

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

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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, 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 demersal species with a low maximum length ($L_{\max}$) 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 generally proceed up to recent years, although both size and $L_{\max}$ spectra suggest some levelling off, or even recovery in one of the surveys. Indeed, significant correlations between all community metrics and exploitation rate were obtained only if time lags ≥ 6 years were introduced.

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Introduction

The primary effect of fishing on a population is an increase in total mortality because the removals 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. Fishing may have additional, indirect effects on natural mortality. The removal of large piscivorous fish diminishes predation pressure on the size classes that they eat, thus lowering natural mortality on their prey (Pope, 1991).

Similar direct and indirect effects of fishing may also be expected at the fish community level (Rice and Gislason,

1996; Shin *et al.*, 2005), because the community simply integrates the accumulated species-specific effects: an increase in exploitation rate of the entire 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 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. Existing single- and multispecies models clearly provide a theoretical basis for testable predictions of relative effects of exploitation rate on the size spectrum, but the quantitative results depend strongly on assumptions about growth rates and recruitment patterns (Gislason and Rice, 1998). Also, the statistical interpretation of slopes and intercepts is not straightforward, because the two parameters are mutually correlated. Thus, it has remained unclear whether the spectrum changes frequently observed involve only a reduction in the absolute abundance of large fish, an increase in the absolute abundance of small fish released from predation, or a combination of both.

Fishing also may directly affect species composition via 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 (F) represents a greater relative increase in total mortality. Unfortunately, reliable information on M for non-target species is rarely available, except on very coarse scales (Musick, 1999). Therefore, we must reason our way to predictions about patterns to be observed. Even with differences in growth rate, fish must survive a relatively long time to grow large. Therefore, overall M should be inversely correlated with maximum size ($L_{\max}$), and changes in $L_{\max}$ spectra might be expected to provide a measure of the indirect 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 and 1989/1997 in the proportion of demersal fish with $L_{\max} < 30$ cm in surveys around the British Isles, while Jennings *et al.* (1999a) showed that the mean (von Bertalanffy) L_{∞} of demersal fish in the northern North Sea declined during the twentieth century. However, the metrics used (fractions, means) do not allow clear interpretations and the changes observed might be accounted for entirely by direct effects of fishing, because the number of large fish affects the proportion of fish with large $L_{\max}$ as well as the mean $L_{\max}$ (or L_{∞}).

In interpreting potential impacts of fishing on the community, direct effects have to be separated from indirect effects. Are the direct effects of increased mortality and reduced abundance of larger fish, and the proportionate reduction of fish with the potential to grow large, adequate to explain the observed changes, or is there evidence of indirect, compensatory effects in small fish, whether due to less predation mortality or to stock-recruit responses?

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 analyses aimed at testing hypotheses about community properties and dynamics is that all gears are necessarily species- and

size-selective, different surveys being biased differently. Hence, if comparative analyses using independent data sets reveal similar emergent patterns and allow a consistent interpretation, confidence in the results is increased.

Because declines in large fish or in high- $L_{\max}$ species may reflect selective removals and thus a direct effect, we are particularly interested whether small fish, or low- $L_{\max}$ species, reveal increases in absolute abundance, because these should be indicative of indirect effects. To relate observed changes in community metrics to changes in fishing intensity, we also develop measures of the overall exploitation of the North Sea fish community.

First-order spatial effects in spectra dynamics may be 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, 1994; Jennings *et al.*, 1999b). Spatial patterns in the metrics provide opportunities to investigate the mechanisms behind the changes observed. If the indirect effects are primarily caused by changes in species interactions, the metrics should vary fairly smoothly across the area as predators, prey, and competitors redistribute themselves in response to fishing-induced changes in their local abundance.

Competition theory (Pimm and Hyman, 1987) would predict that individuals try to compensate for size-dependent mortality with (size-dependent) redistribution to take advantage of the less competitive environment where fishing has occurred, resulting in less spatial variation in the spectra. More complex foodweb interactions would also be expected to blur spatial patterns introduced by fishing. The North Sea foodweb is sufficiently reticulate that, if prey abundance increases in response to predator declines, the release will spread diffusely through the web, and be unlikely to be restricted to only a few prey species or only a few areas (Rice, 1995; Bax, 1998; Yodzis, 2001). Causal explanations invoking size-dependent responses to trawl impacts on seafloor habitats would on the other hand be expected to make the change in the metrics follow the distribution of trawl effort more directly (Rijnsdorp *et al.*, 1998; Dinmore *et al.*, 2003).

