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Redundancy in metrics describing the composition, structure, and functioning of the North Sea demersal fish community

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Broader ecosystem management objectives for North Sea demersal fish currently focus on restoring community size structure. However, most policy drivers explicitly concentrate on restoring and conserving biodiversity, and it has not yet been established that simply restoring demersal fish size composition will be sufficient to reverse declines in biodiversity and ensure a generally healthy community. If different aspects of community composition, structure, and function vary independently, then to monitor all aspects of community general health will require application of a suite of metrics. This assumes low redundancy among the metrics used in any such suite and implies that addressing biodiversity issues specifically will require explicit management objectives for particular biodiversity metrics. This issue of metric redundancy is addressed, and 15 metrics covering five main attributes of community composition, structure, and function are applied to groundfish survey data. Factor analysis suggested a new interpretation of the metric information and indicated that a minimum suite of seven metrics was necessary to ensure that all changes in the general health of the North Sea demersal fish community were monitored properly. Covariance among size-based and species-diversity metrics was low, implying that restoration of community size structure would not necessarily reverse declines in species diversity.

Keywords: community health, community size structure, ecosystem approach to management, life-history-trait metrics, metric suites, species diversity, state indicators.

Introduction

The 1997 Bergen North Sea Intermediate Ministerial Meeting formally recognized the need to adopt an ecosystem approach to management (EAM; Misund and Skjoldal, 2005). Although not having the legislative competence to manage fisheries directly, the Oslo/Paris Commission (OSPAR) was recognized as the competent authority to develop ecological objectives for an EAM (Johnson, 2008). OSPAR subsequently asked ICES to recommend a metric that would best support an Ecological Quality Objective (EcoQO) for the North Sea fish community. Application of the ICES criteria for good state indicators (ICES, 2001a) suggested that size-based metrics would likely perform best (ICES, 2001b; Greenstreet, 2008). The theoretical relationship between fishing mortality and fish population age (and consequently size) composition was well established (Beverton and Holt, 1957), and the effect of fishing pressure on fish community size composition

was already well known from many empirical studies (Bianchi et al., 2000; Daan et al., 2005; Shin et al., 2005). Changes in the proportion of large fish and hence the average weight and average maximum length of the fish community therefore emerged as the Element of Ecological Quality for Fish Communities at the Bergen 2002 North Sea Ministerial Conference (Heslenfeld and Enserink, 2008). Subsequent work has focused on developing the most effective size-based indicator metric and setting the EcoQO; accordingly, the proportion (by weight) of fish >40 cm long should be >0.3 (Heslenfeld and Enserink, 2008; Greenstreet et al., 2011).

Current ecosystem management objectives for the North Sea demersal fish community therefore focus on restoring its size structure. However, before the.5 Bergen Ministerial Declaration in 2002, the Convention on Biological Diversity and Annex V (Protection and Conservation of the Ecosystems and Biological.

Diversity of the Maritime Area) of the OSPAR convention (Protection of the Marine Environment of the Northeast Atlantic) both focused on the conservation and restoration of biological diversity (Barange, 2003). This early emphasis on biodiversity prompted early studies of marine fish communities to examine trends in species diversity and to explore the role of fishing as a possible cause of change (Greenstreet and Hall, 1996; Greenstreet *et al.*, 1999; Rogers *et al.*, 1999a, b; Rogers and Ellis, 2000). [Note that the Convention on Biological Diversity considers biological diversity to include genetic variability between individuals within populations, variability between species within communities, and variability between communities (ecosystems/ habitats) within regions. Here, as with all the papers we cite, we focus only on the second of these three aspects, the diversity of species within fish communities.] Declines in fish species diversity in the northwestern North Sea were, for example, greatest in the areas that had been the most heavily fished (Greenstreet and Rogers, 2006). More recently, the European Union's Marine Strategy Framework Directive (MSFD) continues to stress the need to halt biodiversity loss and ultimately provide biologically diverse and dynamic oceans and seas (Greenstreet, 2008). Given the ongoing political emphasis on biodiversity, the question whether simply restoring fish community size composition will also be sufficient to conserve and restore fish biodiversity needs to be examined.

A strong mechanistic relationship between fish community size composition and species diversity implies redundancy among size-based and species-diversity metrics; achieving the fish community EcoQO and restoring fish size structure should simultaneously contribute to conserving and restoring fish biodiversity. However, it has often been assumed that different aspects of the composition, structure, and functioning of natural communities vary independently (Fulton *et al.*, 2005; Piet and Jennings, 2005; Greenstreet and Rogers, 2006) and that redundancy between different univariate community metrics is low. If so, then a broad suite of metrics is needed to cover all types of change possible in a community (Blanchard *et al.*, 2010; Bundy *et al.*, 2010). Under such circumstances, establishing the necessary monitoring programmes and advisory frameworks could have significant resource implications. Determining the level of covariation among potential state indicators, to identify the minimum number necessary to cover all community attributes of ecological and political concern, is therefore a high priority for scientists concerned with the future development of an EAM.

In all, 15 univariate community metrics were applied to ICES International Bottom-Trawl Survey (IBTS) demersal fish species abundance and abundance-at-length data collected between 1983 and 2008. Following the methodology used to determine the North Sea large fish index (LFI), trends in the metrics were reported at the whole Greater North Sea regional scale (OSPAR Region II). The LFI was 1 of the 15 metrics used. The metrics were selected to cover five broad attributes of the composition, structure, and functioning of the demersal fish community of the North Sea: (i) abundance/biomass/productivity, (ii) size composition, (iii) species richness, (iv) species evenness, and (v) life-history trait composition. Factor analysis was carried out to determine the level of redundancy among the 15 metrics and to identify the minimum number of metrics necessary to ensure that variation in all five attributes was monitored adequately. The merits of using just the LFI to monitor the health of the North Sea demersal fish community, and as the basis for implementing a broader ecosystem approach for its management, are discussed.

Methods

ICES (2007b) advised that the fish community EcoQO be based on the LFI determined using data collected by the IBTS undertaken in the first quarter of the year (Q1). This survey, coordinated through ICES, aims to obtain two 30-min trawl samples from each ICES rectangle ($0.5°$ latitude by $1.0°$ longitude) in each year and has almost complete coverage of the North Sea (ICES Area IV) and Kattegat/Skagerrak region (ICES Area IIIa). Since 1983, all vessels involved have used the same Grande Ouverture Verticale (GOV) demersal trawl, providing the longest time-series of consistent sampling in the North Sea, i.e. from 1983 to 2008. Because of this dependence of the fish community EcoQO on the Q1 IBTS, all analyses undertaken here used the same dataset. The GOV trawl is more selective for bottom-dwelling species. Many earlier studies that have derived univariate community metrics from North Sea groundfish survey data therefore excluded pelagic species from their analyses (Greenstreet and Hall, 1996; Greenstreet *et al.*, 1999; Piet and Jennings, 2005; Greenstreet and Rogers, 2006). Development of the North Sea fish community EcoQO followed the same logic and only considers demersal fish (ICES, 2006; Greenstreet *et al.*, 2011). The same approach has been adopted here, primarily because of the need to derive indicators that are directly comparable with the current LFI, and to be able to relate the results to those of earlier studies. However, addressing the biodiversity needs of the MSFD will ultimately require the development of indicators that take account of all components of fish communities, including pelagic species.

Despite there being a clear sampling protocol, species counts without length frequency data, and failures to identify fish to species level do arise in the IBTS database (Daan, 2001). Size-based metrics require length frequency summaries. They are also affected by the lack of specific taxonomic information if weight-at-length relationships need to be applied to derive biomass-based metrics, such as the North Sea LFI, or mean weight. Productivity metrics depend on both identification to species and the provision of appropriate length frequency data. Species diversity metrics can only be applied to survey data recorded to a consistent level of taxonomic resolution, preferably to species. Similarly, life-history metrics require species identification to apply appropriate parameter appellations to abundance data. Simply excluding whole trawl samples with incomplete records would have caused significant loss of data, compromised time-series analyses, older samples tending to be less complete, and could have potentially introduced a systematic bias because shortcuts in data recording were more likely when larger-than-normal trawl samples were taken on board.

