*, *Neptunea antiqua*, *Pagurus bernhardus*, *Ascidella* spp. and *Galathea* spp.

Species with unchanged spatial presence

Across the North Sea, 7 taxa, 5 of them echinoderms, showed less than 20% change in spatial presence from the beginning to the end of the last century (Table 2). Widely distributed species such as *Asterias rubens* fell into this category (Fig. 6). These taxa stayed broadly within the same geographical borders from 1902 to 1912 up to 2000. More taxa remained unchanged in the north (10) than in the central and southern North Sea (6) (Table 2).

Taxonomic distinctness

Compared with the 95% confidence funnel, 4 ICES rectangles in survey 3 had significantly lower values for AvTD than theoretically expected (Fig. 7). Three of the ICES rectangles were located in the central and southern North Sea, one off the Scottish coast (Fig. 1). All values for Survey 1 and Survey 2 were within the expected range.

The mean AvTD did not change significantly from Survey 1 to Surveys 2 or 3, but in Survey 3 it was

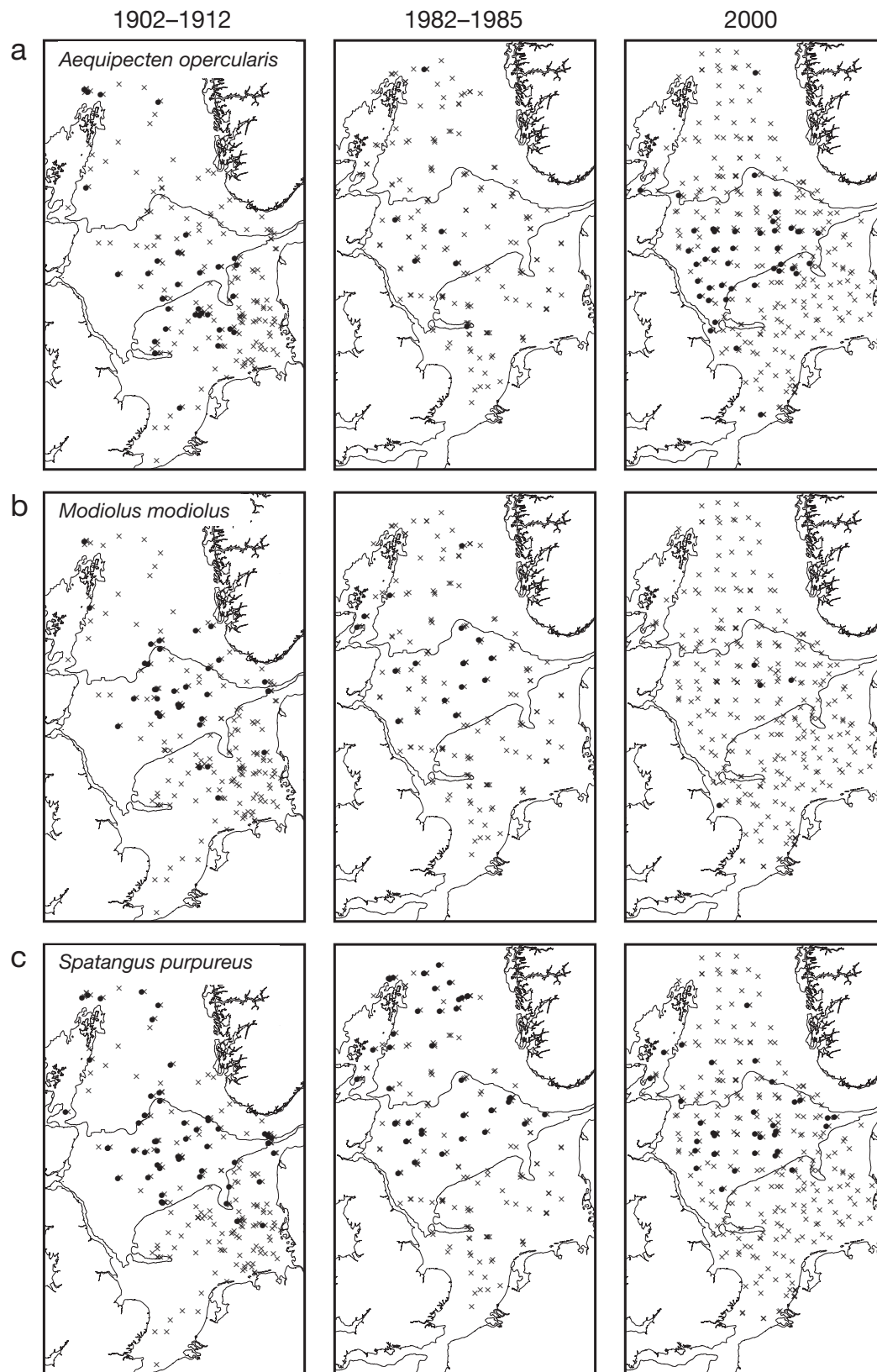


Fig. 4. (a) *Aequipecten opercularis*, (b) *Modiolus modiolus* and (c) *Spatangus purpureus*. Species with reduced spatial presence in 1982–1985 and 2000 compared to 1902–1912; species present (•), sampled station (x)

