

Assessing the sampling effort required to estimate α species diversity in the groundfish assemblages of the North Sea

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ABSTRACT: Conserving and restoring biodiversity are key objectives for an ecosystem approach to management in the North Sea, but ecological quality objectives for the groundfish community instead concentrate on restoring size structure. Species richness and diversity estimates are strongly influenced by sampling effort. Failure to account for this has led to the belief that species richness and diversity indices are not adequate indicators of 'state' for the groundfish community. However, adherence to a standard procedure that is robust within respect to sampling effort influence should allow these metrics to perform a state indicator role. The Arrhenius power and Gleason semi-log species–area relationships are examined to determine whether they can provide modelled estimates of species richness at the ICES (International Council for the Exploration of the Sea) rectangle scale. Of these, the Gleason semi-log appears most reliable, particularly when a randomised aggregation process is followed. Aggregation of at least 20 trawl samples is required to provide empirically derived index values that are representative of the communities sampled, and therefore sensitive to drivers of change in these communities. However, given current groundfish survey sampling levels, combining 20 half-hour trawl samples to provide single estimates of species richness and diversity will require considerable aggregation over time and/or space. This can lead to estimates of α or local richness/diversity becoming inflated through the inclusion of elements of β or regional richness/diversity. For the North Sea groundfish assemblage, this occurs when the distance between the focal position and the location of the most distant sample exceeds 49 km.

KEY WORDS: Ecosystem approach to management · State indicators · Sample-size dependency · Species–area relationships · α -diversity · β -diversity · Management frameworks

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INTRODUCTION

Several policy commitments to protect marine biodiversity, both globally and regionally, underpin the recent moves towards an 'ecosystem approach to management' (EAM) in the North Sea (Greenstreet 2008). The convention for the protection of the marine environment of the north-east Atlantic, OSPAR, deemed the competent authority to develop the EAM, identified 10 key ecological quality issues for the North Sea and requested relevant expert bodies, such as the International Council for the Exploration of the Sea (ICES), to define ecological quality objectives (Eco-QOs) for each issue. Developing the EAM along these lines requires indicators that portray the 'state' of dif-

ferent components of marine ecosystems (Jennings & Reynolds 2000, Frid 2003, Garcia & Cochrane 2005).

Groundfish surveys, carried out for decades in support of traditional fisheries management, provide data on the numbers at length of all species sampled (Heessen 1996, Heessen & Daan 1996). Such data are ideal for the computation of many multi-species community descriptors (e.g. Washington 1984). Since 'fish communities' was the fifth in OSPAR's list of 10 ecological quality issues (Johnson 2008, Heslenfeld & Enserink 2008), examining long-term change of different aspects of the North Sea demersal fish community received considerable attention (Greenstreet & Hall 1996, Hall & Greenstreet 1996, 1998, Rice & Gislason 1996, Greenstreet et al. 1999, Jennings et al. 1999, 2002,

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Rogers et al. 1999, Rogers & Ellis 2000, Piet & Jennings 2005). Long-term declines in species richness and diversity were revealed (e.g. Greenstreet & Hall 1996, Rijnsdorp et al. 1996, Greenstreet et al. 1999), and shown to be a result of fishing activity (Greenstreet & Rogers 2006). Given the political concern over biodiversity, one might have anticipated that the EcoQO for fish communities would address this decline in fish species diversity. Instead, the EcoQO is directed towards restoring the size structure of demersal fish in the North Sea (ICES 2007, Greenstreet 2008). How did this change in focus arise?

When asked by OSPAR to recommend appropriate state indicators to support an EcoQO for Fish Communities, ICES proposed 7 criteria on which to base their judgement (ICES 2001). These criteria, listed in Table 1, place considerable emphasis on the linkage between indicator performance and the anthropogenic activity in question. Species diversity indices performed poorly against several of these criteria, and so were discarded as possible state indicators for the fish community EcoQO (Greenstreet 2008). Explaining why species diversity indices performed so poorly was the main purpose of this study. To do this, attention was directed towards 3 of the criteria (criteria b, c, and d; Table 1) that proved to be the most serious impediments to using species diversity indices.

Criterion b in Table 1 requires a good state indicator to be 'sensitive to a manageable human activity'. In the northern North Sea, analysis of Scottish August groundfish survey (SAGFS) data revealed steeper declines in groundfish species diversity in areas where fishing activity levels were highest (Greenstreet & Hall 1996, Greenstreet et al. 1999, Greenstreet & Rogers 2006), suggesting that species diversity indices were

Table 1. Traffic light system showing results of the application of the ICES criteria for a 'good state indicator' to species diversity indices (after ICES 2001). Green indicates no appreciable concerns; amber indicates some concerns; red indicates serious concerns

Criterion	Property
a	Relatively easy to understand by non-scientists and those who will decide on their use
b	Sensitive to a manageable human activity
c	Relatively tightly linked in time to that activity
d	Easily and accurately measured, with a low error rate
e	Responsive primarily to a human activity, with low responsiveness to other causes of change
f	Measureable over a large proportion of the area to which the EcoQ metric is to apply
g	Based on an existing body or time-series of data to allow a realistic setting of objectives

sensitive to fishing activity. However, other studies revealed no, or even positive, trends in species diversity, depending on the data set analysed (e.g. Rogers & Ellis 2000, Piet & Jennings 2005). This inconsistency led ICES (2001) to conclude that diversity indices were not particularly sensitive to fisheries-related impacts on the marine ecosystem (see also Chadwick & Canton 1984, Robinson & Sandgren 1984). Most diversity indices are sample-size dependent (Magurran 1988, Colwell et al. 2004). Frequently, problems have arisen through failure to appreciate the influence of sampling effort on index performance. If sampling effort requirements are not assessed *a priori*, the application of diversity indices to samples of inadequate size leads to insensitive metrics that fail to detect real differences in diversity (Soetaert & Heip 1990, Boulinier et al. 1998).

The problem is exemplified by island biogeography theory, wherein species richness increases as a (Arrhenius) power function of the area sampled:

$$S = cA^z \quad (1)$$

where S is the species richness count, A the area sampled, and c and z are constants (MacArthur & Wilson 1967, Rosenzweig 1995).

This implies that local (α) species richness (Hill's [1973] index N_0) cannot be determined empirically without sampling the entire habitat area. Instead, by sequentially aggregating samples and tracking both the total aggregated species richness and the total aggregated area sampled, the species–area relationship (SAR) can be parameterised and used to model species richness in the area in question (e.g. Palmer 1988, 1990, Colwell & Coddington 1994, Keating et al. 1998, Gotelli & Colwell 2001, Storch et al. 2003, Ugland et al. 2003, Fridley et al. 2005, O'Hara 2005, van Gemerden et al. 2005). Species diversity indices that take account of relative species abundance are similarly influenced by sampling effort. Hill's (1973) N_1 and N_2 are, respectively, mathematically defined as:

$$N_1 = e^{-\sum_{s=1}^S p_s \cdot \ln(p_s)} \quad \text{and} \quad N_2 = \frac{1}{\sum_{s=1}^S p_s^2} \quad (2)$$

where p_s is the proportion of the total number of individuals sampled contributed by each of the S species recorded in the sample (Magurran 1988).

The inclusion of additional species with increasing sampling effort increases the number of p_s values in each of the summation terms, thereby affecting both indices.

Piet & Jennings (2005) computed their richness and diversity index values as the 'mean value per haul' in each year of the 2 groundfish survey time-series that they analysed. However, as illustrated above, species richness of the community will always be higher than

the number of species in any single sample (e.g. Brose et al. 2003). Calculating the mean species richness per sample still only provides an estimate of the average species richness in the average area covered in each sample, and therefore remains a poor indicator of the actual species richness of the community (e.g. Colwell et al. 2004). Reporting species richness as richness per unit sampling effort is theoretically unsound because, as indicated by the SAR, species richness (S) is proportional to A^z , and not just to A alone (Rosenzweig 1995). Since z is a parameter that is characteristic of each community sampled, in each case, it is a parameter that needs to be estimated.

Application of the traditional Arrhenius power function assumes that local species assemblages are simply sub-sets of the regional species pool (Cornell & Lawton 1992, Angermeier & Winston 1998, Cornell & Karlson 1997, Findley & Findley 2001). However, studies examining the role of regional and local processes in dictating local species richness have demonstrated a phenomenon termed 'saturation'. After an initial sharp rise as the first samples are aggregated, the species accumulation rate drops markedly compared with the ever-increasing traditional Arrhenius power function (Findley & Findley 2001, Cottenie et al. 2003, Heino et al. 2003, Kiflawi et al. 2003, Wright et al. 2003). This has led to debate over which function best fits the SAR. There may be a fundamental difference between local- and regional-scale SARs; the latter may be best fitted by the Arrhenius power function, while the former are best fitted by the Gleason semi-log plot, $S = c + z(\log A)$ (Whittaker 1972, van der Maarel 1988, Stohlgren et al. 1995). At local spatial scales, extrapolation from a traditional Arrhenius power function SAR could overestimate species richness in specified areas, such as ICES 0.5° latitude by 1° longitude statistical rectangles (Fridley et al. 2005).

