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Use and Information Content of Ecosystem Metrics and Reference Points

A spatial and temporal diversity index taking into account species rarity, with an application to the North Sea fish community

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Abstract

A spatial and temporal diversity index is proposed that is based on species rarity. The rarity index integrates information on relative abundance and on the relative extent of the geographical distribution. An application to the North Sea, Skagerrak and Kattegat fish community is presented on the basis of three sets of survey data (International Bottom Trawl Survey, Beam Trawl Survey and Demersal Young Fish Survey). To limit the analysis to 'truly' North Sea fish, 91 species were selected to define the fish community at depths <200m based on bio-geographic region, main habitat and presence in the data set. Because major identification problems in the database prohibit a definitive analysis, the conclusions are limited to the potential utility of the approach. The spatial rarity index seems to be largely unaffected by geographical variations in sampling intensity and may for instance prove useful as an objective criterion for selecting marine protected areas. The temporal rarity index might be a useful indicator of ecosystem effects of fishing, but the interpretation is problematic, because it is directly influenced by annual variations in sampling intensity. Also the index will be sensitive to possible changes in reliable identifications over time.

Introduction

The community metrics commonly used to evaluate effects of fishing on marine ecosystems (e.g., species richness, evenness, dominance; Rice, 2000) describe properties of the fauna that can be compared as time series, among areas and across systems. Although these metrics may signal disquieting developments, their use in formulating ecological quality targets is limited, because the direction of change under influence of human activities is in essence unpredictable. Also the very nature of these metrics dictates that information on individual species constituting the community is lost. Thus, two identical values for any of these metrics in two different years or two different areas may reflect totally different communities. Therefore, they are of limited value for management policies aimed at conservation of biodiversity, which tend to prioritise measures to protect rare and vulnerable species (Red Lists) or habitats.

The terrestrial nature policy of the Netherlands has been concentrated on the identification of target species and target habitats (Bal *et al*., 1995) and the development of management measures aimed at protecting, or even enhancing, these. The selection of target species is based on three types of quantitative criteria (itz): i - international importance of the reproductive population present in the Netherlands (measured either in absolute numbers or in area inhabited by the species); t – downward trend in abundance or area inhabited; and z – relative rarity (also either in abundance or area inhabited). This policy is presently being extended to the marine environment, in particular to the Dutch sector of the continental shelf. Whereas applying i- and t-criteria is relatively straightforward, there are few, if any, studies of species rarity in the North Sea. Therefore, I concentrate here on this latter issue.

The obvious source for fish community analysis is the information collected during research vessel surveys, including both inshore and offshore waters. However, integration of data sets from different surveys is not straightforward. Varying catchability within gears among species and within species among gears obviously presents a major problem in estimating relative abundance over heterogeneously sampled areas.

Another problem is related to what species constitute "the North Sea fish community". A comprehensive checklist of fish species that have been observed in the North Sea does not exist, although there may be such information at the national level for restricted areas. Moreover, marine fish inhabit largely a 'borderless world', i.e., individual specimens may disperse widely and be caught in atypical habitat. From the conservation point of view, many of these irregular visitors and vagrants are of no direct interest and emphasis should be put on species for which the North Sea provides essential habitat. The Dutch policy considers that only species that reproduce on the NCP, or that depend on this area for their survival during some important life stage, are eligible as target species for management. However, also such information is not readily available. Although various handbooks and guides (Wheeler, 1978;

Whitehead *et al*., 1984, Muus *et al*., 1999) include generalized distribution maps, these charts provide not enough detail to assign species to the spawning fish community of a particular area. To exclude vagrants and irregular visitors, a qualitative approach has been taken of defining bio-geographical regions and main habitats within these regions to define 'the North Sea fish community'.

A most awkward problem is the quality of the data collected. In another paper (Daan, 2001), I have outlined some of the inconsistencies in the species composition reported by different countries participating in the International Bottom Trawl Surveys (IBTS) that served as a major input to this exercise. Although I made a personal judgement to exclude many unrealistic data, other inconsistencies were found only after the analysis had been completed. Species mis-identifications obviously undermine the value of the results. The primary aim is, therefore, to describe an approach that may be more generally applicable in the context of conservation policies for the marine environment rather than to provide ultimate answers for this particular area.

Material and methods

• *The North Sea fish community*

Based on Wheeler (1978), Whitehead *et al*. (1984) and Muus *et al*. (1999), 265 fish species were listed as (potentially) having been observed in the North Sea, Skagerrak and Kattegat as defined by ICES (Sub-area IV and Division IIIa). Based on the centre of their broad distribution, each species was assigned to bio-geographic regions (Figure 1). The shelf regions follow largely the pioneering work of Ekman (1953), but I distinguished 'Slope' as a separate bio-geographic region, because the distribution of deep-water species does not seem to follow the apparent borders observed in the shelf fauna. This is undoubtedly related to the much more uniform temperature conditions at larger depths. Also anadromous species did not fit the marine bio-geographic regions too well and they were assigned to a 'Continental' region. In a similar exercise based also on Ekman (1953), Jiming (1982) assigned North Sea species to either a Boreal or Lusitanian origin. However, because species may be distributed over more than one region, I assigned those to one or more regions rather than arbitrarily choosing one with the main area up front (e.g., Boreal-Lusitanian; Lusitanian-Boreal).

Secondly, habitat descriptions for individual species were used to assign depth zone characteristics as a definition of their main habitat (Coastal zone <20m; Shallow shelf <50m; Deep shelf 50-200m; Shelf <200m; Slope 200-1500m; Deep sea >1500m; Oceanic: pelagic and beyond the shelf edge). Other characterizations were also added (Ecological type – marine, brackish water, anadromous, catadromous; Life style – pelagic, demersal, benthic; Reproductive type – ovoparous, ovoviviparous, viviparous; Parental care; Maximum length). A complete listing with the characterisations may be obtained directly from the author.

These characterisations allowed a more or less objective classification of the status of each species in the North Sea as spawner, migrant (essentially diadromous species), regular visitor, vagrant or as non-indigenous. If a species belonged (partly) to the Boreal fauna and had its main habitat the shelf sea (<200m; Figure 2), a species was assigned to the typical North Sea fish fauna. Anadromous migrants were also included. Although the Norwegian Trough and also the northern edge of the slope fall within the North Sea (Sub-area IV), these waters are characterised by a completely different fish community (Bergstad, 1990), that is not sampled systematically during the routine surveys available for analysis. Therefore, Slope species have been excluded from the analysis.

The selection applied reduces the typical North Sea fish community at depth <200m to 124 species.

• *Material*

The analysis is based on three data sets: IBTS (International Bottom Trawl Survey), BTS (Beam Trawl Survey) and DYFS (Demersal Young Fish Survey). These surveys differ in geographical coverage (Figure 3), gears used and procedures, but catches by haul have always been sampled, sorted to species and measured.