Estimators for missing data were therefore derived and applied. Where only species count data were provided, length frequency distributions equal to those observed for the same species in the same year and locality were assumed. Similarly, abundance-at-length data for fish identified only to genus, family, or order were assumed to have a species composition equal to the relative abundance of the constituent species sampled in the same local region, general length range, and year. When inserting missing species composition information in this way, variation in length was taken into account in estimating appropriate species relative abundances. For example, for unidentified weever fish (Trachinidae), all fish >15 cm were assumed to
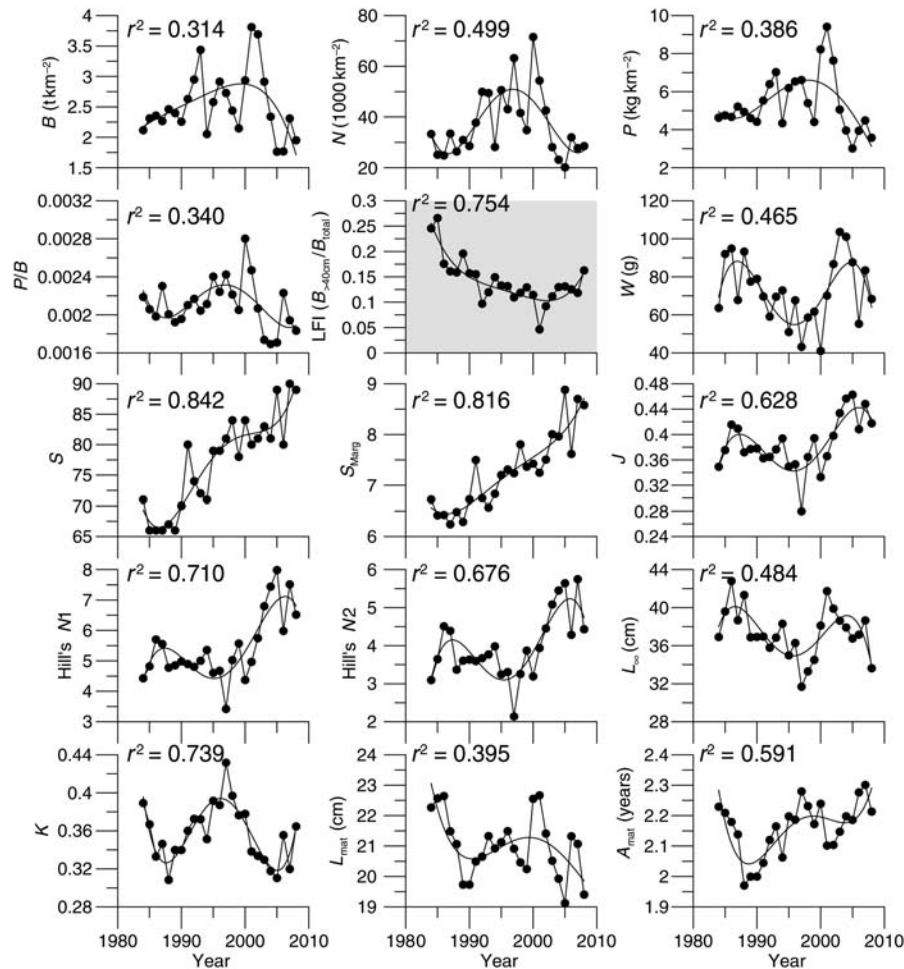
Figure 1. Trends in 15 indicator metrics applied to the IBTS Q1 groundfish survey data for the whole North Sea (see Table 1 for an explanation of the metrics, the *y*-axis labels). The LFI on which the North Sea fish community EcoQO is based is highlighted in grey. Fitted smoothers are fourth-degree polynomials, and the Pearson r^2 values indicate goodness of fit, which if $r^2 > 0.151$ (two-tailed), means that the correlation is significant at $p < 0.05$.

be greater weever *Trachinus draco*. Smaller than that, unidentified weever fish were assigned to *T. draco* or to lesser weever *Echiichthys vipera*, depending on their relative abundance within defined length classes, e.g. 12–15 cm, <12 cm. Species abundance-at-length data were checked to eliminate records of impossibly large fish. All records where the species length exceeded the maximum length for the species (L_{max}) recorded in FishBase (http://www.fishbase.org/search.php) were examined. Outliers were either deleted, or the length was changed to the L_{max} for the species if this length appeared to fit the general length frequency distribution observed in the rest of the data. If the length recorded was only marginally greater than L_{max} in FishBase (e.g. no more than 5% greater), and it seemed to fit the general length frequency distribution, then no action was taken. In all, these corrections affected 0.16% of the 29 million fish recorded in the analysed subset of the Q1 IBTS database. In applying these corrections, we followed procedures established in several earlier studies (Greenstreet and Hall, 1996; Greenstreet et al., 1999; Daan, 2001; Daan et al., 2005; Greenstreet and Rogers, 2006). To ensure that our corrections could not have influenced our conclusions, the analyses depicted in Figure 1 were repeated,

but with all corrected records in the database excluded. No appreciable differences in the temporal trends were detected.

Although haul duration was standardized to 30-min tows (except that Scotland continued to tow for 1 h until 1999), there was some variation attributable to variable operational circumstances. Only trawl samples of 25–35 min duration were analysed (except for Scottish trawls up to 1999, where 55–65 min trawls were considered valid). Tow speeds also varied as a consequence of variable weather conditions and differences between vessels. To standardize the data further, all individual trawl catch abundances-at-length ($n_{s,l,t}$), where the subscripts s, l, and t represent the particular species, length class, and trawl sample in question, were converted to densities-at-length ($d_{s,l,t}$; expressed as numbers per km², n km^{-2}) within the area swept by the trawl, where the latter was determined as the product of the distance towed between shooting and hauling positions ($\Lambda_{tow,t}$) and the average distance between the two wings of the trawl ($\Lambda_{wing,t}$) over the course of the tow:

$$d_{s,l,t} = \frac{n_{s,l,t}}{\Lambda_{tow,t}\Lambda_{wing,t}}.$$

Table 1. Descriptions, abbreviations (with units in parentheses; note that t km^{-2} and g m^{-2} are equivalent), and derivations of the 15 univariate community metrics applied to the groundfish survey data.