Neither the Gleason nor the Arrhenius model is asymptotic in nature; both imply that additional sampling will always reveal new species. Species saturation could suggest that an asymptotic model, such as the Michaelis-Menton equation, might be more suitable to estimate local (α) diversity (e.g. Soberón & Llorente 1993, Denslow 1995, Keating & Quinn 1998). However, asymptotic models are only appropriate when the local habitat is absolutely defined (e.g. a mountain slope, Denslow 1995) and sampling is exhaustive (Magurran 2004). ICES statistical rectangles are arbitrarily defined and cover an area of approximately 3640 km². The average groundfish survey rarely includes more than 4 trawl samples per rectangle, each covering an area of 0.07 km², so sampling is not exhaustive. Asymptotic models therefore do not provide appropriate SARs to estimate ICES rectangle-scale species richness.

The sample aggregation method may also influence the resultant SAR. Several authors (e.g. Rosenzweig 1995, Fridley et al. 2005) have suggested that samples be nested (each new area sampled is contiguous with the area sampled in samples lower in the aggregation order). In randomised aggregation, samples adjacent in the aggregation order may be separated in space, increasing the probability that the new sample will include new habitats, and hence add new species more quickly. Nested aggregation, focusing on α -diversity, produces shallower species accumulation curves (Palmer 1990, Rosenzweig 1995), while a randomised approach may more rapidly incorporate elements of β -diversity (Colwell et al. 2004). The type of aggregation could have an influence on which SAR best fits the data: nested aggregation may be better fitted by the Arrhenius power function, while the Gleason semi-log plot may provide a better fit to randomised aggregations.

An alternative approach is to estimate the sample size required to derive indices of species richness and species diversity that reflect actual rankings in species richness and diversity in sampled communities. This may not provide estimates of actual species richness and diversity, but should allow temporal or spatial trends to be detected. This approach was adopted in the SAGFS studies discussed above. Preliminary analysis revealed that 10 h of Aberdeen 48-foot otter trawl effort was necessary before the aggregated sample obtained produced reliable estimates of Hill's N_0 , N_1 and N_2 (Greenstreet & Hall 1996, Greenstreet et al. 1999, Greenstreet & Rogers 2006). Accounting for sample-size dependency in this way provided indices sensitive enough to detect long-term, fishing-related declines in demersal fish species richness and diversity in the northwestern North Sea.

This approach, however, also has drawbacks. Marine sampling is difficult and expensive, limiting the level of sampling effort that is feasible. The best supported North Sea groundfish surveys, the ICES first (Q1) and third quarter (Q3) International Bottom Trawl Survey (IBTS), rarely achieve more than 3 trawl samples per ICES rectangle surveyed per year. Addressing spatial questions will therefore require the aggregation of samples collected over several years; conversely, investigating temporal issues will require the aggregation of samples collected across several ICES rectangles (e.g. Greenstreet & Rogers 2006). Most studies will be directed towards estimating α -diversity; the diversity in a particular location (habitat, ICES rectangle, etc.) at a given point in time. Aggregation across space risks including new species as new habitats get included in the aggregated sample area, thus confounding α -diversity with β -diversity (Whittaker 1972, Lande 1996, Kiflawi & Spencer 2004). Similarly,

temporal turnover of vagrant species may lead to over-estimation of species richness when samples are aggregated over time (Hadley & Maurer 2001, Adler & Lauenroth 2003, Adler et al. 2005, White et al. 2006, Magurran 2007, Shurin 2007). Both processes would therefore tend to inflate estimates of α -species richness.

The lack of a consistent approach to estimating species diversity and species richness from groundfish species abundance data has produced inconsistent results. In the past, studies that took account of sample size dependency showed significant trends and demonstrated fishing effects, while studies that ignored sample size dependency produced results that were difficult to interpret. This inconsistency led ICES (2001) to conclude that metrics of species diversity and richness were either insensitive to a manageable human activity, or not tightly linked to the activity, illustrating that the use of diversity indices is not straightforward. Depending on how they are determined, indices of species richness and species diversity may not be easily and accurately measured. In a more recent treatise on the characteristics desirable in a state indicator, the capacity to convey information on aspects of the ecosystem that are of societal concern was assigned high priority (Rice & Rochet 2005). Conserving and restoring biodiversity remain key principal policy drivers underlying the implementation of an EAM, which underlines the need for operational biodiversity state indicators. Addressing the problems identified by the application of the ICES criteria to biodiversity metrics is therefore an urgent priority for marine scientists.

A systematic approach to applying species diversity and richness metrics to groundfish survey data should rectify many of these problems, enabling such metrics to perform the role of state indicators and allowing the conservation and restoration of biodiversity to be addressed directly. Therefore, this study examines the sample size dependency of Hill's (1973) indices of species richness and diversity (N_0 , N_1 and N_2) in order to establish a standard procedure for their use. To demonstrate such a procedure, the question of mapping groundfish species richness and diversity across the North Sea is addressed. First, spatial variation in species composition is examined to ensure that, when selecting samples for sequential aggregation to explore the effect of sampling effort on metric performance, samples are drawn from similar species assemblages. Six such sites are selected covering a wide geographic area and 3 different assemblages. Having established a suitable procedure to estimate species richness and diversity in each ICES rectangle, spatial variation in the 3 Hill's metrics is determined by aggregating the necessary number of samples closest to the

centre point of all rectangles included in the survey. The extent to which this spatial aggregation results in confounding elements of β -diversity into each of the individual ICES rectangle estimates of α -diversity is then explored, and the impact this has on qualitative assessment of the resulting diversity maps is examined.

METHODS

The Q3 IBTS survey effort is approximately evenly distributed over ICES statistical rectangles across the whole North Sea. Each rectangle is usually fished by ships belonging to 2 participating countries using a grande ouverture verticale (GOV) trawl, resulting in at least 2 hauls per rectangle in most rectangles in most years. Numbers at length of all species caught are determined, and information on location, distance towed, and area swept by the gear is noted. Following previous practice (e.g. Greenstreet & Hall 1996, Greenstreet et al. 1999), only data for species considered to be members of the 'demersal fish community' were analysed. Prior to 1998, not all participating countries used the same trawl gear, and tow durations varied. After 1998 all participating countries used the GOV trawl gear and tow duration was standardised to 30 min across the entire survey. Therefore, only data covering the period 1998 to 2004 were analysed. This produced the most consistent data set in terms of sampling procedure on which to base analyses of species diversity.

Data for a total of 2076 hauls were available. Despite fairly rigid protocols being laid down for the IBTS, these trawl samples varied markedly in terms of their swept area. Because of the sensitivity of diversity metrics to variation in sampling effort, 'valid' trawl samples were defined on the basis of swept area (Fraser et al. 2008), and only trawl samples conforming to this standard were analysed. This process resulted in approximately 8% of the IBTS trawl samples being excluded, leaving 1909 trawl samples with swept areas ranging from 51 473 to 80 835 m² available for analysis.

Similarity in the species composition of the demersal fish community sampled in different ICES rectangles was assessed using the Bray-Curtis similarity index. Data for all trawl samples in each ICES rectangle were combined to provide a single species abundance 'sample'. Abundance data were root-root transformed to down-weight the effects of the more abundant species. Similarity between all pairs of ICES rectangles was determined. The resulting similarity matrix was subjected to hierarchical group-average cluster analysis to identify groups of ICES rectangles with demersal fish communities of similar species composition. These

analyses were performed using the PRIMER software (Clarke & Warwick 2001). Six ICES rectangles were chosen for detailed analysis of the influence of sampling effort on the performance of 3 species diversity indices. Criteria for selection were:

- the focal rectangles should be widely dispersed across the North Sea
- the focal rectangles should belong to at least 3 different species composition groups
- the number of trawls in the focal rectangles should be relatively high
- all rectangles adjacent to the focal rectangles should belong to the same species composition group.

There are 2 different aspects to species diversity: the actual number of species included in any particular sample, and the evenness of the distribution of individuals between all species encountered. Three metrics commonly used in analyses of groundfish survey data were applied (e.g. Greenstreet & Hall 1996, Greenstreet et al. 1999, Piet & Jennings 2005), each differing in the extent to which they are influenced by these aspects of species diversity (Southwood 1978). Hill's N_0 is simply the count of all species (species richness) encountered in a sample, a metric strongly influenced by sampling effort variation. Two indices of species diversity (Hill's N_1 and N_2 , the exponential of the Shannon-Weiner index and the reciprocal of Simpson's index, respectively) were also applied. The mathematical notation for both N_1 and N_2 is provided in Eq. (2). N_1 is more sensitive to variation in the number of species recorded in a sample, whereas N_2 is more sensitive to variation in the evenness of the distribution of individuals between species. All diversity metrics were determined using PRIMER (Clarke & Warwick 2001).