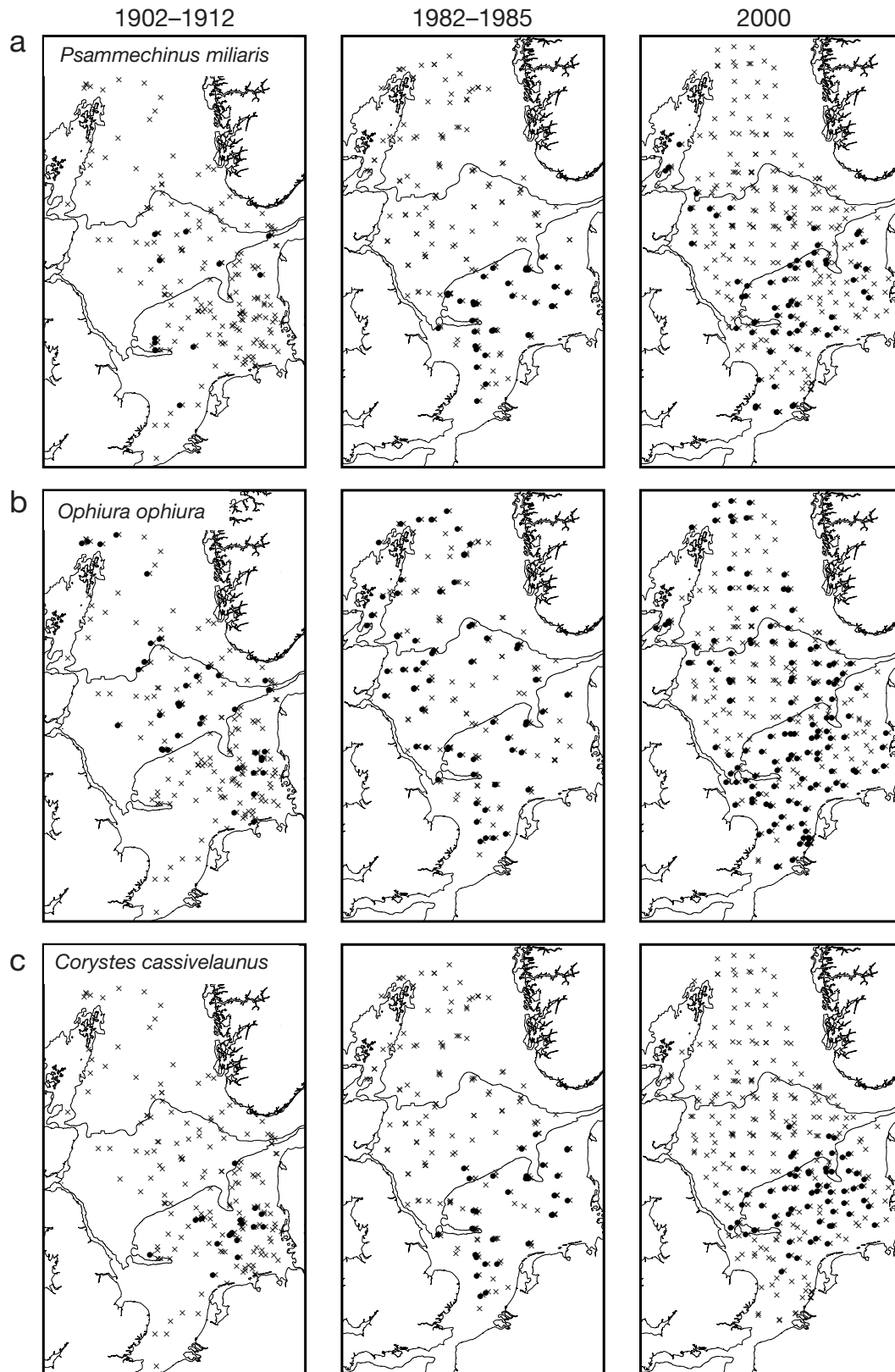


Fig. 5. (a) *Psammechinus miliaris*, (b) *Ophiura ophiura* and (c) *Corystes cassivelaunus*. Species with increased spatial presence in 1982–1985 and 2000 compared to 1902–1912; species present (•), sampled station (x)

