Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. IV. Can comparisons of species diversity be used to assess human impacts on demersal fish faunas?

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Abstract

Patterns in the abundance of commercially important and non-target demersal fish species collected by beam trawl survey from the coastal waters of the northeast Atlantic are described. Catches were dominated by a small number of species, which occurred in large numbers and at high biomass. The most abundant species (plaice and dab) were typical of shallow, uniform sandy and muddy seabed which occurred extensively throughout the southern North Sea, and to a limited extent in UK western waters. Renyi’s diversity index family was used to rank the diversity of coastal sectors throughout the region. The less species-rich North Sea fauna, partly a result of the uniform nature of the seabed, was largely responsible for lower diversity of North Sea coastal faunas compared to those in the Channel and west of the UK. West of the Dover Strait, the more heterogeneous substrate supported a more diverse fauna of smaller sized fish, with the occurrence of southern species such as red gurnard and thicketback sole and an increasing abundance of elasmobranchs. In the Irish Sea, fish biomass was dominated by plaice and dab, but to a lesser extent than on the continental coast of the North Sea. Sole, lesser spotted dogfish and cod were also important in this assemblage. Patterns in community structure over such a wide spatial scale, and without historical perspective, can be explained by biogeographic factors, seabed structure and the influence of regional hydrography. Inferring from these patterns an impact of anthropogenic factors (such as towed fishing gears) is unlikely to be achieved. Identifying vulnerable species, and use of fishing effort distribution data of high resolution, may be a more fruitful approach. Crown copyright © 1999 Published by Elsevier Science B.V. All rights reserved.

Keywords: Diversity; Fishing impact; Assemblage; Demersal; Beam trawl

1. Introduction

Recent interest in the impact of human activities on marine demersal communities, particularly by towed demersal fishing gears, has focused on the results of
experimental studies quantifying impacts on a range of seabed faunas (Bergman and Hup, 1992; Kaiser and Spencer, 1996; Collie et al., 1997), and on interpreting spatial and temporal changes to seabed assemblages (Pope and Knights, 1982: ICES, 1992; Greensstreet and Hall, 1996; Rijnsdorp et al., 1996b). Considerable effort has also been devoted to developing more sophisticated methods for describing community structure and identifying subtle changes to it, in addition to the classical diversity indices which are already widely used by ecologists. For example, improvements in the measurement and interpretation of diversity have recently been made using methods of diversity ordering (Tothmeresz, 1995), where a range of diversity indices within a family show varying sensitivities to rare and abundant species. The use of the taxonomic relatedness of species within the community has also proved to be an effective means of identifying changes to some infaunal communities (Sommerfield and Clarke, 1995). Despite this progress, basic descriptions of demersal fish faunas comprising both commercially exploited species as well as the non-target component, are not yet widely available for many coastal and offshore regions (but see for example Fargo and Tyler, 1991; Farina et al., 1997), although their value with respect to understanding possible fishing effects may be high. The distribution of selected species has been presented in most detail for the North Sea (Daan et al., 1990: Knijn et al., 1993), but difficulties with combining catches by gears with different selectivity have prevented more widespread analyses beyond this region.

One of the most likely direct effects of towed gears on seabed communities will involve changes in the relative abundance of predators and/or their prey, and the reduction in abundance of vulnerable species. The size structure of the fish assemblage will also be strongly affected by fishing pressure (Rice and Gislason, 1996; Rijnsdorp and Leeuwen, 1996). Analysis of North Sea populations (Greensstreet and Hall, 1996) has shown that while changes in the demersal community since the 1930s were evident, only subtle changes had occurred to the non-target assemblage. Analysis of North Sea survey data since the 1970s also showed changes in diversity and evidence of some community-level effects of fishing, especially during the 1980s (Rice and Gislason, 1996). A decline in the abundance of non-target species such as grey gurnard *Eutrigla gurnardus* has been observed in the North Sea (Rijnsdorp et al., 1996b), and also in some elasmobranch species including, for example, spurdog *Squalus acanthias* (Brander, 1981; Heessen and Daan, 1996; Walker and Heessen, 1996). Some of the elasmobranchs are considered to be particularly vulnerable to increased fishing mortality because of their low fecundity and high age and length at maturity (Walker and Heessen, 1996). Finding causal relationships between human impacts such as trawling or eutrophication, and temporal trends in abundance of species, has been difficult. Interpreting the likely effects of these impacts on community structure over a large spatial scale, covering many degrees of latitude and longitude, will be even more complex.

