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The taxonomic distinctness of coastal bottom-dwelling fish communities of the North-east Atlantic

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Summary

1. New techniques for identifying the average taxonomic range of species assemblages were applied to an extensive dataset of bottom-dwelling fish in the coastal waters of NW Europe. These taxonomic distinctness indices provided much greater resolution than traditional diversity indices as they incorporated information on taxonomic relationships into an index which measures species dominance. Unlike standard measures of species richness and diversity, the mean value of these statistics is independent of sampling effort, and this allows objective comparisons to be made between samples from studies where sampling effort is not standardized.

2. A reduction in the average taxonomic range between the fauna of western waters of the UK and that of the southern North Sea was consistent with the general decline in species richness observed between these regions, and suggests that these two factors may be spatially positively correlated. Indices calculated for individual samples of fish on a local scale, however, did not all fit this trend.

3. Much of the variability in taxonomic diversity within the coastal waters of NW Europe was caused by the variable geographical distribution of the elasmobranchs. Of all the families which comprise the fish communities, this group has life-history characteristics which make it most susceptible to impact by commercial trawl fisheries.

4. The use of taxonomic distinctness measures provided additional insights, of relevance to biodiversity assessment, suggesting that they might usefully be applied to other aquatic and terrestrial fauna.

Key-words: taxonomic diversity, groundfish, community structure, fishing impact, NW Europe.

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Introduction

Explaining the large-scale patterns in species distribution and abundance of both marine and terrestrial environments requires information on habitat extent and complexity (Magurran 1988; Rosenzweig 1995), the rates and effects of disturbance and levels of productivity (Connell 1978; Sousa 1979; Petraitis, Latham & Niesenbaum 1989; Baltz 1991), and also the impact of environmental gradients on species richness (Pianka 1966; Ekman 1967; Nelson 1994). Rarely are there sufficient environmental data to be able to fully explain patterns on a smaller provincial or regional scale, but it has become increasingly necessary to at least understand the relative role of natural and anthropogenic perturbation.

The response of benthic marine assemblages to disturbance is thought to be more easily detected at higher taxonomic levels, because of the confounding influence of abiotic factors such as water depth and temperature which will affect small-scale diversity at the species level (Warwick & Clarke 1993). This hierarchical response to stress, first proposed by Pearson & Rosenberg (1978), exploits the fact that various phyla differ in their sensitivity to disturbance. Benthic environments which have been perturbed are generally kept in an early successional stage with low species diversity, and often consist of species which

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are closely related, while unperturbed benthic communities in a late successional stage often consist of a wider range of taxonomically distinct species (Warwick & Clarke 1995). It is not clear, however, whether all communities which have a small number of species should, by definition, have a more limited taxonomic range than those with many species. Assuming that taxonomic diversity translates into ecological diversity, then the taxonomic range of an assemblage may be crucial in maintaining ecosystem stability during natural or anthropogenic perturbations (Hughes 1994; Tilman 1996).

Obscuring these patterns are the underlying biogeographic processes, such as rates of speciation, immigration and extinction, which determine total species richness of a province (Rosenzweig 1995). The resulting species diversity gradients are largely determined by the influence of environmental factors on rates of diversity generation and extinction. For marine organisms, the species richness between the tropics and polar regions generally, although not always, shows consistently decreasing trends (Findley & Findley 1985; Pauly 1994) but see also Gee & Warwick (1996).

These observations influence the way we interpret species diversity trends in marine environments, yet the conventional indices of community diversity, which use only the relative abundance of species, do not describe the degree of taxonomic relatedness of those species. Assemblages with the same species richness may either comprise species which are closely related to one another taxonomically, or they may be more distantly related (Ludwig & Reynolds 1988; Warwick & Clarke 1995). To quantify such changes in taxonomic relatedness, Warwick & Clarke (1995) and Clarke & Warwick (1998b) have defined three biodiversity indices, which quantify the taxonomic diversity and taxonomic distinctness of a faunal assemblage using the path lengths between fish grouped by their taxonomic relationships. They show that taxonomic diversity (Δ) is a natural extension of Simpson diversity, incorporating information on taxonomic relationships within a sample into an index measuring species dominance. Taxonomic distinctness (Δ^*) is a form of taxonomic diversity that limits the influence of patterns in species dominance by dividing Δ by a form of Simpson diversity, thus constructing a measure which more nearly reflects pure taxonomic relatedness. A third index, taxonomic distinctness (Δ)$^+$, considers only the special case where abundance information is not available or is ignored (i.e. presence/absence data). Clarke & Warwick (1998b) show that these statistics are largely independent of sampling effort, which makes their use attractive in spatially extensive or long time-series studies where total sampling effort in different areas or at different times is rarely standardized. Standard diversity indices such as species richness, Shannons' index and evenness measures can be highly influenced by differing sample sizes, making meaningful comparisons impossible (Rogers *et al.* 1999). In addition, the presence of a statistical testing framework for the Δ^+ index enables a comparison to be made between an observed taxonomic distinctness measure and its expected range of variation.

These measures of taxonomic distinctness have been applied to macrobenthos samples from the Ekofisk oil-field in the North Sea (Warwick & Clarke 1995). This study identified a high degree of sensitivity to subtle environmental impacts at this site, although these patterns have not been supported by data from other North Sea oil fields (Somerfield, Olsgard & Carr 1997). Taxonomic distinctness measures have also been applied to literature data on marine benthic nematodes from various intertidal/subtidal and coastal/estuarine sites in the UK, and also coastal habitats in Chile (Warwick & Clarke 1998). These analyses demonstrate a decrease in taxonomic distinctness Δ^+ at polluted sites, such as the UK's Clyde Estuary and Liverpool Bay, compared with taxonomic distinctness at 'clean' sites in the Exe Estuary, the Scilly Isles and the Northumberland coast.

The majority of published studies in which these indices have been applied have used data from soft-sediment macro-and meiobenthic faunas, yet some of the most extensive marine datasets describe the temporal and spatial abundance of fish. In the only known application of these indices to vertebrate populations, Hall & Greenstreet (1998) show that, for a long time-series dataset for bottom-dwelling fish from the northern North Sea, trends in taxonomic distinctness and diversity were identical to those shown by conventional indices. Their observed positive correlation between Δ^* and Hills N1 and N2 diversity indices suggests that assemblages that are more diverse (species-rich) always contain species that have a wider average taxonomic range than assemblages which are less diverse, but this has yet to be tested at a range of spatial scales.

In contrast to these large-scale patterns in species diversity, little is known about the processes which structure the diversity of smaller regional environments. In this paper we re-examine an extensive dataset describing the relative abundance of bottom-dwelling fish in the coastal waters of NW Europe (Rogers *et al.* 1998, 1999) to test whether these new taxonomic diversity indices can mirror changes in species diversity at different scales, ranging from the entire study area to individual sample sites. Using a comprehensive taxonomy of the bottom-dwelling fish found in the North-east Atlantic, we first calculate indices of taxonomic diversity using fish relative abundance, and also using simple presence and absence data. We then test whether these taxonomic diversity indices correspond to known patterns of species diversity, at intermediate and at small spatial scales. We also describe how local factors which may structure the community, such as the effect of man made disturbance on sensitive taxa, can influence the diversity of the entire demersal fauna.