Finally, a major indirect response in the production of small fish might be due to stock-recruit relationships. Recruitment processes are generally considered to operate on the scale of the unit stock. In reality, spawning may be localized and the distribution of recruits in space should reflect size-specific habitat preferences of the different species. These would not be expected to be random over the entire area, but any inhomogeneity should be stable over time and not reflect the impacts of fishing on their parents unless spawning aggregations were selectively eliminated.

The different patterns expected depending on the causal mechanism involved were an incentive to study also variations in spectra on different spatial scales.

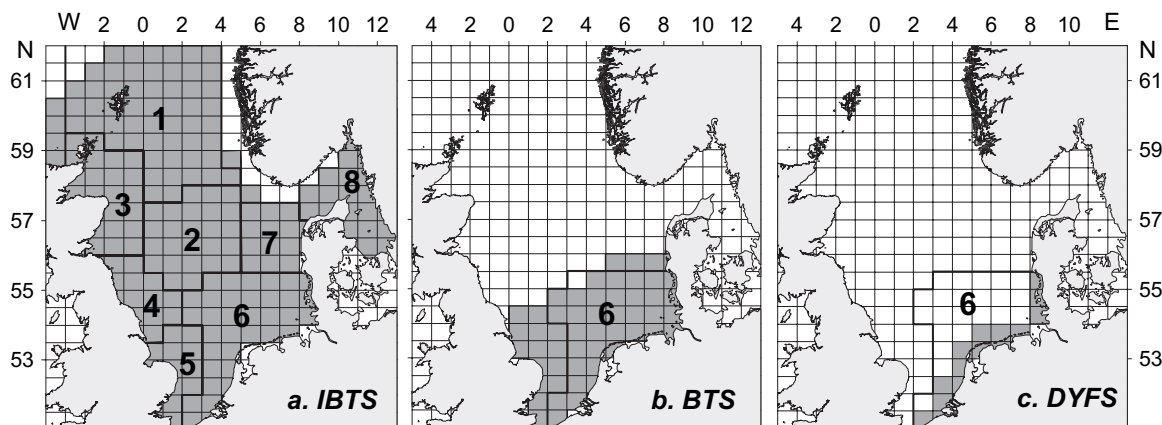


Figure 1. Spatial extent of the three surveys: (a) International Bottom-Trawl Survey, (b) Beam Trawl Survey, (c) Demersal Young Fish Survey with the definition of roundfish areas (RFA) 1–8.

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.

- (i) The IBTS (Heessen *et al.*, 1997; ICES, 1999) has been carried out annually in February since 1966. Initially, different countries used different gears and the area covered gradually extended northwards. 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 data for 1977–2000, and occasional 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 codend has a 20-mm 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 by size or Lmax class per hour fishing), and assume that bias remains constant over time. Based on the estimated horizontal net opening (excluding the area covered by the sweeps) and prescribed towing speed, on average 150 000 m² are fished during a 1-h haul (Knijn *et al.*, 1993).
- (ii) The BTS (Van Beek, 1997) is an international August survey that has been carried out since 1985 in

the southeastern North Sea and has been extended northwards since 1996. The gear is a 8-m beam trawl with four chains running between the shoes and four tickler chains connecting the groundrope (codend mesh size: 20 mm). Beam height is 50 cm and the swept area per haul is ca. 60 000 m². Analyses were restricted to Dutch data and to the consistently sampled roundfish area 6 (Figure 1b).

- (iii) The 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 Wadden Sea. Originally, surveys were carried out twice a year, but only the autumn survey has survived. Because participation of other countries has been irregular, the analysis has been restricted to the Dutch autumn data. During the initial years, many of the smaller species (such as gobies) were counted only so data collected before 1977 were excluded. One seagoing and two inshore vessels operate simultaneously, employing a 6-m and 3-m 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. Beam height is 40 and 30 cm, respectively, and swept area per haul is 16 000 and 8000 m², respectively.