There are many factors which will influence the distribution and abundance of fish, and one of the most fundamental is regional biogeography. Although it is assumed that the tropics contain by far the greatest diversity of genera and species of fish (Norman, 1963), there are few references to the precise rate of decrease in species richness between the equatorial and polar faunas (Ekman, 1967: Henderson, 1989). Indeed, other marine groups, such as seaweeds, reach their greatest diversity in temperate regions, and there are equal numbers of infaunal invertebrate species in soft substrates in Arctic and tropical regions (Gee and Warwick, 1996). So, an understanding of the biogeographic influences which control fish population diversity will underlie subsequent interpretations which relate to possible changes caused by human activity.

The recent development within the International Council for the Exploration of the Sea (ICES) of an extensive database describing the beam trawl catches of demersal fish throughout the coastal waters of the northeast Atlantic (Rogers et al., 1998), has provided a unique opportunity to further develop our knowledge of fish populations. Results from an initial analysis grouped assemblages into broad categories, two of which represented areas of relatively high diversity in the western waters of the UK and off Denmark, and other less diverse assemblages in the eastern Channel and the southern North Sea (Rogers et al., 1998).

This paper develops this initial classification and describes the results of more detailed comparisons of the diversity of demersal assemblages between regions. Its purpose is to identify aspects of community structure which, on a large spatial scale, are most
likely to reveal evidence of anthropogenic impact. Together with more detailed information of the distribution of trawl effort, these data could in future be used for more precise examination of casual relationships.

2. Materials and methods

2.1. The surveys

The beam trawl surveys of the UK, Netherlands, Germany and Belgium which contribute to this data set cover an area comprising the southern and eastern North Sea (ICES Division IVb and IVc), the English Channel (ICES Division VIIId and VIle), the Bristol Channel (ICES Divisions VIIIf and VIIlg) and the Irish Sea (ICES Division VIIa). Although the earliest beam trawl survey began in the North Sea in 1985, a consistent data set for all participating countries is only available from 1990. For the analyses presented in this paper, data for the entire area from 1990 to 1996 inclusive have been used, and the ICES Divisions in which sampling occurred have been subdivided into smaller coastal sectors which generally group fishing stations with the nearest coastline (Fig. 1(a)).
Although the precise details of the sampling methodology have been described elsewhere (ICES, 1994; Rogers et al., 1997), the following summary describes the basic sampling procedure.

Beam trawls were used to survey the demersal fish populations of the coastal waters (10–120 m depth) of northwestern Europe, and different sized trawls were used during the surveys, depending on the ability of the different vessels to deploy them, and the varying nature of the seabed in different parts of the region (Rogers et al., 1998). All samples were collected during the third quarter of the year. In general, fishing stations sampled were at fixed positions, except in Dutch and German surveys where the station positions were stratified by ICES rectangle and selected annually on a pseudo-random basis. The positions of the fixed stations in UK waters were stratified by depth band and by ICES rectangle, with the number of station positions in each depth band allocated in proportion to the catch of pre-recruit flatfish during preliminary surveys. Station positions of the Belgian surveys in the North Sea were stratified by rectangle. In the North Sea, where station positions fished by some countries were not fixed from year to year, all
hauls were grouped by the quarter ICES rectangle in which the shooting position occurred, and the mean catch by species of these hauls was allocated to a nominal fixed position at the centre of the quarter rectangle (Fig. 1(b)).

At each station the fin-fish catch was identified to species where possible, measured, and the numbers recorded. The weight of each species caught at each haul during UK surveys was recorded. The mean weight of an individual of each of these species, based on the total weight and total number of the species captured, was used to estimate the weight of catches in North Sea surveys. Larger catches were subsampled, and more complex strategies adopted when fishing with two beam trawls towed in parallel (ICES, 1994).

The purpose of all sampling methods was to provide catch rates of each species raised to a standard 8 m beam trawl tow, and for a duration of 1 h. Mean catch rates of each species (number 8 m beam trawl-l h tow-l and weight 8 m beam trawl-l h tow-l) at each fixed station position for the period 1990-1996 were calculated and used in all analyses. Only those fish species which were classified as commercially important, or as demersal non-target species, were used in analyses of community structure (Rogers et al., 1998).

2.2. Statistical methods

To describe the distribution of fish biomass with depth, species which have been identified as important contributors to the total demersal fish fauna were combined into six groups, and the total weight of fish in these groups was calculated for 1 m depth intervals within groups of ICES Divisions, over the entire depth range of the survey (Rogers et al., 1998). These weights were then expressed as a cumulative frequency. The six fish groups used were rays (Rajidae), gadoids (gadidae), sharks (all other elasmobranchs excluding the rays), all flatfish, all weevers/blennies and gobies (Families Trachinidae, Blenniidae, Stichaeidae, Pholidae, Callionymidae and Gobiidae) and all gurnards. (Families Triglidae, Cottidae and Agonidae.)

