Spatial and temporal trends in species richness and abundance for the southerly and northerly components of the North Sea fish community separately, based on IBTS data 1977-2005

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Abstract

Based on the North Sea International Bottom Trawl Survey, the number of species recorded after 20 hauls is used as an index of biodiversity at a spatial scale of 10*10nm. The results show a clear pattern: species richness is lowest in the central North Sea and highest in Scottish waters, in the Kattegat and in the Channel area. When the community is split into its northerly and southerly components, the former reaches its highest diversity in waters typically deeper than 100m and the latter in waters less than 50m. The area of high richness of northerly species extends from Scottish waters along the Norwegian trench into the Kattegat. High richness of southerly species is not restricted to the southern North Sea but is observed also along the Scottish coast and in the Kattegat. These patterns are discussed in relation to hydrographical features that may control these differences. Temporal trends indicate that both components are characterized by a gradual increase in species richness over the past 25 years, a process that has affected the whole area while rates of change did hardly differ between the components or areas. A standardized index of abundance also indicates long-term gradual increases for both northerly and southerly species, although in this case the increase in southern species is larger. I argue that overexploitation is a more plausible explanation for the observed phenomena, although climate change may have had add-on effects.

Keywords: Fish community, North Sea, northerly species, southerly species, species richness, trends, climate change, overexploitation.

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Introduction

Biodiversity is a concept that does not lend itself easily for objective measurement, because it has so many facets that the number of possible indicators, and their interpretation, is virtually unlimited. Moreover, large variations in the abundance of individual species appear to be of all times, and measures of diversity can be expected to vary correspondingly, even without man's interference with the system. In the absence of a comprehensive theory on how direct effects of human activities in terms of changes in the abundance of individual species propagate through the system, it becomes an almost impossible task to disentangle the causes of changes in diversity indices. Before any progress can be made in this respect, a comprehensive description of spatial and temporal patterns in diversity indices is needed that can be empirically linked to spatial and temporal indicators of anthropogenic pressure (Daan, 2005).

Many published papers dealing with changes in fish communities in response to climate change deal with an *ad hoc* selection of 'southerly' species (Heessen, 1996; Corten and van de Kamp, 1996; Beare *et al*., 2004, 2005) that may have been guided by *a priori* knowledge on whether they have or have not increased in abundance in recent years. Given the evidence that climate is changing globally, the reasoning that climate change is the causal factor responsible for an observed increase of southerly species becomes almost axiomatic. However, the factual support is often limited because many anthropogenic activities and their impacts develop concurrently and the exact timing of the presumed causes and their effects is often treated superficially (e.g., Perry *et al*., 2005).

Many changes in North Sea fish communities have been reported, but only those related to size and maximum-attainable-size (Lmax) distributions can, on the basis of first principles, be more likely linked to heavy exploitation, although even those may be confounded by climate change (Daan *et al*., 2005). It seems equally possible that increases in southerly species have been confounded with effects of exploitation, because the overexploitation of the community originally

present may have opened up space for new species that were formerly out-competed.

The effect of climate change on the abundance of southerly and northerly fish species might be expected to be mirrorlike, leading to expansion and retreat, respectively. In contrast, exploitation should not affect the two groups differentially. So there is a testable hypothesis. With regard to the North Sea fish communities, I address three main questions:

- Can species-rich areas be identified and are these different for northerly and southerly species?
- Are temporal trends in species richness and /or abundance significantly different?
- Can it be made plausible that observed trends are related to climate change and/or exploitation?

Characterizing the spatial distribution of species richness is useful in this context in order to elucidate possible regional differences as well as factors affecting these.

Based on the International Bottom Trawl Surveys (IBTS; Heessen *et al*., 1997), the most comprehensive North Sea survey data seta, two biodiversity indicators were calculated for the total fish community and for the two groups separately: (1) species richness (number of species reported per unit of effort); and (2) average standardized abundance. However, using these data for community analyses is by no means straightforward and beforehand treatment of the data is inevitable (Daan, 2001; Daan *et al*., 2005).

Methods

Database
Since 1977, the IBTS covers the entire shelf area <200m, including Skagerrak and Kattegat, annually during February. Additional surveys in other quarters have been carried out since 1991 (see for details Heessen *et al*, 1997). Data for 1983-2005 were extracted from the ICES database DATRAS and for earlier years from the former IBTS database. The gear used is a high-opening bottom-trawl (chalut à Grande Ouverture Verticale or GOV-trawl), with a 20mm stretched mesh size in the codend. The distance between the boards is susually 80-100m, the horizontal opening of the trawl itself is approximately 20m and the vertical opening 5-6m. The standard groundrope is relatively light, but bobbins have been used on rough grounds to prevent damage to the gear.

The survey is stratified according to a grid of approximately 30*30nm rectangles (0.5° latitude; 1° longitude), with each rectangle being annually sampled by two countries. The total number of hauls that has been taken since 1977 is in the order of 15 000. Although there is

a tendency to return to the same fishing location within a rectangle, there is enough variation over the years to analyse the data by a finer grid and we have chosen a resolution by squares of approximately 10*10nm (10' latitude; 20' longitude).

