Mapping spatial variation in demersal fish species diversity and composition in the North Sea: accounting for species- and size-related catchability in survey trawls

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The paper maps spatial patterns of groundfish species diversity. It considers how the catchability of different fish species in two different types of bottom trawls, the IBTS GOV and the 8-m beam trawl, influences the estimates of species diversity. Maps of groundfish species diversity derived from these two survey trawls are compared to determine the extent to which the maps of spatial variation in groundfish species diversity are influenced by gear type. Catchability-at-length coefficients were applied to the IBTS data to raise the observed catches to estimates of "actual" numbers of fish present in the path of the trawl, which are then used to produce maps of "actual" species diversity across the North Sea. Finally, these raised maps of "actual" groundfish species diversity are shown to be more explainable based on physical environmental parameters such as depth. We suggest that species diversity maps that take account of catchability provide more reliable information on which to base management decisions than "gear-biased" views. The implications for management are discussed, with particular emphasis on using closed areas to conserve marine biodiversity.

Keywords: groundfish survey data, marine protected areas, size-related catchability, species diversity, species-related catchability, species richness.

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Introduction

Fishing activity in the North Sea has increased markedly over the course of the 20th century (Daan *et al.*, 1990; Greenstreet *et al.*, 1999a), and consideration of the effects this has on various attributes of the demersal fish community has generated considerable interest (Gislason and Rice, 1998; Jennings *et al.*, 1999a, 2002; Piet and Jennings, 2005). There is now a large body of evidence to suggest that fish species diversity has been adversely affected (Greenstreet and Hall, 1996; Rijnsdorp *et al.*, 1996; Hall and Greenstreet, 1998; Greenstreet *et al.*, 1999b; Greenstreet and Rogers, 2000, 2006). Policy drivers such as the Convention on Biological Diversity (CBD), Annex V of the Convention Protection of the Marine Environment of the North-East Atlantic (OSPAR), and the EC Marine Directive all stress the importance of conserving biodiversity. Such a goal should therefore feature highly in any ecosystem approach to the management of natural resources in the North Sea. The use of protected areas to achieve ecological and conservation objectives is explicitly mentioned in several of these policy drivers. Article 8 of the CBD, for example, suggests that a system of protected areas be established where special measures are taken to conserve biological diversity. UK marine strategy documents ("Seas the Opportunity" and "Charting Progress") and the EC Marine Strategy Directive explicitly consider the use of marine protected areas (MPAs) to achieve their goals of "clean, healthy, safe, productive, and biologically diverse oceans and seas". Indeed, MPAs are widely considered as potentially one of the most useful tools available to managers tackling ecological objectives for marine ecosystems (Agardy, 1994; Lindeboom, 1995; Allison *et al.*, 1998; Hastings and Botsford, 2003; Micheli *et al.*, 2004). Most analyses of North Sea groundfish survey data to date have involved time-series analyses, linking changes in the community over time to temporal variation in fishing activity to demonstrate fishing effects (see the references cited at the beginning of the Introduction). However, the use of MPAs to conserve groundfish species diversity in the North Sea clearly requires detailed knowledge of spatial variation in this component of the marine ecosystem, making spatial analysis of these data and mapping of groundfish species diversity now a priority for marine scientists.

It is known that different species of fish and size classes of the same species have different "catchabilities" in particular types of fishing gear (Harley and Myers, 2001; Winger *et al.*, 2004; Fraser *et al.*, 2007). The catchability coefficient, *q*, of a fishing gear determines what fraction of the number of a given category of fish of a particular species and size present in the path of the trawl actually gets caught. Therefore, the Grande Overture Verticale otter trawl (GOV) used in the ICES quarter 1 (Q1) and quarter 3 (Q3) International Bottom Trawl Surveys (IBTS) provides a GOV-biased view of the fish community, and likewise the 8-m beam trawl (8BT) fishing gear used in the Q3 Dutch Beam