Diversity profiles, a graphical display of a family of diversity indices, were calculated for the fish catches (number 8 m beam trawl-l h tow-l) within each of the sectors identified in the coastal waters of the northeast Atlantic. This family of diversity indices was obtained by changing the scale parameter (\(\alpha\)). There are several forms available, but one that is recommended for large data sets is Renyi's diversity index family \(H_{\alpha}\) (Patil and Taillie, 1982; Tothmeresz, 1995):

\[
H_{\alpha} = \frac{\log p_i}{1 - \alpha},
\]

where \(p_i\) is the proportion of individuals belonging to the \(i\)th species. When substituting 0, 1 and 2 for the scale parameter \(\alpha\), \(H_{\alpha}\) will be directly related to the species richness (i.e. \(\alpha\) is the log of the species number), Shannon's entropy and Simpson's dominance index, respectively (Hill, 1973). Thus for \(\alpha\) near zero, richness will have more effect on \(H_{\alpha}\), but for larger values of the scale parameter, species evenness has more effect. For scale parameters which increase from 1 to 4 the influence of rare species will be gradually replaced by the influence of dominant species. One community is more diverse than another if its diversity profile is equal to or above that of another, over the whole range of the scale parameter. If the two profiles intersect at any point then they can be considered non-comparable (i.e. different diversity indices would rank the communities differently).

Relative abundances and biomass of demersal species (\(k\)-dominance curves) were superimposed using the ABC method of Warwick (1986) to provide information on the size of the most dominant species.

To compliment these descriptions, mean species abundances (numbers and biomass 8 m beam trawl-l h tow-l) were ranked and presented graphically for the 18 species which comprised 95% of the total catch number throughout the survey area. The presentation of abundance data for individual named species allows the community structure to be interpreted in terms of the contribution of individual species, rather than anonymous ranked species abundances. This can be used to distinguish identical profiles of diversity, or of ranked abundance such as ABC plots, in two communities which have identical relative abundances, yet in which the species themselves are different.

A similarity of percentages analysis (SIMPER) identified those species which typified the catches within sectors, and also those species most responsible for the dissimilarity in catches between sectors, using raised data. A full description of SIMPER analysis is provided by Clarke (1993). Non-metric multi-dimen-
sional scaling (MDS) was used for ordination and clustering of the data to describe the inter-relationships between sectors, taking into account individual species abundances (Clarke and Ainsworth, 1993). A Bray–Curtis similarity matrix of root transformed mean catch numbers and weight in each sector was calculated. This allowed the species abundances to be described in terms of their ranked similarities, and these were plotted as Euclidean distances in a two-dimensional plot, where the distance apart of each sample represented their relative similarity. A low value of stress for such a plot (<0.1) indicated that the technique gave a good representation of relationships between sectors and that only two dimensions were required for displaying the ordination.

3. Results

The coastal waters of the northeast Atlantic cover a wide range of marine environments, from shallow, sheltered areas in the North Sea with several large estuaries, to exposed and more steeply shelving areas on the southwest coast of the UK (Fig. 1(a)). The depth distribution of groups of demersal species showed that up to 60% of the total biomass of some groups sampled occurred within the depth range 10–30 m, but this proportion was highly variable and depended on the depth profile of each region and the prevailing environmental conditions. The most notable differences in cumulative biomass between ICES Divisions were evident for ‘rays’ in the North Sea, which were restricted to the deeper parts of Division IVb (Fig. 2(a)), in contrast to the Channel and western waters (Fig. 2(b) and (c)). In the Channel, the biomass of demersal species in the ‘shark’ and ‘gurnard’ groups was more associated with deep water than in either the North Sea or the Irish Sea (Fig. 2(b)).

3.1. The fish assemblage: variation within sectors

Throughout the entire survey area, 39 demersal commercial and non-target species provided 99% of the total numerical abundance of fish, and 38% of this total consisted of dab *Limanda limanda* and plaice *Pleuronectes platessa*, while poor cod, dragonet and solenette were also important contributors (Table 1). When expressed in terms of biomass, the total contribution of plaice and dab increased to over 50%, and these species dominated the fauna. The relative rank of species changed slightly when their percentage contribution was expressed in terms of biomass, due to differences in the mean weight of each species. For example, larger species, such as sole, lesser spotted dogfish, and thornback ray all showed increased proportions of the total biomass and increased their rank order. Smaller species such as poor cod and solenette, decreased in rank, as illustrated by the negative values
Table 1
Comparison of total catch number and total catch weight for selected species from all regions, which comprise 99% of the total abundance of all fish