- IBTS (Heessen *et al*., 1997; ICES, 1999): The survey has been carried out annually in February since 1966. The area covered gradually extended northward until from 1974 onwards the entire North Sea within the 200 m depth limit, including the Skagerrak and Kattegat has been sampled. From 1991 onwards, surveys have been carried out quarterly. The standard gear is the GOV (Chalut à Grande Ouverture Verticale), which has a vertical opening of approximately 5 m and a distance between the boards of up to 100 m. Both values depend on depth and warp length. The horizontal opening of the net itself is assumed to be some 20 m and towing speed is 4 knots (Knijn *et al*., 1993). Catches are reported per hour fishing (cpue), during which on average ca 150 000 m^2 are fished (excluding the area between the doors and the net). Excluding hauls at depth >200 m, 15402 valid hauls remained, distributed over 188 ICES rectangles (30*30 miles).

- BTS (van Beek, 1997): This August survey has been carried since 1985 and is specifically aimed at the older year classes of plaice and sole. The area covered includes the south-eastern North Sea, but has been extended northward since 1996. The gear is a 8 m beam trawl with 4 chains from the shoes and 4 tickler chains from the ground rope. The height of the beam is 50 cm, haul duration 30 min and towing speed 4 knots. Thus, the area fished per haul is ca 60 000 m^2. Only Dutch data were available, in total 1447 valid hauls covering 97 ICES rectangles.
- DYFS (Boddeke *et al*., 1970; van Beek, 1997): This (Dutch) survey started in 1970 and is aimed at estimating the abundance of juvenile sole and plaice in inshore waters. It covers the entire area from the Belgian coast to Esbjerg, including the estuaries and the Dutch part of the Wadden Sea. Originally, the survey was carried out in spring and autumn, but only the autumn survey has survived and the spring surveys have not yet been fully computerised. Three vessels take part simultaneously, employing a 6-m beam trawl for the sea-going vessel and 3-m beam trawls for the inshore vessels. The narrow-meshed trawl is rigged like a shrimp trawl without chains and a line with wooden rollers in front of the groundrope. Vertical net opening is 40 and 30 cm respectively, haul duration 15 min and towing speed 1.5 knots. Area fished per haul is 16 000 and 8000 m^2, respectively.

Table 1 provides a summary of the number of hauls, the number of ICES rectangles fished and the number of taxa reported by survey, year and quarter.

As a first check of the quality of the data in the different data bases, a summary by species of the number of positive hauls, the number of specimens caught and their size ranges were checked against reported maximum size from the literature. Daan (2001) gives a detailed description of the kind of inconsistencies that were found. If species identifications were considered unreliable, data were either corrected (Dutch data only; based on comparison with original data sheets), changed to reflect more likely species identifications (based on personal judgement), entirely removed or assigned to a lower taxon (genus or family) to reflect the uncertainty. The algorithm used in the analysis allowed for redistributing lower taxa among the constituting species based on information for species identifications considered reliable from the same square in the same year, or in the absence of appropriate information, in adjacent rectangles in an average year. No effort was undertaken to try and split the genera *Salmo, Syngnathus, Ammodytes, Hyperoplus, Pomatoschistus* into species. The few reliable species identifications for these were assigned to the genus level. After making these adjustments, all species not belonging to the reproductive North Sea fish community (including diadromous species) were removed from the data set.

Although 114 of the potential 124 species have been reported in the surveys, some were excluded because they were only reported incidentally and their abundance would seem to be truly underestimated. This applies in particular to wrasses and other inhabitants of rocky coasts, where no trawls can be operated, and small pelagic species (e.g., *Crystallogobius*). The final list thus includes 91 taxa, 5 of which are anadromous migrants and the rest marine spawners (Table 2).

• *Analysis*

Quantitative rarity indices depend on the geographical resolution of the data and the possibility for discriminating among species increases with the number of rectangles considered. While the IBTS hauls are stratified by ICES rectangle (generally 2 stations per rectangle per year), the other two surveys are characterised by a much higher station density. After trying a sub-division of ICES rectangles in 4 (15*15 nm) and 9 sub-rectangles (10*10 nm), the latter one was selected, because the distribution of hauls (starting position) over all years revealed relatively few empty cells (Figure 4). Overall, data are available for 1323 sub-rectangles based on a (approximately) 10*10 nm grid. Intensity of sampling differed markedly between areas, with a concentration along the Dutch coast.

The integration of data obtained from different surveys is problematic because of differences in catchability by species and gear. However, in any analysis of fish communities, this problem equally applies to data obtained within a single survey. Essentially we are interested in the best estimate of the number caught per swept area (cpsa), which is given by the gear with the highest catch rate. Thus, the procedures were as follows. First, cpue from the same sub-rectangle in the same year by the same gear (in the case of the IBTS after 1991, all data from the 4 quarters) were averaged to obtain a single estimate by survey type. The average cpue was then transformed into an average cpsa. Considering that trawling gear can never catch more than is present per unit area (catchability = 1), the average cpsa by sub-rectangle per survey type were compared and the highest value was selected to represent the best approximation of the true abundance of each species in each year and sub-rectangle. Subsequently, these values were averaged over all years.

Species rarity involves 3 aspects: the geographical area considered, the numerical abundance and the extent of the area occupied. The assignment of target species within the framework of the Dutch nature conservation policy is based on rarity within the borders of the NCP. However, because of the open borders in the marine environment, this might not give sensible answers and therefore, I present information on rarity only for the entire North Sea. Three indices were calculated: one based on average cpsa summed over all squares, one based on the fraction of the squares fished from which a species had been reported, and one which integrated the two aspects in a single value.

The equation used for numbers is:

$$Z_i^N = \{\sum_{j=1}^{J} \sqrt{(N_j+1)}\} / \sqrt{(N_i+1)}, \qquad [1]$$

where N_i is the sum of the average abundance of species i over all rectangles and the sum term sums over all J species. Values were then adjusted to ensure that the sum of all Z is 1 (in practice 1000 was used to avoid rounding errors resulting from very small numbers). The square root is taken to reduce the influence of extremely abundant species and 1 was added to allow comparable calculations for sub-areas, in which not all species might be represented (for the analysis reported here, this adjustment is actually redundant).

Similarly, the index based on sub-rectangles with positive observations (n_i) is calculated from:

$$Z_i^N = \{\sum_{j=1}^{J} (n_j+1)\} / (n_i+1), \qquad [2]$$

where n is the number of sub-rectangles fished.

Finally, these two can be easily integrated as:

$$Z_i^N = \{\sum_{j=1}^{J} (n_j+1)\cdot\sqrt{(N_j+1)}\} / \{(n_j+1)\cdot\sqrt{(N_i+1)}\}. \qquad [3]$$

For a sensible integrated index, the two components should contribute preferably by similar amounts. In this specific application, the maximum value for (n_i+1) is 1324 and for $\sqrt{(N_i+1)}$ 1976 (Norway pout). Therefore, the contribution of the two components to the integrated index appears to be fairly well balanced, abundance contributing only little more than sub-rectangles.

