Changes in the North Sea fish community: evidence of indirect effects of fishing?[*]

Niels Daan[1], Henrik Gislason[2], John Pope[3], and Jake Rice[4]

[1]) Netherlands Institute for Fishery Investigations, P.O.Box 68, 1970 AB, The Netherlands - niels@rivo.wag-ur.nl
[2]) Danish Institute for Fishery Research, Charlottenlund Slot, DK-2920 Charlottenlund, Denmark - hg@dfu.min.dk
[3]) The Old Rectory, Staithe Road, Burgh St. Peter, Beccles, Suffolk NR34 0BT, U.K. - PopeJG@aol.com
[4]) Department of Fisheries and Oceans, Canadian Science Advisory Secretariat, 200 Kent Street, Ottawa, Ontario, Canada K1A OE6 - RICEJ@DFO-MPO.GC.CA

Abstract

We investigate changes in the North Sea fish community with particular reference to possible indirect effects of fishing, mediated through the ecosystem. In the past, long-term changes in the slope of size spectra of research vessel catches have been related to changes in fishing effort, but such changes may simply reflect the cumulative effect of direct effects of fishing through selective removal of large individuals. If there is resilience in a fish community towards fishing, we may expect increases in specific components, for instance as a consequence of an associated reduction in predation and/or competition. We show on the basis of three long-term trawl surveys that abundance of small fish (all species) as well as abundance of species with a low maximum length (demersal species only) have steadily and significantly increased in absolute numbers over large parts of the North Sea during the last 30 years. Taking average fishing mortality of assessed commercial species as an index of exploitation rate of the fish community, it appears that fishing effort reached its maximum in the mid 1980s and has declined slightly since. If the observed changes in the community are caused by indirect effects of fishing, there must be a considerable delay in response time, because the observed changes proceed up to recent years.

Introduction

The primary effect of fishing on a population is an increase in total mortality because the fish removed by fishing are added to the other sources of mortality (Beverton and Holt, 1957). Increased post-juvenile mortality necessarily results in reduced survival and a decrease in the number of old (large) fish. Consequently, changes in age distributions are commonly used for estimating fishing mortality (Gulland, 1957).

Fishing may have additional, indirect effects on natural mortality. The removal of large piscivorous fish diminishes predation pressure on the size classes eaten by those. Multispecies Virtual Population Analysis (MSVPA; Pope, 1991; Sparre, 1991) has been developed to estimate such indirect effects of fishing on commercially exploited fish stocks by accounting for internal age-specific predation among species included in the model.

Where many species of fish are taken in fisheries (whether as catch or bycatch), similar direct and indirect effects of fishing may also be expected at the community level (Rice and Gislason, 1996), because the fish community should reflect the accumulated and integrated species-specific effects. A general increase in exploitation rate of the community should lead to a reduction in the abundance of large predators and to an increase in the abundance of small prey. Both responses would make the slope of the log-linear size spectrum of the total fish community steeper, as first demonstrated by Pope and Knights (1982) for survey data. Later investigations indicated that changes in the slope of size spectra are indeed related to changes in exploitation rate (Pope et al., 1987; Murawski and Idoine, 1992; Gobert, 1994; Bianchi et al., 2000; Zwanenburg, 2000). For the North Sea, Rice and Gislason (1996) showed that, as predicted, spectrum slope had steepened and intercept had increased over time both in survey data and in a simulated community of exploited fish stocks.

However, the statistical interpretation of slopes and intercepts is not straightforward, because the two are mutually correlated. Moreover, intercepts represent extrapolations outside the range of lengths observed in survey catches, and hence have large confidence intervals. Thus, it has remained unclear whether the changes in slopes and intercepts frequently observed in survey data involve only a reduction in the absolute abundance of large fish, an increase in the absolute abundance of small fish, or a combination of both. Gislason and Rice (1998) showed that existing single- and multi-species models provide a theoretical basis for quantitative and testable predictions of (relative) effects of exploitation rate on slope and intercept, but the quantitative results depended strongly on assumptions about growth rates and recruitment patterns.

Apart from changes in size spectra, fishing may have additional effects on species composition that are related to the relative sensitivity of species to increased mortality (Jennings et al., 1998). As a general rule, species with a low natural mortality (M) should be more sensitive to exploitation than species with a high M, if only because a given fishing mortality represents a greater increase in total mortality. Unfortunately, reliable information on M for non-target species is rarely available, so we must reason our way to predictions about patterns to be observed. Even with differences in growth rate (Von Bertalanffy K), it takes more time to grow to a large size, so overall natural mortality should be inversely correlated with maximum size (Lmax). Therefore, changes in Lmax spectra might be expected to provide a sensitive measure of secondary effects of fishing, by reflecting changes in total mortality of the species in the community. Indeed, Rogers and Ellis (2000) reported relative increases between 1901/1907

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and 1989/1997 in the proportion of demersal fish with Lmax <30 cm in surveys in three areas around the British Isles, while Jennings *et al.* (1999a) showed that the mean (Von Bertalanffy) L∞ of demersal fish in the northern North Sea has declined during the 20th century. However, these metrics (fractions, means) represent relative measures and the decreases observed might be accounted for entirely by direct effects of fishing (fewer fish with large Lmax or L∞).

In interpreting potential impacts of fishing on the fish community, it would be of considerable interest to be able to separate primary effects from secondary effects. In other words, do the direct effects of increased mortality and reduced population size for larger fish explain the observed changes sufficiently well or is there evidence of important indirect, compensatory effects in small fish?

We address these issues for the North Sea, where several surveys using different gears have been carried out routinely for many years. A universal problem in fish-community analyses aimed at testing hypotheses about community properties and dynamics is that all survey gears are necessarily species- and size-selective. Therefore, survey data will provide biased information relative to the actual community present. As a consequence, different surveys may display different patterns, and comparative analyses using several independent data sets are useful to identify consistent patterns among the specific assemblages sampled by each of them. Because declines in particular components of the community, especially larger sizes and species with a high Lmax, may reflect selective removals and thus a direct effect, we are particularly interested whether small or intermediate size components reveal increases in abundance, because these should be indicative of potential indirect effects. To relate observed changes in community metrics to changes in fishing intensity, we also develop a measure of the overall exploitation of the North Sea fish community.