<table>
<thead>
<tr>
<th>No.</th>
<th>Species</th>
<th>Percentage of total catch number (%N)</th>
<th>Percentage of total catch weight (%W)</th>
<th>%W-%N</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Dab</td>
<td>27.1</td>
<td>19.7</td>
<td>-7.3</td>
</tr>
<tr>
<td>2</td>
<td>Plaice</td>
<td>11.8</td>
<td>32.6</td>
<td>20.8</td>
</tr>
<tr>
<td>3</td>
<td>Poor cod</td>
<td>8.7</td>
<td>1.6</td>
<td>-7.1</td>
</tr>
<tr>
<td>4</td>
<td>Dragonet family</td>
<td>8.6</td>
<td>3.4</td>
<td>-5.2</td>
</tr>
<tr>
<td>5</td>
<td>Sole</td>
<td>8.3</td>
<td>1.1</td>
<td>-7.2</td>
</tr>
<tr>
<td>6</td>
<td>Whiting</td>
<td>4.6</td>
<td>3.3</td>
<td>-1.3</td>
</tr>
<tr>
<td>7</td>
<td>Soleo solea</td>
<td>4.1</td>
<td>7.4</td>
<td>3.3</td>
</tr>
<tr>
<td>8</td>
<td>Hook-nose</td>
<td>3.9</td>
<td>0.4</td>
<td>-3.6</td>
</tr>
<tr>
<td>9</td>
<td>Grey gumard</td>
<td>3.1</td>
<td>1.2</td>
<td>-1.9</td>
</tr>
<tr>
<td>10</td>
<td>Scalfish</td>
<td>3.0</td>
<td>0.5</td>
<td>-2.5</td>
</tr>
<tr>
<td>11</td>
<td>Bib</td>
<td>2.8</td>
<td>1.8</td>
<td>-1.0</td>
</tr>
<tr>
<td>12</td>
<td>Goby family</td>
<td>2.0</td>
<td>0.1</td>
<td>-2.0</td>
</tr>
<tr>
<td>13</td>
<td>Lesser weever</td>
<td>1.9</td>
<td>0.4</td>
<td>-1.5</td>
</tr>
<tr>
<td>14</td>
<td>Thick back sole</td>
<td>1.7</td>
<td>0.5</td>
<td>-1.2</td>
</tr>
<tr>
<td>15</td>
<td>Lesser spotted dogfish</td>
<td>1.2</td>
<td>7.3</td>
<td>6.1</td>
</tr>
<tr>
<td>16</td>
<td>Lemon sole</td>
<td>0.9</td>
<td>1.4</td>
<td>0.6</td>
</tr>
<tr>
<td>17</td>
<td>Cod</td>
<td>0.8</td>
<td>2.4</td>
<td>1.6</td>
</tr>
<tr>
<td>18</td>
<td>Red gumard</td>
<td>0.7</td>
<td>0.8</td>
<td>0.2</td>
</tr>
<tr>
<td>19</td>
<td>Long rough dab</td>
<td>0.7</td>
<td>0.2</td>
<td>-0.5</td>
</tr>
<tr>
<td>20</td>
<td>Tub gumard</td>
<td>0.4</td>
<td>0.9</td>
<td>0.5</td>
</tr>
<tr>
<td>21</td>
<td>Thornback ray</td>
<td>0.4</td>
<td>2.8</td>
<td>2.4</td>
</tr>
<tr>
<td>22</td>
<td>Bull-rout</td>
<td>0.3</td>
<td>0.2</td>
<td>-0.1</td>
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<tr>
<td>23</td>
<td>Flounder</td>
<td>0.3</td>
<td>0.9</td>
<td>0.6</td>
</tr>
<tr>
<td>24</td>
<td>Haddock</td>
<td>0.3</td>
<td>0.5</td>
<td>0.2</td>
</tr>
<tr>
<td>25</td>
<td>Angler</td>
<td>0.2</td>
<td>1.6</td>
<td>1.3</td>
</tr>
<tr>
<td>26</td>
<td>Spotted ray</td>
<td>0.2</td>
<td>0.8</td>
<td>0.6</td>
</tr>
<tr>
<td>27</td>
<td>Brill</td>
<td>0.2</td>
<td>1.0</td>
<td>0.8</td>
</tr>
<tr>
<td>28</td>
<td>Hake</td>
<td>0.1</td>
<td>0.4</td>
<td>0.2</td>
</tr>
<tr>
<td>29</td>
<td>Norwegian topknot</td>
<td>0.1</td>
<td>0.0</td>
<td>-0.1</td>
</tr>
<tr>
<td>30</td>
<td>Witch</td>
<td>0.1</td>
<td>0.2</td>
<td>0.0</td>
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<td>31</td>
<td>Four-bearded rockling</td>
<td>0.1</td>
<td>0.0</td>
<td>-0.1</td>
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<tr>
<td>32</td>
<td>Cuckoo ray</td>
<td>0.1</td>
<td>0.0</td>
<td>0.5</td>
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<tr>
<td>33</td>
<td>Red mullet</td>
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<td>0.0</td>
<td>0.5</td>
</tr>
<tr>
<td>34</td>
<td>Turbot</td>
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<td>0.7</td>
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<tr>
<td>35</td>
<td>Greater pipefish</td>
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<td>-0.1</td>
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<tr>
<td>36</td>
<td>Blonde ray</td>
<td>0.1</td>
<td>0.4</td>
<td>0.3</td>
</tr>
<tr>
<td>37</td>
<td>John dory</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>38</td>
<td>Streaked gumard</td>
<td>0.1</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>39</td>
<td>Butterfish</td>
<td>0.1</td>
<td>0.0</td>
<td>-0.1</td>
</tr>
</tbody>
</table>