Trawl Survey (DBTS) provides an 8BT-biased view of the fish community. The species composition of the groundfish assemblage of the North Sea varies markedly, being dominated by roundfish species in the north and flatfish species in the south (Daan *et al.*, 1990). Catchabilities of roundfish are much higher than flatfish in otter trawl gears such as the GOV, whereas the converse is true in respect to beam trawls (ICES, 2004). Hence, the dominance of commercial otter trawling in the northern North Sea, and beam trawling in the south (Jennings *et al.*, 1999b). Spatial patterns of the species diversity of the demersal fish community derived from the GOV and 8BT may therefore be strongly gear-dependent and differ considerably. Moreover, neither may reflect the real spatial pattern in species diversity of the demersal fish community present across the North Sea. Under such circumstances, their use in underpinning the advice on which to base closed area management could be seriously flawed. Issues of species catchability in IBTS trawls have come to the fore in previous studies that attempted to estimate the total biomass of fish in the North Sea (Yang, 1982; Daan *et al.*, 1990; Sparholt, 1990). These studies equated groundfish survey catch rates of the main assessed commercial species with estimates of their biomass in the North Sea derived from the ICES stock assessment process. All the non-assessed species were then assigned to a "fish-type" group, each of which was headed by one or more of the assessed species. Within each of the "fish-type" groups, the biomass of the non-assessed species was estimated as a ratio of the two catch rates multiplied by the biomass of the assessed species. A more recent study has further developed this approach, utilizing data collected on two surveys using very different research trawls, the GOV and the 8BT, to model the variation in q for each 1-cm size class of every species sampled by the GOV trawl in the ICES Q3 IBTS (Fraser *et al.*, 2007).

Here, we carry out spatial analysis of the Q3 IBTS and the Q3 DBTS data to compare maps of species composition, species richness, and species diversity derived from two towed fishing gears: the GOV otter trawl and the 8BT. We then apply the estimated catchability at length coefficients for each species in the GOV samples in an attempt to remove the "gear bias" and to determine the "real" spatial patterns of these attributes of the "actual" demersal fish community present in the North Sea. For the purposes of this study, only data covering the period 1998–2004 were analysed, because before this, not all countries participating in the ICES Q3 IBTS used the same GOV trawl gear, and tow durations also varied.

Methods

Sample standardization

Despite fairly rigid protocols being laid down for each survey, the trawl samples contained in both the IBTS and DBTS datasets were not fully standardized with respect to tow duration and speed. Although standard trawl duration was set at 30 min, hauls up to ± 5 min of this were common. Furthermore, as the area swept in IBTS hauls of given duration and tow distance was not consistent, door and wing spread must also have differed from tow to tow. To reduce as far as possible the chance of variable sampling effort influencing our results, we defined "standard" tows for both surveys, and our analyses were restricted to these "standard" tows.

We defined "standard" trawls for both surveys based on area swept. First, we examined the area swept in trawl samples that were within ± 3 min of the stipulated time of 30 min and identified the upper and lower 5 percentile swept area values for this subset. Then from both complete datasets, we extracted all trawl samples with swept areas between these two bounds, regardless of trawl duration. We again determined the upper and lower 5 percentile swept area values for these new subsets of both datasets and excluded all samples that were outside these bounds. This standardization process resulted in ~8% of both survey datasets being excluded from our analysis.

Diversity metrics

There are two different aspects to species diversity: the number of species, and the evenness of the distribution of individuals between species. We used three different metrics each differing in the extent to which they are influenced by the two aspects of species diversity (Southwood, 1978). Species richness (S) was simply the count of all species encountered in a sample, a metric strongly influenced by sampling effort variation, equivalent to Hill's (1973) N_0. We also apply two indices of species diversity; Hill's N_1 and N_2, N_1 being the exponential of the Shannon–Weiner index, and N_2 the reciprocal of Simpson's index. All diversity metrics were calculated using the PRIMER software package (Clark and Warwick, 2001). N_1 is more sensitive to the number of species recorded in the sample, whereas N_2 is more sensitive to the evenness of the distribution of individuals between species.

Similarity in the species composition of the demersal fish community sampled in different ICES rectangles was assessed using the Bray–Curtis Similarity Index. Abundance data were first $\sqrt{\sqrt{}}$ transformed to downweight the effects of the more abundant species. The similarity matrix between all pairs of ICES rectangles was subjected to hierarchical group-average cluster analysis to identify groups of ICES rectangles with similar species composition. These analyses were again performed using the PRIMER software.