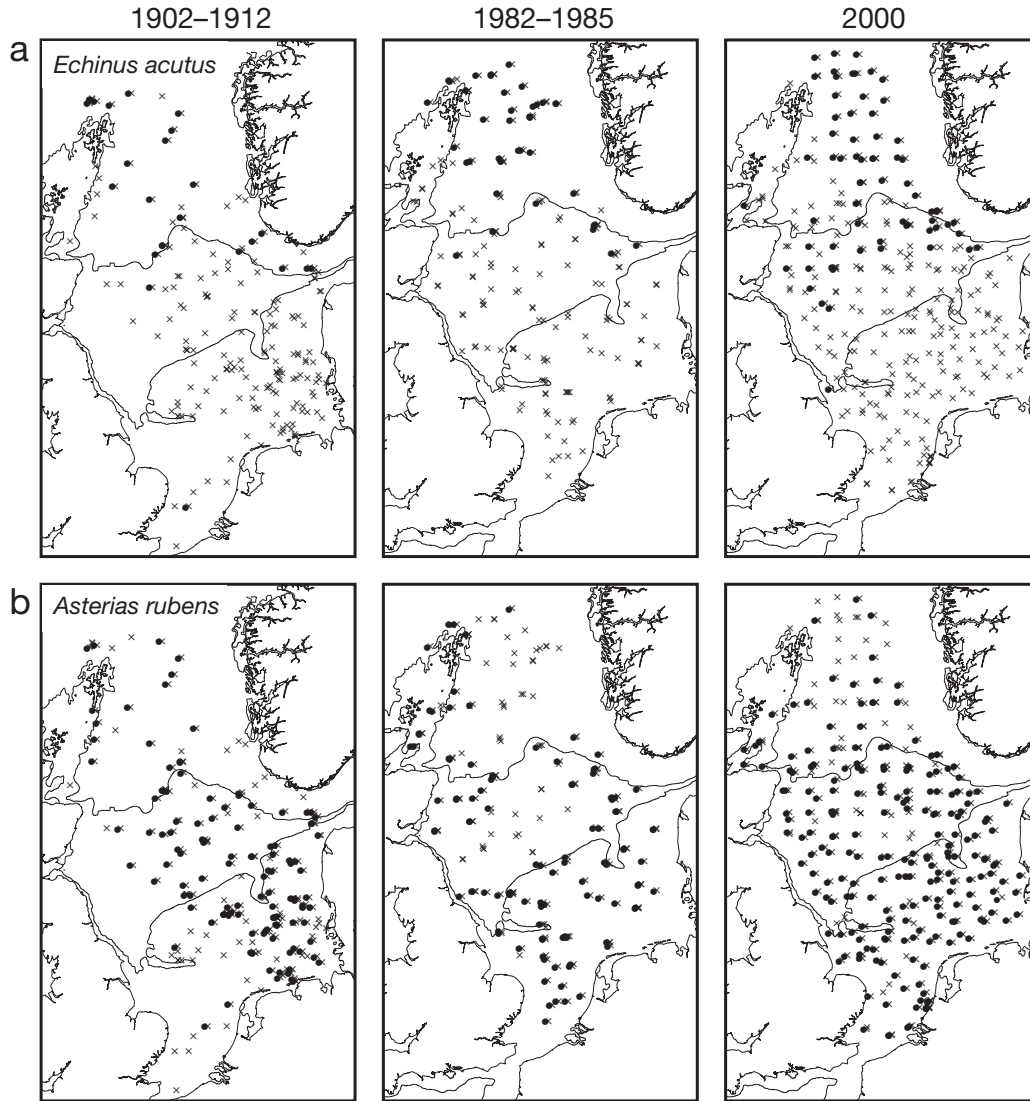


Fig. 6. (a) *Echinus acutus* and (b) *Asterias rubens*. Species with broadly unchanged spatial presence; species present (•), sampled station (x)

depth in Survey 1 (Table 4). In Survey 3, summer bottom water temperatures and longitude were the 2 significant factors explaining 38% of the variance in AvTD. Longitude and depth were significantly correlated in Survey 1 ($r = -0.635$, $p < 0.05$, $n = 22$) and summer temperature and longitude in Survey 3 ($r = 0.537$, $p < 0.05$, $n = 32$). Due to a lack of environmental information, these analyses could not be carried out for Survey 2.