Data selection and treatment
The database contains in principle numbers-at-length caught for all fish species. However, among countries many inconsistencies exist in the identification (Daan, 2001; ter Hofstede and Daan, 2006): differences in taxonomic level, disproportionate catch rates of similar species among countries, incredibly large catches of essentially rare species, implausible size distributions, etc. This greatly reduces the value of the survey for community analyses, because one improper identification in a haul makes all the difference between a biased and a correct diversity index. The procedure outlined in Daan *et al.* (2005) has been applied to correct for the deficiencies encountered, although a comprehensive analysis of all potential problems is still lacking.

The distinction between northerly and southerly species is a relative one and area-specific. Biogeographical studies generally consider the Channel area as the approximate border between the Boreal and Lusitanian fauna (Ekman, 1953). For the North Sea, this is a convenient border and, based on available distribution maps (Wheeler, 1978; Whitehead *et al*., 1984), each species was characterized by having its main area of distribution north ('northerly') or south ('southerly') of this border.

Most amphidromous and deep-water species were excluded, because these are difficult to assign in terms of northerly or southerly. We also had to exclude genus information if both southerly and northerly representatives might be found within a genus and a reliable split in species could not be made (e.g. *Ammodytes* and *Hyperoplus*). Thus, the final list of taxa that could be characterized contained 107 (49 northerly and 58 southerly) species (Table 1).

Spatial analysis
The actual number of species recorded by 10*10nm rectangle (N_r) are heavily influenced by differences in the local sampling effort exercised (n_r) and, because n_r varied widely across rectangles (Figure 1), effort must be accounted for in a suitable species richness index (Daan *et al*., 2005). Taking the average number of species per haul does not resolve this problem, because the probability of a rare species having been observed depends on the total number of hauls and therefore the average number per haul is heavily biased towards the

more common species (two hauls with 10 identical species would receive the same value in the final index as two hauls with 10 completely different species).
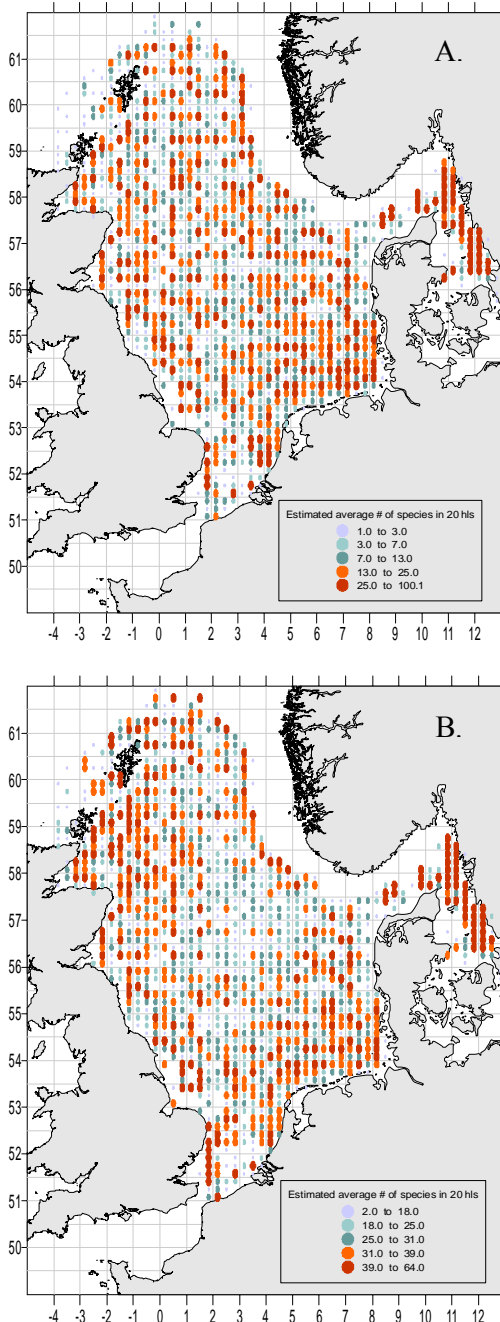

Figure 1. (A) Total number of hauls and (B) actual number of species recorded by 10*10nm rectangle (source DATRAS).

To use all species information available and get rid of potential temporal trends, we created a data set with all species recorded by haul by rectangle and then randomly selected a sequence of hauls for each rectangle and calculated the number of species (N_{ir}) recorded after $i_r=1 \ldots n_r$ hauls. This random selection was repeated 20 times and the results were averaged.