At least 91 trawl samples (across all 7 years) were available for analysis in each of the 6 focal rectangles and their immediate neighbours. To apply the randomised aggregation method, 90 samples were selected at random (without replacement) from the available sample pool and sequentially aggregated. After the addition of each new sample, the total area swept by all aggregated samples was determined and the value of each of the 3 metrics calculated on the combined species abundance data. The order in which samples are aggregated affects the shape of the SAR, depending on whether the first sample in the accumulation order happens to be relatively species rich or species poor, compared with the remaining samples (Palmer 1990). To counter this, the sequential sample aggregation process was repeated 10 times, so that the order of aggregation was also randomised. Arrhenius power and Gleason semi-log functions were fitted to the data for all 10 randomisations. A true nested aggregation could not be carried out, because the IBTS trawl samples were not adjacent to each other in space. Such

sampling has never been a survey requirement. However, as an approximation to this approach, 90 samples were aggregated in order of their distance from the centre-point of each of the 6 focal rectangles. Only one aggregation order fitted this criterion, so no replication was possible. Again, both the Arrhenius power and Gleason semi-log functions were fitted to the resulting accumulation curves.

As samples were aggregated to estimate ICES rectangle-scale index values for each of Hill's metrics, the actual extent of the area from which these samples were obtained also increased. Variation in the area from which the samples were collected was measured using a metric termed the 'search radius'. This was defined as the distance from the sample focal point (e.g. the centre position of an ICES rectangle) and the location of the most distant sample in the sample aggregation.

RESULTS

Cluster analysis of the ICES rectangle species abundance data revealed distinct groups of rectangles with similar species composition. When these clusters were mapped, clear spatial organisation was apparent (Fig. 1). On the basis of the data shown in Fig. 1 and the criteria given above, 6 ICES rectangles ('assemblages') were selected for investigation of the effect of sampling effort on species diversity index performance.

Randomised aggregations

In 5 of the 6 assemblages (the exception being Red2), the R^2 values obtained (Table 2) suggested that species richness (Hill's N_0) was best fitted by the Gleason semi-log function, rather than by the Arrhenius power function (Fig. 2). Residuals to the Arrhenius power function showed a significant negative departure from the expected distribution at high sample aggregation levels (large A) in 4 (Red1, Green1, Green2 and Pink1) of the 6 rectangles (Fig. 2). Consequently, estimates of ICES statistical rectangle-scale (3642 km² in the central North Sea) species richness based on extrapolation of the fitted Arrhenius power functions were unrealistically high (Table 2). The total North Sea fish species inventory, including pelagic species excluded from this analysis, has been estimated at around 224 species (Yang 1982). Extrapolation of the Gleason semi-log functions provided more reasonable estimates of rectangle-scale species richness (Table 2). However, residuals to the Gleason semi-log function showed a significant positive departure from the expected distribution at high sample aggregation levels in the other

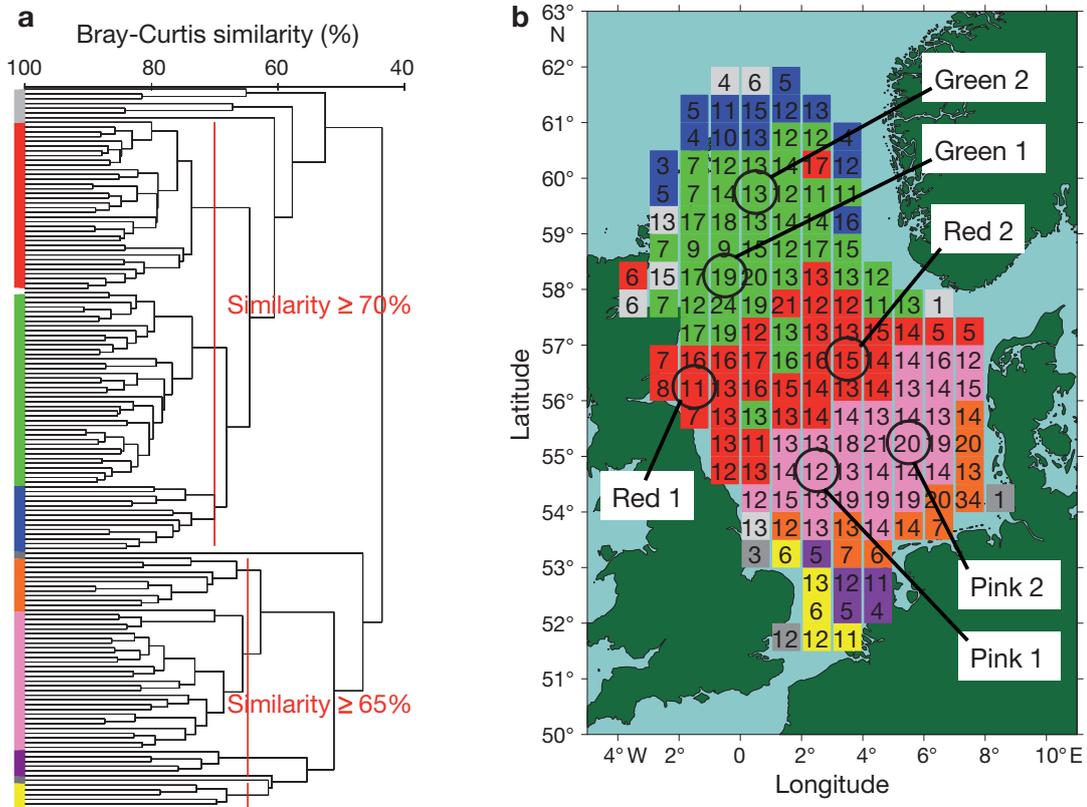


Fig. 1. (a) Results of hierarchical group-averaging cluster analysis of the Bray-Curtis similarity matrix constructed for the International Bottom Trawl Survey (IBTS) grande ouverture verticale (GOV) data set. Clusters of ICES rectangles grouped at similarity levels of 65 and 70 % are colour coded. (b) Chart of spatial distribution of groups from (a). The chart indicates the number of GOV trawl samples available for analysis in each ICES rectangle over the full period 1998 to 2004. The 6 focal rectangles (assemblages) selected for 'sample-size' analyses are annotated

2 assemblages, Red2 and Pink2 (Fig. 2), suggesting that, in these cases, the Gleason semi-log function might under-estimate ICES rectangle-scale species richness. In summary, 5 of the assemblages (Red1, Green1, Green2, Pink1 and Pink2) were better fitted by the Gleason semi-log function, but with Pink2, showing significant positive deviations from the fit at high sample aggregation levels, and 1 assemblage, Red2, was best fitted by the Arrhenius power function.

The Arrhenius and Gleason functions produced a similar, but not identical, ranking of the 6 assemblages in terms of their ICES rectangle-scale species richness (Table 2). The Arrhenius power function ranked the assemblages Pink1 > Green1 > Red1 > Green2 > Pink2 > Red2, while the Gleason semi-log function interchanged the first and second, and third and fourth rectangles to rank the assemblages Green1 > Pink1 > Green2 > Red1 > Pink2 > Red2. However, 95% confidence limits (CLs) around the ICES rectangle-scale estimates of species richness of both the interchanged assemblage pairs overlapped, regardless of the SAR applied to the data (Table 2). Neither of the SARs could therefore provide a definitive ranking order for these 2

assemblage pairs. Given that the Gleason semi-log function provided the best fit to the data from the 4 top-ranked assemblages, the latter ranking is probably the most reliable. Even though the Gleason semi-log function probably underestimated species richness in the 2 lowest-ranked assemblages, these same 2 assemblages were also ranked lowest, and in the same order, by the Arrhenius power function.

More critically, the assemblage rankings were not established until both SARs had been extrapolated to areas greater than 40 km². At aggregation levels of 90 trawl samples, the total area sampled was approximately 7 km² (Fig. 3), suggesting that the sampling required to rank fish communities using empirical estimates of ICES rectangle-scale groundfish species richness (i.e. based simply on aggregated sample species counts) would be too onerous and well beyond current, or likely, levels of groundfish survey activity. However, the situation is not as stark as this initial assessment suggests. Deciding relative species richness rankings between the Red1 and Green2 and between the Pink1 and Green1 assemblages posed the greatest difficulty when using the Arrhenius power function (Fig. 3).