Fig. 7. Average taxonomic distinctness (AvTD, Δ^+). Values are superimposed on 95% probability funnels for AvTD constructed from 1000 independent simulations for subsets of species drawn randomly from a master list of 188 species assembled from all 3 surveys. Labels of stations outside the probability funnel are ICES rectangles (see Fig. 1)

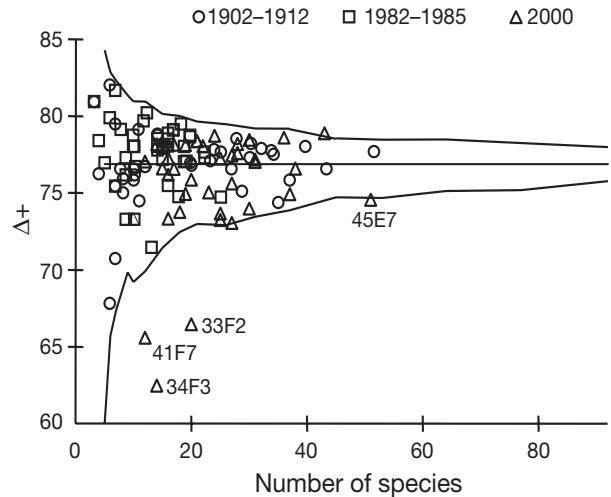


Table 3. Mean (\pm SD) average taxonomic distinctness (AvTD) in the northern (ICES sub-area IVa; $n = 14$) and central southern North Sea (IVb,c; $n = 25$). Survey 1: 1902–1912; Survey 2: 1982–1985; Survey 3: 2000

	Survey 1	Survey 2	Survey 3
IVa	76.9 \pm 3.2	77.3 \pm 2.4	75.8 \pm 1.7
IVb,c	77.1 \pm 2.1	77.9 \pm 1.9	75.6 \pm 4.4