Figure 2 shows the resulting patterns for a selection of some of the most frequently fished

rectangles. Although N_i appears to stabilize on a linear scale after some 40 hauls, the index keeps in fact almost linearly increasing on a log-scale, reflecting that ever more rare species are being caught after ever more hauls. Secondly, the lines may cross over at any point, indicating that any relative measure of biodiversity across rectangles in terms of N_i depends on i. Choosing a higher value would seem preferable in terms of obtaining maximum resolution, but of course not all squares have been fished with the same intensity and in many cases the expected value after x hauls (N_{xr}) has to be estimated based on the trend observed between i=1 ... n_r. We estimated the linear regression for all sub-rectangles with $3 \leq n_r <20$ and estimated the expected number of species caught after x=20 hauls accordingly. In addition, we used the average N_{xr} 'observed' after x=20 hauls for $n_r \geq 20$, and the actual number of species observed (N_r) for $n_r<3$. The choice for x is arbitrary, but represents a compromise between increasing bias through extrapolation and not making use of the available information for rare species.
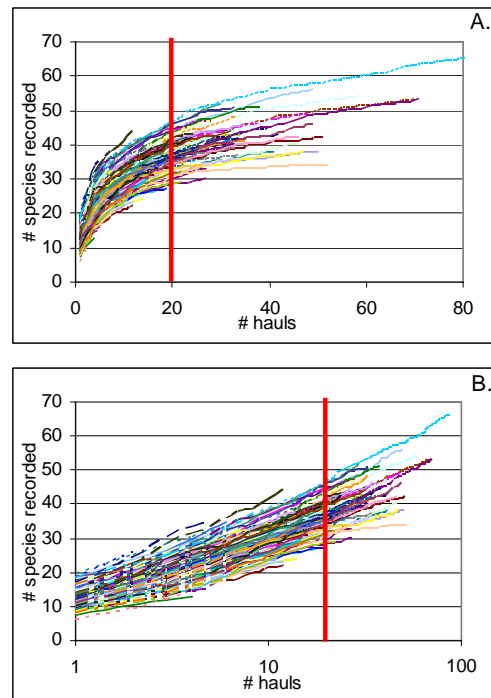

Figure 2. Average number of species recorded after 1… n hauls within a rectangle (based on 20 sequences of randomly selected hauls: (A) arithmetic plot and (B) after log transformation of the number of hauls.

For the spatial analysis, surveys from all seasons were combined to derive the most comprehensive picture of the distribution of species richness. The resulting values were plotted on a map to identify the hotspots. Similar plots were made for 'northerly' and 'southerly' species separately.

Temporal analysis

The number of hauls by survey (n_s) is too restrictive for estimating trends in richness at a local scale. A similar approach was used as for the spatial analysis: all hauls within any one survey were randomized and after 20 simulations of randomly selected hauls, the average number of species recorded (N_s) after i=1 ... n_s hauls was calculated (Figure 3). Because of the much larger number of hauls available by survey, the estimated (or observed) average N_s after 300 hauls was selected as an arbitrary but appropriate measure of annual species richness. In this case, only the February surveys were used for reasons of consistency. N_s were also calculated for 'northerly' and 'southerly' species for the entire North Sea and by region.
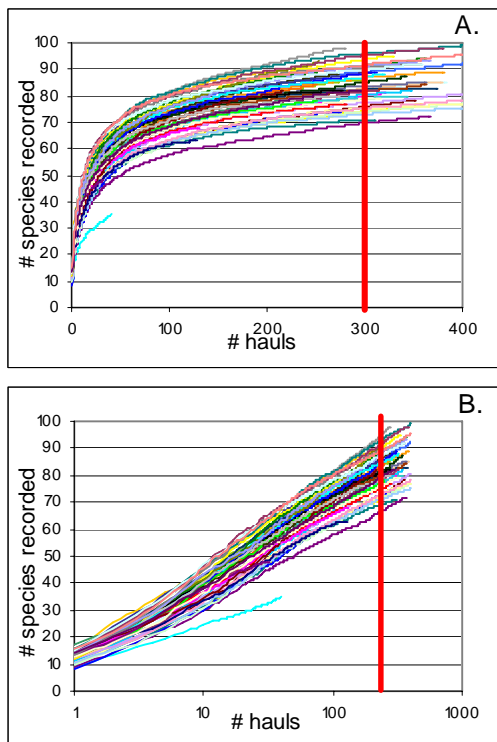

Figure 3. Average number of species recorded after 1… n hauls within individual surveys (based on 20 sequences of randomly selected hauls: (A) arithmetic plot and (B) after log transformation of the number of hauls.

For the analysis of trends in abundance, standardized indices by species were calculated by dividing the average annual catch rate over the total North Sea by the cumulative catch rate over all years. This brings the data for the different species to the same scale so that the average trend can be calculated.