The difference in percentage contribution when using weight and abundance, is shown.

The results of a SIMPER analysis of the fish catches within each sector identified those species which contributed a large proportion to the total within sector similarity, and also those species which were found at consistent abundance amongst all catches and which thus typified the catches within each sector (Table 2).
Table 2
Percentage contributions (>6%) of demersal species to the average within-sector similarity, identified using SIMPER analysis of Bray-Curtis dissimilarities (Clarke, 1993)

<table>
<thead>
<tr>
<th>Species</th>
<th>IVb(e)</th>
<th>IVc(e)</th>
<th>IVc(w)</th>
<th>VIIId(n)</th>
<th>VIIId(s)</th>
<th>VIIe</th>
<th>VIIf&amp;g</th>
<th>VIIa(e)</th>
<th>VIIa(s)</th>
</tr>
</thead>
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<tr>
<td>Dragonet family</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Callionymidae</td>
<td>8.03</td>
<td>8.26*</td>
<td>8.27</td>
<td>12.11*</td>
<td>15.01*</td>
<td>12.20</td>
<td>7.72</td>
<td>8.91</td>
<td>9.05</td>
</tr>
<tr>
<td>Dab</td>
<td>20.05</td>
<td>13.13*</td>
<td>9.66</td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>6.76</td>
<td>8.63</td>
</tr>
<tr>
<td>Plaice</td>
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<td>9.26*</td>
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<td></td>
<td>6.44</td>
<td>7.36</td>
<td>-</td>
<td>6.24</td>
<td>8.20</td>
</tr>
<tr>
<td>Sole</td>
<td></td>
<td>7.12*</td>
<td>11.00</td>
<td>6.28</td>
<td>8.59</td>
<td>7.82</td>
<td>-</td>
<td>7.42</td>
<td></td>
</tr>
<tr>
<td>Hook-nose</td>
<td>6.20</td>
<td>-</td>
<td>7.84</td>
<td>6.75</td>
<td>8.97*</td>
<td>-</td>
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<td>6.40</td>
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<tr>
<td>Poor cod</td>
<td>8.70</td>
<td>-</td>
<td>7.19</td>
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<td></td>
<td>-</td>
<td>-</td>
<td>10.75</td>
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<td>Whiting</td>
<td>8.37</td>
<td>-</td>
<td>8.26</td>
<td>9.89</td>
<td></td>
<td>-</td>
<td>-</td>
<td>10.51</td>
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<tr>
<td>Grey gurnard</td>
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<td>8.85*</td>
<td>-</td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>7.49</td>
<td>6.40</td>
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<td>Lesser spotted dogfish</td>
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<td>6.90</td>
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<td>Skaldfish</td>
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<td>-</td>
<td>7.49</td>
<td>6.40</td>
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<td></td>
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</table>

Within-sector similarity (%) 68.75 73.66 60.97 51.10 53.88 53.87 54.61 58.44 45.32

*Species consistent in typifying the community (mean/SD≥4).

The presence of whiting *Merlangius merlangus*, contributed most to the within-sector similarity (Table 2). In both sectors the lesser spotted dogfish had the greatest mean weight of all species sampled (Fig. 3(b)). This mixture of large and small species, each with a different rank in terms of abundance and biomass, produced k-dominance curves which crossed for those catches taken from the Bristol Channel, and in the western Channel, resembled those further to the east (Fig. 3(a) and (b); Fig. 4(f) and (g)).