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

Size spectra

Length measurements refer to total length (standard: 1 cm below; herring and sprat: 0.5 cm below; fish above 60 cm: 5-cm interval below). For the size spectra analyses, all fish were grouped by 5-cm (DYFS) or 10-cm (IBTS and BTS) classes and the natural logarithm of the average cpue within each class was calculated. After inspection of the size range conforming to a ln-linear slope (Figure 2a), size classes at the lower (poor retention in the gear) and upper (captures too infrequent for robust estimates) end of the range were excluded. To avoid the problem of slopes and intercepts being correlated, the midpoints of the size classes used for each survey were re-scaled with the mid-length of each range (IBTS: range = 20–100 cm, midpoint = 60; BTS: 10–60 cm, 35; DYFS: 10–55 cm, 32.5) fixed at zero. Thus,

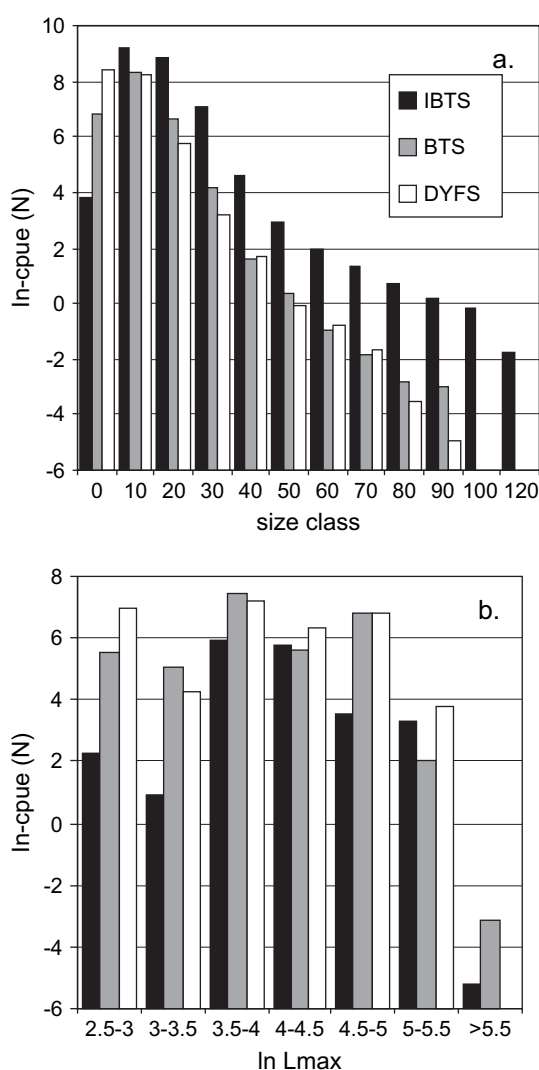


Figure 2. Overall (a) size and (b) Lmax spectra by survey (ln-cpue in numbers by 10-cm class and ln-Lmax class, respectively).

intercept values reflect the “height” of the spectrum and depend largely on total ln-abundance. Indeed, correlations between height and slope were not significant for any of the three surveys (r^2 : 0.22, 0.09, and 0.04, respectively). To investigate spatial variation, average annual slopes and heights were derived also by statistical rectangle (IBTS only).

Although size spectrum parameters capture the overall features, more subtle changes in the relative and absolute abundance of individual size classes may be lost. Therefore, we also plotted trends in ln-abundance by size class using appropriate groupings. To investigate whether patterns were consistent across the entire North Sea, trends in ln-abundance by size class for the IBTS were derived by roundfish area (RFA 1–8; Figure 1a). For BTS and DYFS, detailed spatial analyses were not warranted because of their restricted spatial coverage.

If length measurements for one or more species were missing for a particular haul, all information from that haul was excluded. All species were included to obtain the most complete picture of the assemblage caught by the gear. However, we did investigate whether patterns observed differed among guilds (pelagics, gadoids, flatfish, other demersal, and elasmobranchs) in the IBTS and BTS data sets.

Lmax spectra

The analysis of Lmax spectra was focused on the assemblage typically exploited by demersal gear so pelagic species were excluded. In addition, elasmobranchs as well as vagrant species were excluded because they merely created noise in the data owing to their overall rarity and contagious occurrences.