Results

Spatial patterns in species richness

The highest biodiversity in the North Sea in terms of fish species recorded after 20 hauls is found around the edges, with remarkably low values in the central North Sea (Figure 4). Three hotspots may be identified: around the Orkneys and Shetlands and entering Scottish mainland waters, the Kattegat and the English east coast.
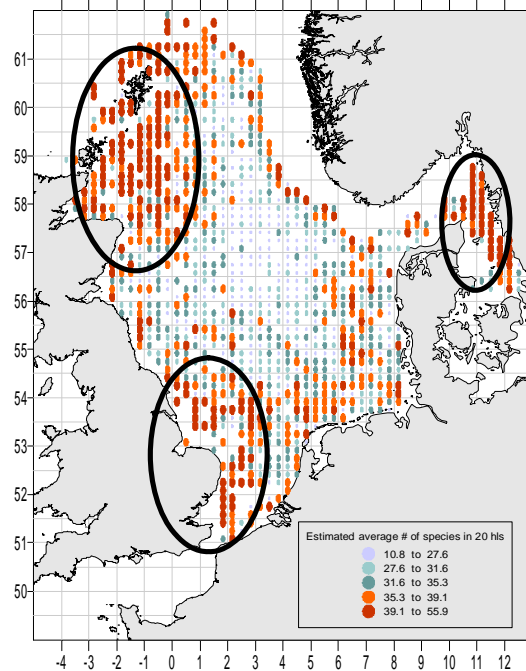

Figure 4. Estimated total number of species recorded after 20 hauls by 10*10nm rectangle (source: DATRAS).

When the community is split into its northerly and southerly components, some markedly different patterns appear (Figure 5). The area of high diversity of the northerly component is restricted to Scottish waters and all along the Norwegian deeps into the Skagerrak/Kattegat region. Off the continental and east-Anglia coasts, diversity of this group is remarkably low. In contrast, diversity within the southerly component is highest over a large area in the southern North Sea extending from the Channel up to the Dogger Bank. However, hotspots are also present in Scottish waters (but more westerly located than for the northern component) and also in the Kattegat.

Temporal trends in species richness

Considering the pronounced differences in diversity patterns of the two groups, the temporal trends in species richness were calculated for both the total North Sea and for three regions separately (cf. Figure 6): the northwestern North Sea (NNS; RNDF1,2,3,and 4), the southeastern North Sea (SNS; RNDF5, 6 and 7) and the Skagerrak/Kattegat (SKK; RNDF8). These three areas largely correspond with the three major hotspots identified.
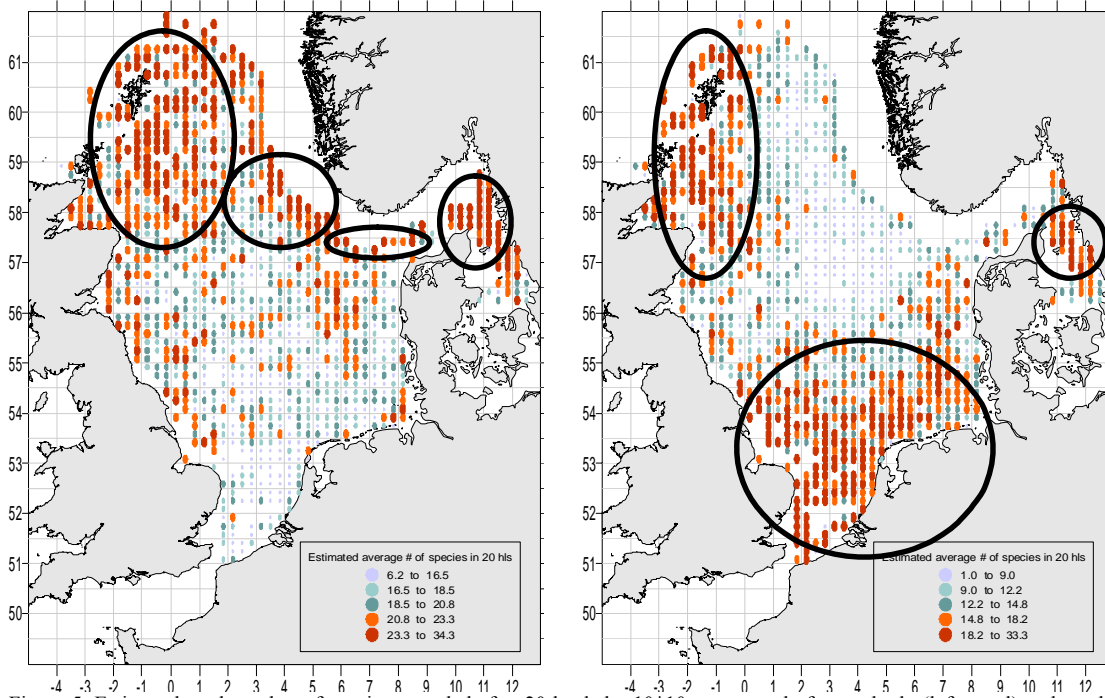
Figure 5. Estimated total number of species recorded after 20 hauls by 10*10nm rectangle for northerly (left panel) and southerly (right panel) species separately (source DATRAS).
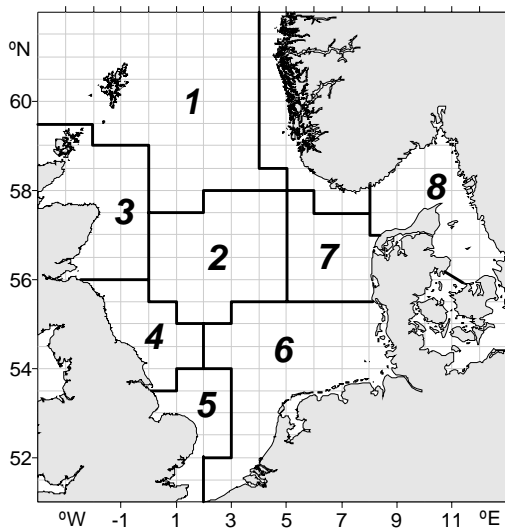

Figure 6. Standard Roundfish areas (RNDF) traditionally used for analysing demersal species caught in the IBTS .