Materials and methods

SURVEYS

A series of international beam trawl surveys of north-east Atlantic coastal waters have sampled the abundance of coastal (10–120 m depth) bottom-dwelling species since the late 1980s, using sampling techniques described in detail by Rogers *et al.* (1998). Different beam 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. All samples were collected during the third quarter of the year, at which time most fish were dispersed and not undergoing migrations to or from spawning grounds. In general, fishing stations sampled were at fixed positions, except in Dutch and German surveys where the station positions were stratified by International Council for the Exploration of the Sea (ICES) rectangle (1 degree of longitude × 0·5 degree latitude) and selected annually on a pseudo-random basis. In the North Sea, all stations were grouped by quarter ICES rectangle, and the centre of this unit was used as the nominal fixed station position. The duration of each tow was either 15 or 30 min. At each station the fin-fish catch was identified to species where possible, measured, and their numbers recorded (Rogers *et al.* 1998). Mean catch rates of each species or taxa (raised to the number per 8 m beam trawl per hour tow) at each fixed station position between 6 m to 35 m depth, and for the period 1990–96, were calculated. Only those fish species which were classified as bottom-dwelling species, and were therefore well sampled by beam trawls, were used in analyses of community structure (Rogers *et al.* 1998). The ICES Divisions surveyed were subdivided into nine coastal sectors (Fig. 1).

TAXONOMIC DIVERSITY INDICES

A taxonomy of bottom-dwelling fish species was used to determine their relatedness (Fig. 2). We compiled a composite taxonomy based primarily on Nelson (1994), with additional information for Chondrichthyes based on McEachran & Miyake (1990) and McEachran, Dunn & Miyake (1996). In addition to the five taxonomic levels shown in Fig. 2, we included subgenera, tribes, subfamilies, superfamilies, suborders, series, superorders, and subdivisions where possible. Three biodiversity indices defined by Clarke & Warwick (1998b) were then calculated from the bottom-dwelling fish abundances:

$$\Delta = [\Sigma\Sigma_{i<j}\omega_{ij}x_ix_j]/[n(n-1)/2] \qquad \text{eqn 1}$$

$$\Delta^* = [\Sigma\Sigma_{i<j}\omega_{ij}x_ix_j]/[\Sigma\Sigma\delta_{i<j}x_ix_j] \qquad \text{eqn 2}$$

$$\Delta^+ = [\Sigma\Sigma_{i<j}\omega_{ij}]/[s(s-1)/2] \qquad \text{eqn 3}$$

where x_i denotes the abundance of the *i*th of *s* species observed, n ($=\Sigma_i x_i$) is the total number of individuals in the sample and ω_{ij} is the weight given to the path length linking species *i* and *j* in the taxonomy. Taxonomic diversity (Δ) can be thought of as the average path length between any two randomly chosen *individuals* from the sample (including individuals of the same species), whereas taxonomic distinctness (Δ^*) is the average path length between two randomly chosen individuals, conditional on them being from different species. When only presence/absence data are used (i.e. $x_i \equiv 1$ for all species present) both equations reduce to an even simpler form of taxonomic distinctness, Δ^+, which can be thought of as the average path length between any two randomly chosen *species* present in the sample. All three indices were calculated for the groundfish data, including an additional modified form of eqn 2 in which the abundances were square root transformed, to downweight the contribution to the index of the numerically dominant species.

Following Warwick & Clarke (1995), the simplest form of path length weighting was adopted for the 13 taxonomic levels (Table 1), namely: $\omega = 0$ for two individuals of the same species; $\omega = 1$ for two individuals in the same subgenus but of different species; $\omega = 2$ for species in the same genus but different subgenera; $\omega = 3$ for species in the same tribe but different genera, etc. Where finer subdivisions do not exist within some groups of taxa, the path length is defined as that for the first existing link. For example, if a particular genus does not possess subgenera then all links between its constituent species carry a weight of $\omega = 2$.

There is a degree of arbitrariness about a constant path length of one unit between each taxonomic level in the hierarchy; for example, if a wholly unused level is inserted, the relative distinctness values for the set of samples will change. Where there is a comprehensive regional list for a group of species, it is possible to refine the weighting to reflect the reduced number of representatives at each taxonomic level. An alternative weighting assessed here ($\{\omega^{\circ}\}$, Table 1) sets the path length from one group to the next coarsest classification as proportional to the percentage by which taxon richness decreases. The path lengths are then summed and the final path lengths scaled so that the total weight linking two species that belong to different subdivisions (the top category of the hierarchy) is set equal to 100. It can be seen from Table 1 that this alternative weighting achieves the desired balance. For example, from genus ($s_3 = 72$) to tribe ($s_4 = 67$) now adds only 3·6 to the path length whereas that from suborder ($s_8 = 33$) to order ($s_9 = 14$) adds 10·5, and addition or deletion of an unused category will now have no effect at all. The relative taxonomic distinctness indices are computed and compared for both ω and ω° forms of weighting.

When the data are reduced simply to pres-

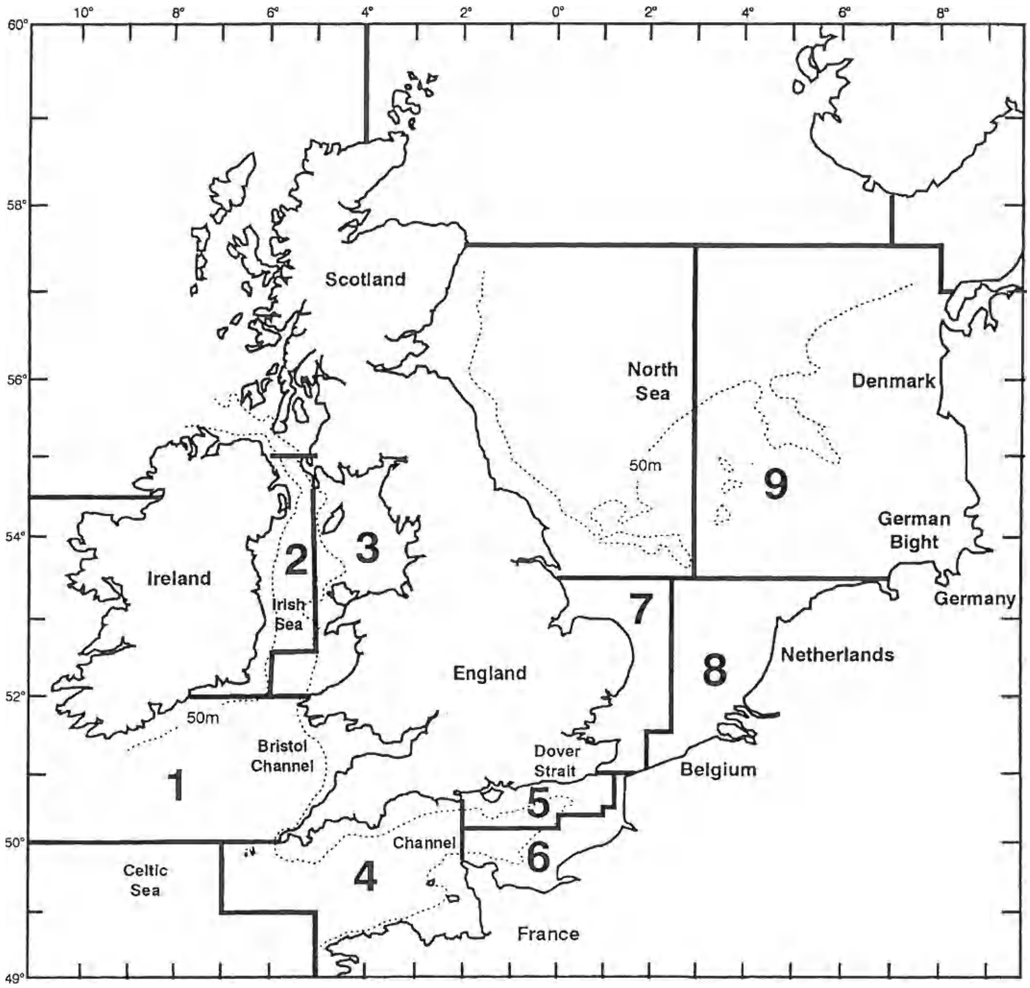

Fig. 1. The shelf seas of continental NW Europe, showing the 50 m depth contour and the nine coastal sectors used in these analyses: (1) = Bristol Channel; (2) = Western Irish Sea; (3) = Eastern Irish Sea; (4) = Western Channel; (5) = North-eastern Channel; (6) = South-eastern Channel; (7) = South-western North Sea; (8) = South-eastern North Sea; (9) = East Central North Sea.

ence/absence, not only can distinctness Δ^+ still be calculated, and compared across samples of different size, but a significance test can also be carried out. This tests for the departure of Δ_m^+, the distinctness measure for any sample of *m* species, from the overall value Δ^+ for a 'global' species list for that region. The test is based on the theoretical mean and variance of Δ_m^+, values obtained by random sampling of *m* species (without replacement) from the total list of *s* species (Clarke and Warwick 1998b). Although the theoretical mean remains constant, the variance naturally increases as *m* decreases, and so the approximate 95% confidence intervals take the form of a 'funnel'. The values of Δ^+ for any particular set of samples can then be related to this confidence 'funnel', to gauge the extent to which their taxonomic distinctness falls significantly below (or above) that expected. Assuming a null hypothesis that each sample is a random selection from the total species list, all values of Δ^+ should fall within the confidence funnel.