In the Irish Sea (sectors VIIa(e) and VIIa(w)), not only were gadoids important contributors to the within-sector similarity (Table 2), but dab, plaice, poor cod, and dragonet each provided more than 10% of the total mean abundance (Fig. 3(a)). Biomass in the Irish Sea was dominated by dab and plaice, but to a lesser extent than on the Continental coast of the North Sea, while sole, lesser spotted dogfish and cod were also important (Fig. 3(b)). Plots of k-dominance reflected the similarity with North Sea catches, as biomass curves were generally more elevated than those for abundance (Fig. 4(h) and (i)). The absence of typifying species throughout western waters of the UK compared to the North Sea (Table 2), and the relatively low within-sector similarity of these sectors indicated the heterogeneous nature of the population sampled.
Fig. 3. Mean species abundances, expressed as numbers (a) and biomass (b) per 8 m beam trawl h⁻¹, by coastal region, for the 18 species which comprised 95% of the total catch number throughout the survey area. Species reference numbers on the x-axis can be interpreted using Table 1.
Fig. 4. Cumulative biomass (triangle) and cumulative abundance (filled circle) for ranked species (expressed on a logarithmic scale) in c sectors IVc(e) (a); IVc(e) (b); IVc(w) (c); VIIId(s) (d); VIIId(n) (e); VIIf and g (f); VIIe (g); VIIa(w) (h) and VIIa(e) (i).
3.2. Variation between sectors

Diversity profiles for each sector were used to identify those demersal communities which were more or less diverse than each other, and those which were non-comparable (Fig. 5(a)-(c)). A summary of these diversity relationships between each sector (Table 3) showed that the samples from the continental coast of the North Sea (sectors IVb(e) and IVc(e)) had low diversity, both because of the limited total number of species present (low value at $\alpha=0$), and the effect of high dab and plaice abundance creating a population in which species abundances were unevenly distributed (low evenness at $\alpha=3$). These two sectors had lower diversity than all others except the Continental coast of the eastern Channel, VIIId(s) (Table 3).

Those species responsible for discriminating between sectors were identified by their contribution to the average dissimilarity, using SIMPER analysis (Table 4). The between-sector dissimilarity value for North Sea sectors IVb(e) and IVc(e) of 35.27% was the lowest of all comparisons made, confirming the similarity of the demersal faunas in each sector. The lesser weever, with greater abundance in sector IVc(e), was the only species which consistently discriminated between these two communities (Table 4). The higher mean catch rate of bib and lemon sole *Microstomus kitt* in the western part of the southern North Sea, IVc(w), contributed to the discrimination between these catches and those to the east IVc(e), and also to its greater diversity (Tables 3 and 4).

In contrast to the North Sea, communities in eastern Irish Sea (VIIa(e)) were more diverse than sectors except those in the northern part of the eastern Channel, VIIId(n), the Bristol Channel, VIIIf and VIIg, and the English coast of the southern North Sea, IVc(w), which were all non-comparable. The eastern part of the Irish sea was more diverse than the Continental coast of the eastern Channel, VIIId(s), in part due to the relatively higher catch of sole and solenette, and lower mean catch of *Microstomus kitt* (Fig. 3(a); Table 4).

All other sectors identified in Fig. 1 had diversity profiles which occurred between those of the Irish and Continental North Sea coasts. This reflected the range in total species richness values for each sector, and the way in which the abundances of species were distributed relative to each other (Table 3).

On the English coast in the southwest, communities in the western Channel (VII) were less diverse than those to the east (VIIId(n)) and to the north (VIIIf and VIIg). This was mainly caused by a slightly lower species richness for this sector when compared to VIIId(n), even though communities were of similar evenness (Fig. 5). In sector VIIIf and VIIg, there were more species with a moderate (5–10%) percentage of the catch, and this was partly due to the percentage of dragonet and solenette in these catches (Fig. 3(a)).

The inter-relationships between sectors were further described by MDS ordination and cluster plots using both mean numerical abundance and species weight. The distinctiveness between the...
Fig. 5. Families of Renyi’s diversity indices for fish catches (number per 8 m beam trawl h⁻¹) within each of the coastal sectors. These profiles display graphically a family of diversity indices obtained by changing the scale parameter α, which for values of 0, 1 and 2 will be directly related to the species richness (i.e. α is the log of the species number), Shannon’s entropy and Simpsons dominance index, respectively. One community is more diverse than another if its diversity profile is equal to or above that of another, over the whole range of the scale parameter. Diversity profiles are shown for sectors in the North Sea (a), the Channel (b) and western waters of the UK (c).
Table 4
Percentage contributions (>3.5%) of discriminating demersal species to the average dissimilarity between selected sectors, identified using SIMPER analysis (Clarke, 1993)