Table 2. Parameter values and ICES rectangle scale Hill's N_0 , species richness values obtained by the application of the Arrhenius power ($N_0 = cA^z$) and Gleason semi-log ($N_0 = c + z \log A$) functions to species-area accumulation data derived from the randomised and nested sequential aggregation of 90 Q3 IBTS trawl samples in each of 6 focal ICES rectangles and their immediate neighbouring rectangles. 95% confidence limit (CL) ranges around each estimate of ICES rectangle-scale species richness are also indicated

Assemblage	c	z	R ²	N ₀	95% CL range
Arrhenius power					
Randomised					
Red1	0.5226	0.2744	0.926	220	205–235
Red2	0.6748	0.2353	0.891	120	112–129
Green1	0.6466	0.2674	0.914	233	217–250
Green2	0.8483	0.2467	0.908	194	181–207
Pink1	0.3697	0.3004	0.857	275	247–307
Pink2	0.5619	0.2646	0.871	190	174–208
Nested					
Red1	0.2493	0.3179	0.968	273	230–324
Red2	0.3492	0.2841	0.913	182	140–235
Green1	0.2917	0.3166	0.963	310	259–372
Green2	0.4356	0.2875	0.960	244	205–290
Pink1	0.0226	0.4824	0.956	926	680–1260
Pink2	0.1994	0.3241	0.909	250	185–339
Gleason semi-log					
Randomised					
Red1	-60.8624	14.206	0.945	75	73–77
Red2	-39.3651	9.578	0.872	52	50–54
Green1	-65.3583	15.455	0.954	82	81–84
Green2	-58.1251	14.154	0.933	77	75–79
Pink1	-66.7891	15.297	0.879	79	77–82
Pink2	-54.1805	12.838	0.879	69	66–71
Nested					
Red1	-66.1030	14.600	0.946	73	69–78
Red2	-47.0834	10.966	0.945	58	54–62
Green1	-74.8645	16.602	0.987	84	81–87
Green2	-68.8151	15.543	0.945	80	75–85
Pink1	-98.2670	19.795	0.913	91	83–99
Pink2	-68.9492	14.650	0.825	71	62–80

Similarly, defining the ranking order of the Pink1 and Green2 assemblages was hardest when using the Gleason semi-log function (Fig. 3). For clarity, 95% CLs were not shown in Fig. 3, but reference to Table 2 reveals that the 95% CLs around the species richness estimates of each assemblage within these assemblage pairs overlap. Within each pair, the assemblage ranking order could not therefore be conclusively defined, and if this is the case, Fig. 3 suggests that extrapolation of the SARs to an area of 7 km² was sufficient to provide relative species richness rankings. Estimates of species richness capable of ranking the species richness of different ICES rectangle groundfish assemblages might therefore be empirically derived from aggregated collections of 90 half-hour GOV trawl samples.

The sample aggregation–species diversity plots for the 2 species diversity indices, Hill's N_1 and N_2 ,

revealed horizontal, funnel-shaped forms that differed markedly from the species richness (Hill's N_0) 'data clouds' (Fig. 2). This is because N_1 and N_2 take account of both aspects of diversity, species richness and species evenness. With species richness, it is possible that the first sample in the accumulation order might be particularly species rich or particularly species poor, thereby causing the observed spread of data at the left of the data clouds (Fig. 2). However, it is also inevitable that, as the combined area sampled increases, new species will be added to the aggregated total, no matter how high the initial start point. Stochastic variation in the species richness of the first samples aggregated also affects N_1 and N_2 in a similar fashion, causing the generally positive convex shape of the data clouds in many of the plots (Fig. 2). However, the degree of evenness also varies in a stochastic manner, so that the first samples in an aggregation order might be characterized by relatively low levels of dominance (unusually low abundance of normally dominant species, or higher-than-usual abundance of some less common species), resulting in unusually high N_1 and N_2 values. Further accumulation of additional samples characterized by more normal levels of dominance then causes aggregated N_1 and N_2 values to fall. This gives rise to the characteristic funnel-shaped data clouds prevalent in Fig. 2.

Since neither of the SARs can be consistently fitted to either of the diversity indices, a similar statistical model-fitting approach to estimating species diversity at the ICES rectangle spatial scale was not possible. However, once the total aggregated area sampled was sufficiently large, the data tended to stabilize around mean index values. Therefore, the mean index value, calculated across all 10 randomised aggregations of 90 samples, probably provides the most reliable estimate of species diversity at the ICES rectangle scale for each of the 6 assemblages (Table 3).

Nested aggregations

Arrhenius power functions provided marginally higher R^2 values for 4 (Red1, Green2, Pink1 and Pink2)

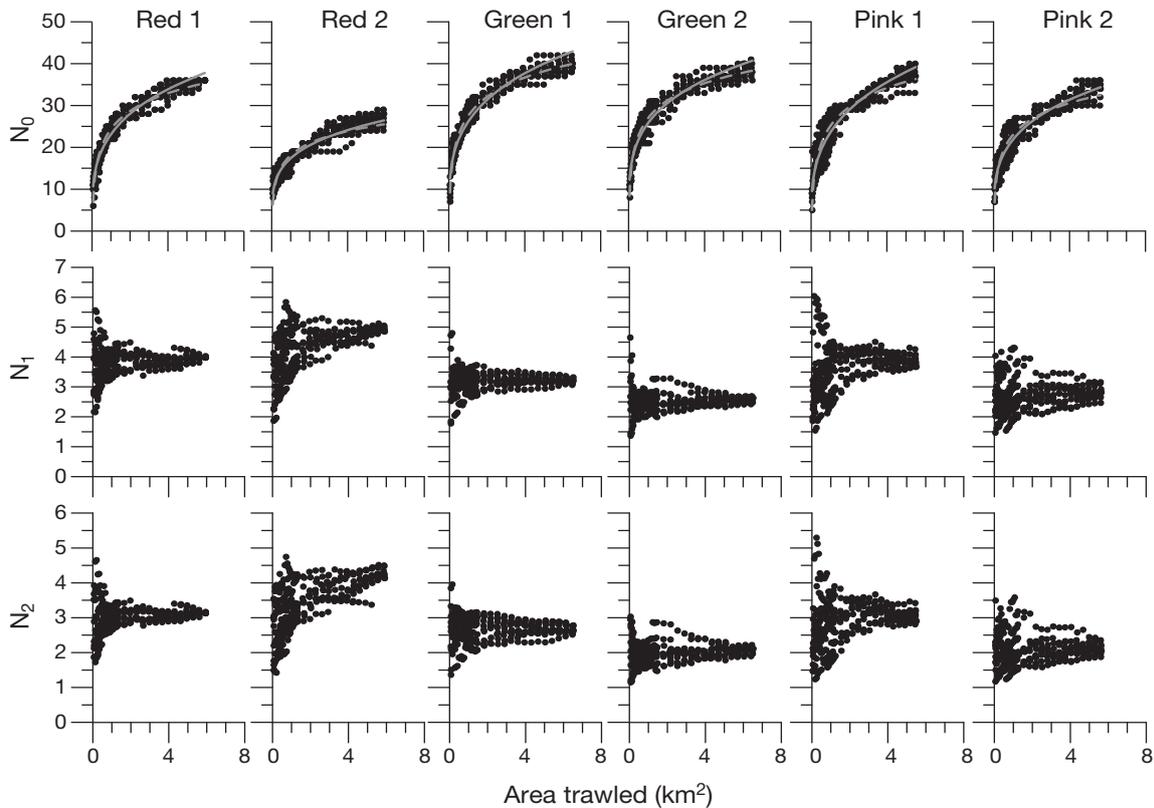


Fig. 2. Effect of increasing area sampled on Hill's N_0 (species richness), N_1 , and N_2 (species diversity) index values for each of the 6 assemblages, using a randomised sequential aggregation of 90 samples. Data for 10 separate randomised aggregations are plotted. For N_0 , solid grey lines show Arrhenius power function fits to the data; dashed grey lines show Gleason semi-log fits to the data

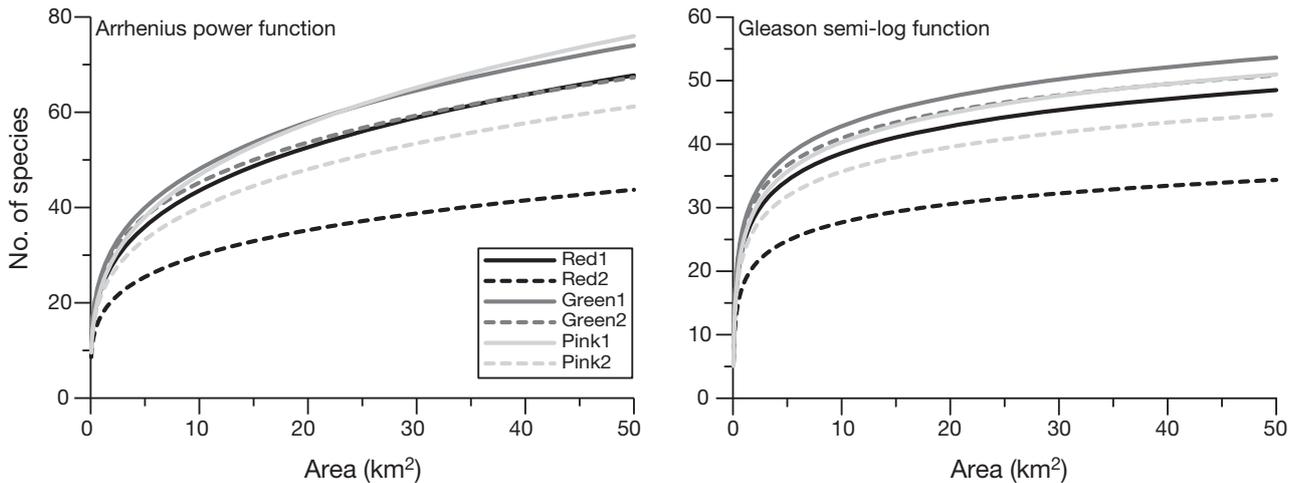


Fig. 3. Extrapolation of the Arrhenius power and Gleason semi-log functions up to 50 km², illustrating overlaps in each type of species–area relationship (SAR) fitted to the 6 assemblages. Final rankings are not established until extrapolation to areas greater than 40 km²

of the 6 assemblages species richness plots (Fig. 4), but in all cases extrapolation to the area of an ICES rectangle again resulted in unrealistically high estimates of species richness (Table 2). Gleason semi-log functions may not have fitted the data quite so well, but the

differences were small, and extrapolation to the ICES rectangle scale resulted in more reasonable estimates of species richness (Table 2). The Arrhenius function ranked the 6 assemblages Pink1 > Green1 > Red1 > Pink2 > Green2 > Red2, while the Gleason function