First-order spatial effects in spectra dynamics are expected, because different parts of the North Sea are inhabited by different communities (Daan *et al.*, 1990) and are subjected to varying fishing effort by different fleets (ICES, 1995; Jennings et al., 1999b). This should provide opportunities to investigate the mechanisms behind the changes observed. If the indirect effects are primarily caused by reduction in predation mortality, different patterns should emerge on spatial scales smaller than the North Sea, but they should vary fairly smoothly as predators and prey redistribute themselves in response to fishing-induced changes in predator fields. Causal explanations invoking size-dependent responses to trawl impacts on seafloor habitats also would have a spatial component but vary more abruptly with spatial scales of trawl effort (Rijnsdorp *et al.*, 1998; Dinmore *et al.*, 2003). Finally, competition theory (Pimm and Hyman, 1987) would predict individuals would try to compensate for size-dependent mortality with size-dependent redistribution of individuals to take advantage of the reduced competitive environment where fishing has occurred, resulting in much less spatial variation in the spectra. The differences in patterns expected depending on the causal mechanism involved were an incentive to study also variations in spectra on different spatial scales.

Methods

• *Survey data*

The analyses are based on three data sets: IBTS (International Bottom Trawl Survey; February surveys only), BTS (Beam Trawl Survey) and DYFS (Demersal Young Fish Survey). These surveys differ in geographical coverage (Figure 1) and gears used, but sampling procedures within surveys are highly standardized. Catches are always sorted to species and samples of each species are measured.
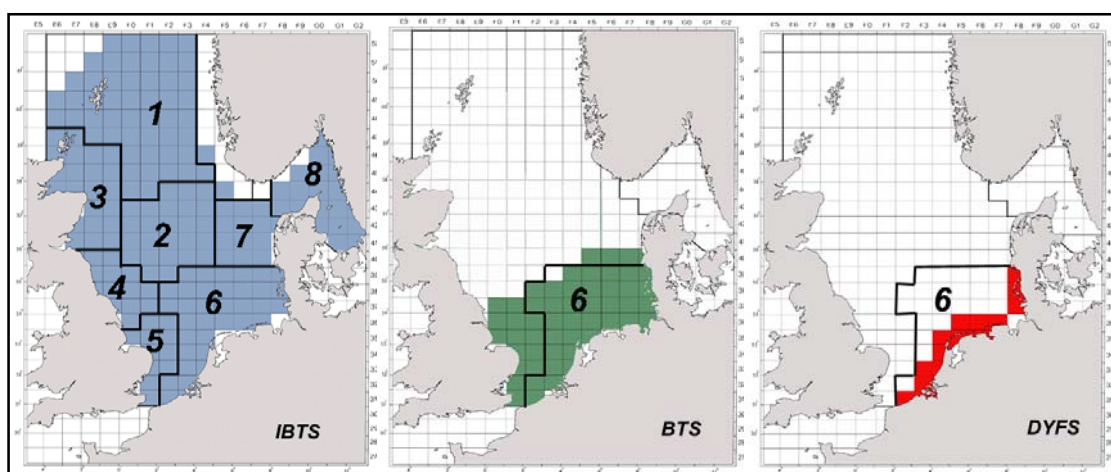

Figure 1. Spatial extent of the three surveys (International Bottom Trawl Survey, Beamtrawl Survey, Demersal Young Fish Survey), with the definition of roundfish areas (RFA) 1-8.

- IBTS (Heessen *et al.*, 1997; ICES, 1999) has been carried out annually in February since 1966. The area

covered gradually extended northward and initially, different countries used different gears. From 1977 onwards, the standard gear has been the Chalut à Grande Ouverture Verticale (GOV) and the entire North Sea within the 200 m depth contour, including the Skagerrak and Kattegat, has been sampled (Figure 1a). Therefore, analyses were restricted to surveys from 1977-2000, and hauls in depths >200 m were excluded. The GOV has a vertical opening of approximately 5 m and a distance between the otter boards of up to 100 m. However, these values vary with depth, warp and sweep length and the effective area swept may be different for different species, sizes, depths and sediment type. Although the cod-end has a 20mm liner, small fish may escape through the front part of the net. In view of these complications, we use a simple cpue (catch in number or weight by size or lmax group per hour fishing), and assume that the inevitable biases in size-dependent selectivity remain constant over time. Given the estimated opening of the net itself (excluding the area covered by the sweeps) and prescribed towing speed, on average 150 000 m2 are fished during 1 hour by the GOV (Knijn *et al.*, 1993).

- BTS (van Beek, 1997) is an international August survey that has been carried out since 1985 in the south-eastern North Sea and is specifically aimed at the older year classes of plaice and sole. Since 1996, it has been extended northwards. The gear is a 8m beam trawl with 4 chains running between the shoes and 4 tickler chains connecting the groundrope (cod-end mesh size: 20 mm). Beam height is 50 cm and the area fished per haul is ca 60 000 m2. Analyses were restricted to Dutch data and the standard area sampled consistently over all years (Figure 1b).

- DYFS (Boddeke *et al.*, 1970; van Beek, 1997) started in 1970 and is aimed at estimating the abundance of juvenile sole and plaice in inshore continental waters. It covers the entire area from the Belgian coast to Esbjerg, including the estuaries of the Scheldt and the Rhine and the Dutch part of the Waddensea. Originally, the survey was carried out in spring and autumn, but only the autumn survey has survived. Other countries have participated irregularly but the analysis has been restricted to the Dutch autumn data, which have been collected consistently. During the initial years, many of the smaller species (e.g., Pomatoschistus sp.) were only counted and therefore data collected before 1977 were excluded. One sea-going and two inshore vessels participate simultaneously employing a 6m and 3m beam trawl, respectively. The narrow-meshed gear is rigged like a shrimp trawl (without chains) with a line with wooden rollers in front of the groundrope. Vertical net opening is 40 and 30 cm, respectively, and average area fished per haul is 16 000 and 8000 m2, respectively.

To obtain roughly comparable cpue estimates in respect of swept area, data collected during the different surveys were raised to match the IBTS (150 000 m2). In the averaging process, hauls made within the same ICES rectangle in a particular year were averaged first before an average was taken over the entire survey. Primary data selections and analyses were made in SAS and followed up in EXCEL.