Formulation [3] allows for the possibility to calculate the contribution of each sub-rectangle k to each species rarity index:

$$Z_{ik}^{N,n} = (N_{ik}/N_i) * Z_i^{N,n} \qquad [4]$$

The values by sub-rectangle can then be summed over all species to provide a 'rarity value', i.e. an overall relative measure of the geographical distribution of rare species (with the sum over all sub-rectangles again being equal to 1):

$$Z_k^{N,n} = \sum_{j=1}^{J} Z_{jk}^{N,n}. \qquad [5]$$

By analogy, the contribution of each year (y) to the catch of rare species may be calculated from:

$$Z_y^{N,n} = \sum_{j=1}^{J} (N_{jy}/N_j) * Z_j^{N,n}. \qquad [6]$$

This allows an evaluation of overall trends in the catch of rare species (with higher values indicating that rare species have become less rare!).

All analyses were performed in SAS.

Results

Figure 5 summarises trends in number of hauls, percentage of potential number of sub-rectangles fished and number of species reported by year. The differences in sampling intensity influence of course the likelihood of catching rare species. For instance, the number of species recorded fits largely a power function of the number of hauls and the percentage of squares fished (Figure 6).

The three rarity indices for individual species are broadly similar, but the ranking deviates in detail (table 3). The species are ranked according to the integrated index. The scale is essentially a logarithmic one that can be used for an objective classification of relative abundance:

Class:	index	# species
Extremely rare	>100	3
Rare	10-100	13
Sparse	1-10	11
Common	0.1-1	32
Numerous	0.01-0.1	19
Abundant	0.001-0.01	8
Extremely abundant	<0.001	5

Figure 7 shows the spatial distribution of the rarity value by sub-rectangle (according to equation [5]). Apparently, the offshore waters in the centre of the North Sea are relatively void of rare species. Along the Norwegian trough, values are slightly higher, but particularly high values occur along the southern coasts and along the north-western edge (Moray Firth, Orkney, Shetland area) and to a lesser extent in the Kattegat. Only very few outliers are observed in the central North Sea.

For comparison, Figure 8 shows the total number of species reported per 100 hauls by sub-rectangle as another measure of species diversity. The correction was based on the overall relationship between number of species reported and the number of hauls within each sub-rectangle, assuming a constant slope (Figure 9).

The pattern in the number of species by sub-rectangle shows some agreement with the distribution of rarity values (high values in the shallow south-eastern North Sea, along the coast of the UK and in the Kattegat), but the rare species appear to be much more confined to particular hotspots. Also the extreme values of the two biodiversity indices do not correspond, indicating that a large number of species recorded does not automatically include a large proportion of rare species.

Figure 10 shows the overall ‘rarity’ value by survey year (equation [6]). In this case, the chance of catching rare species depends of course on sampling intensity (Figure 11) and therefore a tentative correction, again based on a constant slope, has been applied. This procedure appears to flatten the long-term trend, but the marked annual signal remains.

Discussion

In exploring the usefulness of a biodiversity index that takes species rarity into account, there are two main issues to be addressed: differences in catchability and variations in survey intensity.

Survey catches do not provide estimates of the ‘true’ species composition in the sea. For instance, it is quite obvious that sandeels are greatly underrepresented in the data set, because none of the survey gears used catches those fish efficiently. Thus, it would be best to have a multiple of surveys using different gears aimed at different species. Although it should be possible (given enough data) to calculate relative catchability for individual species (e.g. Knijn *et al*., 1993) and to use these multipliers to adjust catch rates, the principle of selecting the highest cpsa among surveys as the best estimate of ‘true’ abundance would seem an acceptable short cut for the time being. Also, we may not need to worry too much about common and abundant species not being caught in their true proportions, because they contribute extremely little to the rarity index. More important is that the rare species are caught in proportion to their more common counterparts and that they are properly identified. The latter clearly presents a major problem (Daan, 2001), that has to be resolved before any such analysis as described here can be expected to provide useful answers. But also the selection of species to be included may need further improvement. Among the extremely rare species, transparent gobies, salmon/trout and lampreys for instance may not be caught efficiently enough in bottom trawls to reflect their relative abundance compared to most of the other species and therefore, should possibly be excluded. In fact, a potential useful additional criterion might be to restrict the analysis to truly demersal species.

The second problem is the imbalance of haul intensity among surveys, within surveys among years (Table 1), and among sub-rectangles (Figure 4). To make the best use of all information on rare species, we cannot afford to exclude part of the information (which is by definition very limited for rare species). Also, for the purpose of evaluating geographical differences in the occurrence of rare species (Figure 7), there is no major objection to merge all available data, if not too much attention is paid to individual outliers and only the general pattern that can be derived from the map is considered. This conclusion can be exemplified by comparing Figure 1 and Figure 6, which suggest no relationship between rarity value and sampling intensity. However, the problem becomes more important when deriving time trends in the reports of rare species (Figure 10), because the likelihood of rare species being caught by year depends on the number of surveys carried out, the number of hauls by survey and even on the number of those sub-rectangles fished where these species are most likely caught. The correction procedure applied is a primitive one and more appropriate ones seem required. More generally the index evokes questions about its statistical properties. I have not endeavoured to apply an evaluation of confidence limits at this stage, but extensive simulations or bootstrapping might resolve this issue.

Nevertheless, the approach would seem useful in relation to nature conservation policies. For instance, the spatial diversity index provides an objective criterion for selecting marine protected areas. The utility might be enhanced further by trying to link the chart to habitat characteristics. The analysis suggests that coastal areas score high in general. This may be because shallow waters represent a spatially limited habitat for species that are restricted to these environments. In addition, the borders of the North Sea, in particular the Channel area and the area off Scotland, may score high because they host species that have their main distribution area outside the North Sea.

In contrast to other diversity indices (number of species, evenness, dominance), the rarity value index cannot be compared across ecosystems. By its nature, the species rarity index will change whenever the set of species is changed or the data set extended. On the other hand, the clear advantage is that it can be decomposed in the individual species contributing to a local or annual value. Also, the temporal rarity value might be a very useful diversity index for investigating ecosystem effects of fishing. Figure 10 suggests that the rarity value by year has increased over time, which in fact means that rare species have become ‘less rare’. This is contra-intuitive for an over-exploited system. The reason may be that a more elaborate procedure is required to correct for differences in sampling intensity by year. However, another possibility is that the increasing trend reflects gradually improving species identifications and increasing attention to non-commercial species. This problem will be even more difficult to tackle, but highlights the importance of good taxonomic knowledge of the scientists on board research vessels when collecting their data.

It is quite clear that, apart from the shallow sandy coast along the continent, the fish community of UK waters is underrepresented in the data set, which is another source of bias. Thus, the relevance of the exercise could be enhanced by incorporating surveys carried out by other countries (e.g., Rogers and Millner, 1996). But we will never know much about the specific communities inhabiting untrawlable habitat such as stony ground and obstacles.

In contrast to the marine environment, a lot of attention has been given to species rarity in terrestrial conservation biology. For instance, Williams *et al*. (1996) and Csuti *et al*. (1997) compare reserve selection algorithms based on a variety of diversity criteria, including range-size rarity. Density rarity seems to be less often used. Other, discontinuous, indices have been based on thresholds for defining rare species (e.g. rare quartile richness: number of species within a subset of the 25% rarest species; Merritt *et al*., 1996). To my knowledge, an integrated range-size/density rarity index has not been applied before.