Table 3. Average Hill's N_0 (species richness), N_1 , and N_2 (species diversity) index values, calculated across 10 randomised aggregations of 90 trawl samples for 6 North Sea groundfish assemblages

Assemblage	N_0	N_1	N_2
Red1	36	3.99	3.14
Red2	27	4.94	4.26
Green1	40	3.19	2.63
Green2	39	2.59	2.07
Pink1	37	3.89	3.07
Pink2	34	2.83	2.12

ranked them Pink1 > Green1 > Green2 > Red1 > Pink2 > Red2, elevating the fifth ranked assemblage into third place. In both cases, the 95% CLs around the ICES rectangle-scale species richness estimates for the assemblages ranked 3, 4 and 5 overlapped, so neither SAR could conclusively rank these 3 assemblages. For each SAR, the aggregation method had little effect on the assemblage rankings. Compared with the randomised aggregation, nested aggregations transposed the fourth- and fifth-ranked assemblages using the Arrhenius function, whilst the first and second assem-

blages were transposed when the Gleason function was used. In both cases, the 95% CLs around the ICES rectangle-scale species richness estimates for the assemblages concerned again overlapped. A Spearman rank correlation matrix, comparing the 4 sets of species richness estimates, confirmed the similarity in ranking order achieved by all 4 methods (Table 4), but no 2 ranking orders were identical.

Nested aggregation plots for Hill's N_1 and N_2 species diversity indices revealed a variety of forms (Fig. 4), demonstrating the interplay between species richness and species evenness in influencing index behaviour with increasing sampling effort. Index values stabilised to some extent, once the aggregated sample area exceeded 1 to 2 km². However, compared with the randomised aggregation plots (Fig. 2), even in the final stages of aggregation, clear positive or negative trends in both indices were still apparent for several of the assemblages, making it difficult to determine appropriate index values.

The nested aggregation plots for all 3 of Hill's indices were not smooth (Fig. 4), suggesting the influence of processes other than simply the effect of increasing the area sampled. Fig. 5 shows similar plots, but here the index values are plotted against search radius (the dis-

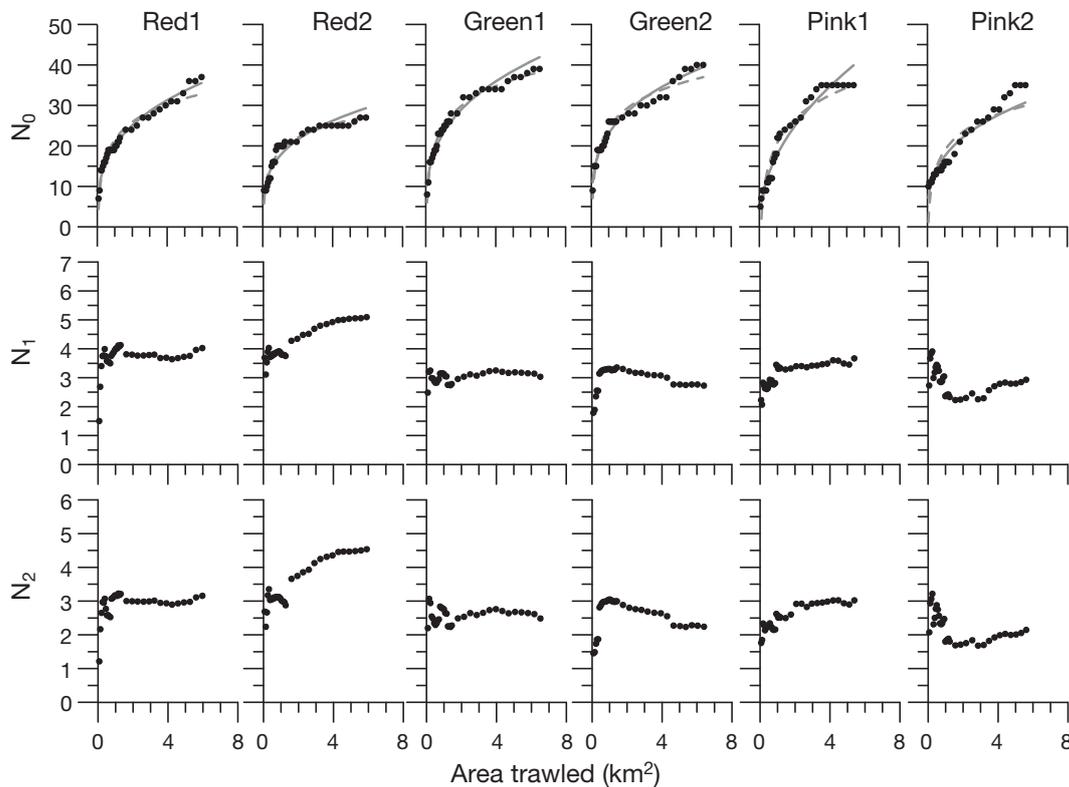


Fig. 4. Effect of increasing the area sampled (km²) on Hill's N_0 (species richness), N_1 , and N_2 (species diversity) index values in each of the 6 assemblages, using a nested sequential aggregation of 90 samples. For N_0 , solid grey lines show Arrhenius power function fits to the data; dashed grey lines show Gleason semi-log fits to the data

Table 4. Spearman correlation coefficients (upper right cells), comparing the ranking order of 6 groundfish assemblages in terms of the species richness determined by extrapolation of Arrhenius power or Gleason semi-log functions, fitted to randomised or nested aggregated sample data up to the spatial scale of the ICES rectangle. Significance levels are indicated (lower left cells; n.s.: $p > 0.05$)

Aggregation	Function	Randomised		Nested	
		Arrhenius	Gleason	Arrhenius	Gleason
Randomised	Arrhenius		0.866	0.943	0.943
	Gleason	$p < 0.05$		0.771	0.943
Nested	Arrhenius	$p < 0.01$	$p = \text{n.s.}$		0.829
	Gleason	$p < 0.01$	$p < 0.01$	$p < 0.05$	

tance between each new sample in the aggregation and the centre of the ICES rectangle concerned). Fifth-order polynomial functions fitted to these data indicated multi-phasic species accumulation curves with marked increases in the species accumulation rate at search distances of around 40 to 50 km. This was almost certainly associated with the incorporation of elements of β -diversity into the estimate of species richness as the region within the expanding search radius included new habitats with different species composition.

Assessing sample size requirements for assemblage ranking

For each of the 6 assemblages, the average index value across each of the 10 randomised aggregations of 90 trawl samples provided the best empirical estimates of each metric for each assemblage (Table 3). This ranked the 6 assemblages, in terms of species richness (Hill's N_0), Green1 > Green2 > Pink1 > Red1 > Pink2 > Red2. Similar to the ranking derived from extrapolation of the randomised

aggregation Gleason semi-log SARs to the ICES rectangle scale, just the second and third ranked assemblages were transposed. This confirms the point made above and illustrated in Fig. 3. Even after aggregating 90 trawl samples, the ranking of empirical estimates of species richness, based on aggregated sample species counts, did not exactly match the ranking obtained by extrapolating Gleason semi-log SARs to the ICES rectangle scale. Hill's N_1 and N_2 both ranked the 6 assemblages in identical order: Red2 > Red1 > Pink1 > Green1 > Pink2 > Green2.