• *Size spectra*

Most length measurements in the survey data refer to total length to the cm below, except for herring and sprat (0.5 cm below) and fish above 60 cm (5cm interval below). A rough estimate of the corresponding weight in each size class (midpoint L) was calculated as W=0.01*L3 (kg). The next step was to group all fish by 5cm (DYFS) or 10cm (IBTS and BTS) classes. After inspection of the spectra for the size range conforming to a log-linear slope (Figure 2a), size classes at the lower (poor retention in the gear) and upper (captures too infrequent for robust estimation of frequency) end of the range were excluded.

To overcome the statistical problem of disentangling slope effects from intercept effects, size spectra were centred around the midpoint of the length range: the midpoints of the size classes used in the calculations (IBTS: 20-100 cm; BTS: 10-60 cm; DYFS: 10-55 cm) were re-scaled with mid-length (60, 35 and 32.5 cm, respectively) fixed at zero. Thus, the intercept value reflects the 'height' of the spectrum and depends largely on total log-abundance. By this procedure, the intercept should be statistically independent of the slope, and not require extrapolation outside the range of observations. Indeed, the correlation between 'height' and slope was not significant for any of the three surveys (R2: 0.22, 0.09, and 0.04, respectively). To investigate spatial variation in slope and height, average values over all years were derived also by statistical rectangle for the IBTS.

Although the overall features of a size spectrum may be captured in height and slope, more subtle changes in the relative and absolute abundance of individual size classes may be lost. Therefore, we also plotted trends in ln-abundance of individual size classes. To investigate whether consistent patterns emerge over the entire North Sea, trends in ln-abundance by size class for the IBTS were also derived by roundfish area (RFA 1-8; Figure 1a). For the other two surveys such analyses were not warranted because of their restricted spatial coverage.

Information from all hauls with missing length measurements for one or more species was rejected a priori. No selection was made in respect of species or guilds, because we were interested in the most complete picture of the community available to the gear. However, we did investigate whether specific patterns could be traced to 5 specific guilds (pelagics, gadoids, flatfish, other demersal and elasmobranchs).

• *Lmax spectra*

When dealing with properties of species composition rather than size composition of survey catches, some problems emerge. Whereas for size spectra, reasonable criteria can be established for setting lower and upper bounds on the size range suitable for analyses, there are less clear grounds for deciding what species are truly part of the "community" whose dynamics are to be analyzed. Nonetheless, such decisions can have substantial influence on estimates of the community metrics, but are necessary to reduce the extraneous noise contaminating potential signals in the Lmax spectra. It seemed appropriate to focus on the assemblage typically exploited by demersal gear and to exclude both pelagic species as well as vagrants. In addition, primary inspection of the data revealed that elasmobranchs created noise in the data

owing to their overall rarity and contagious occurrences. These were therefore also excluded.
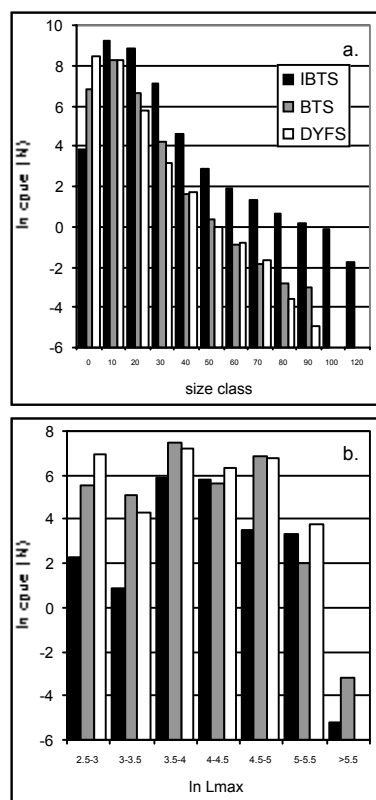

Figure 2. Overall (a) size and (b) Lmax spectra by survey (ln-cpue in numbers by 10 cm class and ln-Lmax class, respectively).

After thus having defined the 'typical' North Sea demersal fish assemblage, a problem of species identification remained. Daan (2001a) provides evidence that several species have been mixed up by different crews at different times, while in other cases identification was restricted to the genus or even family level. We resolved this problem by first assigning apparently mis-identified taxa to their appropriate genus (or family). Subsequently, the associated catch was split among the relevant species according to the fractions observed in hauls with trusted species information made by other countries in the same square and in the same year. If this cell was empty, the average fraction in the same square over the entire survey period was used. Such correction procedures were applied to species belonging to the genera *Callionymus*, *Liparis* and *Sebastes* and the families Soleidae, Bothidae and Cottidae. In the case of *Ammodytes* and *Pomatoschistus*, catches have rarely been identified to species and therefore only the genus name has been retained in the analyses.

For the remaining species retained in the analysis (97, 62 and 46 for IBTS, BTS and DYFS, respectively), Lmax values (cf Daan, 2001b) were derived from Wheeler (1978) or Whitehead et al. (1984). Each record was then assigned a ln-Lmax class (<3, 3-3.5, 3.5-4, 4-4.5, 4.5-5, >5, corresponding to <20.1, 20.1-33.1, 33.1-54.6, 54.6-90.0, 90.0-148.4, >148.4 cm, respectively). Annual ln-Lmax spectra by number and by weight were derived by summing

appropriately over the original length compositions within each ln-Lmax class. Figure 2b provides the average spectra in numbers for RFA 6 over the entire period for the three surveys. Clearly, these spectra do not indicate a log-linear relationship and therefore temporal trends were investigated within each class.

The primary comparisons among surveys were restricted to information from RFA 6, where all surveys allocated sufficient effort to make detection of community patterns likely, if they were present. However, IBTS data were analysed also by RFA to investigate whether similar trends have occurred over larger areas.

• *Trends in exploitation*

To relate observed trends in size and Lmax spectra to effects of fishing, an integrated measure of the exploitation rate of the North Sea fish community is required. We chose to use estimates derived from the most recent run of MSVPA (ICES, 2002a), because it provides a coherent data set with a common scale for cod, haddock, whiting, saithe, plaice, sole, herring, sandeel, sprat and Norway pout and takes historic changes in predation rates fully into account. From this source estimates of fishing mortality are available for 10 exploited target species.
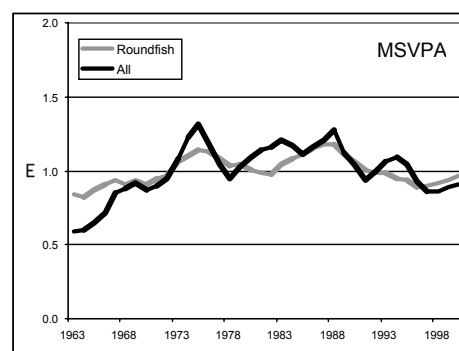

Figure 3. Trends in average (standardized) exploitation rate for all stocks combined and for demersal stocks only (smoothed in threes).