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Table 1. Number of hauls (N), number of ICES rectangles fished (n) and number of species recorded (J) by survey (na: not available).

	IBTS												BTS			DYFS		
	N				n				J				N	n	J	N	n	J
quarter	1	2	3	4	1	2	3	4	1	2	3	4	3	3	3	3	3	3
year																		
196689	-	-	-	36	-	-	-	44	-	-	-	-		-		-		
1967122	-	-	-	64	-	-	-	55	-	-	-	-		-		-		
1968134	-	-	-	60	-	-	-	70	-	-	-	-		-		-		
1969122	-	-	-	68	-	-	-	55	-	-	-	-		-		-		
1970129	-	-	-	81	-	-	-	62	-	-	-	-		-	221	14	44	
1971152	-	-	-	91	-	-	-	64	-	-	-	-		-	209	16	45	
1972187	-	-	-	111	-	-	-	74	-	-	-	-		-	208	13	41	
1973192	-	-	-	108	-	-	-	77	-	-	-	-		-	202	14	41	
1974206	-	-	-	123	-	-	-	72	-	-	-	-		-	226	14	44	
1975248	-	-	-	128	-	-	-	77	-	-	-	-		-	212	14	42	
1976250	-	-	-	115	-	-	-	82	-	-	-	-		-	166	11	38	
1977319	-	-	-	155	-	-	-	88	-	-	-	-		-	228	13	44	
1978357	-	-	-	154	-	-	-	81	-	-	-	-		-	261	17	42	
1979365	-	-	-	152	-	-	-	77	-	-	-	-		-	236	19	42	
1980351	-	-	-	166	-	-	-	83	-	-	-	-		-	265	19	48	
1981311	-	-	-	155	-	-	-	74	-	-	-	-		-	240	16	51	
1982274	-	-	-	159	-	-	-	77	-	-	-	-		-	275	20	51	
1983347	-	-	-	170	-	-	-	85	-	-	-	-		-	254	19	41	
1984383	-	-	-	169	-	-	-	87	-	-	-	-		-	277	18	42	
1985447	-	-	-	171	-	-	-	85	-	-	-	60	32	37	269	19	39	
1986453	-	-	-	168	-	-	-	84	-	-	-	59	25	35	274	18	42	
1987451	-	-	-	164	-	-	-	75	-	-	-	64	26	36	272	19	41	
1988404	-	-	-	167	-	-	-	81	-	-	-	82	34	41	259	18	38	
1989425	-	-	-	166	-	-	-	84	-	-	-	82	34	46	280	19	43	
1990296	-	-	-	157	-	-	-	85	-	-	-	94	36	47	279	19	43	
1991420	338	292	245	170	152	167	149	93	80	85	90	98	38	44	278	19	41	
1992378	249	359	272	171	161	170	157	92	88	86	100	97	38	50	284	20	43	
1993370	227	337	268	173	156	167	143	89	80	91	90	100	38	47	279	18	42	
1994360	307	303	269	166	160	168	143	90	83	92	87	91	33	47	282	18	43	
1995338	276	245	308	168	155	151	153	98	77	77	90	87	32	49	285	19	44	
1996326	128	315	211	169	126	164	137	97	68	86	83	129	71	62	306	19	45	
1997360	128	326	32	172	127	159	32	97	66	95	48	126	73	61	274	14	40	
1998401	na	na	na	173	na	na	na	102	na	na	na	121	75	58	226	12	43	
1999na		na		na		na		na		na		157	94	66	236	13	47	
Totaal	9967	1653	2177	1605	185	171	176	167	143	112	120	116	1447	97	81	7563	22	68
Overall		15402				188				153								

Table 2. List of selected species with ecological characteristics: ET – ecological type, BR – biogeographic region, MH – main habitat, LS – life style, R – reproductive type, Ed – egg deposition, Pc – parental care, Lmax – maximum length, St – Status North Sea.