After having defined the “typical” North Sea demersal fish assemblage, a species identification problem remained. Daan (2001a) provides evidence that several species have been mis-identified by different crews at different times. We resolved this by first assigning apparently mis-identified taxa to the appropriate genus (or family). Subsequently, the associated catch was split among the constituent species according to the fractions observed in hauls with “trusted” species 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 to the families Soleidae, Bothidae, and Cottidae. In the case of *Ammodytes* and *Pomatoschistus*, catches have rarely been identified to species so all species were lumped under the genus. This should not cause problems because the different species included in these genera have approximately similar maximum sizes.

For the demersal species/genera retained in the analysis (97, 62, and 46 for IBTS, BTS, and DYFS, respectively), Lmax values (cf. Daan, 2001b) were derived from the

literature (specifically Wheeler, 1978; 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). The $\ln$ transformation largely balanced the number of species and individuals in each class (Figure 2b). Annual average cpue in number by class was derived by summing over species and sizes.

Comparisons among surveys were restricted to information from RFA 6, where all surveys allocated sufficient effort to make detection of consistent patterns likely. 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 of F derived from the most recent multispecies virtual population analysis (ICES, 2002), because it provides a coherent data set for ten target species (cod, haddock, whiting, saithe, plaice, sole, herring, sandeel, sprat, and Norway pout) and takes historic changes in predation rates fully into account.

Deriving an overall exploitation rate from F estimates for individual species is not straightforward, because demersal species are caught in mixed fisheries. Therefore, species-specific F s are not entirely independent and a risk of double counting exists. Nevertheless, to derive a community exploitation index, some way of averaging is required. To give equal weight to the relative changes in F over time for individual species, annual F s were first divided by the average mortality over the entire period (1963–2000). These relative indices were then averaged over the species, 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 over time, we chose to use the simple arithmetic means (smoothed by taking 3-year running means to reduce noise in the estimates; Figure 3) for all species combined (E_{all}), and for all roundfish and flatfish species only ($E_{demersal}$), for correlation with temporal changes in size and Lmax spectra, respectively. Correlations were restricted to IBTS data for the total North Sea, because no information is available for specific sub-regions such as those covered by BTS and DYFS.

Results

Size spectra

The long-term trends in the size spectra (Figure 4) indicate a significantly ($p < 0.01$) steepening of the slope in the IBTS data, while trends for BTS and DYFS were not significant. However, the residuals around the IBTS trend were not randomly distributed and suggest that the change

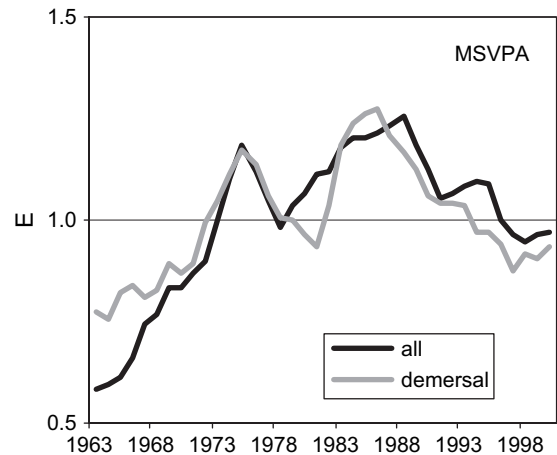


Figure 3. Trends in average (standardized) exploitation rate (3-year running means) for all stocks combined, and for demersal roundfish and flatfish stocks only.

in slope was most pronounced before about 1985 and that the slope remained largely stable thereafter ($r = 0.54$, $p < 0.05$), comparable to the pattern observed in the BTS. The DYFS slopes also steepened during the period before