Deriving an overall exploitation rate from the estimated fishing mortalities for a number of species is not straightforward, because some are caught in mixed fisheries. Therefore, part of the mortality is exercised simultaneously by the same effort and therefore might be counted twice. Moreover, discards are not included for most species and therefore, exploitation may be underestimated even for individual species. Nevertheless, to derive a global trend, some way of averaging is required. First, estimated mortality by year for individual species was divided by the average mortality over the entire period (1963-2000) to place annual estimates on a common scale. These mortality indices were then averaged for different components, both as simple arithmetic means and as means weighted by the average biomass of each species over the entire period. Because the two approaches exhibited virtually the same patterns, we chose to use the simple arithmetic means (smoothed by taking three-year running means to make trends more apparent) for all species combined (as an exploitation index for the

entire North Sea fish community) and for all roundfish and flatfish species (as an index for the demersal fish community) for comparison with changes in size and Lmax spectra, respectively (Figure 3).

Results

• *Size spectra*

Figure 4 shows the annual variation in slope and height of the size spectra for each of the three surveys. The significant ($p < 0.01$) long-term trend in IBTS indicates a gradually steepening slope, while trends for BTS and DYFS are not significant. However, closer inspection of the results reveals that the residuals around the IBTS trend are not randomly distributed. They suggest that the increase in (negative) slope was most pronounced before about 1985 and remained largely stable afterwards ($r=0.54$, $p < 0.05$), during the period covered by the BTS. In contrast, the DYFS slopes steepen during the period before 1986, but have recovered to the original level since that time. Linear regression is apparently not the appropriate tool to investigate these long-term trends.
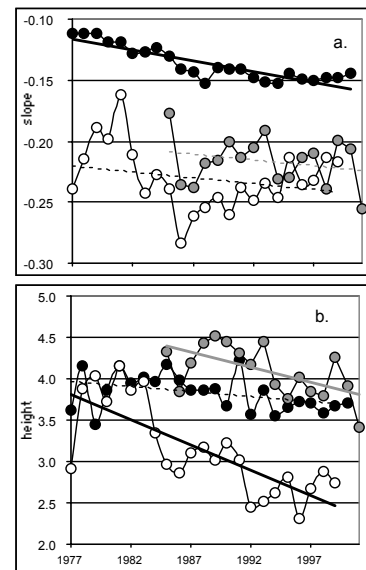

Figure 4. Estimated trends in (a) slope and (b) height of log-linear size spectra of the total fish community sampled by the three surveys (heavy lines: $p < 0.01$; thin lines: $p < 0.05$; dashed lines: not significant).

A.

	E6	E7	E8	E9	F0	F1	F2	F3	F4	F5	F6	F7	F8	F9	G0	G1	G2
51			-0.08	-0.09	-0.07	-0.09	-0.10										
50			-0.10	-0.13	-0.10	-0.07	-0.10	-0.08									
49			-0.18	-0.11	-0.10	-0.11	-0.09	-0.11									
48		-0.10	-0.15	-0.14	-0.13	-0.12	-0.09	-0.09									
47		-0.17	-0.13	-0.14	-0.13	-0.11	-0.11	-0.11									
46	-0.12	-0.15	-0.13	-0.13	-0.13	-0.12	-0.11	-0.11							-0.11		
45	-0.11	-0.15	-0.12	-0.12	-0.10	-0.11	-0.10	-0.10	-0.09					-0.13	-0.11	-0.12	
44	-0.10	-0.09	-0.13	-0.10	-0.13	-0.13	-0.08	-0.10	-0.11				-0.12	-0.12	-0.10	-0.10	
43			-0.14	-0.13	-0.11	-0.10	-0.11	-0.09	-0.08	-0.08	-0.10	-0.09	-0.10		-0.08	-0.14	-0.14
42		-0.11	-0.12	-0.13	-0.10	-0.12	-0.10	-0.06	-0.09	-0.08	-0.09	-0.11				-0.12	-0.12
41		-0.12	-0.12	-0.12	-0.12	-0.10	-0.10	-0.05	-0.08	-0.08	-0.10	-0.09			-0.09	-0.12	-0.12
40			-0.15	-0.14	-0.13	-0.11	-0.09	-0.09	-0.07	-0.09	-0.09	-0.09					
39			0.13	-0.12	-0.12	-0.10	-0.10	-0.07	-0.06	-0.07	-0.09	-0.07	-0.07				
38				-0.11	-0.09	-0.11	-0.09	-0.07	-0.08	-0.08	-0.09	-0.11	-0.10				
37					-0.10	-0.08	-0.10	-0.09	-0.08	-0.07	-0.09	-0.13	-0.12				
36						-0.08	-0.05	-0.08	-0.08	-0.09	-0.10	-0.13	-0.16				
35						-0.09	-0.09	-0.07	-0.08	-0.10							
34							-0.06	-0.06	-0.10	-0.07							
33							-0.08	-0.10	-0.12	-0.11							
32							-0.12	-0.13	-0.12								
31							-0.15										

|value|
- >0.15
- 0.11- 0.15
- 0.08- 0.11
- <0.08

B.