	Scientific name	English name	ET	BR	MH	LS	bH	R	Pc (cm)	Lmax	St
1	*P. marinus*	Sea lamprey	A	C	SS	P	O	B	+	120	**M**
2	*L. fluviatilis*	River lamprey	A	C	SS	P	O	B	+	50	**M**
3	*M. glutinosa*	Hagfish	M	LB	DS	B	O	B		60	**S**
4	*S. canicula*	Lesser spotted dogfish	M	LB	SS	D	O	B		100	**S**
5	*G galeus*	Tope	M	BL	S	SP	OV			200	**S**
6	*M. asterias*	Starry smooyhhound	M	LB	SS	SP	OV			140	**S**
7	*M. mustelus*	Smoothhound	M	LB	SS	D	V			150	**S**
8	*S acanthias*	Spurdog	M	BL	S	SP	OV			110	**S**
9	*R. radiata*	Starry ray	M	AB	DS	B	O	B		60	**S**
10	*R. montagui*	Spotted ray	M	LB	SS	B	O	B		80	**S**
11	*R. batis*	Common skate	M	B	DS	B	O	B		250	**S**
12	*R. naevus*	Cuckoo ray	M	LB	DS	B	O	B		70	**S**
13	*R. clavata*	Thornback ray	M	LB	S	B	O	B		100	**S**
14	*D. pastinaca*	Stingray	M	LB	Cz	B	OV			140	**S**
15	*A. fallax*	Twaite shad	A	C	SS	P	O	B		50	**S**
16	*C. harengus*	Herring	M	B	S	P	O	B		40	**S**
17	*S. sprattus*	Sprat	M	LB	SS	P	O	P		19	**S**
18	*S. pilchardus*	Pilchard	M	LB	SS	P	O	P		25	**S**
19	*E. encrasicolus*	Anckovy	M	LB	SS	P	O	P		20	**S**
20	*Salmo* sp.	Salmon/Trout	A	C	S	P	O	B		150	**M**
21	*O. eperlanus*	Smelt	B	B	Cz	P	O	B		45	**S**
22	*A. sphyraena*	Lesser argentine	M	LB	DS	P	O	P		32	**S**
23	*L. piscatorius*	Monkfish	M	BL	DS	B	O	P		200	**S**
24	*G. morhua*	Cod	M	B	S	D	O	P		150	**S**
25	*P. virens*	Saithe	M	B	DS	D	O	P		130	**S**
26	*P. pollachius*	Pollack	M	BL	DS	D	O	P		130	**S**
27	*B. brosme*	Tusk	M	B	DS	B	O	P		110	**S**
28	*M. aeglefinus*	Haddock	M	B	DS	D	O	P		112	**S**
29	*R. cimbrius*	Four-bearded rockling	M	B	S	B	O	P		41	**S**
30	*T. minutus*	Poor cod	M	BL	S	D	O	P		26	**S**
31	*T. luscus*	Steenbolk	M	LB	SS	B	O	P		47	**S**
32	*T. esmarki*	Bib	M	B	DS	SP	O	P		25	**S**
33	*M. merlangus*	Whiting	M	LB	S	D	O	P		70	**S**
34	*M. molva*	Ling	M	B	DS	B	O	P		200	**S**
35	*G. vulgaris*	Three-bearded rockling	M	LB	S	B	O	P		55	**S**
36	*R. raninus*	Tadpole fish	M	B	Cz	B	O	P		30	**S**
37	*C. mustela*	Five-bearded rockling	M	BL	SS	B	O	P		30	**S**
38	*C. septentrionalis*	Northern rockling	M	B	SS	B	O	B		18	**S**
39	*E. drummondi*	Pearlfish	M	B	DS	D	OV			30	**S**
40	*Z. viviparus*	Viviparous blenny	B	B	Cz	B	V			50	**S**
41	*B. belone*	Garfish	M	B	SS	EP	O	F		95	**S**
42	*A. presbyter*	Sand-smelt	B	LB	Cz	P	O	F		20	**S**
43	*G. aculeatus*	Stickleback	A	C	SS	P	O	B	+	10	**M**
44	*S. spinachia*	15-spined stickleback	B	B	Cz	D	O	B	+	22	**S**
45	*Syngnathus* sp.	Pipefish	M	LB	SS	D	OV		+	46	**S**
46	*E. aequoraeus*	Snake pipefish	M	B	SS	D	OV		+	60	**S**
47	*S. viviparus*	Small redfish	M	B	DS	D	OV			35	**S**
48	*T. lucerna*	Tub gurnard	M	LB	SS	D	O	P		75	**S**
49	*E. gurnardus*	Grey gurnard	M	LB	S	D	O	P		50	**S**
50	*A. cuculus*	Red gurnard	M	LB	SS	D	O	P		50	**S**
51	*M. scorpius*	Bull-rout	M	BA	SS	B	O	B	+	30	**S**
52	*T. murrayi*	Moustache sculpin	M	AB	DS	B	O	B	?	19	**S**
53	*T. bubalis*	Sea scorpion	M	B	SS	B	O	B	+?	17	**S**
54	*A. cataphractus*	Hooknose	M	B	S	B	O	B	?	20	**S**
55	*L. liparis*	Sea-snail	M	AB	SS	B	O	B		18	**S**
56	*L. montagui*	Montagui’s sea-snail	M	B	Cz	B	O	B		10	**S**
57	*C. lumpus*	Lumpsucker	M	AB	S	SP	O	B	+	70	**S**
58	*T. trachurus*	Horse mackerel	M	LB	S	P	O	P		50	**S**
59	*M. surmuletus*	Striped red mullet	M	LB	SS	D	O	P		40	**S**
60	*D. labrax*	Bass	M	LB	S	D	O	P		100	**S**
61	*C. labrosus*	Thick-lipped grey mullet	M	LB	Cz	P	O	P		75	**S**
62	*E. vipera*	Lesser weever	M	LB	SS	B	O	P		17	**S**
63	*T. draco*	Greater weever	M	LB	SS	B	O	P		40	**S**
64	*A. lupus*	Wolffish	M	BA	DS	B	O	B	+	125	**S**
65	*L. lampretaeformis*	Snake blenny	M	AB	DS	B	O	B		49	**S**
66	*P. gunnellus*	Butterfish	M	BA	Cz	B	O	B	+	25	**S**
67	*Ammodytes* sp.	Sandeels	M	B	S	SP	O	B		25	**S**
68	*Hyperoplus* sp.	Greater sandeels	M	LB	S	SP	O	B		40	**S**
69	*C. lyra*	Dragonet	M	LB	SS	B	O	P		30	**S**
70	*C. maculatus*	Spotted dragonet	M	LB	DS	B	O	P		16	**S**
71	*C. reticulatus*	Reticulated dragonet	M	LB	SS	B	O	P		11	**S**
72	*Pomatoschistus* sp.	Gobies	M	LB	SS	D	O	B	+	9	**S**
73	*G. niger*	Black goby	M	LB	Cz	B	O	B	+	15	**S**
74	*A. minuta*	Transparent goby	M	LB	SS	P	0	B	+?	6	**S**
75	*S. scombrus*	Mackerel	M	BL	S	EP	O	P		66	**S**
76	*P. maxima*	Turbot	M	BL	SS	B	O	P		100	**S**
77	*S. rhombus*	Brill	M	LB	SS	B	O	P		75	**S**
78	*A. laterna*	Scaldfish	M	LB	SS	B	O	P		20	**S**
79	*Z. punctatus*	Topknot	M	B	SS	B	O	P		25	**S**
80	*P. norvegicus*	Norwegian topknot	M	B	S	B	O	P		12	**S**
81	*L. whiffiagonis*	Megrim	M	LB	DS	B	O	P		50	**S**
82	*G. cynoglossus*	Witch	M	BA	DS	B	O	P		60	**S**
83	*H. platessoides*	Long rough dab	M	AB	DS	B	O	P		50	**S**
84	*L. limanda*	Dab	M	B	SS	B	O	P		42	**S**
85	*M. kitt*	Lemon sole	M	B	DS	B	O	P		70	**S**
86	*P. flesus*	Flounder	K	BL	SS	B	O	P		60	**S**
87	*P. platessa*	Plaice	M	B	SS	B	O	P		90	**S**
88	*H. hippoglossus*	Halibut	M	AB	DS	B	O	P		400	**S**
89	*S. vulgaris*	Sole	M	LB	SS	B	O	P		70	**S**
90	*B. luteum*	Solenette	M	LB	SS	B	O	P		18	**S**
91	*M. variegatus*	Thickback sole	M	LB	DS	B	O	P		33	**S**

Codes:

Ecological type:	Biogeographic Region	Main habitat:	Life style (LS):
M – marine	A – arctic	Cz – coastal zone (0-20m)	B – benthic
B – brackish waters	B - boreal	SS – shallow shelf (0-50m)	D – demersal
A – anadroous	L – Lusitanian	S - total shelf (0-200m)	P – pelagic
K – katadromous	C - continental	DS – deep shelf (50-200m)	SP – semipelagic
		EP – epipelagic	
Reproduction type:	Egg deposition:	Status North Sea (St):	
O – oviparous	B – benthic	M – migrant	
OV – ovoviviparous	F – on plants	S – spawner	
V – viviparous	P – pelagic		

Table 3. Quantitative species rarity indices based on abundance (Z^N), fraction of positive squares (Z^n) and the integrated index ($Z^{N,n}$) for the North Sea (ranked in descending order).