Sample treatment

Recent studies suggest that it is necessary to aggregate up to 20 GOV trawl samples and 20 8BT trawl samples to derive reliable estimates of local species diversity and species richness (Greenstreet *et al.*, 2007). For each survey, therefore, the entire 7-year period was treated as a single collection of trawl samples, ignoring sample year. For each ICES rectangle, 20 trawl samples in each of the surveys closest to the geographic centre of the rectangle were aggregated to form single-rectangle-level samples of the demersal fish community.

The IBTS GOV abundance data were corrected to account for catchability using the catchability coefficients published by Fraser *et al.* (2007). These coefficients were derived based on geometric mean density estimates. First, therefore, it was necessary to determine the geometric mean density of each 1-cm size class of each species in each rectangle. These density estimates were then raised by the reciprocal of the catchability coefficients provided by Fraser *et al.* (2007). Summing over all length classes then provided raised density estimates for each species. Bray–Curtis, Hill's N_0, Hill's N_1, and Hill's N_2 statistics could then be calculated on the raised species density data. For visualization, the diversity indices were smoothed using a two-dimensional penalized regression spline, with degrees of freedom chosen by generalized cross-validation, assuming gamma errors and a log link (Wood, 2006).

Differences between two sets of diversity indices were assessed by calculating the log ratio of the indices in each rectangle, log (index1/index2), then smoothing the log ratios with a two-dimensional spline, assuming normal errors and an identity link.

The fitted values and standard errors from the smooth were then used to test, on a pointwise basis, whether the log ratio in each rectangle was significantly different from 0. The smoothed log ratios were plotted with contours corresponding to pointwise significance levels of 0.0001, 0.001, 0.01, and 0.05. The 0.05 contour shows where the diversity indices differed at a pointwise significance level of 5%.

Results

The pattern of spatial variation in species richness (S) across the North Sea was similar for both raw survey datasets (Figure 1a), but with the 8BT catching slightly more species than the GOV. However, this was not the case for either Hill's N_1 or Hill's N_2. Figures 1b and 1c show that values of Hill's N_1 and N_2 in the 8BT were significantly higher ($p < 0.0001$) across most of the area common to both surveys. For both diversity indices, our perception as to how species diversity varied across the North Sea was strongly influenced by which survey dataset was used. Examination of the correlation between the three metrics within each dataset also revealed marked differences between the data collected by the GOV otter trawl and the 8-m beam trawl. For both datasets, spatial variation in the two diversity indices, Hill's N_1 and N_2, was positively correlated, but although N_1 and N_2 were both positively correlated with S in the 8BT dataset, they were negatively correlated when the GOV data were examined (Figure 2).

When applying the reciprocal catchability coefficient raising factors to the GOV data, we focused on spatial variation in Hill's