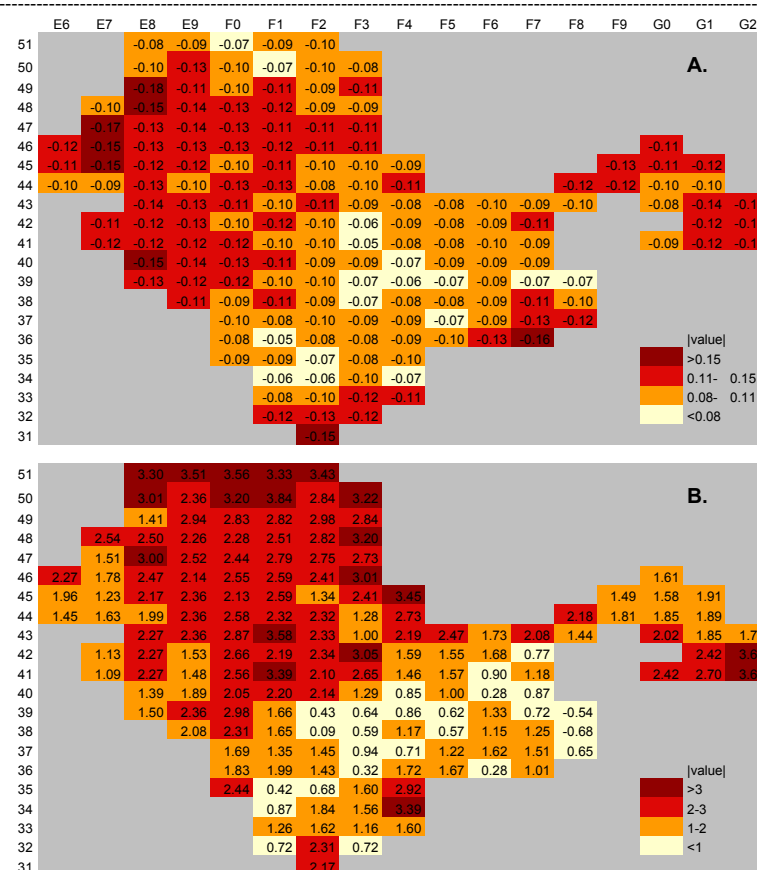|	E6	E7	E8	E9	F0	F1	F2	F3	F4	F5	F6	F7	F8	F9	G0	G1	G2
51			3.30	3.51	3.56	3.33	3.43										
50			3.01	2.36	3.20	3.84	2.84	3.22									
49			1.41	2.94	2.83	2.82	2.98	2.84									
48		2.54	2.50	2.26	2.28	2.51	2.82	3.20									
47		1.51	3.00	2.52	2.44	2.79	2.75	2.73									
46	2.27	1.78	2.47	2.14	2.55	2.59	2.41	3.01							1.61		
45	1.96	1.23	2.17	2.36	2.13	2.59	1.34	2.41	3.45					1.49	1.58	1.91	
44	1.45	1.63	1.99	2.36	2.58	2.32	2.32	1.28	2.73				2.18	1.81	1.85	1.89	
43			2.27	2.36	2.87	3.58	2.33	1.00	2.19	2.47	1.73	2.08	1.44		2.02	1.85	1.72
42		1.13	2.27	1.53	2.66	2.19	2.34	3.05	1.59	1.55	1.68	0.77				2.42	3.67
41		1.09	2.27	1.48	2.56	3.39	2.10	2.65	1.46	1.57	0.90	1.18			2.42	2.70	3.67
40			1.39	1.89	2.05	2.20	2.14	1.29	0.85	1.00	0.28	0.87					
39			1.50	2.36	2.98	1.66	0.43	0.64	0.86	0.62	1.33	0.72	-0.54				
38				2.08	2.31	1.65	0.09	0.59	1.17	0.57	1.15	1.25	-0.68				
37					1.69	1.35	1.45	0.94	0.71	1.22	1.62	1.51	0.65				
36					1.83	1.99	1.43	0.32	1.72	1.67	0.28	1.01					
35				2.44		0.42	0.68	1.60	2.92								
34							0.87	1.84	1.56	3.39							
33							1.26	1.62	1.16	1.60							
32							0.72	2.31	0.72								
31							2.17										

|value|
- >3
- 2-3
- 1-2
- <1

Figure 5. Spatial variation in average (A) slopes and (B) heights of the size spectra (mean ln-cpue 1977-2000 vs 10 cm size classes) in first-quarter IBTS.

In respect of height, a different picture emerges. Height decreased significantly in both BTS and DYFS (p<0.01), suggesting a decline in overall abundance up to the most recent years. The overall trend in IBTS is not significant, but over the period 1985-2000, the negative trend is also significant (r=0.64, p<0.01). It is noteworthy that the scales for slopes are markedly different among surveys, indicating that they sample different assemblages. Although the heights of the spectra also differ among surveys, this may be a trivial artefact that only reflects inaccurate raising factors used to derive comparable swept areas. When compared with the trend in overall exploitation (Figure 3), the steepening of the slopes halts at approximately the time when exploitation rate reached its maximum. In contrast, height, and thus overall abundance, continued to decrease after that time.

The spatial variation in average slope and height by statistical rectangle exhibits a surprisingly coherent pattern (Figure 5). Slopes are generally steeper (more negative) in the northwestern North Sea, the entrance of the Channel, the German Bight and in the Skagerrak/Kattegat area, with the shallowest slopes concentrated in the southern and central North Sea. Spectrum heights are largest along the northern edge of the survey area and at the southern border of the Kattegat, with low values throughout most of the southeastern North Sea. In the absence of integrated information on the distribution of fishing effort by rectangle, interpretation of these patterns is not straightforward, but the different patterns presented by the two metrics reveal that they capture different properties of the community.
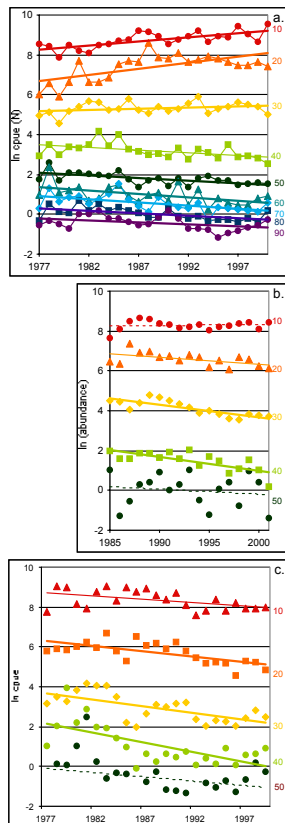
Figure 6. Trends in ln-cpue by size class and survey (a: IBTS; b: BTS; c: DYFS; for line symbols see Fig. 4).