Number	Metric	Abbreviation	Metric calculation	Terminology
1	Biomass	B (t km^{-2} or g m^{-2})	$B_y = \sum_{s=1}^{S_y} \sum_{l=\min}^{l=\max} D_{y,s,l} c_s l^{b_s}$	Where S_y is the total number of species sampled in year y, l the length class for which any given density-at-length in terms of numbers is being converted to an equivalent density-at-length in terms of biomass (this product is then summed for all length classes between the minimum length and the maximum length recorded for each species across the whole North Sea in that year), and $D_{y,s,l}$ the North-Sea-wide estimate of the average density-at-length of each species in each year (see text for detail). The constants c_s and b_s are the constant and exponent values, respectively, in the species-specific weight-at-length relationship
2	Abundance	N (km^{-2})	$N_y = \sum_{s=1}^{S_y} \sum_{l=\min}^{l=\max} D_{y,s,l}$	Where S_y is the total number of species sampled in year y, l the length class (summed for all length classes between the minimum length and the maximum length recorded for each species across the whole North Sea in that year), and $D_{y,s,l}$ the North-Sea-wide estimate of the average density-at-length of each species in each year (see text for detail)
3	Overall daily growth production	P (t km^{-2} or g m^{-2})	$P_y = \sum_{s=1}^{S_y} \sum_{l=\min}^{l=\max} D_{y,s,l} c_s b_s l^{b_s-1} \frac{k_s}{365}[l_\infty - l]$	Where S_y is the total number of species sampled in year y, l the length class, and $D_{y,s,l}$ the North-Sea-wide estimate of the average density-at-length of each species in each year (see text for detail). The constants c_s and b_s are the species-specific weight-at-length relationship constant and exponent values, respectively. The constants k_s and $l_{\infty,s}$ are the species-specific von Bertalanffy growth function and ultimate body length values, respectively. k_s is divided by 365 to convert the annual parameter to a daily parameter
4	Specific daily growth production	P/B	$I_{P/B,y} = \dfrac{P_y}{B_y}$	Where P_y is the total daily growth production and B_y the total biomass of the fish community in any one year (see above; indicators 3 and 1), and $I_{P/B,y}$ is the annual specific daily growth production indicator (P/B) value
5	Large-fish indicator	LFI	$I_{LF,y} = \dfrac{\sum_{s=1}^{S_y} \sum_{l>40cm}^{l=\max} D_{y,s,l} c_s l^{b_s}}{B_y}$	Where the denominator term is described above (indicator 1) and the numerator term is a similar expression, except that the summation is carried out across lengths $>$40 cm only. $I_{LF,y}$ is the resulting annual LFI value
6	Mean weight of fish	W (g)	$W_y = \dfrac{B_y}{N_y}$	Where B_y and N_y are the estimates of average density in terms of biomass and number, respectively, over the whole North Sea (see above; indicators 1 and 2)
7	Species count	S	S_y	Where S_y is the count of the number of species recorded in all IBTS trawl catches collected in any one year
8	Margalef's species richness	S_{Marg}	$S_{Marg,y} = \dfrac{S_y - 1}{\log F_y}$	Where S_y is defined above (indicator 7) and F_y is the total count of all individual fish caught in all IBTS trawl catches in any one year
9	Pielou evenness	J	$J_y = \dfrac{-\sum_{s=1}^{S_y} N_{y,s}/N_y \log(N_{y,s}/N_y)}{\log S_y}$	Where N_y is defined above (indicator 2) and $N_{s,y}$ the average density of fish (individuals km^{-2}) belonging to each species, s, calculated across the whole North Sea, i.e. $N_{y,s} = \sum_{l=\min}^{l=\max} D_{y,s,l}$, without the summation-across-species term defining indicator 2
10	Hill's N1 diversity	$N1$	$N1_y = \exp\left(-\sum_{s=1}^{S_y} \frac{N_{y,s}}{N_y} \log \frac{N_{y,s}}{N_y}\right)$	Where both $N_{s,y}$ and N_s are defined above (indicators 9 and 2, respectively)
11	Hill's N2 dominance	$N2$	$N2_y = \dfrac{1}{\sum_{s=1}^{S_y} (N_{y,s}/N_y)}$	Where S_y, $N_{s,y}$, and N_y are all defined above (indicators 7, 9, and 2, respectively)
12	Mean ultimate body length	L_∞ (cm)	$L_{\infty,y} = \dfrac{\sum_{s=1}^{S_y} \sum_{l=\min}^{l=\max} D_{y,s,l} l_{\infty,s}}{N_y}$	Where $l_{\infty,s}$ is the von Bertalanffy ultimate body length of each species s, $D_{y,s,l}$ the North-Sea-wide estimate of the average density-at-length of each species in each year (see text for details), and S_y, and N_y defined above (indicators 7 and 2, respectively)

Continued

Table 1. *Continued*

Number	Metric	Abbreviation	Metric calculation	Terminology
13	Mean growth coefficient	K	$K_y = \dfrac{\sum_{s=1}^{S_y} \sum_{l=\min}^{l=\max} D_{y,s,l} k_s}{N_y}$	Where k_s is the von Bertalanffy growth parameter for each species s, $D_{y,s,l}$ the North-Sea-wide estimate of the average density-at-length of each species in each year (see text for details), and S_y and N_y defined above (indicators 7 and 2, respectively)
14	Mean length at maturity	L_{mat} (cm)	$L_{mat,y} = \dfrac{\sum_{s=1}^{S_y} \sum_{l=\min}^{l=\max} D_{y,s,l} l_{mat,s}}{N_y}$	Where $l_{mat,s}$ is the length at maturity of each species s, $D_{y,s,l}$ the North-Sea-wide estimate of the average density-at-length of each species in each year (see text for detail), and S_y and N_y defined above (indicators 7 and 2, respectively)
15	Mean age at maturity	A_{mat} (years)	$A_{mat,y} = \dfrac{\sum_{s=1}^{S_y} \sum_{l=\min}^{l=\max} D_{y,s,l} a_{mat,s}}{N_y}$	Where $a_{mat,s}$ is the age at maturity of each species s, $D_{y,s,l}$ the North-Sea-wide estimate of the average density-at-length of each species in each year (see text for detail), and S_y and N_y defined above (indicators 7 and 2, respectively)

Species life-history-trait parameter values ($l_{\infty,s}$, k_s, $l_{mat,s}$, and $a_{mat,s}$) are derived from Jennings *et al.* (1999) and FishBase. Metrics 1–4 are the metrics of abundance/biomass/productivity, 5 and 6 the metrics of size composition, 7 and 8 the metrics of species richness, 9–11 the metrics of species evenness, and 12–15 the life-history-trait composition metrics. Explicit in the derivations of each of the 15 metrics is the fact that a single metric value was calculated for each year covering the whole North Sea. Essentially the entire IBTS for each year was treated as a single sample of the North Sea fish assemblage.

If the distance trawled could not be determined, this was estimated from tow duration, assuming the mean trawl speed for the vessel concerned and year in question. Missing wingspread data were estimated using a relationship between wingspread and water depth following the procedure used by Fraser *et al.* (2007). For each year (y), and for all species and length classes of each species sampled in that year, single whole North-Sea-wide average density-at-length estimates ($D_{y,s,l}$) were derived by dividing the sum of all individual trawl sample densities-at-length estimates across all trawl samples collected in that year by this total number of trawl samples (T_y):

$$D_{y,s,l} = \frac{\sum_{t=1}^{t=T_y} d_{s,l,t}}{T_y}.$$

In essence, this meant that all individual Q1 IBTS trawl samples collected in any one year were combined to provide a single, North-Sea-wide estimate of average density-at-length for each species. These were the raw data used to determine annual values for each of 15 univariate community metrics following the equations listed in Table 1.

Temporal trends in these 15 metrics were examined and factor analysis used to assess the level of covariation among these trends and to identify the minimum number of metrics that explained a large proportion of the total variance (Sokal and Rohlf, 1981), and which would therefore be required to monitor change in all major aspects of the composition, structure, and functioning of the North Sea demersal fish community. This analysis was carried out using the SYSTAT© software package. Only factors with eigenvalues >1 were considered to be significant (the SYSTAT default). To simplify the interpretation of the factors, varimax orthogonal rotation was applied to minimize the number of variables that had high loadings on each factor, thus rendering the linkage of particular indicators to particular factors less ambiguous. Quartimax orthogonal rotation, which minimizes the number of factors needed to explain each indicator, might also be considered appropriate in a study of indicator redundancy. However, repeating the analysis using this rotation method made little

difference. The factor analysis outcome was therefore robust to the orthogonal rotation method applied.

The factor analysis was based on a Pearson correlation matrix between the 15 metrics, assuming each metric to be normally distributed. The outcome of the analysis could therefore have been affected if the different metrics had different underlying distributions. Examination of a scatterplot matrix (each metric plotted against all others) indicated little cause for concern because, in each pairwise comparison, the points generally fell within the ellipsoid characteristic of bivariate, normally distributed data. Despite this, five metrics (B, N, P, LFI, and N1) had distributions that were marginally positively skewed. This was resolved by transforming these metrics by taking natural logarithms (after first adding 1.0 to the LFI values). However, the effect of this on the factor analysis outcome was minimal: the same number of factors was observed with eigenvalues >1; these factors combined explained the same total variation, and each factor individually explained nearly identical percentages of the total variation. Individual metrics linked to the same factors and their loadings on these factors were essentially the same. The level of departure from normality in the underlying metric distributions was so slight as to have negligible impact on the outcome of the factor analysis. Consequently, we report only the results of the analysis performed on the non-transformed metrics on the grounds that these are more easily interpreted.

Results

Clear differences were apparent between the 15 metric temporal trends, highlighted by fitting fourth-degree polynomial smoothers (Figure 1). Factor analysis suggested four significant factors, each explaining between 12.1 and 34.8%, and together explaining 91.9% of the total variance in the metric trends (Table 2). Including a fifth factor (with eigenvalue <1) explained <5% additional variation. Fourth-degree polynomial smoothers fitted to the factor scores suggested clear underlying temporal trends in the first three factors. Conversely, the fourth-factor scores were poorly fitted by the smoother and may simply have reflected residual short-term (i.e. interannual, biannual), or perhaps even random, variation (Figure 2).

Table 2. Summary of factor analysis results showing the Pearson correlations (r^2) between individual annual metric values and annual scores for the four significant factors and between individual annual metric values and fourth-degree polynomial smoothers fitted to the factor scores (Figure 2).