DISCUSSION

The increasing impact of human beings on the marine environment is accompanied by increasing efforts to research the consequences. The assessment is difficult when the anthropogenic interference started more than a century ago, as it was the case for fishing in the North Sea. Information on the 'pristine' state of the environment is sparse. Within limits, historical data compared with contemporary records can provide insight into broad changes that have taken place (Kröncke 1995, Rijnsdorp et al. 1996, Frid et al. 2000). The fishing data collated in this study suffered mainly from inconsistencies in recording the information, while the quality of the benthos data was compromised by the diversity of sampling equipment. The different durations of the 3 benthos surveys (10, 3 and 1 yr) may also have affected the comparison; the 1 yr survey in 2000, although covering more stations than any of the other surveys, may be less representative for the end of the century than the accumulated 10 yr survey at the beginning of the century. However, studies from 1996 and 1999 confirm the epibenthos patterns found in 2000 (Jennings et al. 1999a, Zühlke et al. 2001). Despite these limitations in the quality of data, it was possible to establish general temporal trends for the development in fishing and for changes in the epibenthos, which provide arguments for a possible link between the two.

Demersal fishing

To our knowledge this is the first paper showing trends in total international landings of the main flatfish and roundfish species for the 3 ICES divisions of the North Sea separately and for the major part of the 20th century, with the exception of both World Wars and the intervening years, when only global data are available. Even though changes in landings only partly reflect changes in effort, these figures still provide useful information on long-term trends in the relative levels of demersal fishing in different areas of the North Sea.

Throughout the 20th century large quantities of roundfish (generally > 200 000 t) and flatfish (> 50 000 t) were taken annually from the North Sea. The only

Table 4. Stepwise multiple regression of environmental factors predicting average taxonomic distinctness (AvTD, Δ^*); only significant factors are shown. Beta: standardised regression coefficient, Sign.: significance

Survey	Variable	R ²	Beta	<i>t</i>	Sign. of <i>t</i>
1902–1912	Longitude	0.45	0.87	3.96	0.001
	Depth		0.61	2.79	0.012
2000	Summer temp.	0.38	-0.71	-4.08	0.000
	Longitude		0.53	3.05	0.005

notable reductions occurred during both World Wars, when fishing effort was temporarily much reduced (Borley 1923, Margetts & Holt 1948). The overall pattern, however, implies sustained high trawling activity in the North Sea since a century ago. Indeed, a rapid expansion of steam trawling had already taken place during the last 2 decades of the 19th century (Garstang 1900, Graham 1956, Engelhard 2005), and at the start of our time-series in 1906, the total number of steam trawlers at European North Sea ports was estimated as 1752 (Board of Agriculture and Fisheries 1908). In addition, several thousands of sailing trawlers completed the international trawling fleet. This does not lend credibility to the notion of a 'pristine' North Sea ecosystem at the onset of the 20th century.

Long-term trends in landings are due to variations in both fishing effort and fish abundance. Notably, the very high roundfish landings from the mid-1960s to mid-1980s are generally attributed not only to sustained high effort but particularly to the 'gadoid outburst'. In this period the North Sea cod, haddock and whiting stocks produced some of the largest year-classes on record (Hislop 1996). The peak in roundfish landings from 1969 to 1970 specifically relates to the extremely strong haddock year-class of 1967 (Holden 1978). High abundance levels also explain the high catches of flatfish and roundfish in the years immediately after both World Wars; these resulted from the temporary release of stocks from most fishing pressure during the war years (Borley 1923, Margetts & Holt 1948, Beverton & Holt 1957). The 1966 and 1985 peaks in flatfish landings in the southern North Sea can be related to strong year-classes of plaice (1963, 1981) and sole (1963) (Millner & Whiting 1996, Rijnsdorp & Millner 1996). However, disentangling effects of effort and stock abundance on landings goes beyond the scope of this paper; rather, we sought general patterns allowing comparisons between the 3 divisions of the North Sea.

Roundfish landings per unit area suggest that during the earlier years of the century, roundfish otter trawling was less intensive in the northern North Sea and more so in the central and southern divisions. This pattern is indicated by similar roundfish landings per unit area in

the southern and northern North Sea from 1906 to 1912, but about double those in the central division, in spite of typically far higher roundfish catch rates in the north (e.g. ICES Bulletin Statistiques). The generally deeper grounds of the northern North Sea were more difficult for the early steam trawlers to work compared to shallow grounds in the southern and central North Sea, and were further away from the main landing ports.