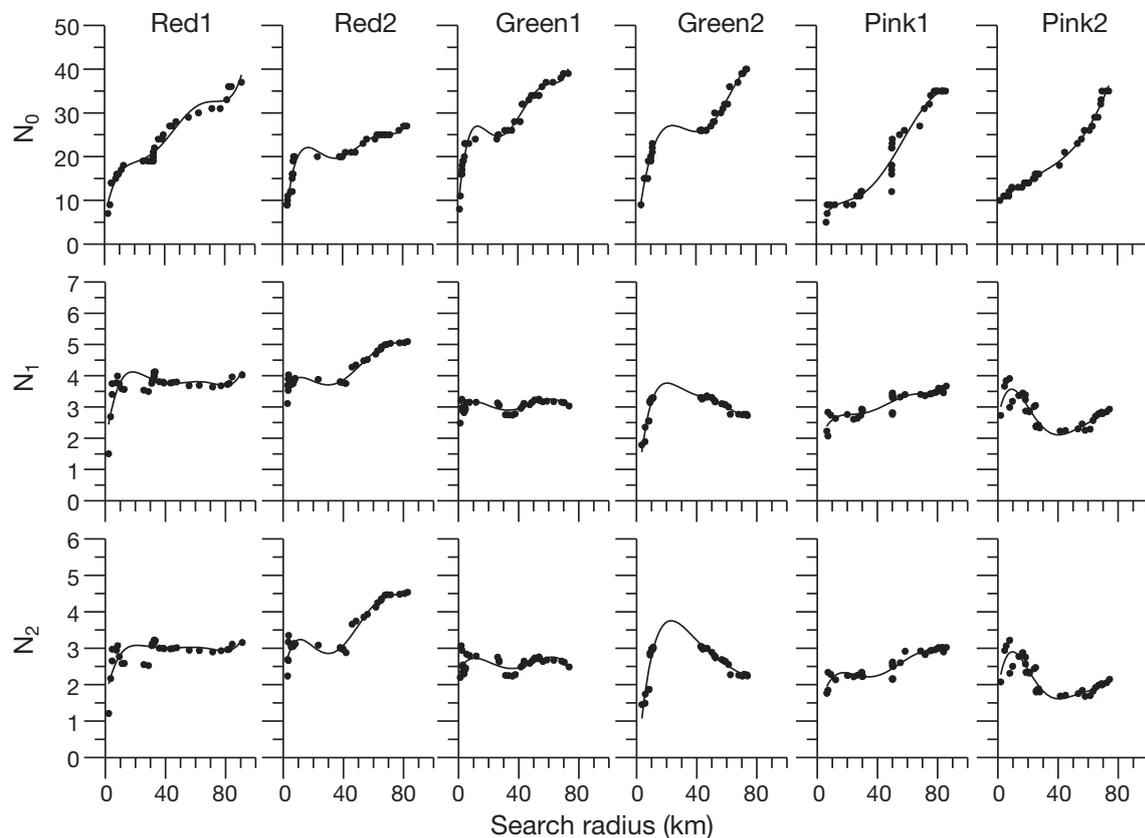


Fig. 5. Effect of increasing search radius (km) on Hill's N_0 (species richness), N_1 , and N_2 (species diversity) index values in each of the 6 assemblages using a nested sequential aggregation of 90 samples. Fitted curves are assemblages fifth-order polynomials

Next, the level of sample aggregation required in order to have a good chance of ranking the assemblages in the correct order was assessed using Pearson's correlation. Values determined for each metric at each aggregation level (as y variables) were compared with the mean values obtained for each metric when 90 trawls samples were aggregated (as x variables; i.e. Table 3). Correlation coefficients approaching 1 indicated good performance, while scores near zero indicated poor performance. Negative coefficients implied a reversal of the correct ranking order. Since 10 randomisations were carried out, means and standard deviations of the correlation coefficient at each aggregation level could be determined (Fig. 6). For each of the 3 metrics, aggregation of at least 20 trawl samples was required. By this point, mean Pearson's R was close to the curve asymptotes (>0.75 in all cases), and the standard deviations around these mean values had declined by more than 66%. This does not mean that estimates of species richness based on 20 GOV trawl samples indicate actual species richness in any given ICES rectangle. Rather, it suggests that measures of species richness based on 20 or more samples are sufficient to compare species richness between different locations or different times.

Mapping species richness and species diversity

Hill's N_0 , N_1 and N_2 indices for each ICES statistical rectangle were derived from the aggregation of the 20 trawl samples closest to each rectangles' central point and maps of spatial variation of species richness and

diversity were plotted (Fig. 7). Species composition of the North Sea groundfish community varied significantly across space; the greater the distance between 2 ICES rectangles, the more different the communities at each location were (Fig. 8). This confirmed the possibility that aggregating samples in space posed a real risk of confounding β -diversity with α -diversity, leading to inflated estimates of the latter. Consequently, in mapping the 3 indices (Fig. 7), ICES rectangles requiring a search radius of >95 km in order to aggregate 20 samples were excluded. Relationships between search radius and each metric were then examined to ensure that this precaution was sufficient to preclude the incorporation of β -diversity.

Since all metric values were based on identical sample size, there was no reason to anticipate that the metric values should be influenced by the search radius. However, this assumption was falsified with respect to Hill's N_0 , the species richness index (Fig. 9). Below a search radius of 49 km, N_0 was independent of search radius, but above this distance, N_0 was significantly linearly related to search radius, suggesting increasing inclusion of β -diversity. For all rectangles where the search radius required to 'capture' 20 trawl samples exceeded 49 km, this linear regression was used to estimate the β diversity contribution ($N_{0,\beta}$) where $N_{0,\beta} = \hat{N}_{0,SR=x} - \hat{N}_{0,SR=49}$. $\hat{N}_{0,SR=x}$ and $\hat{N}_{0,SR=49}$ are the estimates of N_0 obtained from the regression equation at the observed search radius for each of the rectangles concerned and at a search radius of 49 km, respectively. This estimated β -diversity contribution was then subtracted from actual observed estimates of N_0 in each rectangle for which the search radius exceeded

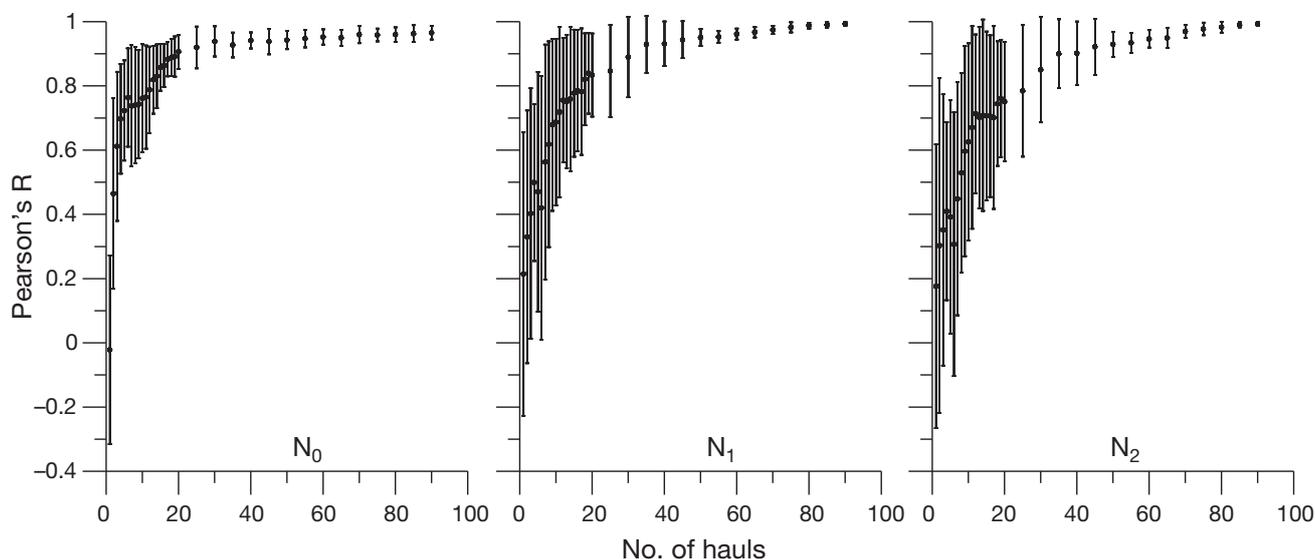


Fig. 6. Mean (± 1 SD) Pearson correlation scores for different sample aggregation levels of Hill's N_0 , N_1 , and N_2 diversity metrics