Correlation	Metric	Factor 1 (34.8%)		Factor 2 (23.5%)		Factor 3 (21.4%)		Factor 4 (12.1%)	
		r^2	$p<$	r^2	$p<$	r^2	$p<$	r^2	$p<$
Factor scores	B	0.000	–	**−0.757**	**0.0001**	−0.025	–	0.019	–
	N	0.383	0.001	**−0.541**	**0.0001**	0.014	–	0.025	–
	P	0.072	–	**−0.802**	**0.0001**	−0.010	–	0.081	–
	P/B	**0.358**	**0.01**	−0.305	0.01	0.000	–	0.177	0.05
	LFI	0.019	–	**0.680**	**0.0001**	−0.140	–	0.047	–
	W	**−0.635**	**0.0001**	0.097	–	−0.057	–	−0.001	–
	S	−0.001	–	−0.054	–	**0.837**	**0.0001**	−0.039	–
	S_{Marg}	−0.058	–	0.000	–	**0.800**	**0.0001**	−0.059	–
	J	**−0.776**	**0.0001**	0.048	–	0.099	–	−0.017	–
	$N1$	**−0.638**	**0.0001**	0.029	–	0.285	0.01	−0.030	–
	$N2$	**−0.777**	**0.0001**	0.003	–	0.171	0.05	−0.004	–
	L_∞	**−0.515**	**0.0001**	−0.075	–	−0.153	–	0.214	0.05
	K	**0.894**	**0.0001**	0.007	–	0.010	–	0.017	–
	A_{mat}	0.077	–	0.067	–	**0.557**	**0.0001**	0.238	0.05
	L_{mat}	0.015	–	−0.062	–	−0.055	–	**0.854**	**0.0001**
Factor smoother	B	0.024	–	**−0.273**	**0.01**	−0.002	–	−0.025	–
	N	0.205	0.05	**−0.286**	**0.01**	0.005	–	−0.093	–
	P	0.074	–	**−0.285**	**0.01**	−0.002	–	−0.030	–
	P/B	**0.138**	**–**	−0.120	–	−0.008	–	−0.022	–
	LFI	0.023	–	**0.702**	**0.0001**	−0.166	–	0.400	0.001
	W	**−0.264**	**0.01**	0.088	–	−0.014	–	0.143	–
	S	−0.008	–	−0.089	–	**0.809**	**0.0001**	−0.079	–
	S_{Marg}	−0.060	–	−0.015	–	**0.789**	**0.0001**	−0.029	–
	J	**−0.544**	**0.0001**	0.004	–	0.109	–	−0.001	–
	$N1$	**−0.489**	**0.0001**	0.000	–	0.281	0.01	−0.006	–
	$N2$	**−0.568**	**0.0001**	−0.001	–	0.170	0.05	−0.005	–
	L_∞	**−0.341**	**0.01**	0.000	–	−0.093	–	0.039	–
	K	**0.691**	**0.0001**	0.005	–	0.000	–	0.005	–
	A_{mat}	0.015	–	0.061	–	**0.336**	**0.01**	0.078	–
	L_{mat}	0.014	–	0.022	–	−0.069	–	**0.187**	**0.05**

The original correlation coefficient signs have been retained to illustrate the directionality of the relationship between each indicator and its associated factor; therefore, where an r^2 value is shown as negative, this means that the indicator varies inversely with variation in the factor scores. The percentage of the total variance explained by each factor is given in parenthesis. Emboldened values indicate the metrics linked to each factor by the factor analysis.

For 14 metrics, variation in the scores of the most strongly correlated factor explained >50% of the variation in actual metric values, the exception being the P/B ratio metric (Table 2). For all but the P/B ratio metric, polynomial smoothers fitted to the factor scores also explained a significant proportion of variation in the original associated metric values (Table 2). Smoothers fitted to the first and the third factor scores explained almost as much variation in both Hill's species evenness and both original species richness metrics, respectively, as the actual scores, whereas the smoother fitted to the second factor scores actually explained more of the variation in the original LFI data than the actual scores. Hence, for the three factors where fourth-degree polynomial smoothers fitted trends in their scores reasonably well, these smoothers explained almost as much, if not the same amount, of variation in the actual metric values as the scores did themselves (Table 3). Assuming that these polynomial smoothers provided an indication of a response to some underlying driver or drivers, this analysis could be used as a diagnostic tool to select particular metrics for inclusion in a suite of state metrics.

The 15 metrics were chosen to portray variation in five main attributes of the composition, structure, and functioning of the demersal fish community. Factor analysis suggested that several of the metrics representing these attributes did indeed vary

independently of each other. For example, the two species-richness metrics correlated closely (Figure 3a) and associated with factor 3 (Table 2), whereas all three species evenness metrics also covaried closely (Figure 3b), but were linked to factor 1 (Table 2). North Sea demersal fish species richness and evenness therefore varied relatively independently of each other (Figure 3c), so a suite of state indicators for the community would need to include both types of diversity metric. However, just one metric would be needed to cover each attribute, reducing the number of biodiversity metrics from the five used here to just two. Similarly, the biomass, abundance, and overall productivity metrics all covaried closely (Figure 4a), but this time linked to the second factor (Table 2). Only one of these metrics would be necessary to perform a state indicator role for this main attribute of the composition, structure, and functioning of the demersal fish community. This also implies that variation in demersal fish abundance, biomass, and productivity was relatively independent of variation in both species richness (Figure 4b) and species evenness (Figure 4c), although to some extent, species evenness varied inversely with abundance (Figure 4c).

Although P/B was linked most closely to factor 1 (Table 2), and indeed P/B correlated with all three species evenness metrics (Figure 5a), the P/B metric also correlated with the factor 2
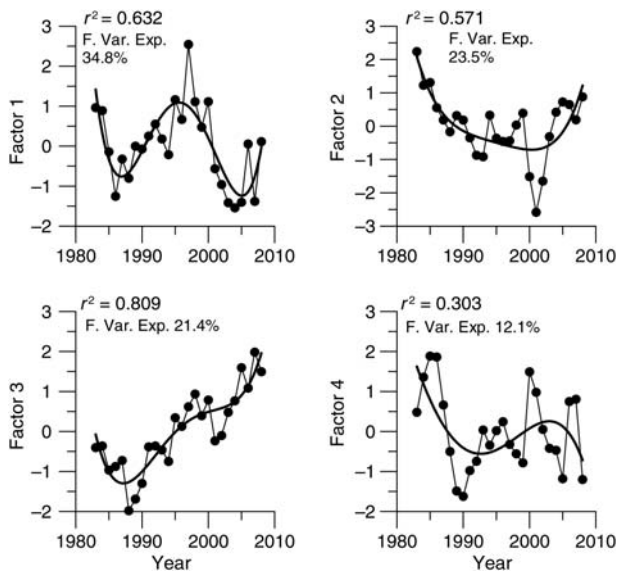
Figure 2. Trends in scores for each of the four significant factors, fitted by fourth-degree polynomial smoothers to define underlying trends. The Pearson r^2 values indicate the goodness of fit of the fourth-degree polynomial smoother to the actual factor scores, which if $r^2 > 0.111$ (one-tailed) or if $r^2 > 0.151$ (two-tailed), means that the correlation is significant at $p < 0.05$. "F. Var. Exp." indicates the percentage of total variation explained by each factor (Table 2).

Table 3. Ratios of the variance explained in the original metric data by the smoothers fitted to the linked factor scores divided by the variance explained by the factor scores themselves (ordered by ranked ratio scores).

Metric	Factor	Ratio
LFI	2	1.0324
S_{Marg}	3	0.9859
S	3	0.9658
K	1	0.7730
$N1$	1	0.7662
$N2$	1	0.7309
J	1	0.7015
L_∞	1	0.6631
A_{mat}	3	0.6035
N	2	0.5279
W	1	0.4151
P/B	1	0.3859
B	2	0.3600
P	2	0.3552
L_{mat}	4	0.2186

scores (Table 2). This arose through the relatively strong correlations between abundance and P/B and between overall productivity and P/B. However, the relationship between biomass and specific productivity was much weaker (Figure 5b). The two size composition metrics (LFI and mean weight) were not closely correlated (Figure 5c) and were split between two different factors (Table 2). The LFI was linked to factor 2 and negatively correlated with the abundance, biomass, and overall productivity metrics (Figure 5d). Mean fish weight was linked to factor 1; it correlated negatively with specific productivity. Mean fish weight was weakly but positively correlated with the three species evenness metrics (Figure 5e).