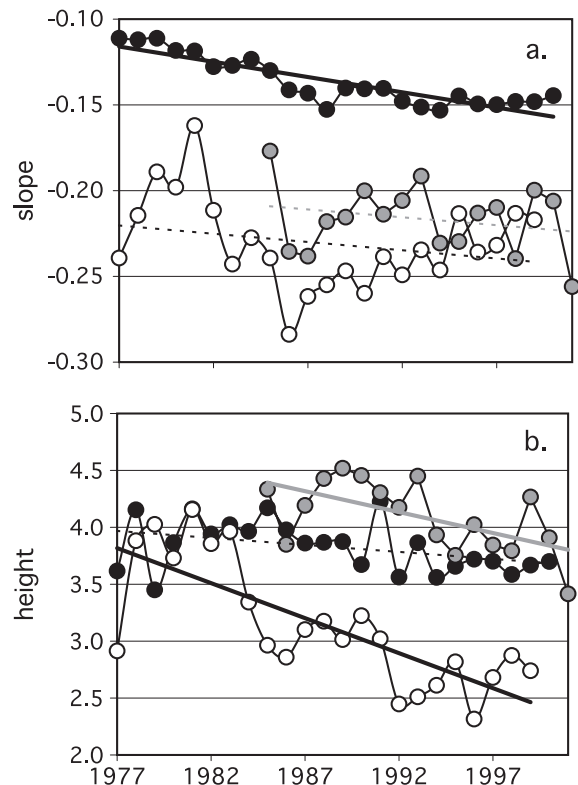


Figure 4. Estimated trends in (a) slope and (b) height of log-linear size spectra of the total fish community sampled by the three surveys (heavy lines: $p < 0.01$; thin lines: $p < 0.05$; dashed lines: not significant).

1986, but gradually recovered thereafter to the original level. Linear regression is apparently not the appropriate tool to investigate the long-term trends involved. The values of the slope differ markedly among surveys, confirming that they sample different assemblages.

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 ($r = 0.64$, $p < 0.01$). Although heights also differ among surveys, this may be an artefact of inaccurate raising factors used to derive comparable swept areas. A qualitative comparison with the trend in E_{all} (Figure 3) suggests that the steepening of the slopes halts at approximately the time when exploitation rate reached its maximum. In contrast, height 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, and shallower 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 indicate that they capture different properties of the community.

Figure 6 presents a detailed view of the temporal change in $\ln\text{-cpue}$ by size class in the three surveys. The IBTS in particular shows a significant ($p < 0.01$) increase in the