Figure 6 presents a detailed view of the temporal change in ln-cpue by size class in the three surveys. The IBTS in particular shows a significant (p<0.01) increase in the smallest three size classes, whereas, through the entire period, the abundance of all larger size classes have declined significantly (40-50: p<0.05; others: P<0.01). The trend for the smallest size class in the BTS was not significant, but for all larger classes trends were significantly negative (20-30: p<0.05; others: p<0.01). Only the DYFS showed significant declines in abundance of both small and large (up to 50-60) size classes (10-20: p<0.05; others: p<0.01).
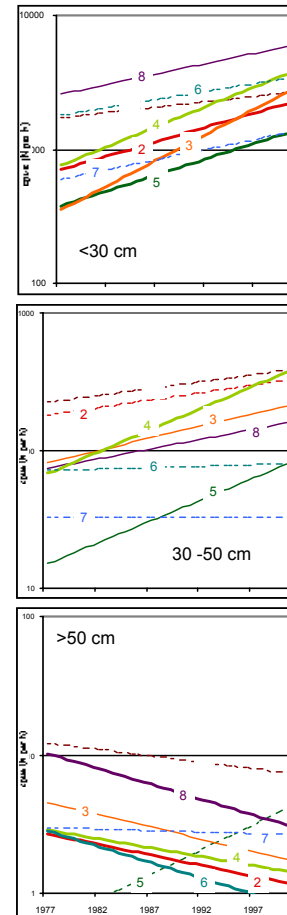

Figure 7. Trends in IBTS ln-cpue by RFA (see Figure 1a) for three size classes (for line symbols see Fig. 4).

Figure 7 compares trends in three broad size classes defined as small (<30 cm), medium (30-50 cm) and large (>50 cm) fish among roundfish areas (IBTS data). Abundance in the smallest size class increased in all eight areas, which has a probability by chance of ~0.004 (binomial test). The increases were significant in five of the areas (4: p<0.01; 1: p<0.05). Also the abundance of medium sized fish increased in all eight areas (P ~ 0.004) and significantly in 4 areas (1: p<0.01; 3: p<0.05), which were largely the same as for the small fish. In contrast, large fish declined in seven out of eight areas (P ~0.03) and significantly so in five (4: p<0.01; 1: p<0.05). Overall, increases in small fish were most pronounced in the central areas (RFA 2, 3, 4, 5, 7) of the North sea and in the Skagerrak/Kattegat (RFA 8), whereas the greatest declines in large fish occurred in

the central-southern areas (RFA 2, 3, 4, 6) and Skagerrak/Kattegat (RFA 8). These results clearly indicate a large spatial coherence in the observed phenomena.
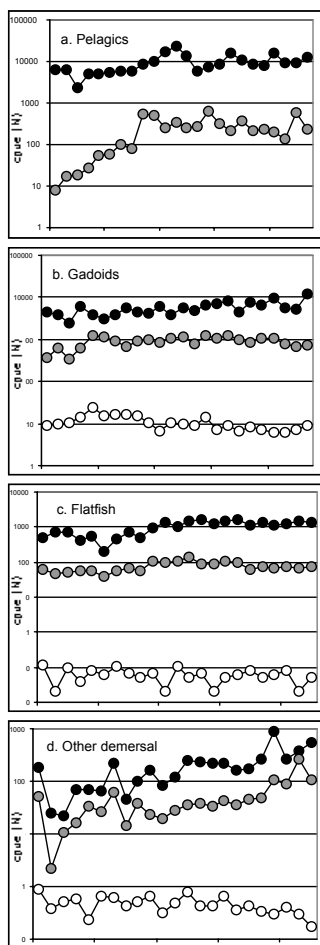

Figure 8. IBTS ln-cpue by guild for three size classes.

These changes appear not to be restricted to particular species groups (Figure 8). Abundance of small roundfish, flatfish, elasmobranchs and other demersal fish have all increased, while medium-sized fish have remained fairly stable (except for an increase in other demersal fish) and large fish have decreased. Among the pelagic species, the medium sized fish have sharply increased during the initial years, which may be attributed largely to the recovery of the herring stock.

• Lmax spectra

Ln-cpue in numbers of successive ln-Lmax classes (demarcation points: 3, 3.5, 4, 4.5, 5 corresponding to 20.1, 33.1, 54.6, 90.0 and 148.4 cm, respectively) in RFA 6 for the three surveys (Figure 9) reveal a consistent pattern with a marked increase in abundance of small species, stable abundance of intermediate species and a decline in abundance of large species. However, the classes involved differ among surveys. In contrast with the slopes of the size spectra, these trends do not stop around 1985, but continue until the most recent years.
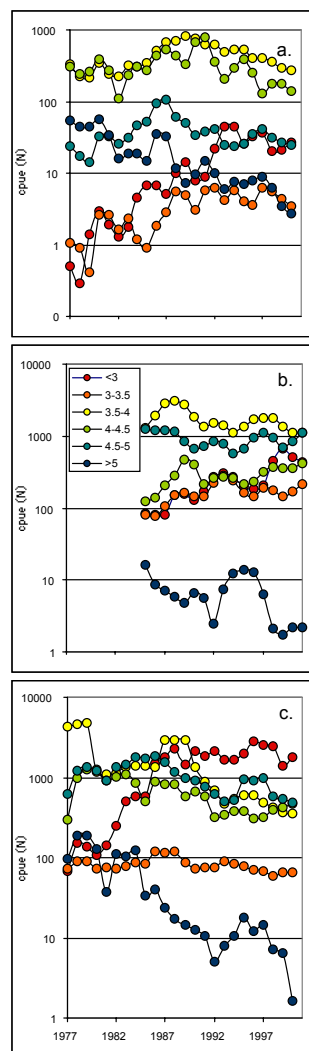
Figure 9. Trends in ln-cpue by ln-Lmax class for demersal fish in roundfish area 6 by survey (a: IBTS; b: BTS; c: DYFS).