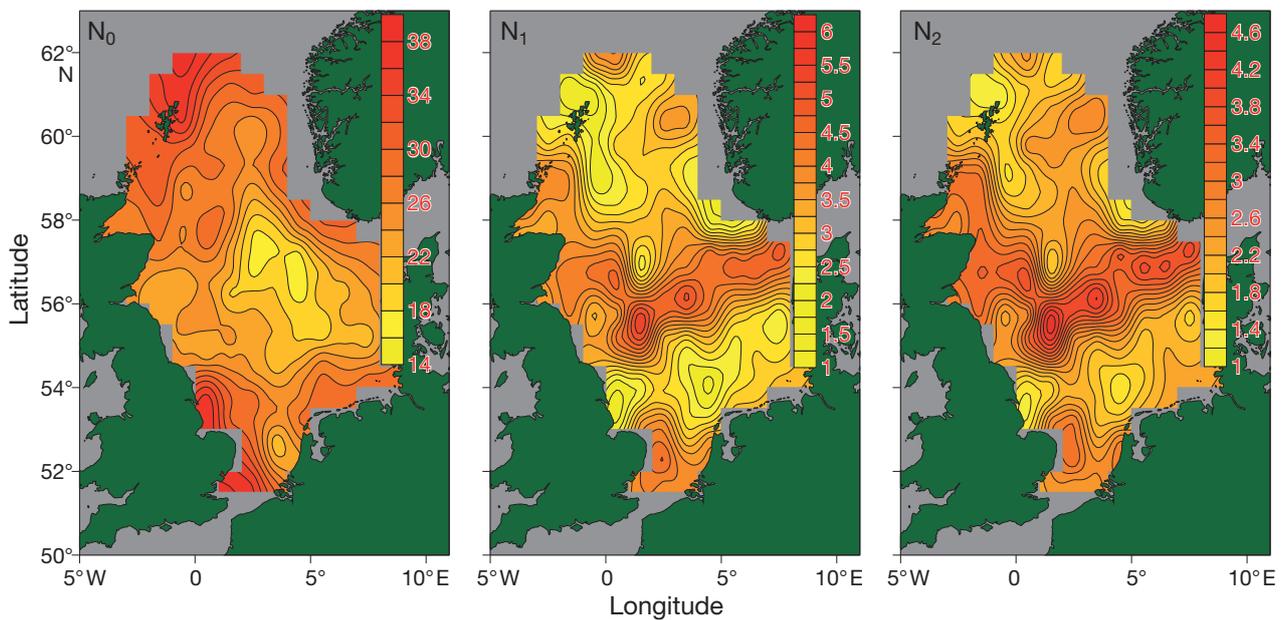


Fig. 7. Spatial variation in Hill's N_0 , N_1 and N_2 across the North Sea, based on aggregation of the 20 Q3 IBTS trawls closest to the central point of each ICES statistical rectangle. Interpolation is by radial basis function in SURFER

49 km. Spatial variation in species richness (N_0) across the North Sea was then re-mapped (Fig. 10). Little difference was apparent between this revised map and the original map (Fig. 7), suggesting that the incorporation of elements of β -diversity in some instances had little effect on qualitative interpretation of spatial variation in α -diversity across the North Sea.

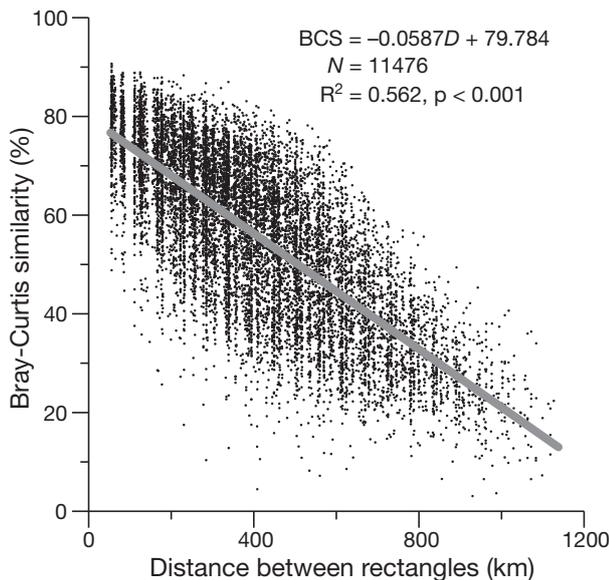


Fig. 8. Relationship between the Euclidean distance between pairs of ICES rectangles and the Bray-Curtis similarity (BCS) in species composition of the groundfish community present in each rectangle

DISCUSSION

The current EcoQO for fish communities in the North Sea concentrates on the restoration of community size structure because fish size metrics were believed to comply with the ICES criteria for good state indicators (ICES 2007). Indices of biodiversity, on the other hand, were considered to violate too many of these criteria to be of use within a management context. Conflicting and inconsistent results in studies undertaken in the North Sea implied that indices of species richness and species diversity were not sensitive to a manageable human activity, not responsive primarily to that human activity, not tightly linked in time to that activity, or not easily and accurately measured. Hill's N_0 , N_1 and N_2 , the indices of species richness and species diversity most commonly applied to North Sea groundfish survey data, are shown here to be strongly influenced by variation in sampling effort. When the influence of sampling effort has been taken into account by *a priori* assessing and then meeting sampling effort requirements, these indices were sensitive to drivers of change in a community (e.g. Greenstreet & Rogers 2006). However, when the influence of sampling effort was ignored, results were less conclusive (e.g. Piet & Jennings 2005). Failure to follow a standard methodology in applying Hill's diversity indices to groundfish survey data, rather than any failing in the indices themselves, may largely be responsible for giving the impression that these metrics are insensitive to drivers of change in the North Sea groundfish community.

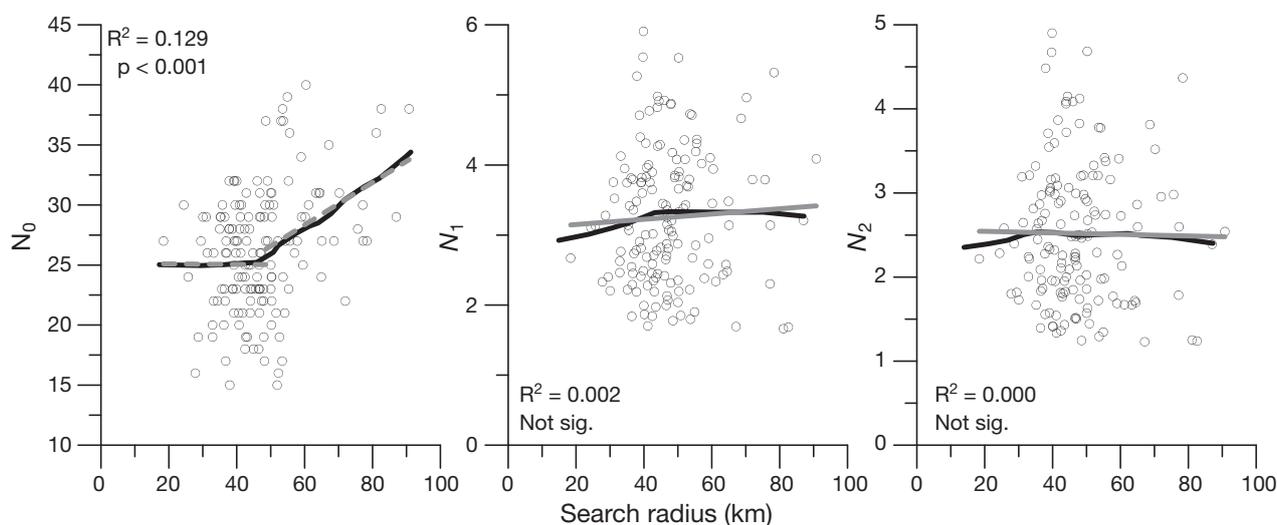


Fig. 9. Effects of ICES rectangle search radius on Hill's N_0 , N_1 , and N_2 , calculated on the 20 trawls 'captured' within the search radius aggregated to provide a single rectangle scale species abundance sample. Black curves show Lowess smoother fits to the data (tension = 0.8; SYSTAT). Grey lines show linear regression fits. On the basis of the shape of the significant Lowess fit to the Hill's N_0 data, the species richness fit was split into 2 components (dashed grey line): rectangles for which search radii ≥ 49 km were required to 'capture' 20 trawl samples, and for which a significant positive relationship ($N_0 = 17.7601 + 0.1764D$, $R^2 = 0.103$, $p < 0.01$) to the data was obtained, and rectangles with search radii < 49 km for which the linear fit was not statistically significant

Furthermore, because Hill's metrics were not believed to be sensitive to a human activity, they were also *de facto* considered not to be tightly linked in time, or to

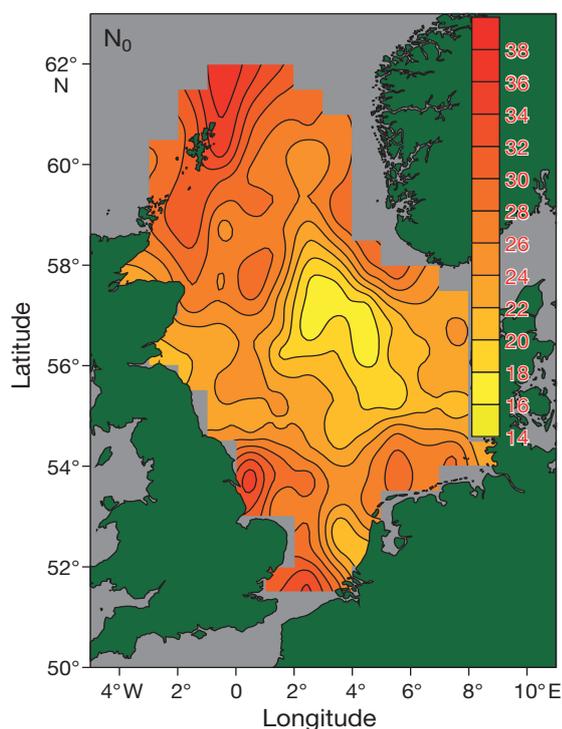


Fig. 10. Spatial variation in species richness (Hill's N_0) after elimination of the β -diversity contribution based on the linear regression for N_0 from Fig. 9

respond primarily to that activity. Methodological failures in the application of diversity indices have therefore blighted them across several of the ICES criteria. Consequently, in the minds of many marine scientists this precluded the use of diversity indices as state indicators, despite the importance of biodiversity as one of the principal drivers at the heart of the EAM.