The four life-history-trait metrics were distributed across three different factors (Table 2). Ultimate body length (L_∞) and the von Bertalanffy growth parameter (K) both linked to factor 1 (Table 2) and, as would be expected, were correlated negatively with each other (Figure 6a). The von Bertalanffy growth parameter was strongly negatively correlated, whereas ultimate body length was only weakly positively correlated with all three species evenness metrics (Figure 6b). Mean age at maturity was linked to factor 3 (Table 2) and was positively correlated with the two species-richness metrics (Figure 6c). Length at maturity was the only metric linked to factor 4.

Discussion

Our initial premise was that the 15 metrics reflected variation in five distinct attributes of the North Sea demersal fish community: (i) abundance/biomass/productivity, (ii) size composition, (iii) species richness, (iv) species evenness, and (v) life-history-trait composition. However, observing only three factors displaying well-defined independent trends suggests a need to re-evaluate this premise. Rather than five separate community attributes, if the metrics instead quantify variation in either the structure of the community or the individual nature of the organisms that make up the community, then the results are more readily interpreted.

Structural attributes include (i) the number of individuals present, measured by the abundance metrics, N, B, and P, (ii) the number of species present, measured by the species richness metrics, S and S_{Marg}, and (iii) the distribution of individuals between species, measured by the species evenness metrics, $N1$, $N2$, and J. Table 2 clearly shows that each of the first three factors was strongly associated with metrics defining variation in one of these structural attributes of the North Sea demersal fish community: factor 1 related to metrics quantifying the species evenness structural attribute, factor 2 linked to metrics quantifying the abundance structural attribute, and factor 3 associated with metrics quantifying the species richness structural attribute. Moreover, because these different sets of structural metrics associated with different factors, covariance in these structural attributes of the North Sea demersal fish community was weak; this independence between the three structural community attribute trends is clearly illustrated in Figure 2. Although calculated as community-wide average values, and so qualifying as community-level metrics, the two size composition and four life-history-trait composition metrics in essence provide information on the individual nature of the fish that make up the North Sea demersal fish community. They indicate whether the community consists on average of large or small fish, fast- or slow-growing fish, early- or late-maturing fish, etc. As these metrics convey quite different information from the structural attribute metrics considered above, it was interesting that they generally linked with one or other of the first three factors, rather than associating together with additional factors.

Variation in the weights of fish within the two length classes that define the LFI, fish >40 cm (in particular) and fish ≤40 cm long, was sufficient to reduce the correlation between the LFI and the mean weight of fish in the community (Figure 5c) to the point that the two size composition metrics associated with different factors. The LFI was related negatively to the abundance factor 2, and mean fish weight was positively related to the species evenness factor 1. The two von Bertalanffy growth parameters generally co-vary when interspecific differences are considered
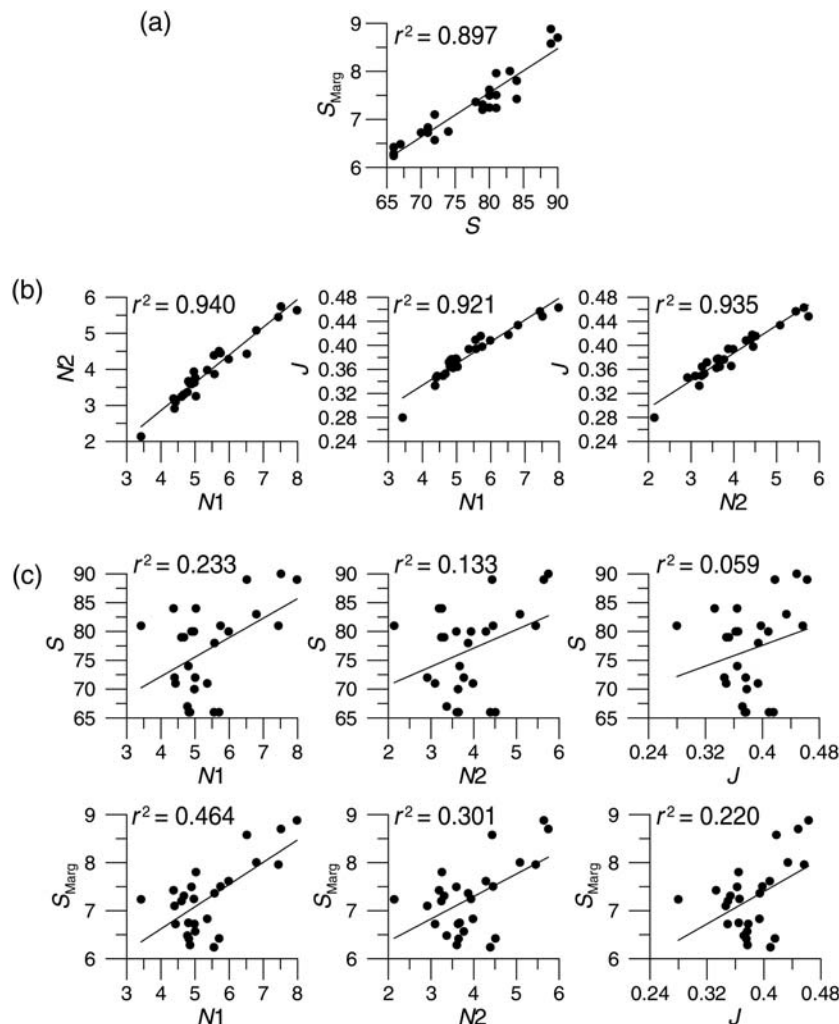
Figure 3. Relationships between (a) the two species-richness metrics, (b) the three species-evenness metrics, and (c) each species-richness and species-evenness metric combination. Pearson correlations r^2 are shown, which if $r^2 > 0.111$ (one-tailed) or if $r^2 > 0.151$ (two-tailed), means that the correlation is significant at $p < 0.05$.

(Jennings *et al.*, 1999); our results show that even when calculated at the community-average level, this inverse relationship still held (Figure 6a). Both von Bertalanffy community metrics therefore linked together with the species evenness factor 1. Interestingly, average age and average length-at-maturity in the North Sea demersal fish community were unrelated. Average age-at-maturity covaried only weakly with the two von Bertalanffy community metrics and was therefore linked to the species richness factor 3. Although weakly correlated with average ultimate body length, average length at maturity in the community was the only metric not linked with one of the first three factors. Instead, it associated with factor 4, reflecting residual, non-trend-related, short-term variability in the community.

With this interpretation of the factor analysis results in place, the question of how many, and which, community metrics should be included in a minimum suite of state metrics aimed at monitoring the health of the North Sea demersal fish community can now be addressed. A minimalistic approach might consider just those metrics most closely associated with each factor, a total of four, or perhaps even three if one elected to ignore the non-trend-related factor 4. Such an approach would result in the