The time series of the proportion of ln-cpue (in weight) in each ln-Lmax class indicate similar trends. However, the patterns are more stable, at least in the IBTS and BTS data (Figure 10), because both the small and large Lmax classes, where the time trend is most pronounced, contribute relatively little to the total abundance. The figure also shows that the assemblages sampled differ markedly among surveys. For instance, the signal for small species is hardly visible in the IBTS data and large species are poorly represented in the BTS.Figure 11 shows the estimated trends (IBTS) for each RFA. With the exception of RFA 2, the abundance in the smallest Lmax class (<20.1 cm) has increased significantly (p<0.01) throughout the North Sea. For intermediate size classes, the results are more variable, but there is a tendency of increasing abundance or no change. Only RFA 6 exhibits a significant decline (p<0.01) of large fish. Major trends also exist in catch rates whether expressed as numbers, weights, or mean weights (Figure 12). Catch weights have significantly declined (p<0.01) in BTS and DYFS, and average weights in all surveys. The decline in catch rates in numbers was not significant in any survey owing to large annual variability.
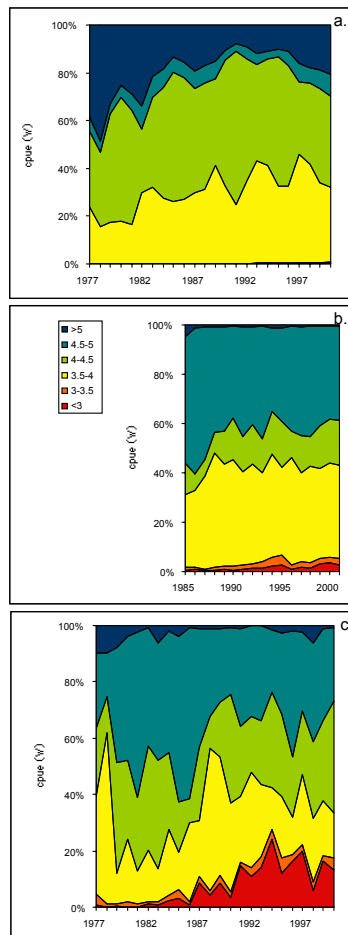
Figure 10. Relative contribution by ln-Lmax class to the cpue in weight of demersal fish in RFA 6 by survey (a: IBTS; b: BTS; c: DYFS).

Figure 11. Trends in IBTS cpue of demersal fish by RFA (Figure 1a) for 3 ln-Lmax classes (for line symbols see Fig. 4).

Discussion

Size-spectra analyses generally reduce the fish community to a two-parameter model (slope and intercept/height). These simplifications are only sensible if the fish community can be characterized sufficiently well by these two parameters that trends in their values can be associated with effects of changes in overall exploitation. Many studies have shown that the slope in particular is a sensitive parameter (see introduction), and the change in slopes of IBTS and BTS data (Figure 4) over time appear to mirror the pattern in average exploitation rate over all species routinely assessed by ICES (Figure 3).

DYFS data deviate in the sense that the slope has flattened markedly since 1986. This survey samples an inshore fish community that may vary independently of overall North Sea trends, particularly because it is an important nursery area for several exploited species (Zijlstra, 1972). The recent recovery suggests a local decline in fishing effort, which is consistent with the introduction of the plaice box in the early 1990s (Pastoors *et al.*, 2000). However, the trend was reversed several years before the plaice box was introduced and additional explanations for the apparent recovery appear to be required.
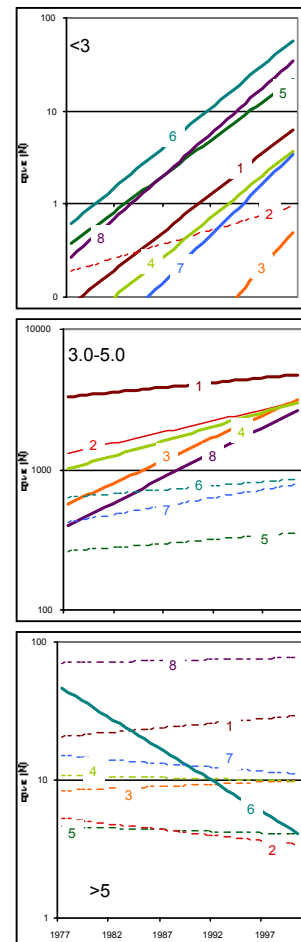
Changes in traditional estimates of the intercept are more difficult to interpret, because these represent extrapolations outside the range of observations and are correlated with estimated slopes. We feel that mid-length height (or intercept of the centred spectrum) may be a more useful descriptor. The height of the IBTS spectrum remained approximately constant up to 1985 and the subsequent drop supports the pattern seen in the shorter BTS data series. Thus, height shows generally a different trend from those shown by the slopes and by exploitation. This suggests that heights and slopes capture two different effects of exploitation. While the slope responds more or less directly to changes in mortality (removal of large fish), the effect on height as a proxy for overall abundance appears to be delayed. If the responses of the small and medium size classes reflect increased survivorship owing to reduced predation, the delay may reflect the time needed for the community to find a new balance between production (increased abundance of small fish) and exploitation (reductions in large fish). These adjustments might take several life cycles.

This explanation presupposes that exploitation of the community is the main cause of the observed changes. This can of course not be proven and other, environmental factors may be involved (Zwanenburg 2000). The steady decline of height in the DYFS data cannot easily be linked to changes in exploitation, indicating that the causes of changes in the spectra

may be complex, and involve more factors than just fishing.
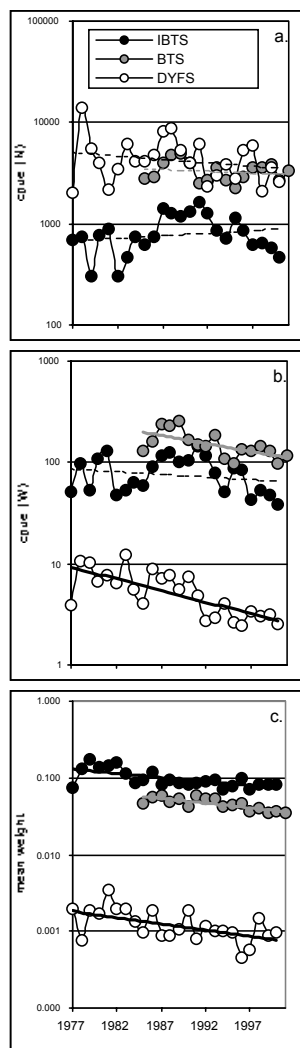

Figure 12. Trends in catch rates of demersal fish in (a) numbers and (b) weights, and (c) in average weights of individuals caught (for line symbols see Fig. 4).