From its construction, the taxonomic distinctness index Δ^* should be independent of the Simpson species diversity index, i.e. they must be quantifying different aspects of diversity. It is thus interesting to show how these two community attributes are correlated across the available, spatially dispersed, sets of samples. Simple scatter plots are used to examine this.

Results

The taxonomic diversity of the untransformed fish abundance matrix showed similar patterns for the three diversity indices Δ, Δ^* and Δ^+ (Fig. 3). Although most coastal sectors showed similar values, the Eastern Central and South-eastern North Sea, and the Western Irish Sea had lower mean values of Δ (taxonomic diversity) than others. Mean values of Δ^* (taxonomic distinctness) maintained the same general pattern (Fig. 3b). The use of square root transformed

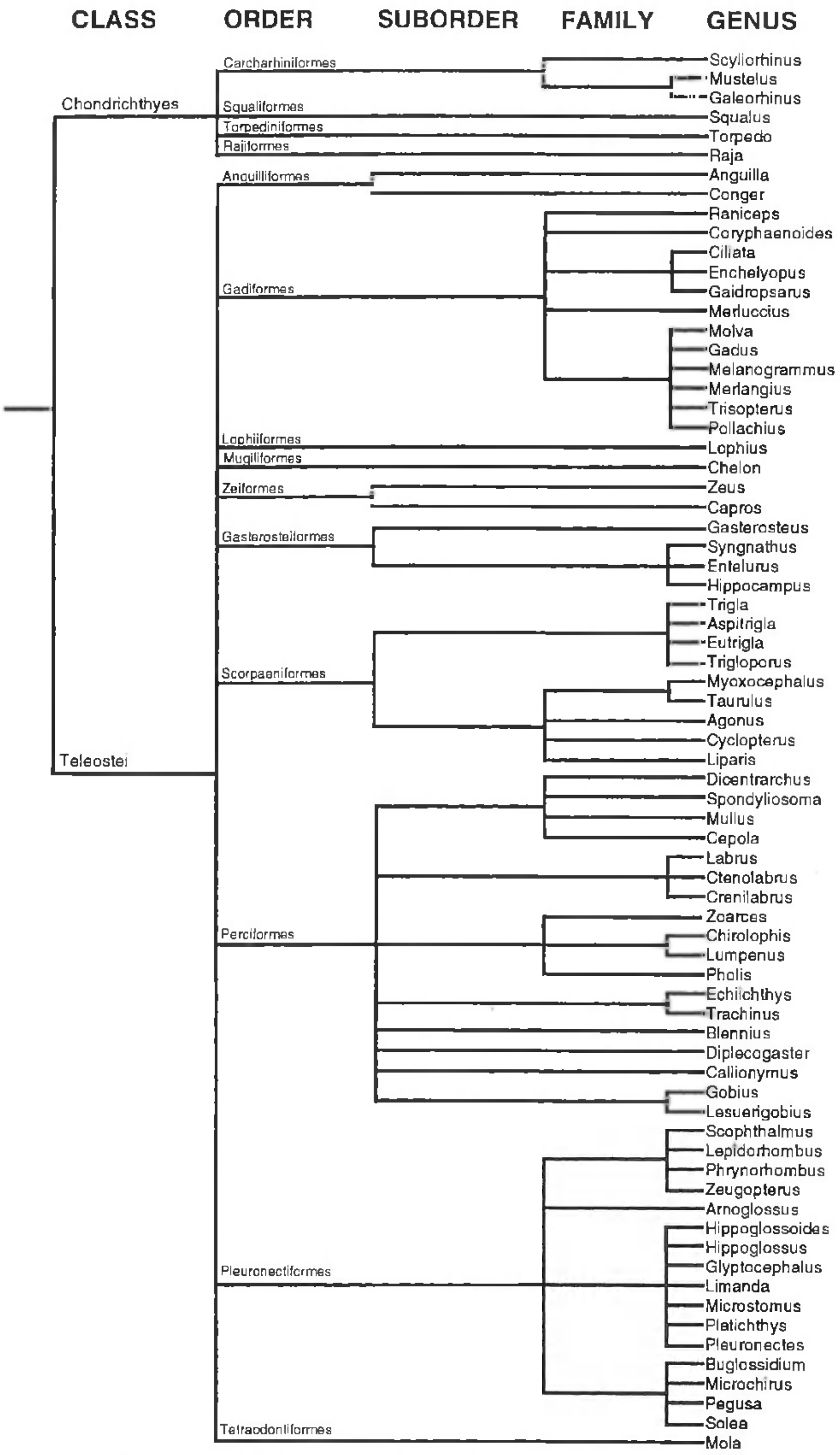

Fig. 2. The taxonomy compiled for this analysis, simplified to show five from a total of 13 levels of classification.

Table 1. The 13 levels of classification (k) used in the bottom-dwelling fish taxonomy, with the number of each type $\{s_k\}$, the 'standard' weighting scheme $\{\omega_k\}$, and an alternative version $\{\omega_k{}^o\}$ utilising an accumulation of the proportional decrease in taxon richness values $\{s_k\}$. More precisely, for a specific k, ω_k is the weighted path length between species belonging to differing taxon group k but the same group $k + 1$

k	Level	s_k	ω_k	$\omega_k{}^o$
1	Species	93	1	1·3
2	Sub-genus	89	2	6·9
3	Genus	72	3	8·9
4	Tribe	67	4	12·5
5	Sub-family	59	5	21·4
6	Family	41	6	22·9
7	Super-family	39	7	27·4
8	Sub-order	33	8	44·4
9	Order	14	9	54·9
10	Series	9	10	61·4
11	Super-order	7	11	65·6
12	Sub-division	6	12	85·3
13	Class	2	13	100

abundance data for the calculation of Δ^*, to downweight the contributions of dominant species, again identified the Eastern Central and Southeastern North Sea as taxonomically depauperate, and generated similar values for all other coastal sectors (Fig. 3c). Using only presence/absence data, the pattern in taxonomic distinctness Δ^+ between sectors was maintained for the Eastern Central and South-eastern North Sea, but the South-eastern Channel also had low values of Δ^+ (Fig. 3d). Mean values of Δ^+ for all sectors except the Bristol Channel fell below that of the theoretical mean, indicating that most of the individual sectors had lower average taxonomic range than the entire survey area.