	ZN	Zn	ZN,n
S. spinachia	51.26	141.34	187.52
D. pastinaca	67.37	88.34	178.29
C. septentrionalis	58.68	70.67	108.49
G. niger	48.19	70.67	88.85
A. minuta	46.09	54.36	65.21
R. raninus	56.75	33.65	49.30
Salmo sp.	53.41	35.33	49.11
E. drummondi	40.13	44.17	46.16
L. montagui	39.19	33.65	34.32
C. labrosus	40.79	27.18	28.87
Z. punctatus	39.50	24.37	25.03
L. fluviatilis	41.14	20.79	22.28
P. marinus	43.82	15.36	17.41
A. presbyter	19.63	30.73	15.00
E. aequoraeus	30.55	17.24	13.66
T. murrayi	22.92	19.10	11.36
M. variegatus	19.23	18.12	9.04
M. asterias	21.16	12.85	7.05
D. labrax	14.90	18.12	7.00
M. mustelus	16.61	15.70	6.77
R. batis	15.92	10.87	4.56
B. belone	14.62	8.62	3.27
G. galeus	14.96	8.03	3.12
P. norvegicus	13.25	6.80	2.34
H. hippoglossus	17.89	4.94	2.29
B. brosme	9.10	5.65	1.32
T. bubalis	5.78	7.14	1.07
M. glutinosa	5.96	5.05	0.78
G. vulgaris	6.65	4.42	0.76
C. reticulatus	7.26	3.74	0.71
P. gunnellus	3.27	8.22	0.70
A. cuculus	4.95	4.77	0.61
R. montagui	5.60	4.06	0.59
C. mustela	3.23	6.04	0.50
G. aculeatus	4.15	4.47	0.48
L. lampretaeformis	3.95	3.93	0.40
A. fallax	3.35	4.50	0.39
T. draco	2.11	7.14	0.39
O. eperlanus	1.40	9.82	0.36
Z. viviparus	1.74	7.68	0.35
M. surmuletus	4.09	3.01	0.32
R. naevus	4.75	2.43	0.30
P. pollachius	3.25	3.45	0.29
L. liparis	2.72	3.59	0.25
S. pilchardus	1.71	5.65	0.25
S. rhombus	5.14	1.86	0.25
S. canicula	3.45	2.54	0.23
L. whiffiagonis	3.23	2.24	0.19
A. lupus	5.08	1.35	0.18
S. viviparus	2.23	3.09	0.18
C. lumpus	4.80	1.15	0.14
Syngnathus sp.	1.47	3.66	0.14
T. lucerna	2.46	2.15	0.14
R. clavata	3.10	1.66	0.13
P. maxima	3.68	1.37	0.13
E. encrasicolus	2.04	2.29	0.12
M. molva	3.30	1.36	0.12
M. scorpius	1.57	2.62	0.11
L. piscatorius	3.65	1.09	0.10
C. maculatus	2.39	1.55	0.10
R. cimbrius	1.93	1.66	0.08
G. cynoglossus	2.35	1.16	0.07
T. luscus	1.09	1.74	0.05
P. flesus	1.19	1.59	0.05
A. laterna	0.86	2.04	0.05
E. vipera	0.66	2.65	0.05
A. sphyraena	0.75	1.85	0.04
S. acanthias	1.17	1.05	0.03
B. luteum	0.64	1.72	0.03
R. radiata	1.36	0.82	0.03
P. virens	0.77	1.16	0.02
Hyperoplus sp.	0.60	1.43	0.02
A. cataphractus	0.75	1.09	0.02
S. vulgaris	0.48	1.41	0.02
M. kitt	0.87	0.63	0.01
Pomatoschistus sp.	0.23	1.92	0.01
C. lyra	0.55	0.78	0.01
T. minutus	0.59	0.69	0.01
S. scombrus	0.39	0.77	0.01
Ammodytes sp.	0.28	1.17	0.01
T. trachurus	0.30	0.81	0.01
G. morhua	0.38	0.54	0.01
H. platessoides	0.29	0.65	0.01
P. platessa	0.21	0.65	0.00
E. gurnardus	0.27	0.59	0.00
L. limanda	0.11	0.57	0.00
C. harengus	0.06	0.56	0.00
S. sprattus	0.06	0.67	0.00
M. merlangus	0.08	0.54	0.00
M. aeglefinus	0.09	0.62	0.00
T. esmarki	0.05	0.76	0.00

Figure 1. North Sea, Skagerrak and Kattegat with depth zones and the Dutch Sector (NCP).

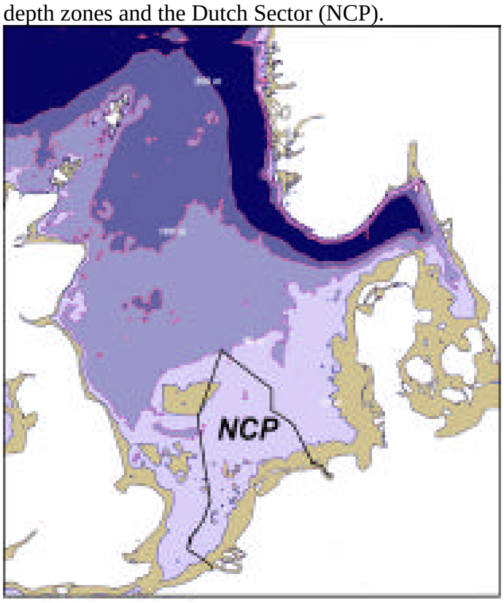


Figure 2. Biogeographical regions in the Northeast Atlantic area (after Ekman, 1953).

Figure 3. Areal extent of the trawl surveys (IBTS, BTS, DTFS). Lighter colour of BTS indicates recent extension.

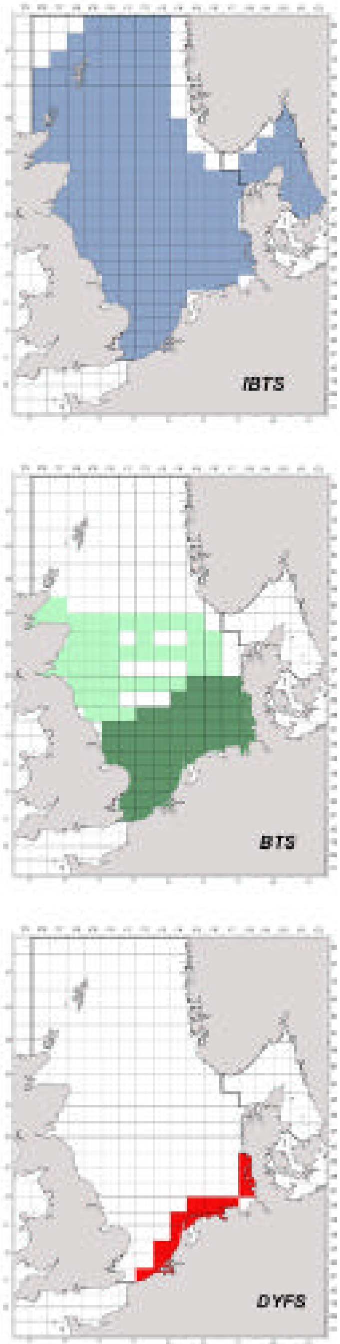


Figure 4. Spatial distribution of sampling intensity (number of hauls by sub-rectangle) for all surveys combined.