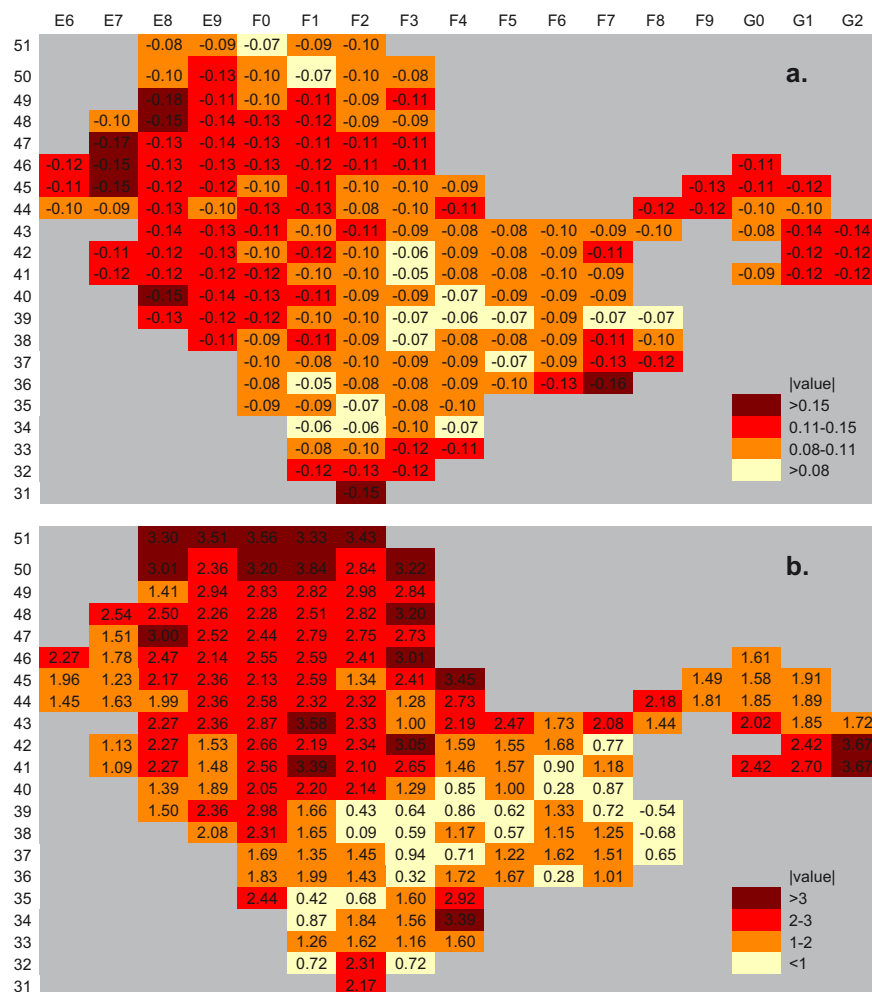


Figure 5. Spatial variation in average (a) slopes and (b) heights of the size spectra (mean $\ln\text{-cpue}$ 1977–2000 vs. 10-cm size classes) in first-quarter IBTS.

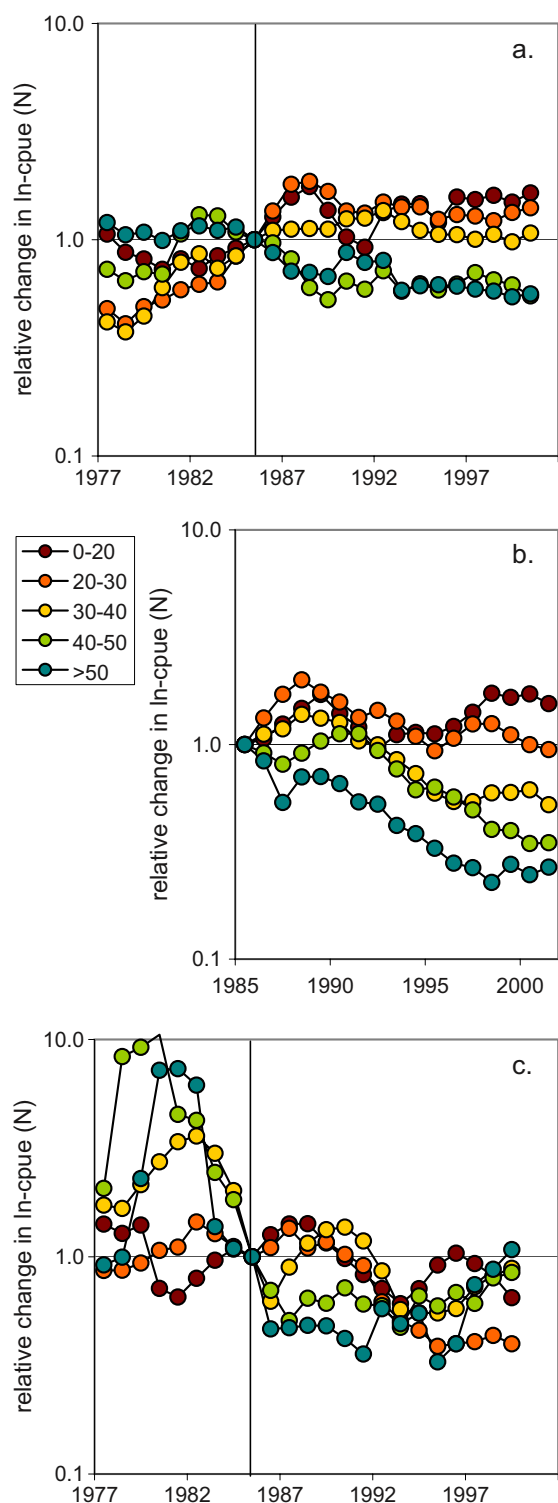


Figure 6. Trends in ln-cpue by size class and survey (for line symbols see Figure 4).

three smallest size classes, whereas the abundance of the larger size classes has declined significantly (40–50: $p < 0.05$; > 50 : $p < 0.01$). The positive 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: $p < 0.01$). The DYFS showed significant declines in abundance of both small and large size classes (10–20: $p < 0.05$; others: $p < 0.01$).