Comparison of taxonomic diversity Δ and taxonomic distinctness Δ^* values determined from fish samples from all fishing station positions (Fig. 4a), showed an underlying positive correlation, but with considerable variability in this relationship to the lower right hand side of the figure. Here, some samples which were highly dominated and so had low values of taxonomic diversity Δ, represented assemblages which were taxonomically broad (i.e. high values of Δ^*). Note that the converse situation, i.e. taxonomically restricted assemblages with high Δ, cannot occur. The effect of data transformation on the calculation of Δ^* was limited, and the correlation between Δ^* calculated using transformed and untransformed data remained positive (Fig. 4b). In contrast, the apparently poor correlation between Δ^+ and Δ^* clearly showed the influence of species abundances when calculating taxonomic distinctness Δ^* (Fig. 4c). Finally, although the use of a more refined weighting to reflect the quantitative reduction in taxon richness on moving up the hierarchy seems logical, in fact the correlation between Δ^+ calculated with and without the modified weighting shows that they are highly correlated (Fig. 4d).

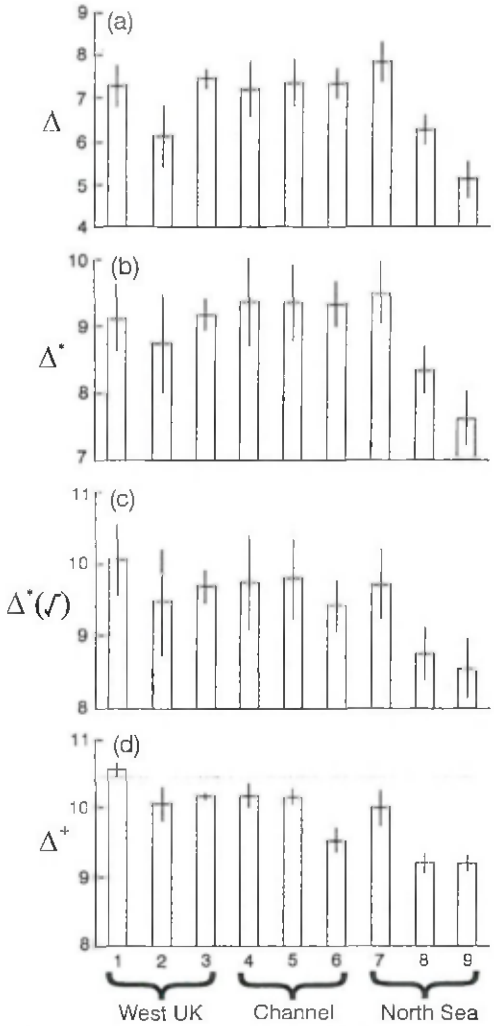

Fig. 3. For the nine coastal sectors in Fig. 1, the taxonomic diversity Δ (a) and the taxonomic distinctness Δ^* (b) of the untransformed fish abundance matrix, and the taxonomic distinctness Δ^* of square root transformed abundance data (c), and the taxonomic distinctness Δ^+ of presence/absence data (d). For each sector the mean value with 95% confidence limits is shown. The theoretical mean value of Δ^+ calculated by random sampling of species from the total species list is marked on Fig.3d.

There was no relationship between the total number of species in individual samples, and their taxonomic distinctness (Δ^+) calculated using presence/absence data (Fig. 5). Many of these Δ^+ values, however, were lower than the theoretical mean determined by random sampling from the entire bottom-dwelling fish fauna, a pattern already evident from Fig. 3d. Although most sample values fell within the 95% confidence limit funnel, a proportion had significantly lower values of Δ^+ than the theoretical mean.

These values of Δ^+ averaged over a quarter ICES rectangle showed consistent trends in taxonomic distinctness from the Eastern Central North Sea to the

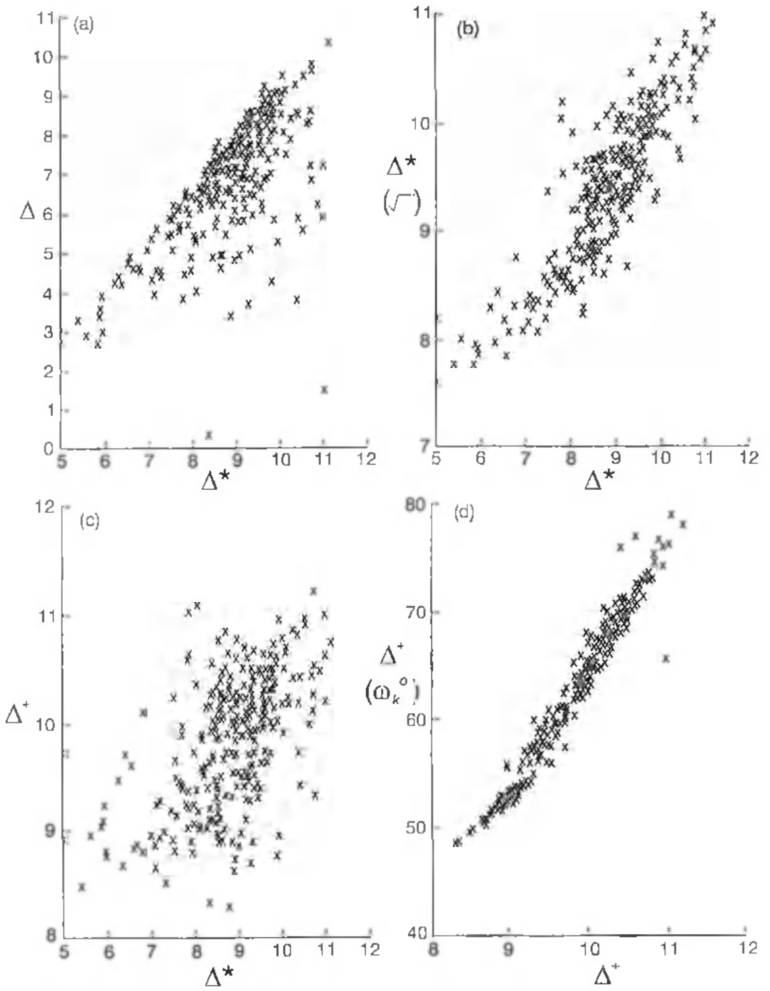

Fig.4. A comparison using all catch data between (a) taxonomic diversity Δ and taxonomic distinctness Δ^*, (b) the root transformed form of Δ^* against ordinary Δ^*, (c) taxonomic distinctness Δ^+ against ordinary Δ^*, and (d) Δ^+ using $\omega_k{}^o$ weights against Δ^+ using ordinary ω_k weights.

coastal waters west of the UK (Fig. 6). The Eastern Central and South-eastern North Sea, and South-eastern Channel, supported assemblages in which average taxonomic distinctness was less than the theoretical mean. Assemblages close to, and occasionally greater than the theoretical mean, occurred in the South-western North Sea, along the south coast of England, in the Bristol Channel and in some parts of the western Irish Sea (Fig. 6).

It is helpful when interpreting these regional differences in taxonomic distinctness to identify which fish taxa have contributed most to patterns in Δ^+. The number of species belonging to each of the 14 orders of bottom-dwelling fish in the dataset were identified (Table 2). In the Eastern Central and South-eastern North Sea, which were the least taxonomically distinct areas of all those surveyed, most species belonged to the orders Gadiformes (cod-like fishes), Perciformes (bottom-dwelling or benthic fish particularly dragonets of the family Callionymidae and gobies of the family Gobiidae), Pleuronectiformes (flatfishes) and Scorpaeniformes (gurnards, Triglidae). These groups contained almost all the species that were identified by Rogers et al. (1999) as numerically most abundant in the entire coastal demersal fauna, and which typified coastal sectors or discriminated between them (Table 3). Only two elasmobranch orders were represented here, and these only by a few species. From a total of 14 orders of fish, only 10 were represented in the North Sea, although the taxonomic distinctness of the South-western North Sea was increased by the presence there of greater numbers of more distantly related cartilaginous species (Carcharhiniformes, Rajiformes and Squaliformes) (Table 2). The bottom-dwelling fish fauna of the Channel was broadly similar to that of the North Sea in terms of the relative distribution of species amongst phyla, but the increased abundance of cartilaginous species (Rajiformes) and species from the order Perciformes, together with members of a more southerly fauna (e.g. Zeiformes,