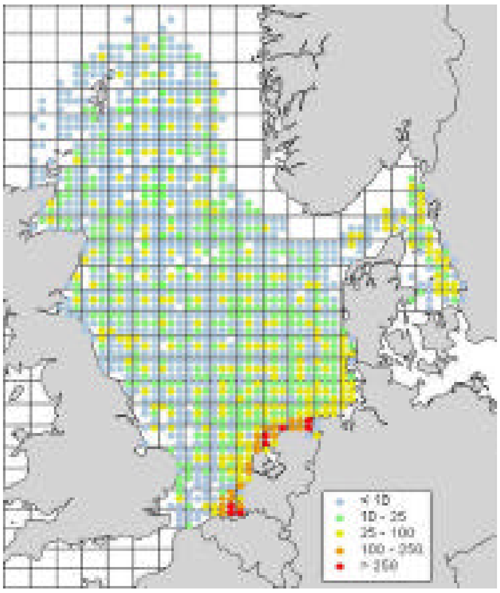


Figure 5. Time trends in (a) number of hauls, (b) percentage of sub-rectangles sampled and (c) number of species reported by year.

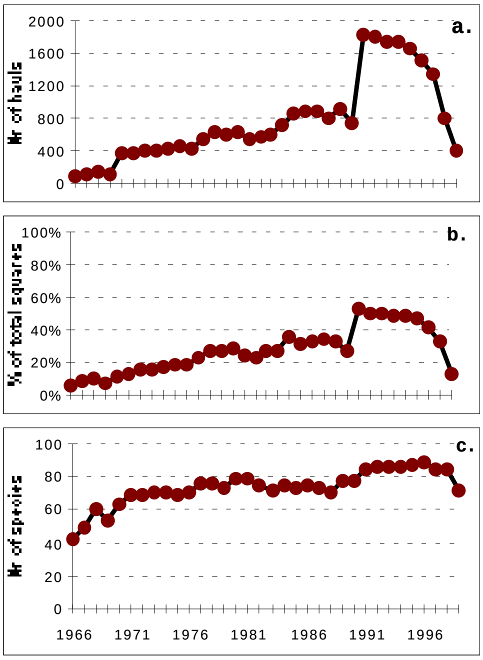


Figure 6. Relationship between number of species reported by year and (a) number of hauls and (b) number of squares fished for the North Sea and NCP (lines represent fitted power functions).

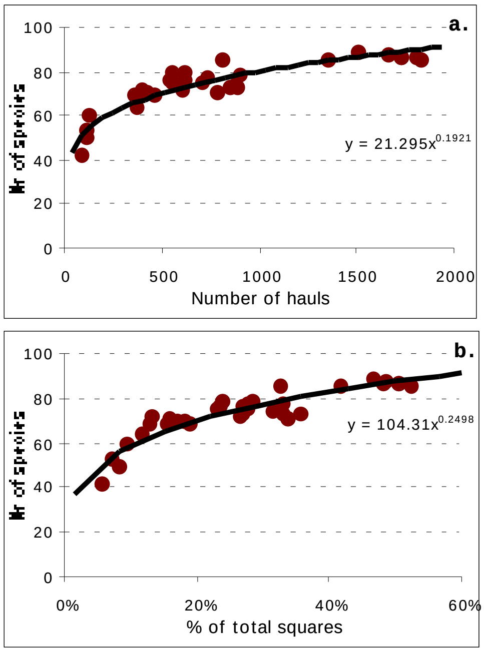


Figure 7. Distribution of estimated ‘rarity values’ by sub-rectangle (relative contribution to the total; sum=1000).

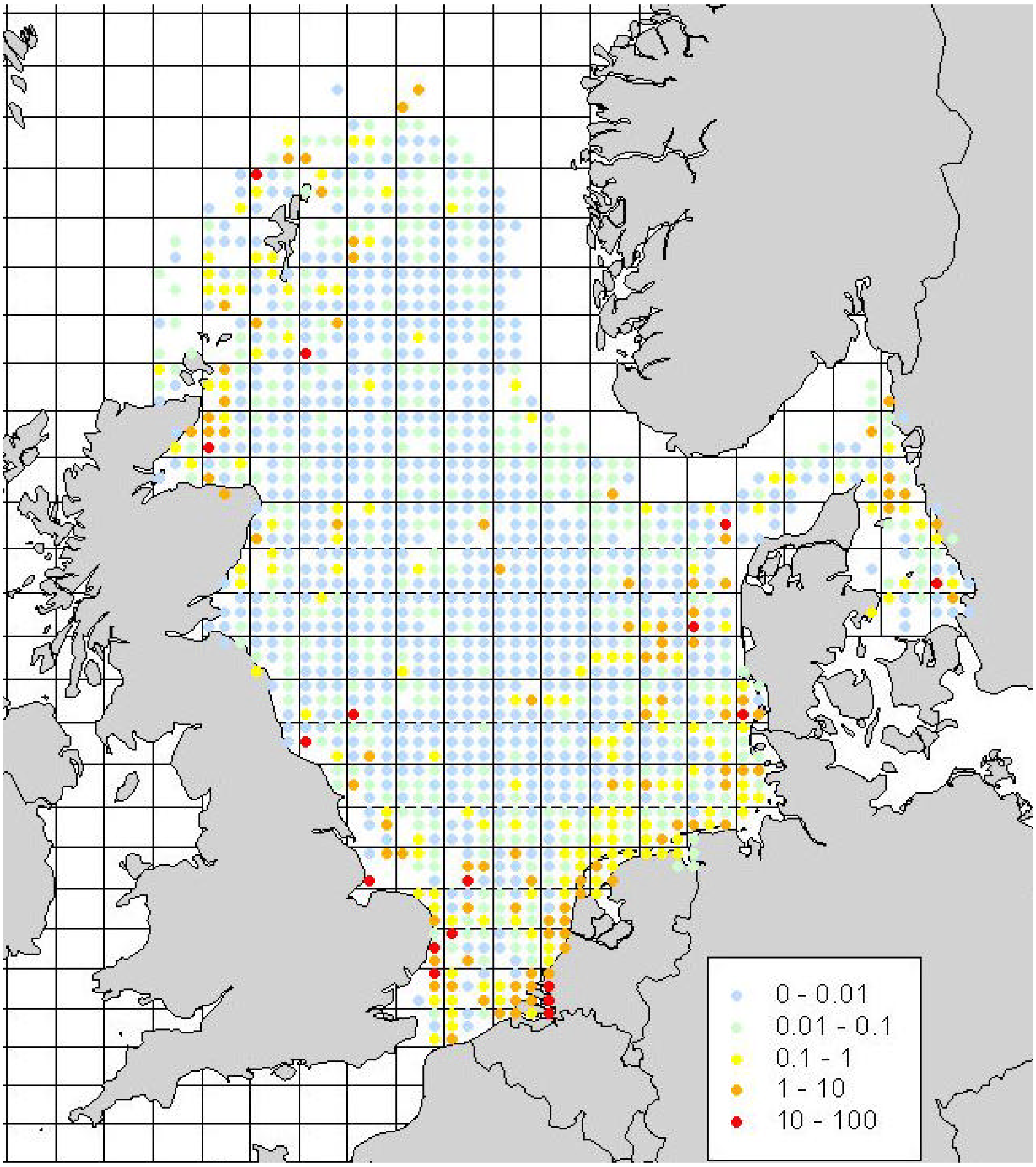


Figure 8. Number of species reported in 100 hauls by sub-rectangle (correction based upon Figure 9).