Vessel improvements and increased roundfish demand led to the expansion of otter trawling in the north, and as a consequence, roundfish landings per unit area increased (Jennings et al. 1999b, Robinson 2000). The results also suggest that in the southern North Sea, roundfish exploitation remained relatively intensive, although by the 1990s otter trawling in this region had become more reduced (Jennings et al. 1999b).

The central and southern North Sea appears also to have received by far the most effort in terms of trawling for flatfish, viz. beam trawl effort. In the southern North Sea, flatfish landings per unit area in 1906 to 1912 were already of a magnitude similar to that of the 1990s. Those in the central North Sea were lower in 1906 to 1912 but became 3 to 4 times higher in the second half of the century. Although the expanding modern twin-beam trawl fleet extended the fished area northward, the southern and south-central North Sea remained the main beam trawl area (Jennings et al. 1999b), receiving intensifying effort, especially from the 1960s onwards.

Epibenthos

The benthos data available for the years 1902 to 1912, reconstructed from museum specimens, dictated the data analyses. Community analysis was restricted to one aspect of biodiversity, the taxonomic distinctness. This index explores the variety of taxonomic groups in samples, is based on the presence and absence of species and is independent from sampling effort (Clarke & Warwick 1998, 2001). However, the descriptive analyses of the biogeography of individual species gave the clearest indication of changes in the epibenthic fauna during the last century.

Taxonomic distinctness

In 2000, 4 ICES rectangles showed AvTD levels significantly below expected values. Three of these 4 rectangles were located in the southern and eastern-central North Sea in areas heavily fished with beam trawls during recent decades (Jennings et al. 1999b) as well as at the beginning of the century (Masterman 1914). This suggests that there may be a link between

beam trawling and diminishing taxonomic diversity, but our data does not provide enough evidence to substantiate the hypothesis.

The spatial patterns of AvTD could only partly be explained by the available environmental parameters for any of the surveys. Variables associated with longitude seemed to play a role, such as summer bottom water temperature in 2000.

The mean AvTD was significantly lower in 2000 than in the 1980s, but not lower than at the beginning of 20th century. The result indicates a change in community characteristics in the last 2 decades of the century, while at the same time it signals long-term persistence in terms of epibenthic taxonomic diversity.

Generally the use of taxonomic distinctness indices for epibenthos studies in the North Sea seems limited and can only be one facet of a more complex analysis. This was also found for other historical comparisons and environmental impact studies for different taxonomic groups (Somerfield et al. 1997, Bates et al. 2005, Raut et al. 2005).

Biogeography

It appears that most of the changes in biogeography of individual species had happened by the 1980s and the presence of only a few species declined or increased in the study rectangles between 1982 to 1985 and 2000. Increases in spatial presence were recorded throughout the entire North Sea from the beginning to the end of the last century, while the central southern North Sea simultaneously saw some drastic declines of individual species, resulting in a northward shift of their southern distribution border. Four species declined in the north, while 17 species showed reductions in spatial presence in the central and southern North Sea. Increases, on the other hand, were about equal in both areas (11 in the central southern area, 13 in the north).

Epibenthos change in relation to demersal fishing

To what extent did fishing cause the changes in the spatial presence of epibenthic species? It is difficult to separate effects of fishing from other factors in the North Sea such as eutrophication or climate change; all impacts increased in the latter part of the century. However, evidence from this study suggests that fishing is the most probable cause for the changes in benthos because of (1) the nature of the species suffering from declining presence, (2) the area in which most reductions were recorded, (3) the timing of changes in the benthos.