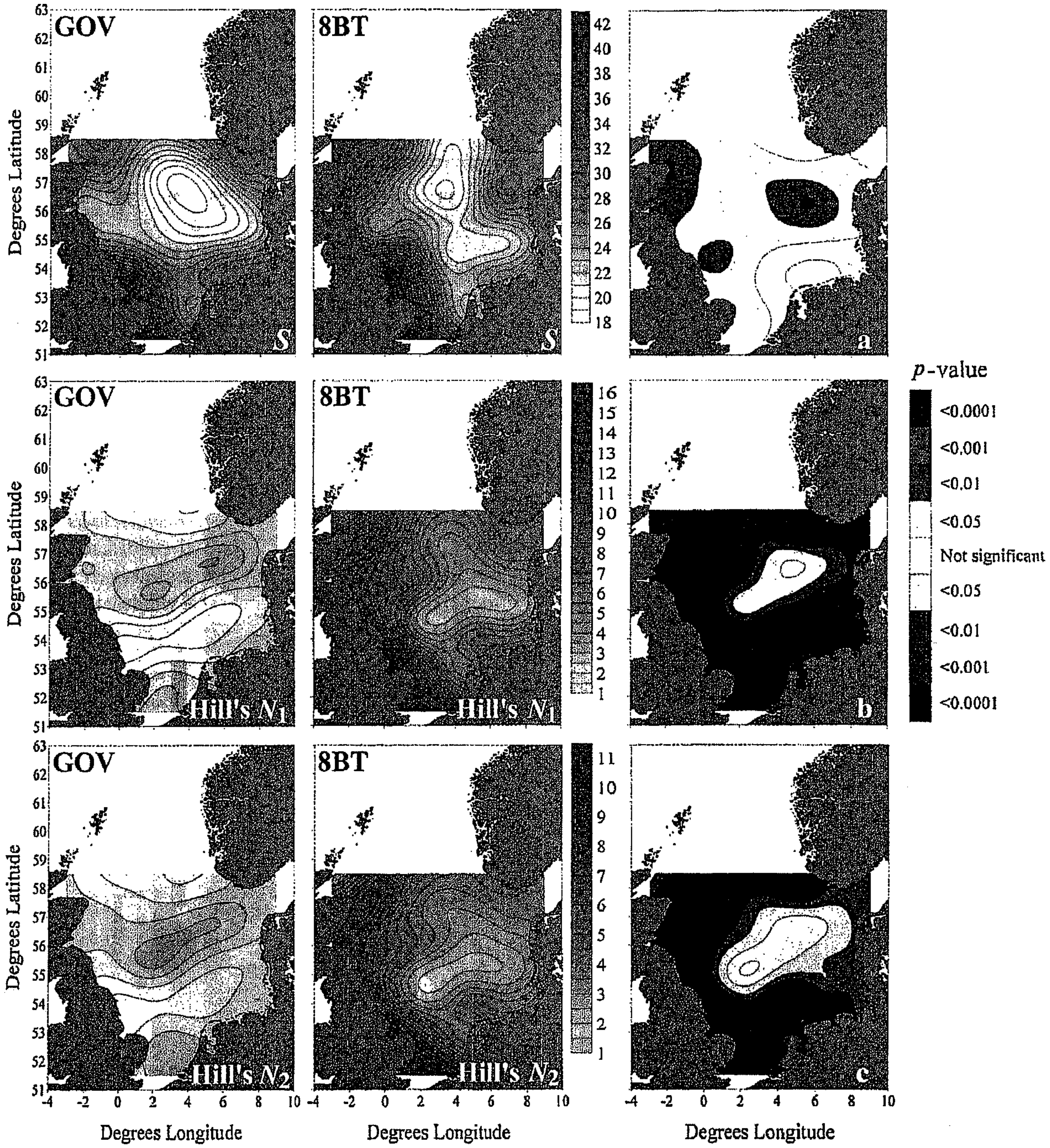

Figure 1. Spatial variation in three diversity metrics (S, species richness; N_1, Hill's N_1 indices of species diversity and N_2, Hill's N_2 indices of species diversity) computed for the IBTS (GOV) and DBTS (8BT) surveys. Differences between the three measures of species diversity are shown in panels (a), (b), and (c), where green/blue indicates that the metric for the GOV is significantly greater/less than that for the 8BT.