<table>
<thead>
<tr>
<th>Species consistent in discriminating between sectors (mean/SD&gt;1.5).</th>
<th>IVb(e) &amp; IVc(e)</th>
<th>IVc(e) &amp; IVc(w)</th>
<th>Vlla(e) &amp; Vlla(w)</th>
<th>Vlla(w) &amp; Vlld(s)</th>
<th>Vlla(w) &amp; Vlla(e)</th>
<th>Vlla(e) &amp; Vlla(e)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solenette</td>
<td>Buglossidium luteum</td>
<td>5.73</td>
<td>5.11</td>
<td>4.77</td>
<td>4.47</td>
<td>4.16</td>
</tr>
<tr>
<td>Poor cod</td>
<td>Trisopterus minutus</td>
<td>–</td>
<td>4.29</td>
<td>4.5</td>
<td>4.71</td>
<td>4.36</td>
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<tr>
<td>Scalfish</td>
<td>Arno glossus laterna</td>
<td>–</td>
<td>4.82</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Dab</td>
<td>Limanda limanda</td>
<td>–</td>
<td>–</td>
<td>4.56</td>
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<tr>
<td>Bib</td>
<td>Trisopterus luscus</td>
<td>4.79</td>
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<tr>
<td>Lesser weever</td>
<td>Echichthys vipera</td>
<td>11.32*</td>
<td>5.57</td>
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<tr>
<td>Grey gurnard</td>
<td>Eutrigla gurnardus</td>
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<td>5.35</td>
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<td>4.23</td>
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<td>Thick back sole</td>
<td>Microchirus variegatus</td>
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<tr>
<td>Hook-nose</td>
<td>Argonous cataphractus</td>
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<td>4.27</td>
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<td>Plaice</td>
<td>Pleuronectes platessa</td>
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<td>–</td>
<td>4.26</td>
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<tr>
<td>Red gurnard</td>
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<td>–</td>
<td>–</td>
<td>4.36</td>
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<td>Gobiidae</td>
<td>5.38</td>
<td>4.41</td>
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*Species consistent in discriminating between sectors (mean/SD>1.5).

diverse North Sea faunas, and more diverse western UK faunas, was clearly identified in clustering plots for both numerical and weight data, where sectors were grouped approximately according to their geographical distance apart (Fig. 6). When using fish biomass, the distinction between the southern North Sea fauna on the English coast (IVc(w)) was less clearly differentiated from the westerly faunas (Fig. 6(b)). The predominance of small species throughout the Channel distinguished this assemblage.

Fig. 6. Multi-dimensional scaling ordination plots for mean catch number (a) and mean catch weight (b), of all fish samples caught within the nine sectors illustrated in Fig. 1.
from others to the west where flatfish, gadoids and other larger species, such as elasmobranchs, became increasingly abundant. In the west, ordination of Irish Sea and Bristol Channel faunas distinguished the less diverse community in the western Channel (VIIe), although the degree of similarity within this group varied depending on whether numerical or biomass data were used to determine sample similarity (Fig. 7(a)-(b)).

3.3. Distribution of the elasmobranchs

The distribution of the five elasmobranch species which occurred in the top 36 ranked species (Table 1), the lesser spotted dogfish, thornback ray *Raja clavata*, spotted ray *Raja montagui*, cuckoo ray *Raja naevus*, and blonde ray, *Raja brachyura*, is shown in Fig. 8(a)-(e). Without exception the centre of abundance of these species is to the west of the UK. Dogfish are widespread throughout the area sampled and even occur in abundance in the southern North Sea off the English coast, but appear to be rare or absent elsewhere in the North Sea (Fig. 8(a)). Thornback, blonde and spotted rays show a similar distribution but are generally less abundant, especially the blonde ray, and more closely associated with coastal areas (Fig. 8(b)-(d)). The cuckoo ray is confined to the western waters of the UK, and is found almost entirely in the Irish Sea and Bristol Channel (Fig. 8(e)).

4. Discussion

These analyses have allowed us for the first time to compare directly the diversity of the demersal fish assemblage of the northeast Atlantic shelf seas, using data collected by beam trawl surveys. The results show that catches were dominated by a few species, which occurred in large numbers and at a high biomass. The most abundant species were those which were typical of shallow, uniform sandy and muddy seabed which occurred predominantly in the southern North Sea, but also to a lesser extent in the Irish Sea and Bristol Channel (Knijn et al., 1993). The high level of dominance of catches by plaice and dab, and the limited total number of species present, were partly responsible for the generally low diversity of demersal assemblages on the Continental coast of the North Sea, compared to those in the Channel and west of the UK. One of the few species which helped to differentiate between these populations in the North Sea was the lesser weever, which occurred in lower abundance in the waters off Germany and Denmark, while off the coast of southeast England, bib and lemon sole occurred in larger numbers.