selection of the average von Bertalanffy growth parameter (K), the total daily growth production metric (P), the species-richness index (S), and perhaps the average length at maturity (L_{mat}) metric. Such a suite would, however, exclude any size-based metrics, already determined to be among the most effective at detecting the effects of fishing on the fish community (ICES, 2001b; Shin *et al.*, 2005; Piet *et al.*, 2008), and in particular the LFI, which is already the state indicator on which the fish community EcoQO is based (Heslenfeld and Enserink, 2008; Greenstreet *et al.*, 2011). Interpretation of the information available from such a limited suite of community metrics could present problems, making it difficult to indentify underlying causes and advise on appropriate remedial action. Therefore, an alternative approach might be to select, for each of the first three trend-related factors at least, one metric to quantify variation in the structure of the community, and one metric to quantify variation in the individual nature of fish making up that community. The information presented in Tables 2 and 3 and the fits of the polynomial smoothers to the original metric values (Figure 1) were used to provide the basis for such a selection, first considering metrics of community structure and then metrics of individual nature.
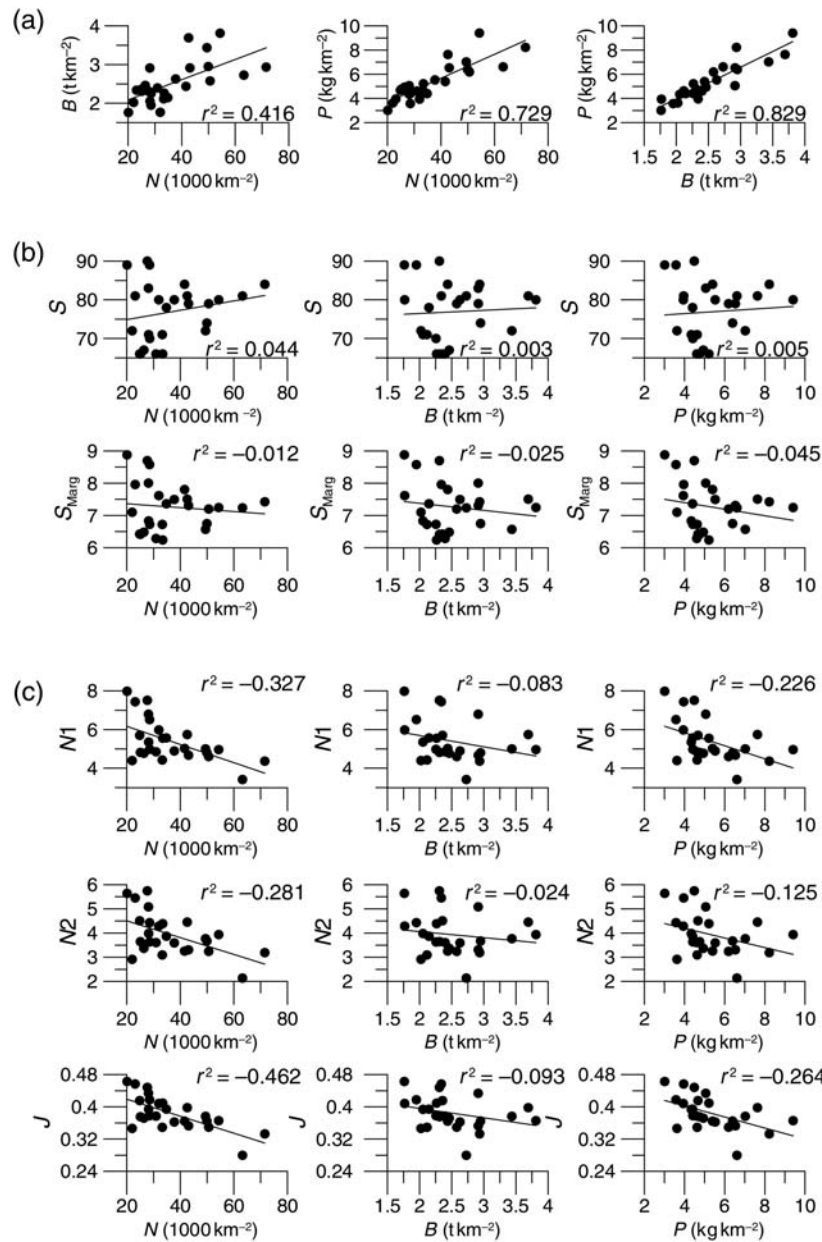
Figure 4. Relationships between (a) three abundance/biomass/productivity attribute metrics linked to Factor 2, (b) the three Factor 2 abundance/biomass/productivity attribute metrics and the two Factor 3 species richness attribute metrics, and (c) the three Factor 2 abundance/biomass/productivity attribute metrics and the three Factor 1 species-evenness attribute metrics. Pearson correlations r^2 are shown, which if $r^2 > 0.111$ (one-tailed) or if $r^2 > 0.151$ (two-tailed), means that the correlation is significant at $p < 0.05$. Where negative Pearson correlations r^2 are shown, these simply confirm the direction of the relationship.

Three metrics linked to factor 2 quantified variation in the quantity of individuals in the community; abundance (N), biomass (B), and total daily growth production (P). Of these, N ranked highest in Table 3 and was best fitted by the polynomial smoother in Figure 1, i.e. had the smoothest time-trend or lowest noise. Data provided by the IBTS are used directly to calculate N with no requirement for further transformation, such as the application of weight- or production-at-length relationships (Table 1). This metric is therefore more comprehensible to non-scientists and less prone to calculation error, so complies better with key criteria established by ICES (2001a) for a good state indicator. Two metrics linked to factor 3 quantified variation in the

number of species in the community; the simple species count (S) and Margalef's species richness index (S_{Marg}). The analyses summarized in Table 3 suggested that little separated these two metrics, S_{Marg} performing only marginally better than S. Conversely, the polynomial smoother fitted to the original data showed S to be slightly less noisy (Figure 1), and agreement between the original metric data and the factor 3 scores, or the smoother fitted to these scores, was closest for S, implying a slightly better signal-to-noise ratio. On balance, the simple species count is probably the best choice to include in any suite of state metrics. Like N, it is obtained directly from the IBTS data and is better understood by non-scientists. Only if the use of S was
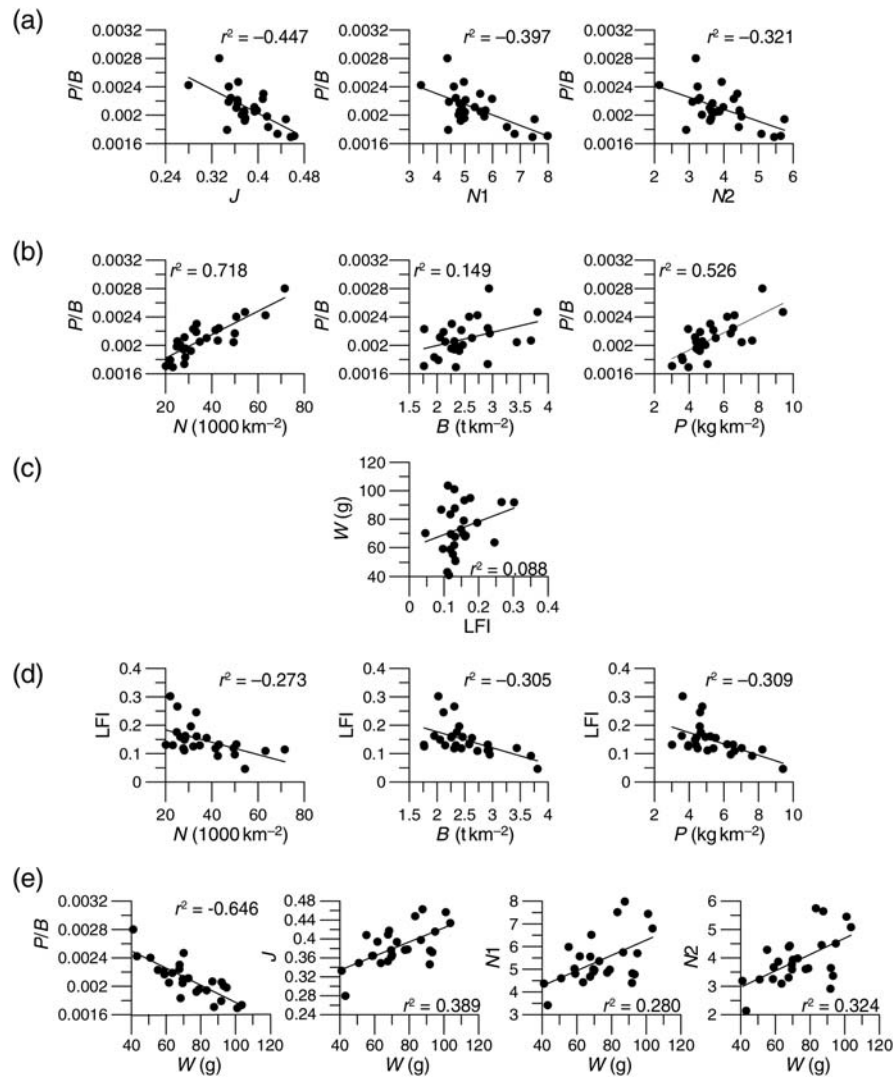
Figure 5. Relationships between (a) specific productivity and the three species-evenness metrics linked together with Factor 1, (b) specific productivity and the three abundance/biomass/productivity attribute metrics, (c) the two size composition metrics, split between Factors 1 and 2, (d) the LFI and the three abundance/biomass/productivity attribute metrics, linked together to Factor 2, and (e) the mean fish weight metric and the specific productivity and three species evenness metrics linked together with Factor 1. Pearson correlations r^2 are shown, which if $r^2 > 0.111$ (one-tailed) or if $r^2 > 0.151$ (two-tailed), means that the correlation is significant at $p < 0.05$. Where negative Pearson correlations r^2 are shown, these simply confirm the direction of the relationship.

compromised by sampling effort limitations might S_{Marg} prove to be the better choice (Greenstreet and Piet, 2008). Three metrics linked to factor 1 quantified variation in the distribution of individuals between species in the community: Hill's $N1$, Hill's $N2$, and Pielou species evenness (J). Data in Table 3 and the polynomial smooth fit to the original metrics suggest that Hill's $N1$ might have a marginally better signal-to-noise ratio, whereas the fits reported in Table 2 support Hill's $N2$. However, differences between the performance of the metrics were small and essentially either metric, or even J, could serve. The Shannon–Wiener metric is one of the most widely used diversity indices in the ecological literature (Magurran, 2007); being simply the exponential of this index, Hill's $N1$ would perhaps be the most readily recognized by the scientific community. However, if control of sampling effort bias was an issue, then the use of $N2$ might be the more appropriate (Soetaert and Heip, 1990).