The spatial patterns of slopes and heights by rectangle support the view that these metrics capture different characteristics of the community, because there appears to be little spatial correlation. The coherence in the estimates of both metrics at the scale of hundreds of miles would suggest that reduced predation by large fish provides a more likely explanation than local trawling impacts or competition, because for instance a major predator such as cod migrates and disperses on an annual basis at a comparable scale (Daan, 1978). The area off Scotland, where slopes were steepest seems to largely coincide with an intensive Scottish fishery (Jennings *et al*., 1999b). However, it seems unlikely that all spatial variations can be accounted for entirely by differential fishing effort in different regions, because the area, where an extensive beam trawl fishery operates, is characterized by shallower slopes than anywhere else in the North Sea. Also, the German Bight area with steep slopes is within the plaice box and not likely to be heavily exploited in recent years. Thus, these regional differences in size spectra are

presumably partly related to fundamental differences in overall abundance, size and species composition of local fish communities.

The hypothesis stated in the introduction was that the direct effect of fishing (increased mortality) should lead to a decrease in numbers of large fish, and the reduction in size-dependent predation to a subsequent increase in absolute numbers of small fish. A lower abundance of large fish is supported directly by the patterns in slopes over time. Additional inferences may be made for the abundance of small fish on the basis of slope and height combined. For instance, if height is constant and slope has steepened, it follows that the amount of small fish must have increased. This was apparently the case in the IBTS data before 1985. However, when both slopes and heights vary, the interpretation is more difficult, as other factors may be involved (see Introduction). In these cases, the limitations of a two-parameter model to describe a complex spectrum become obvious. Thus, detailed patterns should be investigated more directly on the basis of individual size classes.

The IBTS results provide strong support for the hypothesis that small fish have increased in absolute numbers over time, while medium-sized fish have remained more or less constant and large fish have declined. Although the general tendency of more severe declines in larger fish appeared also in the other two data sets, there was no significant trend in the smallest size class in the BTS, and even a slight decline in the DYFS. Differences in species' catchabilities in the various survey gears may contribute to these differences across surveys. Nevertheless, consistent patterns are observed in the IBTS data over large areas, and among different species groups, in the heavily, and at least up to 1985 increasingly, exploited North Sea ecosystem. These common patterns point to a common causal factor and fishing serves as a prime candidate that may explain the observed patterns adequately.

The information on individual size classes clearly allows for a more refined interpretation than is possible from the two-parameter regression model of ln-abundance on size class. This may well be due to the fact that the most significant changes have occurred at the lower and upper end of the size range sampled. These sizes were partly excluded from the regression analysis, because they did not fit the log-linear relationship, but their information content may also have been partially obscured by the more abundant intermediate classes showing less pronounced patterns.

Size spectra tell us little about changes in the species composition of the fish community, because juveniles of large species are always more abundant then adult fish. The Lmax analysis revealed significant changes in RFA 6, which were supported by all three surveys: total abundance (over all sizes) of species with low Lmax have significantly increased, those with medium Lmax have remained stable, and those with high Lmax have declined. This result seems to support the hypothesis that high-Lmax species (as a proxy for high M) are more sensitive to exploitation than low-Lmax species. However, while low-Lmax species increased throughout the North Sea, the reduction of high-

Lmax species has apparently been restricted to the southeastern North Sea (RFA 6).

If changes in the abundance of low-Lmax species are a universal response to variations in fishing pressure, changes in high-Lmax species apparently are not. With a Lmax of 150 cm, cod belongs to the largest species (ln-Lmax >5). The community signal observed in RFA 6 can probably largely be accounted for by the near-extinction of cod in this part of the North Sea. In historic times, the inshore coastal area has proven an important area for 0-group cod in August and so have the offshore areas in the southern North Sea for 1-group cod in winter (Daan, 1978). However, juvenile cod have been virtually absent in RFA 6 in recent years and their distribution has shifted to more northerly areas (ICES, 2003). Thus, the changes in representation of the largest Lmax category in RFA 6 in the three surveys may in fact reflect changes in abundance of juveniles of a single species (cod), which is known to be on the verge of collapse by overexploitation (Cook *et al.*, 1997). Overall, there is no strong indication of an apparent sensitivity of high-Lmax species to exploitation. In contrast, the generalization that fishing appears to favour low-Lmax species is strongly supported by survey data over large areas of the North Sea. The increase in the proportion of fish with an Lmax <30 cm in research vessel catches around the British Isles between the start of the 20th century and the 1990s observed by Rogers and Ellis (2000) points in the same direction. Reduced predation pressure owing to the removal of large predators as indicated by the size spectra analysis provides a simple explanation for these observations.

This analysis cannot prove that the observed increases in small fish and in low-Lmax species are related to secondary effects of fishing through reduced predation. Effects of environmental change (Zwanenburg, 2000) or habitat-mediated effects of fishing cannot be excluded (Hall, 1999). However, there is no established environmental theory that predicts such patterns of change. While relationships may exist between climatological indices and population responses of individual species, these could be either positive or negative and it could only be guessed how the environment would affect associated metrics at the community level. In contrast, the existing theory on effects of fishing, mediated through changes in inter- and intra-specific predation, accounts well for the patterns observed in the North Sea fish community.

One other possibility deserves attention. Could these temporal trends be caused by bias owing to gradual changes in sampling methodology? All surveys started with the primary aim of getting information on annual recruitment estimates for commercially important fish species. As a consequence, most countries involved paid initially more attention to exploited species than to non-target species and many hauls had to be excluded from the initial years because of incomplete coverage of measurements. Indeed, when data were screened for recording quality, interannual variability in the spectra much larger during the early years. Although showing broadly similar trends, we decided to exclude all years before 1977. Given the number of ships and people involved, it is difficult to judge whether sampling has been carried out in a consistent way since that time. However, because several surveys revealed similar main trends and trends were consistently found over large areas, where different countries operated, we feel that it is unlikely that a common bias would apply to all.

Despite showing similar patterns, the actual values of all metrics used - slopes of the size spectra, cpue by size and Lmax classes and average weights alike - vary considerably among surveys. This suggests that the values can only be interpreted in a relative sense. The absolute values have little meaning and only refer to the typical assemblage of species sampled by the gear. The corresponding true values for "the North Sea fish community" may never be known, which complicates things when trying to use them in defining ecosystem-based management goals. Other important questions remain. Are the observed changes reversible with better management or has the ecosystem been permanently altered? Is a steeper slope bad? How big a change can be tolerated before the ecosystem has suffered "serious or irreversible harm". In short, do these changes matter in a management context?

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