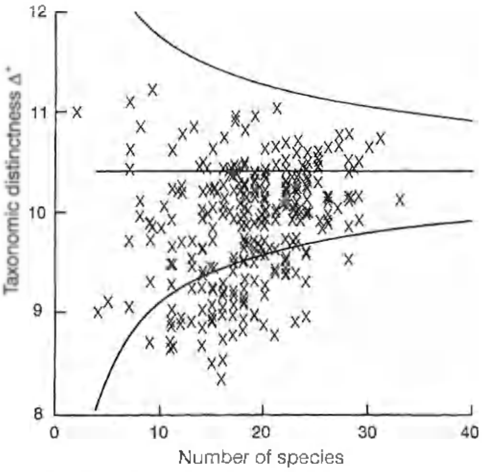

Fig. 5. The departure from the theoretical mean taxonomic distinctness Δ^+, and 95% confidence funnel, of all individual samples of bottom-dwelling fish species calculated using presence/absence data. All values of Δ^+ should fall within the confidence funnel assuming a null hypothesis that each sample contains species randomly selected from the total species list.

Zeus faber (L.)) increased the taxonomic distinctness of the region. This pattern continued into the western waters of the UK, where additional representatives of the southern fauna, for example the electric ray (Torpedinidae), mullet species (Mugiliformes), and sun fish (Tetradontiformes) were found. The most diverse fauna, representing 14 orders of cartilaginous and bony fishes, was found in the Bristol Channel (Table 2).

Discussion

We have found clear spatial patterns in the taxonomic diversity of bottom-dwelling fish assemblages in the coastal waters of NW Europe, at both regional and local scales. The reduction in average taxonomic range between the western waters of the UK and the southern North Sea mirrors similar patterns in the number of taxa represented, and the relative abundance of the species which comprise them (Fig. 6; Rogers et al. 1999). Although this suggests that taxonomic diversity and traditional species diversity may indeed be positively correlated within this limited latitudinal range,

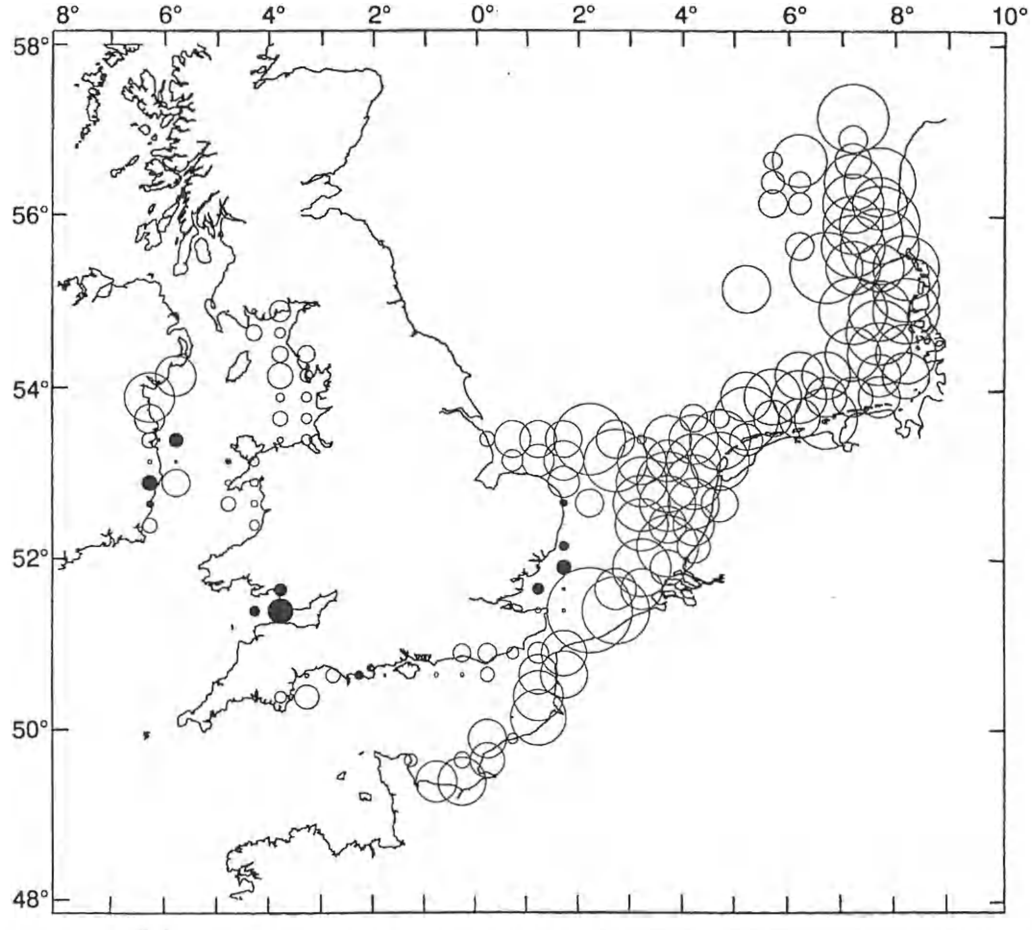

Fig.6. Taxonomic distinctness Δ^+ for samples grouped by quarter ICES rectangles. Filled circles show areas with mean values of Δ^+ above the theoretical mean, and open circles identify those regions with mean values below the theoretical mean. Increasing bubble size reflects the magnitude of departure from the mean.

Table 2. The mean number of species of demersal fish that belong to the same order, in each of the nine sectors sampled

	Sector								
Order	1	2	3	4	5	6	7	8	9
Rajiformes	3.1	2.0	3.5	3.1	2.4	1.3	1.5	0.2	0.1
Torpediniformes	0.1	0.2	0.2	0.6	0	0	0	0	0
Squaliformes	0.1	0	0	0	0	0	0.1	0	0
Carcharhiniformes	2.1	3.2	3.8	1.8	1.0	0.5	1.3	0.1	0.1
Anguilliformes	0.4	0.8	1.2	1.1	0.2	0	0.3	0.2	0.1
Gadiiformes	4.7	0.2	0.5	0.3	2.3	1.8	3.6	2.7	2.9
Lophiiformes	0.6	0	0	0	0	0	0	0	0.1
Gasterosteiformes	0.4	0.3	0.5	0.2	0.3	0.5	0.2	0.3	0.1
Perciformes	3.5	4.4	7.2	5.3	3.8	4.2	2.3	2.6	1.9
Pleuronectiformes	8.1	1.1	1.8	1.6	6.5	7.6	6.8	7.4	7.3
Scorpaeniformes	2.8	0	0	0.1	3.1	3.5	3.5	3.1	3.0
Zeiformes	0.4	0	0	0	0.3	0.2	0	0	0
Tetradontiformes	0.1	0	0	0	0	0	0	0	0
Mugiliformes	0.1	1.7	2.2	2.5	0	0	0	0	0

as suggested by Hall & Greenstreet (1998) for the Northern North Sea, the techniques used to calculate these two types of index quantify different aspects of biodiversity. This observation must therefore be a real effect rather than an artefact of the methodology. Records of samples which were taxonomically broad but had highly dominated species abundances (i.e. low taxonomic diversity) (Fig. 4a), highlight the additional degree of resolution that can be achieved when calculating these new indices on individual rather than regionally aggregated samples. It also shows that correlations of the type described by Hall & Greenstreet (1998) may only apply at relatively large geographical scales.

These new indices incorporate information on taxonomic relationships into diversity measures, and also support a statistical testing framework. They are therefore a valuable additional tool for interpreting assemblage structure. It is reasonable to assume that the observed patterns in taxonomic diversity and distinctness are: (i) the inevitable consequence of the regional patterns in natural processes, or (ii) a result of natural or man-made disturbance at a local scale, or (iii) a combination of both.