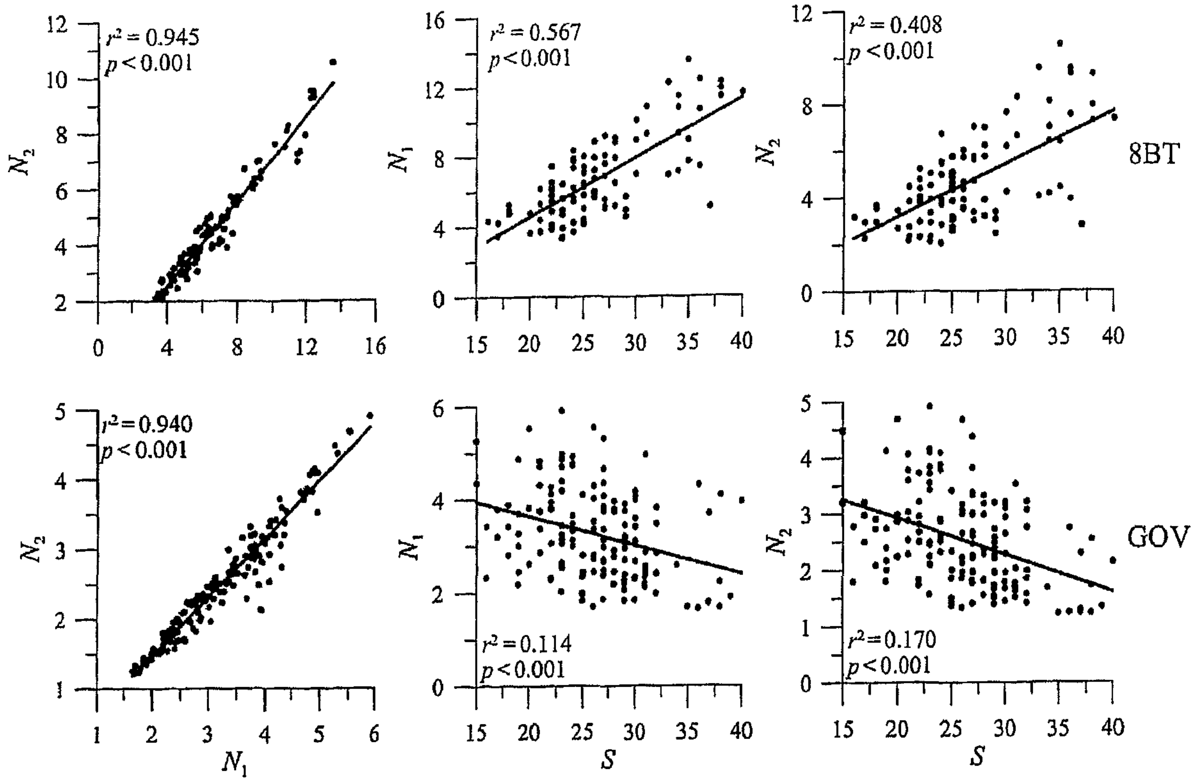

Figure 2. Intercorrelations between the species richness and species diversity metric calculated for both survey datasets, IBTS (GOV) and DBTS (8BT).

N_1 and N_2. The effect of taking catchability into account on both diversity metrics was profound (Figure 3). When based on GOV survey data raised to take account of species- and size-related catchability in the trawl gear, it was obvious that species diversity was highest in the shallower, hydrographically mixed, more productive region of the southern North Sea. Figures 3a and 3b

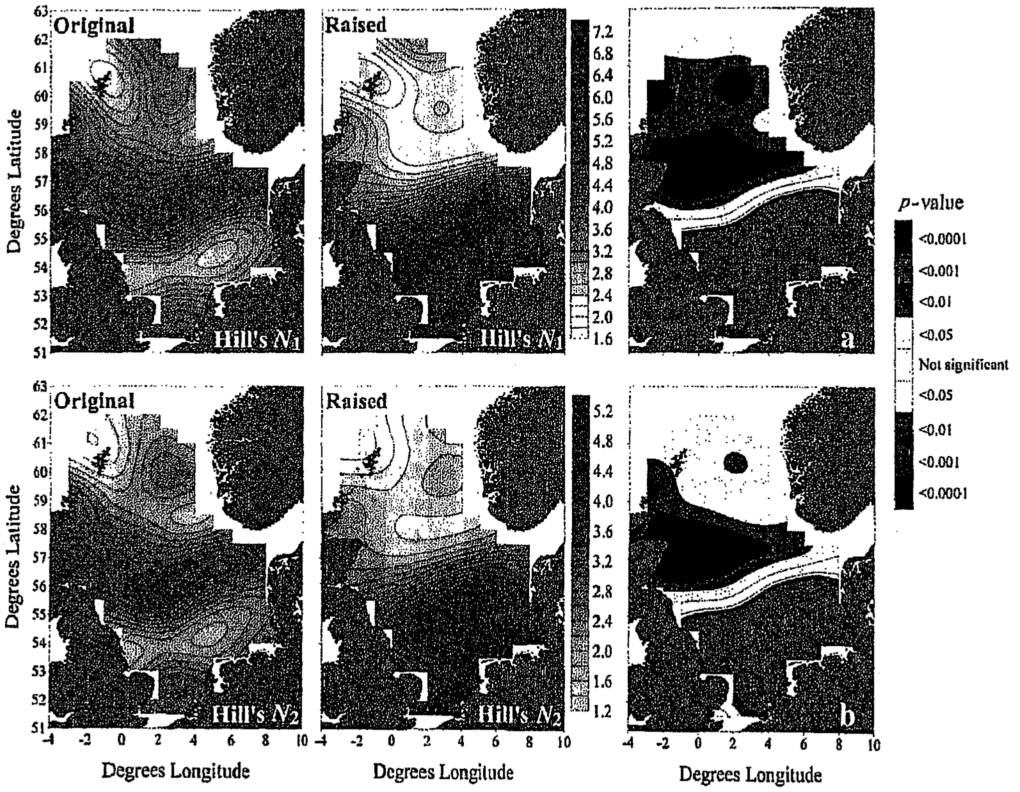

Figure 3. Spatial variation in Hill's N_1 and Hill's N_2 across the North Sea based on the IBTS (GOV) dataset, illustrating the effect of taking into account species- and size-related catchability in the GOV. Differences between the two measures of diversity are shown in panels (a) and (b), where green/blue indicates that the metric for the original data is greater/less than that for the raised GOV data.