Figure 7 shows the trends by region and group. All trends were significant at p<0.01 (see R-values in text table below) and slopes were not significantly different between northerly and southerly species except for the northwestern North Sea, where the increase in northerly species was significantly less than the one in southerly species. However, the overall conclusion can only be that species richness has increased in both groups and this pattern has

been remarkably constant over large areas of the North Sea. On average, species richness increased with slightly less than 1 species per year and this increase was accounted for almost equally by the two groups.

Area	Subset	R	Slope
North Sea	total	0.88	0.90
northerly	0.82	0.43
southerly	0.82	0.47
SNS	total	0.79	0.87
northerly	0.73	0.39
southerly	0.70	0.48
NNS	total	0.69	0.58
northerly	0.47	0.15
southerly	0.70	0.43
SKK	total	0.80	1.16
northerly	0.72	0.59
southerly	0.76	0.57

Temporal trends in species abundance
Figure 8 shows the average trend in abundance within the two components, giving equal weight to all species. In both cases, apparently more species have increased in abundance than declined, although the increase is markedly steeper in the southerly species. What is also remarkable is that this index (as well as the richness index) follows smooth curves, suggesting that it has a conservative character, with very little random noise, even though the annual estimates are completely independent.

Periods of increase appear to alternate with more stable periods or even periods of some decline.
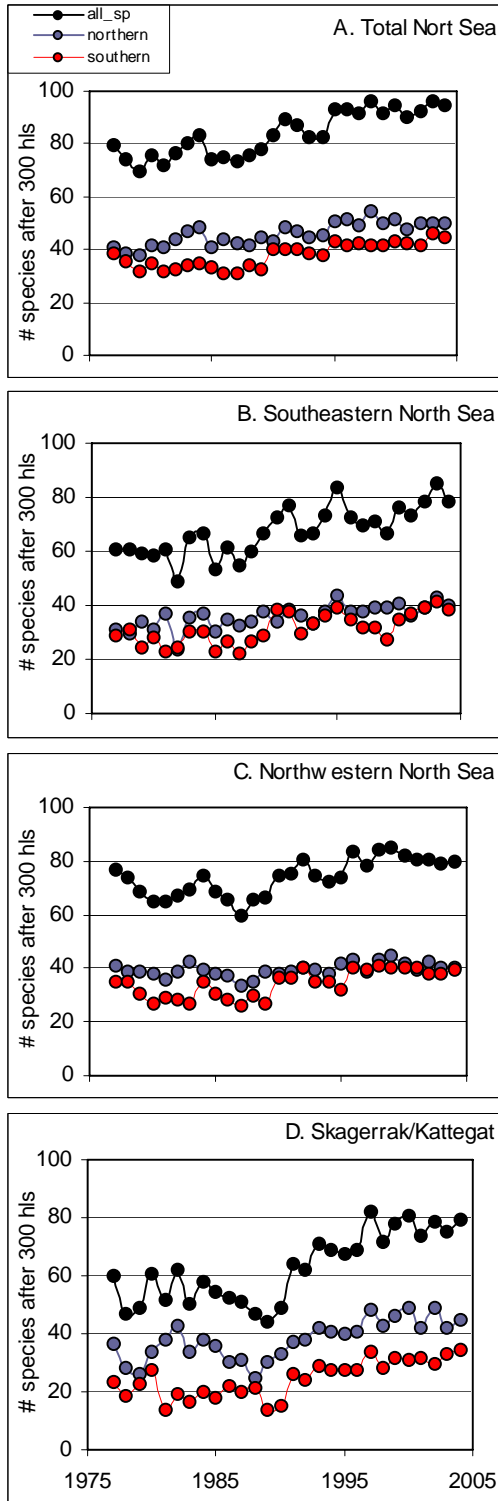

Figure 7. Trends in number of species recorded per year after 300 hauls for the total community and for northerly and southerly species separately and by region: (A) total NS; (B) southeastern NS; (C) northwestern NS; and (D) Skagerrak/Kattegat.
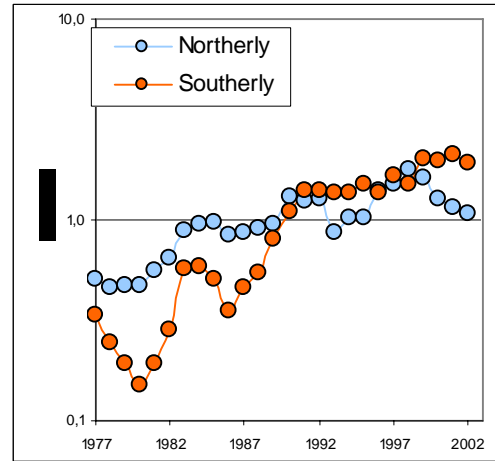

Figure 8. Average standardized trend (log scale) in abundance of northerly and southerly species over the entire North Sea.