Only one individual nature metric, LFI, was associated with the abundance factor 2. As the LFI is the basis for the North Sea fish community EcoQO (ICES 2007a, b; Greenstreet *et al.*, 2011), almost by definition this metric needs to be included in any suite of state metrics. Similarly, age at maturity (A_{mat}) was the only individual nature metric linked to the species richness factor 3, so this metric would also need to be included in our suite of state metrics. Several individual nature metrics were linked to the species evenness factor 1. These included the von Bertalanffy growth (K) and ultimate body length (L_∞) parameters, and mean fish weight (W). We have already remarked on the correlation between the two von Bertalanffy parameters; inclusion of both in a suite of state metrics would therefore probably not be necessary. The stronger performance of K in Tables 2 and 3, and in Figure 1, identifies it as the best choice of the two. Although considered as part of the element of ecological quality for the
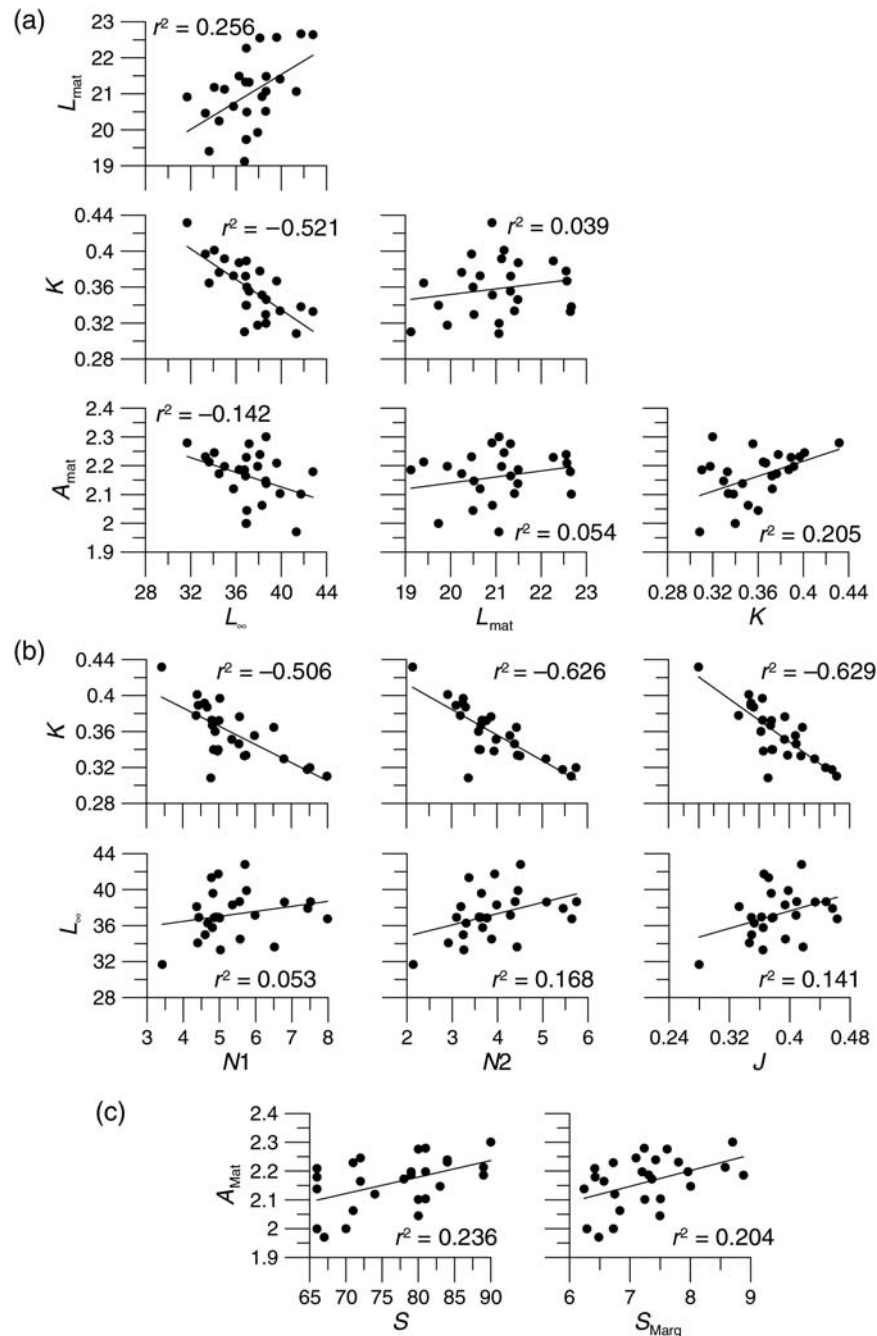
Figure 6. Correlations between (a) the four mean life-history-trait metrics, (b) the von Bertalanffy ultimate body length and growth parameter metrics and the three species evenness metrics, and (c) the mean age at maturity and the two species-richness metrics. Pearson correlations r^2 are shown, which if $r^2 > 0.111$ (one-tailed) or if $r^2 > 0.151$ (two-tailed), means that the correlation is significant at $p < 0.05$. Where negative Pearson correlations r^2 are shown, these simply confirm the direction of the relationship.

North Sea fish community (Heslenfeld and Enserink, 2008), the use of W for the EcoQO has been discounted because its sensitivity to environmentally driven recruitment variability reduces its value as a state indicator for managing the impact of fishing on the fish community (ICES, 2007b; Greenstreet *et al.*, 2011). However, such considerations do not disqualify it from being included as part of a suite of state metrics and instead may argue for its inclusion.

Initially, we considered that both the total daily growth production (P) and specific daily growth productivity metrics (P/B) quantified variation in the abundance/biomass/productivity attribute of the demersal fish community. For P, this belief was borne out: P associated with factor 2 alongside the other abundance structural metrics, and this was entirely intuitive—the greater the quantity of biological material present, the greater the scope for overall increase in biomass/abundance. Indeed, a constant P/B ratio implies a direct proportional relationship between P and B. However, P/B associated with factor 1 and the species evenness structural metrics. Given the new insight provided by our factor analysis, we now consider P/B to be an individual nature metric rather than a structural descriptor,
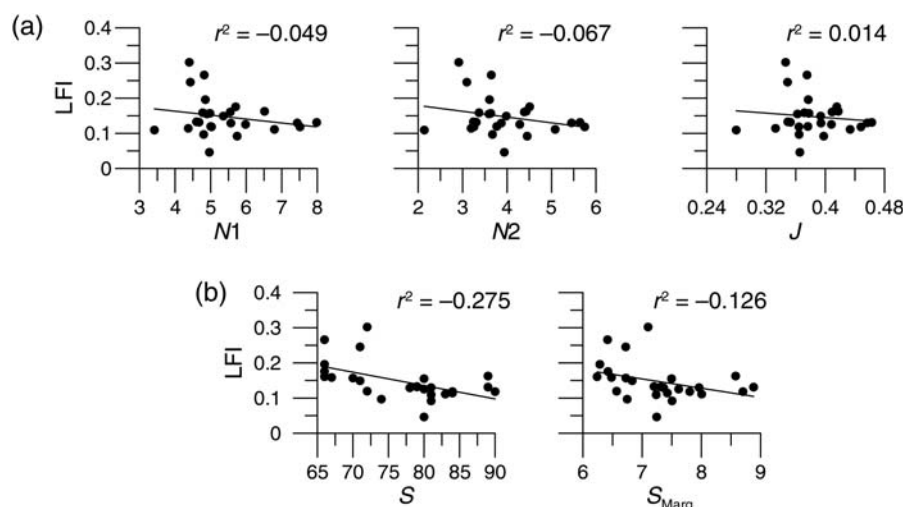
Figure 7. Correlations between the LFI and (a) the three species evenness metrics and (b) the two species richness metrics. Pearson correlations r^2 are shown, which if $r^2 > 0.111$ (one-tailed) or if $r^2 > 0.151$ (two-tailed), the correlation is significant at $p < 0.05$. Where negative Pearson correlation r^2 are shown, these simply confirm the direction of the relationship.

quantifying variation in the productivity, or daily growth potential, of individual fish in the community. Seen in this light, it is no surprise that P/B associated with factor 1 alongside W and the two von Bertalanffy growth parameter individual nature metrics. By definition, fish with high values of K are fast-growing and hence highly productive. Similarly, small fish, with a low value of W, would tend on average to be only a short way along their own von Bertalanffy growth trajectories, and therefore at the highly productive fast-growing phase of their life history.