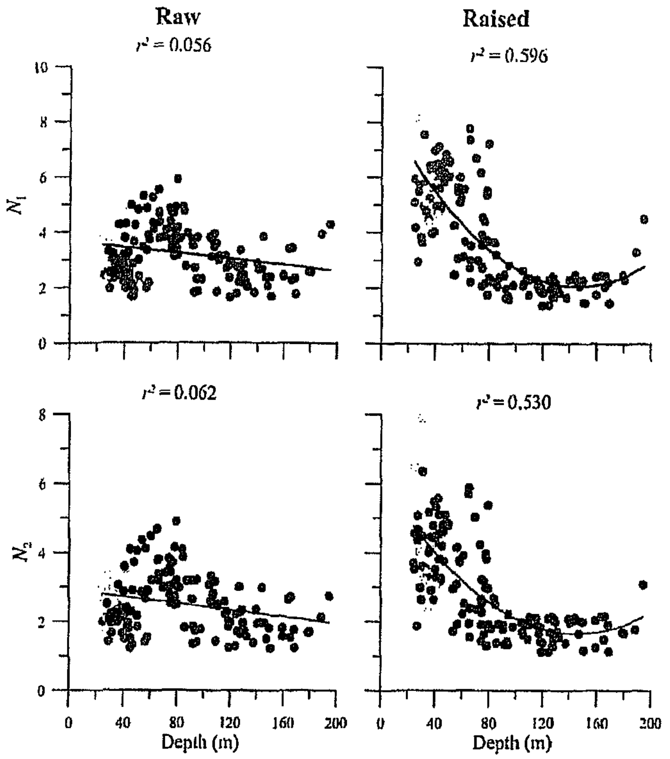

Figure 4. Relationship between Hill's N_1 and N_2 and depth illustrating the effect on this relationship when trawl abundance data are raised to take account of species- and size-related variation in catchability. Data point colour coding corresponds to the cluster identity indicated in Figure 5.

show that when catchability is taken into account, Hill's N_1 and N_2 are significantly lower in the northern North Sea and significantly higher in the southern North Sea. It was not our objective here to examine the processes that control groundfish species diversity across the North Sea. However, to illustrate this point, if species- and size-related catchability in the GOV is ignored, there would be no significant relationships between the diversity indices and depth, but when catchability is taken into account, both relationships would be significant (Figure 4).

Patterns of spatial variation in the species composition of the North Sea demersal fish community revealed by both survey gears were broadly the same (Figure 5a, b). Both suggested four distinct community types and, although there was some variation in the precise location of the boundaries between them, both surveys placed these communities in generally similar regions. Accounting for species- and size-related catchability in the IBTS GOV dataset had little real impact on the basic spatial pattern (Figure 5c). Two community types were grouped, but the same distinctive northwest/southeast pattern in species composition remained. Spatial variation in species composition revealed by the catchability-raised GOV data bore a strong resemblance to the species diversity patterns shown for the same dataset in Figure 3. The data therefore suggested the presence of two high-diversity fish communities in the southern North Sea and a single low-diversity community in the northern North Sea.

Discussion

MPAs have received considerable attention as a means of conserving and restoring biodiversity (Allison *et al.*, 1998; Halpern, 2003). There is some suggestion that MPAs benefit biodiversity in exploited marine regions regardless of their location; species diversity generally increases in most MPAs (Halpern, 2003). Such observations are encouraging if the main purpose is to restore biodiversity, in that they imply that MPAs could be sited almost anywhere in areas impacted by fishing and the effects would be beneficial. However, if the principal objective of management is to conserve species diversity, then more attention needs to be directed towards the geographic placement of MPAs (Roberts *et al.*, 2003). This requires knowledge regarding spatial variation in species diversity, and in respect of fish communities, such information is very likely to be obtained from groundfish surveys that currently take place in support of more traditional fisheries management. The analyses we present here suggest that some aspects of the structure and composition of demersal fish communities are reasonably well represented by such survey data, but others most definitely are not.