Discussion

Spatial aspects

The differences in the spatial patterns of species richness for northerly and southerly species require an explanation. Figure 9 shows relevant hydrographic information. The hotspots in overall diversity appear to be largely explained by the main current system (Figure 9a), oceanic water entering the North Sea mainly through the Orkney and Shetland channels, but moving along the edge of the Norwegian trench into the Skagerrak/Kattegat area. Oceanic water also enters the southern North Sea through the Channel. Apparently, these currents bring atypical species into the system, thereby enhancing diversity around its edges. Because the Baltic fish fauna is essentially an impoverished North Sea fauna (apart from the presence of freshwater species that do not reach the Kattegat), the hotspot in this area cannot be linked to the occurrence of typical Baltic species, although the outflow of Baltic water of relatively low salinity may create conditions under which specific northerly and southerly species may thrive.
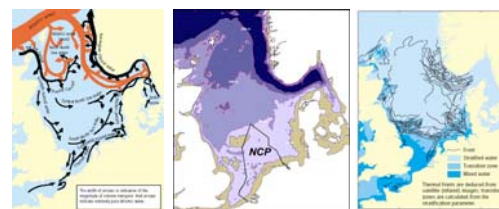

Figure 9. Hydrographical features of the North Sea: (A; left) main current system; (B; middle) isobaths; and (C; right) location of main frontal zones (A and C from OSPAR, 2000).

The different patterns observed between northerly and southerly species can be largely explained by an apparent difference in depth preference (Figure 9b). The highest diversity of

southerly species is largely restricted to waters of less than 50m depth, particularly in the southern area, but also in Scotland diversity is highest in inshore waters. In contrast, areas of high species richness of northerly species overlap to a large extent with waters over 100m depth. The poor diversity of the central North Sea coincides with an area without clear fronts. But of course, all these hydrographical features are closely related, as is also the temperature regime.

The interpretation of North Sea temperature distributions in relation to the distribution of the two groups is a bit more difficult, because in winter there is a gradient running from highest in the north to coldest along the continental coast, whereas in summer the situation is reversed (Figure 10). Thus, while southerly species would be better off in Scottish waters during winter time, because they would avoid relatively colder waters further south, conditions during summer should be better in the south. The summer distribution shows a steep gradient in the central North Sea that coincides approximately with the 50m depth contour (Figure 9), which is related to the development of a thermocline in deeper areas that prevents warming of the bottom waters.

Whatever the real basis for the different preferences among the groups, the existence of three hotspots for southern species suggests that southerly species enter the North Sea through the Channel and around Scotland, with little exchange in between these two areas. The Kattegat seems an extension of the southern hotspot, even though there appears to be a marked gap along the Danish Skagerrak coast. In contrast, the high diversity of northerly species in the Kattegat is clearly linked to the northern North Sea with high diversity observed all along the Norwegian Trench.
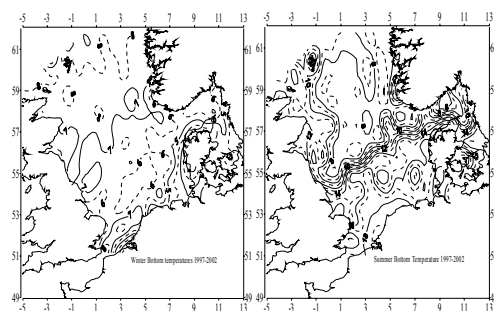

Figure 10. Average bottom temperature distribution during winter (left) and summer (right).

The majority of the spatial data have been collected during February surveys, although data from other quarters have been included. This might have given a bias. However, such bias is considered to be small, because a check on the annual species richness by survey did not

reveal big differences among seasons (Figure 11). In fact, diversity in other seasons was often lower, possibly because the number of hauls was less and the chance of having gaps in the coverage may have been larger.
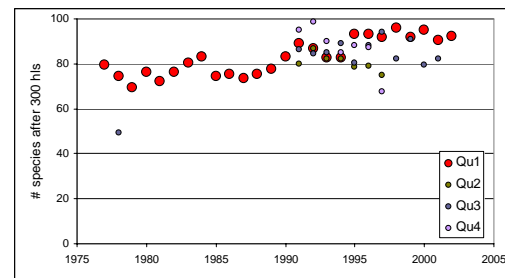

Figure 11. Estimated species richness by year and season for all IBTS surveys.