Nature of species suffering from declining presence

The majority of species that demonstrated decreases in spatial presence are known from other, small-scale studies to be vulnerable to the impact of fishing gear. Generally trawling gear removes large-bodied fauna (e.g. *Modiolus modiolus*, *Aequipecten opercularis*), damages species with fragile shells (e.g. *Phaxas pellucidus*) and tests (e.g. the heart urchins *Echinocyamus pusillus*, *Spatangus purpureus* and *Brissopsis lyrifera*), and removes and injures long-living bivalves (e.g. *Arctica islandica*) (Kaiser et al. 2000). Heavy beams cause direct damage to the shells of bivalves and sweep them to the surface with tickler chains (Bergman & Hup 1992, Witbaard & Klein 1994). Furthermore, larger fauna often represent long-lived and slowly reproducing species that are more prone to decline if mortality is increased due to fishing, in this case *A. islandica*. (Witbaard & Klein 1994)

Small, robust species as the sea urchin *Psammechinus miliaris* appear to survive the impact of fishing gear better than their fragile heart urchin relatives. The brittle star *Ophiura ophiura* and the polynoid polychaete *Aphrodita aculeata* are also relatively unaffected by fishing (Bergman & Hup 1992). These species are among the group of taxa which can escape the direct impact of the trawling gear or have the capability to survive and regenerate damaged body parts (ophiurids, starfish, crabs) and are therefore promoted in fished areas (Kaiser et al. 2000). Their increased spatial presence observed in this study may also be related to the improved availability of resources by the reduced presence of competitors. However, the heart urchin *Echinocardium cordatum* and the masked crab *Corystes cassivelaunus* did not fit into this pattern. These species are vulnerable to the direct damage of fishing gear and show poor survival rates once discarded (Bergman & Hup 1992, Lindeboom & de Groot 1998), but the present study indicated that their presence increased dramatically from the beginning of the century to the 1980s. This result suggests that their reproductive turnover outweighs fishing-induced mortality rates. Rumohr & Kujawski (2000) have hypothesized previously that the scavenging feeding mode of *E. cordatum* helped them to thrive in a grossly fished area where dead and wounded benthic creatures are available as a food resource. However, since the 1980s it appears that its presence has decreased.

Generally sessile species such as hydrozoans, bryozoans and sponges are more vulnerable to the impact of fishing gear than free-living species (Jennings & Kaiser 1998, Watling & Norse 1998, Freese et al. 1999, Kaiser et al. 2000). Unfortunately, there was little infor-

mation on the presence of erect, sessile species, for example the horn wrack *Flustra foliacea* or dead man's finger *Alcyonium digitatum*. However, some of our results for free-living species indicate that there may have been more sessile species, particularly in the southern North Sea, at the beginning of the last century before the onset of intense trawling in fisheries. The presence of the porcelain crab *Pisidia longicornis*, which lives mainly among colonial, branching bryozoans, was much reduced in 2000, as was the presence of the velvet shell *Velutina velutina* associated with tunicates and that of the nudibranch *Tritonia hombergii* (5 records in Survey 1, 1 in Survey 3), which feeds exclusively on dead man's finger *A. digitatum*.

Area with the most reductions

Reduced spatial presence of benthic species was limited mainly to the central and southern North Sea, which coincides with the area of the most dramatic increases in flatfish fisheries since the end of WWII, and particularly since the 1960s, with the introduction of heavy twin-beam trawlers. Beam trawling played a much smaller role in the northern North Sea. This region was subjected to intensified otter trawling during the second half of the last century, which can also reduce the biomass of larger fauna, but is generally less destructive than twin-beam trawling (Prena et al. 1999).

Timing of changes in the benthos

Most of the changes in biogeography of epibenthos had already happened by the 1980s. Due to the discontinuous nature of the data it remains unknown whether the changes had occurred around this time or during earlier decades. By-catch records of fishing vessels suggest that changes in the invertebrate epifauna of the Dutch sector had already started as early as the 1950s (de Voys & van der Meer 1998). It is worth noting that high landings of roundfish and flatfish have been taken from the North Sea throughout the 20th century, apart from both World Wars, so it is reasonable to suggest that changes in biogeography of epibenthos may have taken place at a fairly early stage.