Currently, we are unable to determine for certain whether species- and size-related variation in catchability in survey trawl

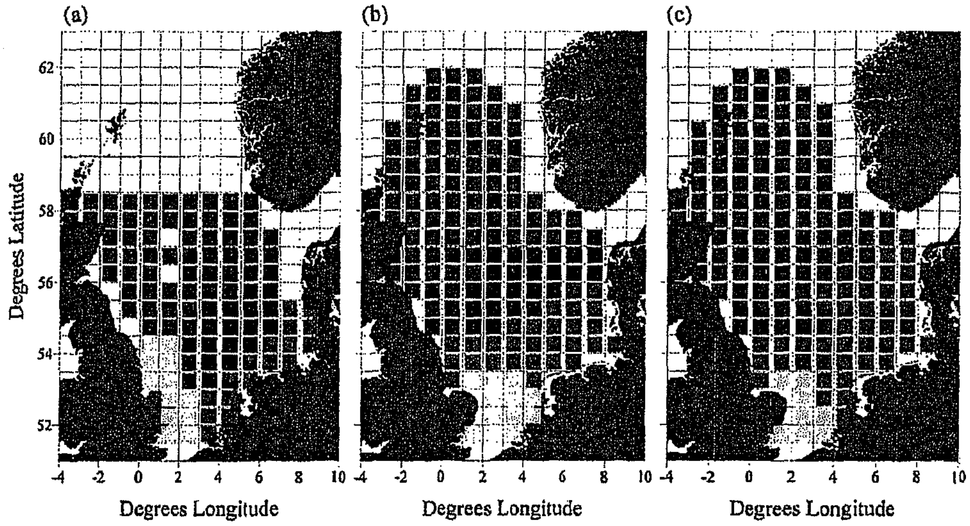

Figure 5. Spatial plots of the results of cluster analysis of the DBTS 8BT data: (a) raw IBTS GOV data; (b) raised (taking account of catchability) IBTS GOV data; (c) plots showing clusters defined at Bray–Curtis Similarity values of 67%, 65%, and 60%, respectively. These similarity levels were selected based on similarity step-length between levels of branching. At higher levels of similarity, step-length reduced markedly, giving a rapid proliferation in the number of individual clusters.

gears affects maps of species richness derived from the analysis of groundfish survey data. Clearly, some species will always remain unsampled, so in absolute terms, species richness at any particular location will inevitably be underestimated using empirical data alone. Several studies have used sequential sample aggregation methods to derive fitted species area relationships (SARs). Extrapolation from these SARs then provides estimates of species richness in a given area (reviewed in Magurran, 2007). This approach has been examined with respect to groundfish survey data collected in the North Sea and found to be unsatisfactory (Greenstreet *et al.*, 2007). Consequently, here we followed the recommendations of Greenstreet *et al.* (2007) and simply plotted the species richness obtained from 20 aggregated trawl samples located closest to the centre of each ICES rectangle. Comparison of maps of North Sea demersal fish species richness derived from two groundfish surveys that used trawl gears with perhaps the greatest difference in catchability characteristics revealed similar patterns of spatial variation, suggesting that each of the surveys portrayed spatial trends in relative species richness reasonably well. Either survey could therefore be used as the basis for advice regarding the location of MPAs intended for the conservation of species richness. Two explanations for this might be considered. First, variation in species- and size-related catchability between the two gears does affect the way species richness analyses respond to the common signal of actual variation in species richness across the North Sea, but the impact of this is relatively minor. Alternatively, the problems involved in adequately sampling rare species at any one location, so obtaining precise estimates of spatial variation in species richness (Brose *et al.*, 2003; Colwell *et al.*, 2004; Wintle *et al.*, 2004; Mao and Colwell, 2005; O'Hara, 2005; Kéry and Schmid, 2006), affects both gears to a similar extent.