West of the Dover Strait, towards regions which were more influenced by southern fish faunas, and which supported a generally more heterogeneous substrate, the total number of demersal species increased (Fig. 5) (Henderson, 1989; Rogers et al.,
Fig. 8. The mean catch rate (numbers per 8 m beam trawl h⁻¹) of lesser spotted dogfish (a), thornback ray (b), spotted ray (c), blonde ray (d), and cuckoo ray (e), by quarter ICES rectangle.
The more steeply shelving substrate here supported a wider range of sediment types, and populations of smaller fish dominated the demersal assemblage. Still further west, towards the Celtic Sea, the presence of southern species such as red gurnard and thickback sole, the increasing abundance of elasmobranchs, and the high catches of gadoids, increased species diversity of these assemblages compared to those to the east. Between the Bristol Channel and the Irish Sea this basic population structure remained but was increasingly dominated by large flatfish populations, which, like those in the North Sea, were able to exploit areas of shallow sandy seabed (Symonds and Rogers, 1995).

These data summarise the diversity of demersal assemblages as sampled by beam trawl on a wide spatial scale, and without a historical perspective. Explanations for the observed patterns in diversity include well-known principles involving the distribution of warm-water and boreal faunas, and the hydrographic influence of the major water current systems in the region (Ekman, 1967; Henderson, 1989; Pauly, 1994). These factors can be assumed not only to influence the relative abundance of resident species, but also the richness of those fish faunas which are accessible to southern migrants. An extensive area of relatively low diversity exists in the southern North Sea, and the comparison of this with other regions, may suggest the involvement of some form of human activity. There is certainly a considerable amount of anthropogenic impact in the region, with fishing activity, eutrophication, pollution and infrequent periods of oxygen depletion (Riesen and Reise, 1982; Rijnsdorp and Leeuwen, 1996). This low diversity fish fauna may also, however, be related to the extreme environmental conditions in this relatively shallow area, which is exposed to larger seasonal fluctuations in temperature and salinity than in the other sectors studied.

A more fruitful approach to finding evidence of impact may not be to use spatially diverse community level indices such as these, but to examine individual parts of the assemblage which may show quantifiable effects of exploitation. For example, the low fecundity and high length and age at maturity of elasmobranchs makes this group particularly vulnerable to towed gears, and thus an additional source of evidence of gear effects. Dogfish and four ray species were absent from the southeast North Sea, where consistently high gear impact has occurred. Not all species are equally sensitive, however, and those with a relatively low length at maturity such as the starry ray *Raja radiata*, have maintained population size (Walker and Heessen, 1996). The size structure of parts of the demersal population is affected by selective removal of larger fish, and a comparison of these patterns in relation to known levels of fishing effort, and at a range of depths, could also be informative (Pope and Knights, 1982; Rice and Gislason, 1996; Rijnsdorp et al., 1996b; Rogers et al., 1998).

In contrast to much of the fish fauna, towed gears have shown quantifiable effects on invertebrate benthic communities, for example, experimental trawling altered the abundance of small invertebrates (Bergman and Hup, 1992), and significantly reduced the number of species in a stable sediment community (Kaiser and Spencer, 1996). These direct effects included the provision of food for other scavenger species through the damage or killing of benthic invertebrates in the passage of the gear, and altered the proportions of short-lived and long-lived species. For example, large numbers of the bivalve *Arctica islandica* have been reported to be damaged by otter trawling in Kiel Bay, and during intense fishing activity this species is more frequently found in the stomachs of cod, *Gadus morhua* (Arntz and Weber, 1970). Thus the possible impact of trawling on demersal fish may also occur through indirect effects via the benthos, and so it has been difficult to attribute observed changes in demersal fish populations to fishing effort. One of the few associations to be documented has involved changes in the growth rate of sole and plaice in the North Sea, where recent increases in mean length at age were thought to be caused by a combination of beam trawl and eutrophication effects (Millner and Whiting, 1996; Rijnsdorp and Leeuwen, 1996).

In subsequent investigations of the impact of trawling on widespread demersal communities, it will be very difficult to disentangle the effect of natural processes from any potential influence of towed gears. Examining specific aspects of the assemblage, with emphasis on selected vulnerable species rather than the community as a whole, may be the best way to interpret such spatially diverse data. The provision of accurate fishing effort data to a high level of resolution
will be a valuable next step in interpreting these observations (Rijnsdorp et al., 1996a).

Acknowledgements

We would like to thank Dr. Peter Henderson who introduced us to diversity profiles, and stimulated the analyses in this paper. We are also grateful to all the scientific staff, ship's officers and crew who have helped to collect data during the Belgian, Dutch, German and UK Beam Trawl Surveys. This work was funded by the Ministry of Agriculture, Fisheries and Food under MOU ‘A’.

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