NATURAL PROCESSES

Although not universally true, many taxa show a clear decrease in their species diversity from the tropics to the poles (Pianka 1966; Ekman 1967). One explanation for this trend is that the tropics are larger in area than temperate or tundra zones, and experience relatively high and uniform annual mean temperatures (Rosenzweig 1992). In marine and freshwater systems, the largest number of fish species occur in the tropics with progressively fewer towards polar areas (Nelson 1994). While this rule can be applied universally to groups that occupy the continental shelf – e.g. coral reef fishes (Findley & Findley 1985) and flatfish (Pauly 1994) – there are some exceptions. For example, the deep water fish fauna of the rise and abyssal regions of the open oceans are more influenced by the temperature difference throughout their depth range than by the latitude, and so for this group, species diversity declines with increasing depth (White 1987). In the North-east Atlantic, the warm water fauna of the Mediterranean and Lusitanean regions reaches its northern boundary on the continental shelf to the west of the British Isles, close to the English Channel (Ekman 1967). In addition to the native fish fauna, there are also representatives of the more southerly Lusitanean fauna, particularly those from the order Perciformes, such as the Sparidae, Mullidae and Labridae, but also species from the families Zeidae, Molidae, and Mugillidae (Table 3). In most of the North Sea, there are two species groupings delimited by the boundary between stratified and mixed water masses approximately at the 40 m depth contour, and in much of the region, gadoids (cod, *Gadus morhua* (L.), whiting, *Merlangius merlangus* (L.) and pleuronectids (dab, *Limanda limanda* (L.)) predominate (Daan *et al.* 1990).

The role of local environmental disturbance and productivity is particularly important in the southern North Sea, which, unlike other regions that we examined, is relatively shallow and supports an extensive and homogeneous sandy substrate. The benthic fauna of this region is dominated by annelids, molluscs and crustaceans, and it is maintained in an early stage of succession partly by the influence of storm events and tides. In addition, the nutrient-rich fresh water from the Rivers Rhine and Elbe which flow into the German Bight, have created extensive eutrophication in inshore waters which has contributed to these patterns (Hickel, Mangelsdorf & Berg 1993). The absence of extensive reef-forming colonial invertebrates, and the varied fauna which can become associated with these biogenic structures, has reduced the range of niches

Table 3. The bottom-dwelling fish taxa caught during the beam trawl surveys, with their taxonomic hierarchy. Those species shown by Rogers et al. (1998a) to comprise 0.4% or more of the total numerical abundance of the bottom-dwelling fish catch are marked by *. Amongst this group, those which they additionally found to be consistent in typifying fish communities within sectors, or consistent in discriminating between them, are shown by **

CLASS	ORDER	FAMILY		
Chondrichthys	Rajiformes	RAJIDAE	blonde ray	*Raja brachyura*
			thornback ray	*Raja clavata**
			small-eyed ray	*Raja microocellata*
			spotted ray	*Raja montagui*
			starry ray	*Raja radiata*
			cuckoo ray	*Raja naevus*
			undulate ray	*Raja undulata*
	Torpediniformes	TORPEDINIDAE	marbled electric ray	*Torpedo marmorata*
			electric ray	*Torpedo nobiliana*
	Squaliformes	SQUALIDAE	spurdog	*Squalus acanthias*
	Carcharhiniformes	SCYLIORHINIDAE	lesser spotted dogfish	*Scyliorhinus canicula**
			nurse hound	*Scyliorhinus stellaris*
		CARCHARINIDAE	tope shark	*Galeorhinus galeus*
		TRIAKIDAE	smooth hound	*Mustelus mustelus*
			starry smooth hound	*Mustelus asterias*
Teleostei	Anguilliformes	ANGUILLIDAE	eel	*Anguilla anguilla*
		CONGRIDAE	Conger eel	*Conger conger*
	Gadiformes	GADIDAE	cod	*Gadus morhua**
			haddock	*Melanogrammus aeglefinus*
			whiting	*Merlangius merlangus**
			poor cod	*Trisopterus minutus**
			bib	*Trisopterus luscus**
			pollack	*Pollachius pollachius*
			common ling	*Molva molva*
		PHYCIDAE	five-bearded rockling	*Ciliata mustela*
			four-bearded rockling	*Enchelyopus cimbrius*
			shore rockling	*Gaidropsarus mediterraneus*
			three-bearded rockling	*Gaidropsarus vulgaris*
			rockling species	*Gaidropsarus spp.*
		RANICIPITIDAE	lesser forkbeard	*Raniceps raninus*
		MACROURIDAE	roundhead rat-tail	*Coryphaenoides rypestris*
		MERLUCCIIDAE	hake	*Merluccius merluccius*
	Lophiiformes	LOPHIIDAE	angler	*Lophius piscatorius*
	Gasterosteiformes	GASTEROSTEIDAE	stickleback	*Gasterosteus aculeatus*
		SYNGNATHIDAE	greater pipefish	*Syngnathus acus*
			Nilsson's pipefish	*Syngnathus rostellatus*
			snake pipefish	*Entelurus aequoreus*
			sea horse	*Hippocampus ramulosus*
			short snouted seahorse	*Hippocampus hippocampus*
		CAPROIDAE	boar-fish	*Capros aper*
	Perciformes	SPARIDAE	black sea-bream	*Spondyliosoma cantharus*
		MULLIDAE	red mullet	*Mullus surmuletus*
		CEPOLIDAE	red bandfish	*Cepola rubescens*
		PERCICHTHYIDAE	sea bass	*Dicentrarchus labrax*
			bass family	*Dicentrarchus spp.*
		LABRIDAE	cuckoo wrasse	*Labrus mixtus*
			ballan wrasse	*Labrus bergylta*
			rock cook	*Centrolabrus exoletus*
			goldsinny	*Ctenolabrus rupestris*
			corkwing wrasse	*Crenilabrus melops*
		ZOARCIDAE	eelpout	*Zoarces viviparus*
		PHOLIDAE	butterfish	*Pholis gunellus*
		STICHAEIDAE	Yarrels blenny	*Chirolophis ascanii*
			snake blenny	*Lumpenus lampretaeformis*
		TRACHINIDAE	greater weever	*Trachinus draco*
			lesser weever	*Echiichthys vipera***
		BLENNIIDAE	butterfly blenny	*Blennius ocellaris*
			tompot blenny	*Blennius gattorugine*
		GOBIESOCIDAE	two-spotted clingfish	*Diplecogaster bimaculata*
			clingfish family	*Gobiesocidae*
		CALLIONYMIIDAE	dragonet family	*Callionymidae***

Table 3.—*continued.*

CLASS	ORDER	FAMILY		
		GOBIIDAE	rock goby	Gobius paganellus
			black goby	Gobius niger
			Stevens goby	Gobius gasteveni
			Fries's goby	Lesuerigobius friesii
			goby family	Gobiidae*
	Pleuronectiformes	SOLEIDAE	sole	Solea solea**
			solenette	Buglossidium luteum*
			sand sole	Pegusa lascaris
			thick back sole	Microchirus variegatus*
		PLEURONECTIDAE	plaice	Pleuronectes platessa**
			flounder	Platichthys flesus
			dab	Limanda limanda**
			lemon sole	Microstomus kitt*
			witch	Glyptocephalus cynoglossus
			long rough dab	Hippoglossoides platessoides*
			halibut	Hippoglossus hippoglossus
		SCOPHTHALMIDAE	brill	Scophthalmus rhombus
			turbot	Scophthalmus maximus
			megrim	Lepidorhombus whiffiagonis
			Ekstroms topknot	Phrynorhombus regius
			Norwegian topknot	Phrynorhombus norvegicus
			topknot	Zeugopterus punctatus
		BOTHIDAE	scaldfish	Arnoglossus laterna*
			Imperial scaldfish	Arnoglossus imperialis
	Scorpaeniformes	TRIGLIDAE	tub gurnard	Trigla lucerna*
			red gurnard	Aspitrigla cuculus*
			grey gurnard	Eutriglia gurnardus*
			streaked gurnard	Trigloporus lastoviza
		COTTIDAE	bull-rout	Myoxocephalus scorpius
			sea scorpion	Taurulus bubalis
		AGONIDAE	hook-nose	Agonus cataphractus**
		CYCLOPTERIDAE	lump sucker	Cyclopterus lumpus
		LIPARIDAE	sea snail	Liparis liparis
			sea snail genus	Liparis spp.
	Zeiformes	ZEIDAE	John dory	Zeus faber
	Tetradontiformes	MOLIDAE	sunfish	Mola mola
	Mugiliformes	MUGILIDAE	thick lipped mullet	Chelon labrosus
			grey mullet family	mugilidae