As said before, the choice of calculating the richness index after 20 hauls is arbitrary and one may wonder to what extent this index differs from taking just the average number of species per haul. Although the two indices are significantly correlated, the correlation explains only 53% of the variance and indeed within individual squares the relative diversity in terms of number of species after 20 hauls may easily differ by a factor of 50-200% from the average number per haul (Figure 12).
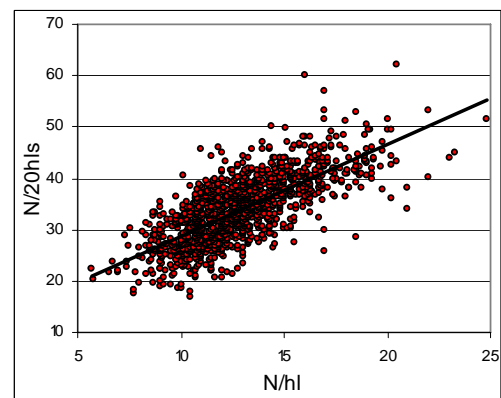.

Figure 12. Correlation between the (estimated) number of species recorded after 20 hauls and the average number of species per haul.

Another methodological aspect is the potential bias in the estimation procedure by extrapolating outside the range covered in the calculations of the log-linear regressions. By selecting all rectangles with $\geq$ 20 hauls and using only the first ten hauls to estimate the number that should have been recorded after 20 hauls, some qualitative evidence can be obtained. Figure 13 provides the frequency distribution of the deviations between the thus estimated and 'observed' values. The median of these deviations is -1 and thus species richness is on average slightly underestimated, but given the much larger spatial differences in species

richness and the consistent patterns in its distribution, the effect seems less important.
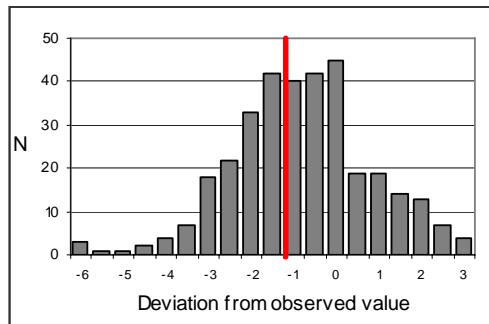

Figure 13. Frequency distribution of deviations of the estimated number of species recorded after 20 hauls from the regression based on the first 10 data points and the observed average after 20 hauls (class intervals: 1=1.0/1.5; -1=-0.5/-1.0. Red line represents median.

Temporal aspects

Because the regression in the temporal analysis is based on much larger number of hauls than in the spatial analysis (minimum of x hauls per survey), the potential bias introduced is substantially smaller and in fact negligible.

The richness index is a presence-absence type of approach, where only the frequency with which a species reported is used, while the abundance analysis is based on catch rates. Both yielded essentially the same result: richness and average abundance of both northerly and southerly species have significantly increased over the last 25 years and these increases appear to have been fairly steady right from the beginning of the series onwards. For richness, the increases are not restricted to particular regions but represent large-scale events. Thus, the hypothesis that climate change is mainly responsible for changes in abundance and distribution of southerly species is not supported by the evidence presented, because the two groups of species have shown similar responses.

The abundance analysis supports this conclusion, although in this case the increase in southerly species has been steeper. Thus, the conclusion should be that climate change has not been the primary factor involved in these changes, but potentially has had an add-on effect.

The observed changes should be seen in the light of other changes observed in the North Sea fish community. Jennings *et al.* (1999) argue that exploitation has been responsible for restructuring the exploited fish community through differential fishing effects on species with contrasting life styles. Daan *et al.* (2005) provide evidence that the system is increasingly dominated by fish of a small size and by fish with a low Lmax, suggesting a restructuring of the community in response to a decline in predation pressure caused by the removal of large fish. The parallel development in northerly and southerly species suggests these small and low-Lmax fish include representatives of both groups, which supports the view that overexploitation is the main cause of the changes that have been seen so far. The decline observed by Daan (2006) in the fraction of 'large fish' (a proxy for the mature fraction within each species), is clearly also related to this major restructuring of the fish community.