In this study, data from the Q3 IBTS were analysed. This is an international survey coordinated through ICES and supported by many countries within and beyond the European Union, particularly those with a fisheries interest in the North Sea. These surveys have operated over at least 2 decades (Heessen 1996, Heessen & Daan 1996, Piet & Jennings 2005), and because of their importance to the traditional stock assessment process (ICES 2006), they will no doubt continue to provide the main source of fisheries-independent groundfish abundance data for many years to come. As well as supporting traditional fisheries management, these surveys also provide an important time-series with which to demonstrate the impacts of human activities on the broader fish community, and to monitor the effectiveness of management action to mitigate these. If biodiversity issues are to be addressed directly in future developments of the EAM, then it is crucial that an effective standard methodology for the application of diversity metrics to these IBTS data is established. Determining the level of sample aggregation required, assessing how these samples should be aggregated, and identifying and resolving any other

issues associated with such sample aggregation are essential components of this.

Cluster analysis revealed spatial zonation in the groundfish community across the North Sea, with different areas being occupied by communities differing in their species composition. Similar zonation has been noted previously (Daan et al. 1990, Fraser et al. 2008). However, our analysis was necessary to ensure that, in examining the influence of sampling effort on the performance of species richness and species diversity indices, each successive sample in the cumulative sample aggregations was drawn from essentially the same community.

Regardless of the aggregation method applied, residuals to the Arrhenius power function fits frequently became increasingly negative at high aggregation levels. Consequently, given previous complete North Sea species inventories (Yang 1982), extrapolation of Arrhenius power function SARs to the ICES rectangle scale produced estimates of species richness that were unrealistically high. Gleason semi-log SARs generally provided the better fit, particularly to the randomised aggregation species richness curves, and extrapolation to the ICES rectangle scale produced more reasonable estimates of species richness. As far as the North Sea groundfish community is concerned, areas as large as an ICES statistical rectangle may be considered 'local' in scale (van der Maarel 1988, Stohlgren et al. 1995). Local resources place a limit on the number of species able to coexist within each rectangle so that the fish communities present are 'saturated': species richness is lower than expected, given the regional species pool (Findley & Findley 2001, Cottenie et al. 2003, Heino et al. 2003, Kiflawi et al. 2003).

The nested aggregations, particularly when plotted against search radius, suggested multi-phasic species accumulations. These have been noted before (Fridley et al. 2005) and indicate the operation of processes not reflected by either of the 2 SARs (Colwell et al. 2004). The marked effect of search radius suggests that the species richness estimates are increasingly influenced by the inclusion of β -diversity as new habitats become incorporated within the aggregated sample's search radius. Second-phase increases in species richness accumulation rates occurred at 'search radii' of 40 to 50 km. Even though the aggregations were all carried out within the major community types defined by the cluster analysis at similarity levels of between 65 and 70%, finer-scale clustering at higher similarity levels must still be critical in distinguishing β - from α -diversity.

In both nested and randomised aggregations, Hill's N_1 and N_2 stabilised at some stage in the sample aggregation process. At this point, the index values obtained may be considered representative of the

community sampled, and so have maximum sensitivity to drivers of change. Both indices are influenced by variation in both species richness and species evenness, so the basic theory underpinning the relationship between species richness and area sampled is contravened (Cam et al. 2002, He & Legendre 1996, 2002). The 2 SARs could therefore not be applied to Hill's N_1 and N_2 and extrapolated to estimate species diversity at ICES rectangle scale.

A minimum of 20 IBTS GOV hauls was required to obtain reliable empirical estimates of all 3 metrics. The 'stopping rule' reflected a balance between gains in estimate sensitivity against the economic costs of marine sampling and concerns over the confounding of β - and α -diversity (see Magurran 2004). The most species-rich areas in the North Sea were adjacent to major inflows—the Fair Isle, East Shetland and Norwegian Trench currents in the North and the English Channel to the south (Turrell 1992, Lenhart et al. 1995)—suggesting that immigration is important in maintaining species richness (e.g. MacArthur & Wilson 1967, Williamson 1981, Earn et al. 2000). Highest species diversity (both N_1 and N_2) occurred across the central North Sea at the border between 2 major community types. Elements of both community types may have been included in the aggregated samples, thus raising estimates of α -diversity. Hill's N_1 and N_2 appeared robust to the inclusion of β -diversity as search radius increased, but this was not so for N_0 . Above search radii of 49 km, estimates of α -species richness were increasingly inflated by the inclusion of β -diversity. However, at a qualitative level, this had little effect on maps of spatial variation in species richness across the North Sea.

While an empirical approach may be the only option with respect to Hill's N_1 and N_2 , this is not the ideal solution for species richness (N_0). Empirical estimates of N_0 produced a fifth ranking order for the 6 assemblages, similar to the ranking obtained by fitting the Gleason semi-log SAR to randomised aggregations. No single method of ranking species richness of the 6 assemblages corresponded exactly with any of the other methods examined. This begs the question: Why should such a high level of sampling aggregation be required to estimate species richness reliably? Catchability of many demersal fish species in the GOV trawl is low (Fraser et al. 2007). When 'detectability' of species in the sampling gear is poor, species richness metrics are much more strongly influenced by chance events. It becomes more difficult to sample rare species, requiring much greater sampling effort to accurately parameterise SARs and to attain a sufficient sample to rank communities accurately (Boulinier et al. 1998, Cam et al. 2002, Wintle et al. 2004, Mao & Colwell 2005).

Hopefully, these analyses will help to establish a recognised methodology for applying species richness and species diversity metrics to groundfish survey data. A standard approach, which takes account of sampling effort requirements, should produce sensitive indices. Once sensitivity has been addressed, species richness and diversity indices should be responsive to drivers of change and more tightly linked in time to such drivers, thereby addressing 3 of the ICES criteria for good state indicators against which these metrics performed so poorly. However, ensuring that metrics are sensitive does not necessarily ensure that they are responsive primarily to human activities, and not responsive to other (e.g. environmental) causes of change. The complexities involved will also do little to reassure scientists that they can easily and accurately be measured with low error rate, and they certainly do not help make such indices easier to understand by policy makers and other non-scientists. Using these metrics within a management context therefore continues to pose some problems.

Previous studies investigated temporal changes in the fish community and thus aggregated samples across space (Greenstreet & Hall 1996, Greenstreet et al. 1999, Greenstreet & Rogers 2006). However, spatial issues (marine spatial planning, marine protected areas, etc.) are becoming more important to managers, so questions concerning spatial variation in species richness and diversity were addressed in the present study. To reduce the need for spatial aggregation, data collected over a 7 yr period (1998 to 2004) were aggregated. The environment of the North Sea is changing gradually, and ecosystem-wide changes have occurred (Heath 2005). Consequently, some changes in North Sea groundfish species richness and diversity may have taken place within the time span of this study, but there is no evidence at present of any major 'regime shift' having occurred. Ignoring such a temporal signal when aggregating samples may, at worst, have served to blur the spatial signal. Despite this, however, clear spatial patterns emerged. Documenting variation in α -diversity was the main objective. At search radii exceeding 49 km, elements of β -diversity started to enter the aggregate samples, inflating estimates of α -diversity. At current IBTS sampling intensities, obtaining 20 trawl samples from a radius of 49 km around each ICES rectangle will require the aggregation of data collected over at least 4 yr. From a management perspective, this is not ideal. Following the implementation of any mitigating management action, 12 yr would be required to attain the minimum 3 data points necessary to confirm a new trend. If restoration of biodiversity remains a political objective, then politicians may have to wait longer than usual to reap the political benefits of their actions (see also Nicholson & Jennings 2004).

Acknowledgements. We thank all our colleagues in the ICES working group on ecosystem effects of fishing activities (WGEKO) who have participated in numerous vigorous debates over the years, all of which served to hone the ideas presented here. We are also indebted to colleagues who participated in the MAFCONS project, where these ideas came to final fruition. We also thank staff at ICES who provided the IBTS data. This work was supported by the Scottish executive environment and rural affairs department under ROAMES MF0753 and MF0168. The MAFCONS (Managing fisheries to conserve groundfish and benthic invertebrate species diversity) project was funded in part by the European Commission (Q5RS-2002-00856). We are indebted to 2 anonymous referees, and to the editor, Jake Rice, whose suggestions greatly improved this paper.

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Editorial responsibility: Jake Rice, Ottawa, Canada

*Submitted: October 24, 2007; Accepted: March 25, 2008
Proofs received from author(s): July 10, 2008*