Managers aiming to conserve species diversity (i.e. Hill's N_1 and N_2, the indices of species diversity that take account of species relative abundance, or "evenness"), and therefore needing to identify areas where species diversity is high, would be faced with a dilemma. This is because our perception as to how groundfish species diversity varied across the North Sea was entirely dependent on which set of groundfish survey data were analysed to produce the maps on which to base the decisions, and differences between the pairs of maps were considerable. Based on the IBTS GOV data, the most suitable sites for such MPAs might appear in the central North Sea, but the DBTS 8BT data indicate that species diversity there is low. The latter data instead suggest optimum locations in the northwestern and southwestern North Sea. Intuitively, one might expect species richness and species diversity to be positively correlated (Cotgreave and Harvey, 1994; Wilsey *et al.*, 2005), relegating the concept of "species diversity" to a single dimension characterized by species richness alone (Rosenzweig, 1995; Gaston, 1996). Observing positive correlations between species richness and the two species diversity indices within the DBTS 8BT dataset, and negative correlations in the IBTS GOV data, might therefore tempt managers to put greater credence in the DBTS-derived maps. However, several studies have demonstrated the two-dimensionality of "species diversity", showing that species richness and the evenness of species relative abundance are not necessarily positively related (Buzas and Hayek, 1996; Stirling and Wilsey, 2001; Stevens and Willig, 2002; Wilsey *et al.*, 2005). Indeed, in dominance-orientated marine communities, such as the North Sea demersal fish community, negative relationships such as those observed in the IBTS GOV dataset may be the norm (Birch, 1981).

Spatial variation in the two species diversity indices was clearly influenced by species- and size-related catchability in the trawl gear deployed during the survey. Application of reciprocal catchability coefficient raising factors to the IBTS species density-at-length data controls for species- and size-related catchability in the GOV trawl used in this survey, so provides an improved representation of actual spatial variation in groundfish species diversity across the North Sea. This analysis produced a third pair of Hill's N_1 and N_2 maps that differed from either of the two pairs of maps based on the raw IBTS and DBTS data. Maps of species diversity based on the raw survey data did little to suggest any obvious underlying regulatory processes. In contrast, the maps of species diversity that took account of catchability in the survey gear revealed species diversity to be greatest in the shallow, hydrodynamically mixed southern North Sea where primary productivity is greatest (Reid *et al.*, 1990). High productivity is widely recognized as a positive correlate of species diversity (Brown, 1975; Davidson, 1977; Adams and Woodward, 1989; Currie, 1991; Hawkins *et al.*, 2003; Whittaker and Heegaard, 2003; Rex *et al.*, 2005).

Like species richness, maps of spatial variation in the species composition of the demersal fish community derived from analysis of the two groundfish surveys' raw data were remarkably similar. Moreover, when the IBTS data were corrected to account for species- and size-related catchability in the GOV trawl, the resulting map showing the location of different types of groundfish community bore a strong resemblance to the maps derived from the raw data. This does not mean that characterization of the different communities portrayed in these maps (i.e. their species composition) would be the same, simply that the placement of boundaries between different communities appears to be reasonably robust to gear-related differences in catchability. The maps suggest that there are three or four main demersal fish community types, although of course the actual number of community types is entirely dependent on the subjective interpretation of the cluster analysis dendrogram. Using a higher level of similarity to define clusters would have produced a greater number of community types. Previous cluster analyses of variation in the species composition of the fish community in the North Sea suggest a similar number and location of different community types (Daan *et al.*, 1990; Callaway *et al.*, 2002).

To identify appropriate sites for MPAs aimed at conserving demersal fish species richness and species diversity in the North Sea, the maps we include here provide a basic starting point. From these, areas with the highest current species richness and species diversity can be identified. However, with respect to species diversity, careful consideration is required over which maps are used to inform any decision. Failure to take account of species- and size-related catchability in the survey trawl could easily result in the selection of MPAs in areas where species diversity, although apparently high, is in fact relatively low. Such decisions could result in fishing activity being displaced into the very areas that we wish to protect (Kaiser, 2005). Furthermore, our analyses confirm the existence of several different types of demersal fish community occupying distinct geographic regions of the North Sea that appear reasonably consistent over time (between studies). This raises the question: should species richness or species diversity be the sole criteria for our choice of sites for MPAs, or should we be selecting areas of great species richness and/or species diversity in each of these different communities? If the latter, then we need to be aware that species diversity in areas selected for MPAs in the northern North Sea will be considerably lower than in southern North Sea MPAs.

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