One of the problems of climate change is that there is a large uncertainty as to when its effects actually might be expected to have become expressed (i.e. when annual anomalies became systematically different from the fluctuations seen in the past). Figure 14a shows the temperature and salinity anomalies in the Fair Isle Current (Hughes and Lavin, 2003), one of the few North Sea time series that can be used for identifying climate change. These data suggest that the cyclical patterns in the two parameters run in parallel up to around 2000, but then temperature suddenly takes off relative to the salinity cycle. If this reflects the first signs of climate change, we should look for causal relations after this date rather than before. However, none of the long-term trends observed, also those by Beare *et al.* (2004) and Perry *et al.* (2005), would fit into this picture. Still, it may be that the recent downward trend observed in the abundance of northerly species after 1999 (Figure 8) is a first sign of this change in ocean climate.
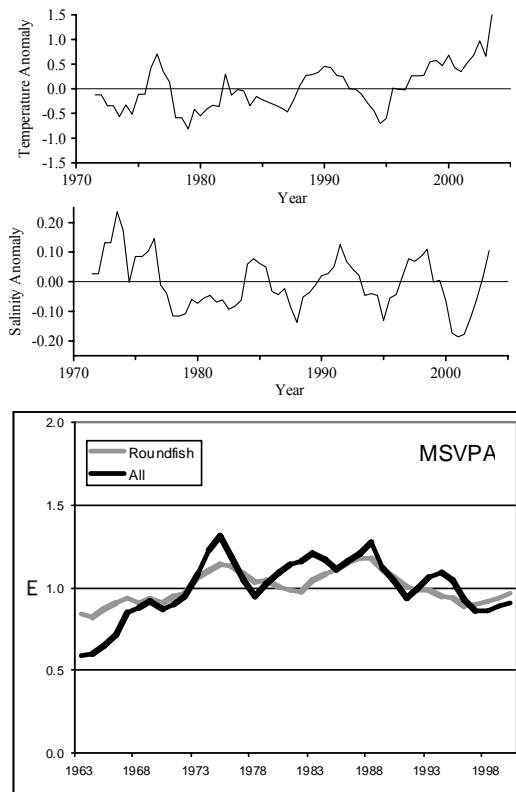
Figure 14. (A) Annual temperature and salinity anomalies in the Fair Isle Current (top panel; from Hughes and Lavin, 2003), and (B) an index of the exploitation rate of the North Sea fish community based on standardized trends in various commercial species (bottom; from Daan et al., 2005).

Although overexploitation appears to be a better candidate for having caused the large changes observed, it is extremely difficult to obtain an overall pressure indicator on a fish community (Daan, 2005). Still, all information we do have indicates that exploitation reached its maximum in the seventies and has somewhat decreased in the 1990s (Figure 14b). Correlations between changes in the fish community and exploitation rate were not significant (Daan et al., 2005) and, if overexploitation is the main cause, the response of fish communities must be characterized by considerable delay effects.

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Table 1. Listing of northerly and southerly species included in the analysis.

Northerly species	Southerly species
Agonus cataphractus	*Aphia minuta*
Anarhichas lupus	*Argentina sphyraena*
Artediellus atlanticus	*Arnoglossus imperialis*
Belone belone	*Arnoglossus laterna*
Brosme brosme	*Aspitrigla cuculus*
Ciliata mustela	*Atherina presbyter*
Ciliata septentrionalis	*Buglossidium luteum*
Clupea harengus	*Callionymus lyra*
Cyclopterus lumpus	*Callionymus maculatus*
Echiodon drummondi	*Callionymus reticulatus*
Entelurus aequoraeus	*Capros aper*
Gadus morhua	*Chelon labrosus*
Galeorhinus galeus	*Crystallogobius linearis*
Glyptocephalus cynoglossus	*Ctenolabrus rupestris*
Hippoglossoides platessoides	*Dasyatis pastinaca*
Hippoglossus hippoglossus	*Dicentrarchus labrax*
Limanda limanda	*Diplecogaster bimaculata*
Liparis liparis	*Echiichthys vipera*
Liparis montagui	*Engraulis encrasicolus*
Lophius piscatorius	*Eutrigla gurnardus*
Lumpenus lampretaeformis	*Gaidropsurus vulgaris*
Melanogrammus aeglefinus	*Gobius niger*
Micrenophrys lilljeborgi	*Labrus bergylta*
Microstomus kitt	*Labrus mixtus*
Molva molva	*Lepidorhombus whiffiagonis*
Myoxocephalus scorpius	*Lesueurigobius friesii*
Osmerus eperlanus	*Liza aurata*
Pholis gunnellus	*Lophius budegassa*
Phrynorhombus norvegicus	*Merlangius merlangus*
Phrynorhombus regius	*Merluccius merluccius*
Platichthys flesus	*Microchirus variegatus*
Pleuronectes platessa	*Mullus surmuletus*
Pollachius pollachius	*Mustelus spp.*
Pollachius virens	*Myxine glutinosa*
Psetta maxima	*Pagellus erythrinus*
Raja batis	*Phycis blennoides*
Raja radiata	*Pomatochistus spp.*
Raniceps raninus	*Raja brachyura*
Rhinonemus cimbrius	*Raja circularis*
Scomber scombrus	*Raja clavata*
Sebastes viviparus	*Raja montagui*
Spinachia spinachia	*Raja naevus*
Squalus acanthias	*Raja undulata*
Taurulus bubalis	*Sardina pilchardus*
Triglops murrayi	*Scophthalmus rhombus*
Trisopterus esmarki	*Scyliorhinus canicula*
Trisopterus minutus	*Scyliorhinus stellaris*
Zeugopterus punctatus	*Solea lascaris*
Zoarces viviparus	*Solea solea*
	Spondyliosoma cantharus
	Sprattus sprattus
	Symphodus melops
	Trachinus draco
	Trachurus trachurus
	Trigla lucerna
	Trigloporus lastoviza
	Trisopterus luscus
	Zeus faber