On a regional scale, eutrophication can be an important factor for shifts in the benthic community (Rosenberg et al. 1987, Kröncke 1990, Rachor 1990). From the 1950s to the 1980s a shift from long-lived to opportunistic, short-lived species on the Dogger Bank was considered to be related to eutrophication (Kröncke 1990). The timing overlaps with the increase in fishing

activity and both factors, eutrophication and fishing, could have had additive or synergistic effects on the benthic community.

For the last 2 decades of the century there is compelling evidence of climate change and its impact on the North Sea fauna (Beaugrand et al. 2002, Edwards et al. 2002, Hays et al. 2005, Perry et al. 2005). Generally, climatic changes are expected to significantly affect the biogeography of benthic species (Kröncke et al. 1998); particularly their planktonic larvae are likely to be affected by temperature variations (Beaugrand et al. 2003). It was suggested that an ecosystem regime shift occurred in the North Sea around 1982 to 1988 (Beaugrand 2004) or in 1978 and 1988 (Weijerman et al. 2005).

For the last 2 decades of the century it is impossible, based on the present study, to weigh the contribution of fishing effort in comparison with other factors to the observed changes in epibenthos. The significant difference in taxonomic distinctness between the 1980s and 2000 suggests that characteristics of the epibenthic community changed during this period, but this change is not clearly linked to fishing.

Overall, although we consider that sustained high trawling effort has significantly affected North Sea epibenthos during the past century, this does not exclude eutrophication and/or climate change as additional, potentially important factors contributing to the epibenthos changes that this study demonstrates.

Finally, it should be mentioned that many taxa, particularly echinoderms and hermit crabs, were persistently present over great areas of the North Sea in all 3 surveys. This does not mean that species within these groups were evenly distributed. The starfish *Asterias rubens*, for example, is ubiquitous in the North Sea but its abundance is much higher in the south than in the north (Callaway et al. 2002). Its biogeographical distribution pattern, however, appears to be remarkably persistent over time, despite natural and anthropogenic impacts. Species of hermit crabs, ophiurids and starfish would possibly remain in a species assemblage subjected to even greater anthropogenic interference. Thus, assuming that these taxa continue to be widely present in the North Sea for the foreseeable future, they may contain useful 'indicator' species if any of their population parameters (e.g. abundance, biomass, size spectrum or shell condition) could be linked to environmental impacts.

CONCLUSIONS

Long-term trends in landings indicate that substantial trawling effort has taken place in the North Sea throughout the entire 20th century. Central and south-

ern areas were not only trawled more intensively than the north, but also with more invasive gear. Especially in the earlier decades, the northern North Sea was less exploited and trawling only gradually expanded and intensified from south to north.

Over the century, the biogeography of many epibenthic species changed, with species' presence variously spreading and declining in the different areas. Reductions in spatial presence occurred especially in the central and southern North Sea, where beam trawl effort has been highest. The affected species are known to be sensitive to damage by fishing gear.

Conversely, the benthic species expanding their distribution over the last century are relatively tolerant to fishing gear or likely to benefit from reduced competition by other species and high numbers of damaged species suitable as prey.

Overall, the most profound changes in the epibenthos appear to have taken place before the 1980s; since then there has been further change, but the communities of recent decades probably reflect faunal assemblages adapted to long-term impacts.

Climate change, eutrophication and other factors are highly likely to have contributed to the observed changes. The nature of the changes, however, indicates that to a considerable extent, and especially in the central and southern North Sea, long-term changes in epibenthos can be linked to a century of sustained, high trawling effort.

Acknowledgements: We thank the officers, crew and scientists on board the various research vessels involved in all surveys that have provided the data analysed in this study. Four anonymous reviewers, R. Rosenberg and A. Rowden made valuable comments on the first draft of the manuscript. P. Somerfield made helpful remarks on the analyses of taxonomic diversity. G.H.E. was supported by the Department for Environment, Food & Rural Affairs of the United Kingdom (Contracts MF0322 and MA018).

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Editorial responsibility: Howard Browman (Associate Editor-in-Chief), Storebø, Norway

*Submitted: November 16, 2005; Accepted: May 6, 2007
Proofs received from author(s): September 5, 2007*