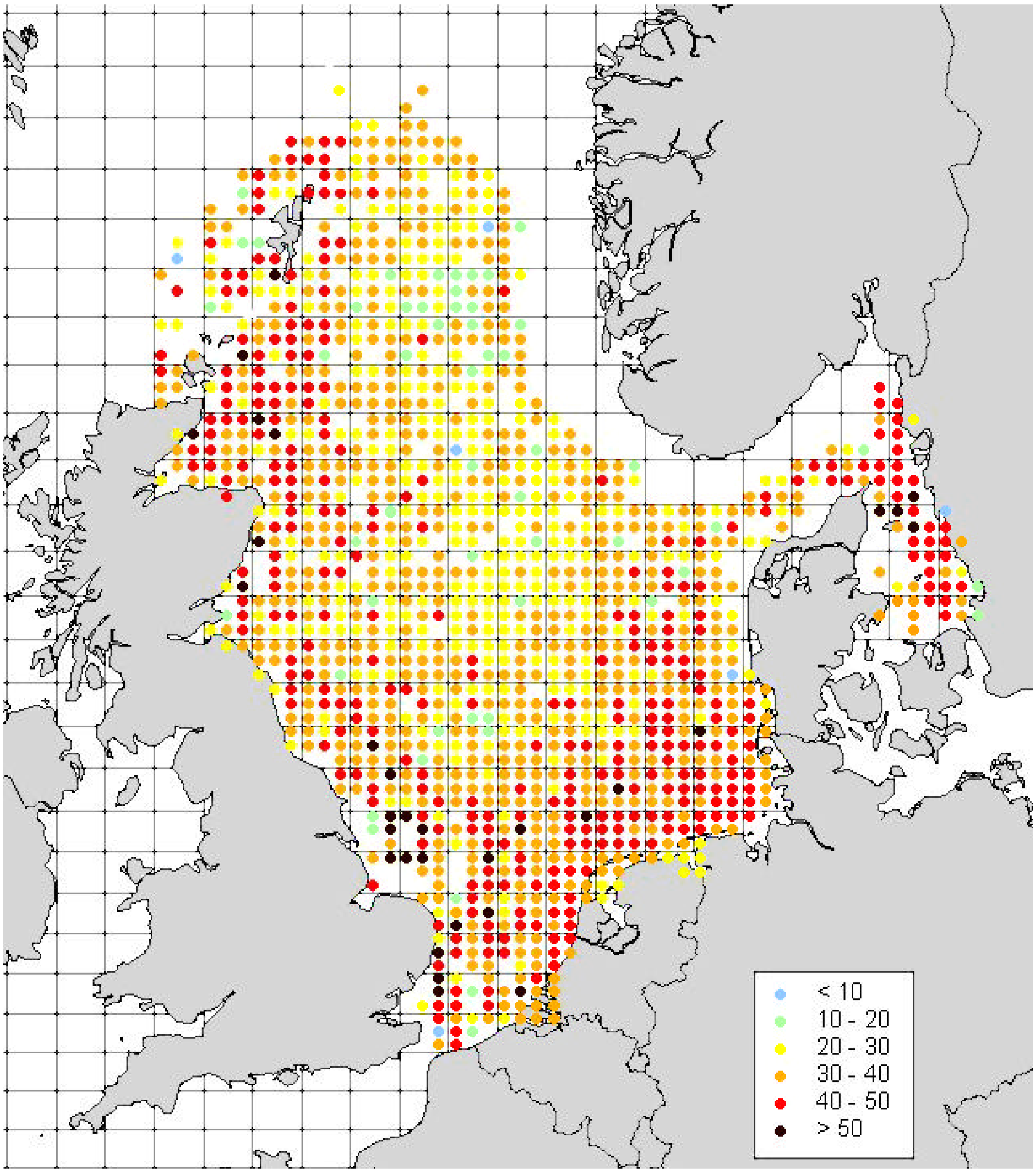


Figure 9. Relationship between number of species recorded by sub-rectangle and the number of hauls (line represents fitted logarithmic function).

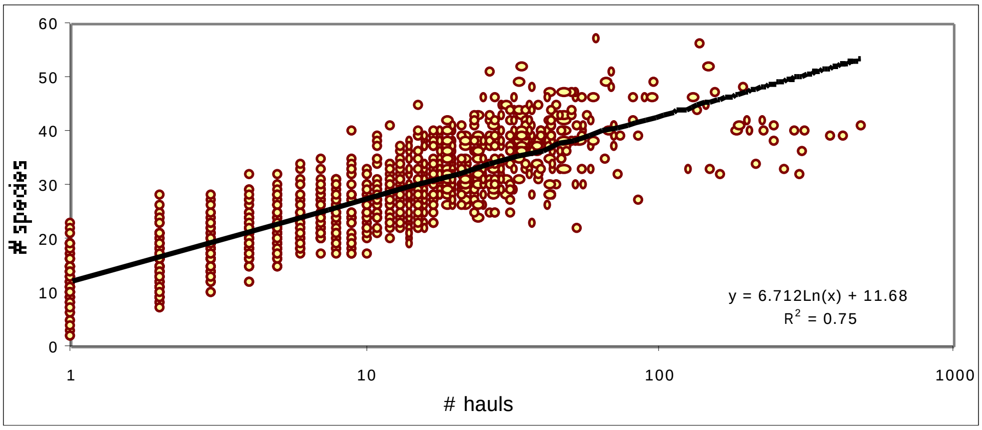
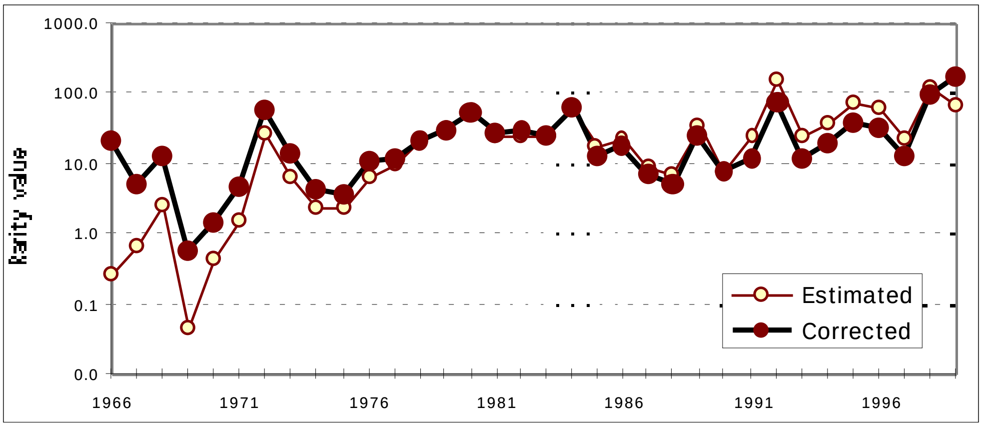


Figure 10. Rarity value by survey year as estimated directly and corrected for variations in sampling intensity (cf. Figure 11).



igure 11. Relationship between estimated annual rarity value and number of hauls by year.