We have already argued that including both K and L_∞ in the suite of state indicators would be unnecessary, preferring K over L_∞. The question now is whether P/B, W, and K are all required, or would just one, or perhaps two, of these metrics provide all the information necessary to interpret variation in the overall suite of metrics? Tables 2 and 3 suggest that P/B performed weakest of the three in terms of its sensitivity to any underlying trend. Likewise, Figure 1 showed P/B to be the least well fitted by a polynomial smoother. We consider P/B to be superfluous, believing that if the two metrics K and W suggest a shift towards a community consisting of smaller, faster-growing fish, any scientist with an understanding of fish biology would interpret this as an increase in the overall productivity of the community.

We posed two questions at the start of this paper. First, would focusing solely on the restoration of size composition as the main thrust of an EAM for the North Sea demersal fish community be sufficient to ensure that political obligations related to biodiversity conservation are met? Second, how many metrics would need to be included in a suite of state indicators to monitor changes in all aspects of the general health of the North Sea demersal fish community of political or ecological concern? Our analyses suggest that the answer to the first question is no. The LFI associated with factor 2, and the three species-evenness and two species-richness metrics aligned with factors 1 and 3, respectively, implying that the LFI varied relatively independently of either variation in species richness or species evenness. Figure 7, showing the lack of any correlation between the LFI and these two sets of metrics, explicitly confirms this supposition. Our conclusions regarding the selection of a suite of state indicators for the North Sea demersal fish community, summarized in Table 4,

Table 4. Suite of state indicators to describe variation in the "health" of the North Sea demersal fish community.

Factor	Structural indicators	Individual nature indicators
First	Hills species evenness (N1)	Mean von Bertalanffy growth parameter (K) Mean individual fish weight (W)
Second	Total abundance (N)	Large fish indicator (LFI)
Third	Species richness (S)	Mean age at maturity (A_{mat})
Fourth		Mean length at maturity (L_{mat})

suggest that the answer to the second question is 7, or 8 if the metric L_{mat} associated with the residual variability factor 4, is also included.

The patterns of covariation between different community metrics identified by our factor analysis present some interesting insights regarding the processes involved. These are discussed below.

(i) Variation in the LFI was inversely related to changes in abundance, biomass, and production of the demersal fish community. To increase the LFI from its current value of ~0.2 and achieve the EcoQO target of 0.3, overall abundance, biomass, and productivity of the fish community may decline. Greenstreet *et al.* (2011) point out on theoretical grounds that any increase in small-fish biomass, linked to fishery removals of large predatory fish and consequent alteration of top−down predation control processes, is likely to be five times the reduction in large-fish biomass (see also Daan *et al.,* 2005). It is to be hoped that, in raising the LFI to the EcoQO target of 0.3, the actual biomass of large fish would increase. However, most change in the metric value is likely to be attributable to the far greater reduction in small-fish biomass, leading to an overall decrease in biomass within the community as a whole.

(ii) All the species evenness metrics involve summation terms over the number of species sampled. A degree of positive association between species-richness and species-evenness metrics was therefore to be expected (Figure 3). However,

the level of correlation observed was sufficiently low that the two sets of diversity metric aligned with different factors. Weak relationships between species richness and species evenness in marine communities have been remarked on before (Birch, 1981). Assuming that variation in species richness in a region such as the North Sea is limited by the number of species in the NE Atlantic species pool acting as a source for the region (Cornell and Lawton, 1992; Caley and Schluter, 1997; Cornell and Karlson, 1997; Angermeier and Winston, 1998; Findley and Findley, 2001), this simply implies that processes driving variation in species relative abundance, particularly among the more-abundant species that predominantly drive variation in the species-evenness metrics, occur independently, and with greater variability, than the four processes that govern variation in the number of species in the region: speciation, extinction, immigration, and emigration.

(iii) Species richness has increased steadily over the 26 years of the IBTS time-series analysed here. No fish species new to science has been recorded in the North Sea in this time, discounting speciation as a cause of the increase. Some introductions, or reintroductions, of species into the North Sea from surrounding regions have been noted (Heessen *et al.*, 1996; Beare *et al.*, 2004), but the number of potential species involved is too small for immigration to account solely for the increase in species richness by >20 species. Further, the two species-richness metrics were positively linked with mean age at maturity to factor 3. Dispersive species, the type of species that generally drive regional immigration processes, tend to have *r*-strategy-type life-history characteristics. If the arrival of such species into the North Sea were the cause of the increase in species richness, then this would be more likely to be associated with a decrease in average age at maturity than an increase. The linkage of the species richness structural metrics with the age-at-maturity individual-nature metric is therefore counter-intuitive and perhaps a topic worthy of further investigation. One possible explanation is that species always present, but rare, in the North Sea, and with above-average age at maturity have increased in abundance in recent years, so becoming more consistently sampled by the IBTS and giving rise to an apparent increase in species richness (Cam *et al.*, 2002; Mao and Colwell, 2005). Population outbreaks of species such as the snake pipefish *Entelurus aequoreus* (Harris *et al.*, 2007) and the recent increases in the abundance of species with southern biogeographic affinity (Beare *et al.*, 2004) suggest that this could be a possible mechanism.

(iv) The "individual nature" metrics linked to factor 1 along with the species-evenness metrics implied that as species evenness declined, the community was increasingly dominated by small-bodied, fast-growing fish with high daily specific productivity, and vice versa. The functional role of biodiversity has been the focus of considerable research activity over the past 10 years or so, with many studies attributing greater productivity to the more biodiverse communities (Kinzig *et al.*, 2001; Loreau *et al.*, 2002). Our results appear to counter this belief. The positive relationship between diversity and productivity has tended to be linked to bottom–up processes; the more species present, the greater the range of resources utilized by the community, resulting in greater productivity overall (Tilman and Lehman, 2001; Tilman *et al.*, 2001, 2002; Emmerson and Huxham, 2002). Reductions in North Sea demersal fish species evenness have, in the past, reflected increased dominance of the community by small-bodied, fast-growing, highly productive species such as Norway pout (Greenstreet and Hall, 1996; Greenstreet *et al.*, 1999) and have been attributed to increased fishing mortality, a top–down process (Greenstreet and Rogers, 2006). It follows that to maintain a relatively constant standing-stock biomass, specific productivity of the fish community would have had to increase to meet the increasing biomass-removal demands of fisheries. Achieving this would have required the community to become increasingly dominated by fish with high specific growth productivity: small-bodied, fast-growing individuals. Not all species have these characteristics, so the community would have become increasingly dominated by those that did, resulting in reduced species evenness. Other studies also suggest that the directionality of diversity–productivity relationships does indeed depend on the trophic level (Aoki, 2003) and is influenced by disturbance regimes (Cardinale *et al.*, 2005).

Finally, it should be noted that in drawing up our list of state indicators for the North Sea demersal fish community (Table 4), we examined just 15 potential candidates; other metrics exist, which some may argue should also be included. We suggest that such metrics be subjected to a similar selection process, then if found to perform better in a particular role than the metrics listed in Table 4, it would be appropriate to replace the metrics we suggest with those alternatives. However, if alternative metrics simply duplicate the information portrayed by our metric selection, then there would be no real need to add them to the list. We would be particularly interested to consider new metrics that either quantified new aspects of the structure of the North Sea demersal fish community, or which described additional characteristics of the individual nature of the fish making up the community, particularly if the latter provided further insight into the underlying processes causing changes in structure.

Acknowledgements

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