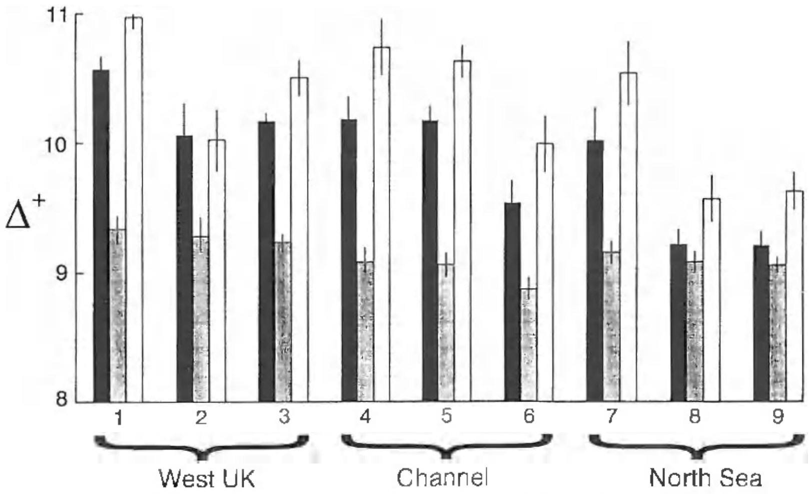

Fig. 7. Taxonomic distinctness Δ^+ of the nine coastal sectors using presence/absence data (solid bars) (shown also in Fig. 3d), showing the effect of removing all elasmobranch species (tinted bars), and all flatfish (pleuronectidae) (open bars) on the calculation of the index.

which the region can support. This in turn has limited the range of fish species which can use these environments for food and shelter, such as the herbivorous mullets (Mugillidae) (Daan *et al.* 1990).

HUMAN IMPACTS

The North Sea has also experienced extensive manipulation of its fish communities by commercial fishing activity, and the extent of this disturbance, and its potential impact on the bottom-dwelling fish assemblage, deserves particular attention. As one may expect from a consistently high level of fishing activity, the most obvious effects of the removal of fish from the higher trophic levels have been on the temporal changes in size structure of communities (Pope 1989; Greenstreet & Hall 1996; Rice & Gislason 1996; Rice & Kronlund 1997). The reduction in the abundance of larger fish (Pope & Knights 1982; Rice & Gislason 1996; Jennings, Reynolds & Mills 1998) has caused changes in the dominance of the smaller target and non-target components of the assemblage, as well as the species composition of the catch. Although several studies undertaken in tropical waters show that locally intense fishing activity can cause reductions in species richness, there are few examples of this effect in temperate waters (Greenstreet & Hall 1996; Rice & Gislason 1996); and see review by (Jennings & Kaiser 1998). Is there any evidence that anthropogenic activity has contributed to the lower taxonomic range of populations in the southern North Sea, compared to elsewhere on the continental shelf?

There are some examples of commercial groundfish species in the North-east Atlantic disappearing from large parts of their former range (Heessen & Daan 1996; Rijnsdorp *et al.* 1996; Walker & Heessen 1996). Perhaps one of the best known involves the common skate, *Raja batis* (L.), (Brander 1981). The combination of late age at maturity (11 years) large maximum size (>2 m) and a low potential rate of population increase, are thought to have been responsible for its decline. A similar decline has recently been documented for the barndoor skate *Raja laevis* (Mitchill) (Casey & Myers 1998). The presence of these life-history characteristics was also directly linked to decreasing trends in abundance of 18 intensively exploited fish stocks, after accounting for differences in their fishing mortality (Jennings *et al.* 1998). The elasmobranchs have some or all of these characteristics, and dogfish, and several species of ray (Squaliformes and Carcharhiniformes), which generally have a widespread distribution throughout the North-east Atlantic, are exploited by commercial fisheries (Holden 1974; Quero & Cendrero 1996; ICES 1997; Walker, Howlett & Millner 1997). In the Bay of Biscay, the long-term decline in abundance of three species of ray (*Raja batis* (L.), *Raja brachyura* (Lafont) and *Raja clavata* (L.)), and other species of large bodied carcharhiniform sharks, was attributed to the long-term effects of bottom trawling throughout the area (Quero & Cendrero 1996). Of all the families which comprise the total fish assemblage therefore the elasmobranchs are the most likely to show effects of commercial activity, if it is present.

To what extent do the elasmobranchs influence the spatial patterns in taxonomic distinctness that we identified in Fig. 6? To investigate this further, values of Δ^+ were recalculated for each sector, but using a revised dataset in which all elasmobranchs, i.e. members of the Chondrichthyes (Table 3)) were assumed to be absent from catches. The result of this analysis describes the taxonomic distinctness of the bottom-dwelling, non-elasmobranch fishes, and should exclude the potentially confounding effects of human activity on this group to reveal the underlying biogeographic pattern. Differences in mean Δ^+ between sectors using this revised dataset were less significant (F statistic = 8·4) than when previously calculated using the full dataset ($F = 42{\cdot}9$) (Fig. 7). In particular, mean taxonomic distinctness in all sectors of the North Sea appeared only marginally less than those west of the UK (Fig. 7). This is not simply a scale effect in which a reduced dataset leads to reduced discrimination. When the calculations were repeated but with all the flatfish (Pleuronectiformes, a similar-sized group) excluded from the dataset instead of the elasmobranchs, the effect was barely detectable (Fig. 7). Mean values of Δ^+ retained the same general relationships between sectors, and the differences between sector means were still relatively large ($F = 31.7$). This analysis confirms that the elasmobranchs have a major influence on the taxonomic distinctness of the North-east Atlantic fauna, and that when they are artifically excluded from the samples, the remaining species have a more uniform taxonomic range throughout the region. In such a widely distributed bottom-dwelling group, this effect is surprising. One possible explanation is that the adverse effects of high fishing mortality have influenced the distribution and abundance of some elasmobranch species to create an artificial pattern. Alternatively, it may result from different levels of fishing activity within coastal waters. Further analysis of time-series changes in the distribution and abundance of elasmobranchs, their life-history characteristics and their patterns of exploitation, will be necessary to confirm the extent of the role of high fishing effort in the decline of some of these species.

In the event of perturbations caused by either human impact or changing environmental conditions, Tilman (1996) claims that the taxonomic range of an assemblage will be important for maintaining the stability of the ecosystem. In some marine invertebrate communities there is considerable redundancy at the species level, such that similar patterns in structure can be identified at a higher taxonomic level. This suggests that there may also be several species which perform the same functional role (Ferraro & Cole

1992; Clarke & Warwick 1998a). Marine fish communities with low levels of species redundancy and where few species fulfil key functional roles, for example some coral reef ecosystems, may be least able to withstand environmental change (Hughes 1994; Jennings & Kaiser 1998). These indices of taxonomic diversity and distinctness can therefore provide valuable information on the extent to which fish assemblages are able to resist change, and this will become increasingly relevant in our interpretation of changes in assemblage structure.

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References

Baltz, D.M. (1991) Introduced fishes in marine systems and inland seas. *Biological Conservation*, **56**, 151–177.

Brander, K. (1981) Disappearance of common skate *Raia batis* from the Irish Sea. *Nature*, **290**, 48–49.

Casey, J.M. & Myers, R.A. (1998) Near extinction of a large, widely distributed fish. *Science*, **281**, 690–692.

Clarke, K.R. & Warwick, R.M. (1998a) Quantifying structural redundancy in ecological communities. *Oecologia*, **113**, 278–289.

Clarke, K.R. & Warwick, R.M. (1998b) A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology*, **35**, 523–531.

Connell, J.H. (1978) Diversity in tropical rain forests. *Science*, **199**, 1302–1310.

Daan, N., Bromley, P.J., Hislop, J.R.G. & Nielsen, N.A. (1990) Ecology of North Sea fish. *Netherlands Journal of Sea Research*, **26**, 343–386.

Ekman, S. (1967) *Zoogeography of the Sea.* Sidgwick and Jackson, London.

Ferraro, S.P. & Cole, F.A. (1992) Taxonomic level sufficient for assessing a moderate impact on macrobenthic communities in Puget Sound, Washington, USA. *Canadian Journal of Fisheries and Aquatic Science*, **49**, 1184–1188.

Findley, J.S. & Findley, M.T. (1985) A search for pattern in butterfly fish communities. *American Naturalist*, **126**, 800–816.

Gee, J.M. & Warwick, R.M. (1996) A study of global biodiversity patterns in the marine motile fauna of hard substrata. *Journal of the Marine Biological Association, UK*, **76**, 177–184.

Greenstreet, S.P.R. & Hall, S.J. (1996) Fishing and the ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. *Journal of Animal Ecology*, **65**, 577–598.

Hall, S.J. & Greenstreet, S.P.R. (1998) Taxonomic distinctness and diversity measures: responses in marine fish communities. *Marine Ecology Progress in Series*, **166**, 227–229.

Heessen, H.J.L. & Daan, N. (1996) Long-term trends in ten non-target North Sea fish species. *ICES Journal of Marine Science*, **53**, 1060–1078.

Hickel, W., Mangelsdorf, P. & Berg, J. (1993) The human impact in the German Bight: eutrophication during three decades (1962–91). *Helgolander Meeresunters*, **47**, 243–263.

Holden, M.J. (1974) Problems in the rational exploitation of elasmobranch populations and some suggested solutions. *Sea Fisheries Research* (ed. F.R. Harden Jones), pp. 117–137. Elek Science, London.

Hughes, T.P. (1994) Catastrophes, phase shifts and large-scale degradation of a Caribbean reef. *Science*, **265**, 1547–1551.ICES. (1997) *Report of the Study Group on Elasmobranch Fishes* ICES CM 1997/G: 2.

Jennings, S. & Kaiser, M.J. (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology*, **34**, 201–352.

Jennings, S., Reynolds, J.D. & Mills, S.D. (1998) Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of, London*, **265**, 333–339.

Ludwig, J.A. & Reynolds, J.F. (1988) *Statistical Ecology: a Primer on Methods and Computing.* John Wiley and Sons, New York.

Magurran, A.E. (1988) *Ecological Diversity and its Measurement.* Chapman & Hall, London.

McEachran, J.D. & Miyake, T. (1990) Phylogenetic interrelationships of skates: a working hypothesis (Chondrichthyes, Rajoidei). *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries* (eds H.L. Pratt, S.H. Gruber & T. Taniuchi), pp. 285–304. *NOAA Technical Report NMFS 90*.

McEachran, J.D., Dunn, K.A. & Miyake, T. (1996) Interrelationships of the Batoid fishes (Chondrichthyes: Batoidea). *Interrelationships of Fishes* (eds M.L.J. Stiassny, L.R. Parenti & G.D. Johnston), pp. 63–84. Academic Press, San Diego.

Nelson, J.S. (1994) *Fishes of the World*, 3rd edn. John Wiley & Sons, New York.

Pauly, D. (1994) A framework for latitudinal comparisons of flatfish recruitment. *Netherlands Journal of Sea Research*, **32**, 107–118.

Pearson, T.H. & Rosenberg, R. (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology, Annual Review*, **16**, 229–311.

Petraitis, P.S., Latham, R.E. & Niesenbaum, R.A. (1989) The maintenance of species diversity by disturbance. *Quarterly Review of Biology*, **64**, 393–418.

Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist*, **100**, 33–46.

Pope, J.G. & Knights, B.J. (1982) Comparison of the length distributions of combined catches of all demersal fishes in surveys in the North Sea and at Faroe Bank. *Canadian Special Publication of Fisheries and Aquatic Sciences, Vol 59* (ed. M.C. Mercer), pp. 116–118. Government of Canada, Ottawa.

Pope, J.G. (1989) Fisheries research and management for the North Sea: the next hundred years. *Dana*, **8**, 33–43.

Quero, J.-C. & Cendrero, O. (1996) Incidence de la pêche sur la biodiversité ichtyologique marine: Le bassin d'Arcachon et le plateau continental sud Gascogne. *Cybium*, **20**, 323–356.

Rice, J. & Gislason, H. (1996) Patterns of change in the size spectra of numbers and diversity of the North Sea assemblage, as reflected in surveys and models. *ICES Journal of Marine Science*, **53**, 1214–1225.

Rice, J.C. & Kronlund, A.R. (1997) Community analysis and flatfish: diagnostic patterns, processes, and inference. *Journal of Sea Research*, **37**, 301–320.

Rijnsdorp, A.D., Van Leewen, P.I., Daan, N. & Heessen, H.J.L. (1996) Changes in abundance of demersal fish species in the North Sea between 1906 and 1909 and 1990–95. *ICES Journal of Marine Science*, **53**, 1054–1062.

Rogers, S.I., Maxwell, D., Rijnsdorp, A.D., Damm, U. & Vanhee, W. (1999) 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 coastal demersal fish faunas in the Northeast Atlantic? *Fisheries Research*, **40**, 135–152.

Rogers, S.I., Rijnsdorp, A.D., Damm, U. & Vanhee, W. (1998) Demersal fish populations in the coastal waters of the UK and continental NW Europe from beam trawl survey data collected from 1990 to 1995. *Journal of Sea Research*, **37**, 79–102.

Rosenzweig, M.L. (1992) Species diversity gradients: we know more and less than we thought. *Journal of Mammology*, **73**, 715–730.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Somerfield, P.J., Olsgard, F. & Carr, K.R. (1997) A further examination of two new taxonomic distinctness measures. *Marine Ecology Progress in Series*, **154**, 303–306.

Sousa, W.P. (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, **60**, 1225–1239.

Tilman, D. (1996) Biodiversity: population versus ecosystem stability. *Ecology*, **77**, 350–363.

Walker, P., Howlett, G. & Millner, R. (1997) Distribution, movement and stock structure of three ray species in the North Sea and eastern Channel. *ICES Journal of Marine Science*, **54**, 797–808.

Walker, P.A. & Heessen, H.J.L. (1996) Long-term changes in ray populations in the North Sea. *ICES Journal of Marine Science*, **53**, 1085–1093.

Warwick, R.M. & Clarke, K.R. (1993) Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. *Marine Ecology Progress in Series*, **92**, 221–231.

Warwick, R.M. & Clarke, K.R. (1995) New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress in Series*, **129**, 301–305.

Warwick, R.M. & Clarke, K.R. (1998) Taxonomic distinctness and environmental assessment. *Journal of Applied Ecology*, **35**, 532–543.

White, B.N. (1987) Oceanic anoxic events and allopatric speciation in the deep sea. *Biological Oceanography*, **5**, 243–259.

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