To investigate spatial coherence in these patterns among roundfish areas (IBTS data) and species groups (IBTS and BTS), three broad size classes were defined: small (< 30 cm), medium (30–50 cm), and large (> 50 cm) fish (Table 1). Abundance in the smallest size class increased in all eight areas, which has a probability by chance of ~ 0.004 (binomial test; assuming a 50/50 chance of an increase; samples by area are independent). The increases were significant ($p < 0.05$) in five areas. Also the abundance of medium-sized fish increased in all eight areas ($p \sim 0.004$) and significantly so in four (the areas corresponding largely with those for small fish). In contrast, large fish declined in seven out of eight areas ($p \sim 0.03$) and significantly so in five. Overall, increases in small fish were most pronounced in the central North Sea (RFA 2, 3,

Table 1. Estimated slopes of the regression of ln-cpue (in numbers) on year (IBTS and DYFS: 1977–2001 — $n = 24$; BTS: 1985–2001 — $n = 16$) by size class for various subsets (RFA: roundfish area) of survey data (bold: $p < 0.01$; regular: $p < 0.05$; +/–n.s.: not significant positive/negative trend; —: sparse data; otherwise: $p < 0.05$).

Survey	Subset	Size class		
		< 30 cm	30–50 cm	> 50 cm
IBTS	Total North Sea	0.039	0.034	–0.035
	RFA 1	+n.s.	+n.s.	–n.s.
	RFA 2	0.049	+n.s.	–0.035
	RFA 3	0.088	0.041	–0.041
	RFA 4	0.068	0.074	–0.030
	RFA 5	0.054	0.072	+n.s.
	RFA 6	+n.s.	+n.s.	–0.053
	RFA 7	+n.s.	+n.s.	–n.s.
	RFA 8	0.036	0.033	–0.051
	Pelagics	0.039	0.124	—
BTS	Gadoids	0.035	+n.s.	–0.033
	Flatfish	0.057	0.020	–n.s.
	Elasmobranchs	0.070	0.050	–n.s.
	Other demersal	0.100	0.099	–0.025
	RFA 6	+n.s.	–0.064	–0.087
	Pelagics	0.190	–n.s.	—
DYFS	Gadoids	0.084	–0.065	–0.121
	Flatfish	+n.s.	–0.069	–0.076
	Elasmobranchs	—	—	—
	Other demersal	0.032	$\pm$ n.s.	–0.193
	RFA 6	–0.018	–0.080	–0.079

4, 5, 7) and 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.

These changes were not restricted to particular species groups (Table 1). Abundance of small pelagics, roundfish, flatfish, elasmobranchs, and other demersal fish has increased (only flatfish in BTS not being significant), while medium-sized fish yielded different responses in the two surveys: positive for all groups in the IBTS (all areas combined), negative for most groups in the BTS (RFA 6 only). Large fish within all species groups consistently decreased, though not always significantly so. Because trends are based on $\ln$ -cpue, slope values may be interpreted directly in terms of percentage change per year. Taking into account the length of the period over which these trends were estimated, some of the overall changes are considerable. For instance, a slope of 0.1 for other demersal in the IBTS means a 10% increase per year or an increase by a factor of 16 over a 24-year period!

Lmax spectra

$\ln$ -cpue in numbers of successive $\ln$ -Lmax classes in RFA 6 by year for the three surveys also (Figure 7) reveals consistent patterns. There has been a marked increase in abundance of small species, a stable abundance of intermediate species, and a decline in abundance of large species. In contrast with the size spectra, trends in Lmax do not stop around 1985, but continue during the more recent years. Table 2 provides the estimated slopes by RFA (IBTS) and their significance. 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, corroborating the pattern observed in BTS and DYFS. However, significant trends of different sign are observed among the intermediate classes and surveys.

Correlations with exploitation rate

To investigate whether the observed changes in the community metrics for the total North Sea may be explained by changes in exploitation rate, slopes and heights of the size spectra and annual abundance by size class were correlated with E_{all} , while annual abundances by $\ln$ -Lmax class were correlated with $E_{demersal}$ (IBTS data only; Table 3). Without introducing time lags, none of the regressions were significant. However, indirect community responses to exploitation may not appear immediately. Therefore, correlations were also investigated for time lags up to 12 years ($n = 24$ in all cases). Correlations for the

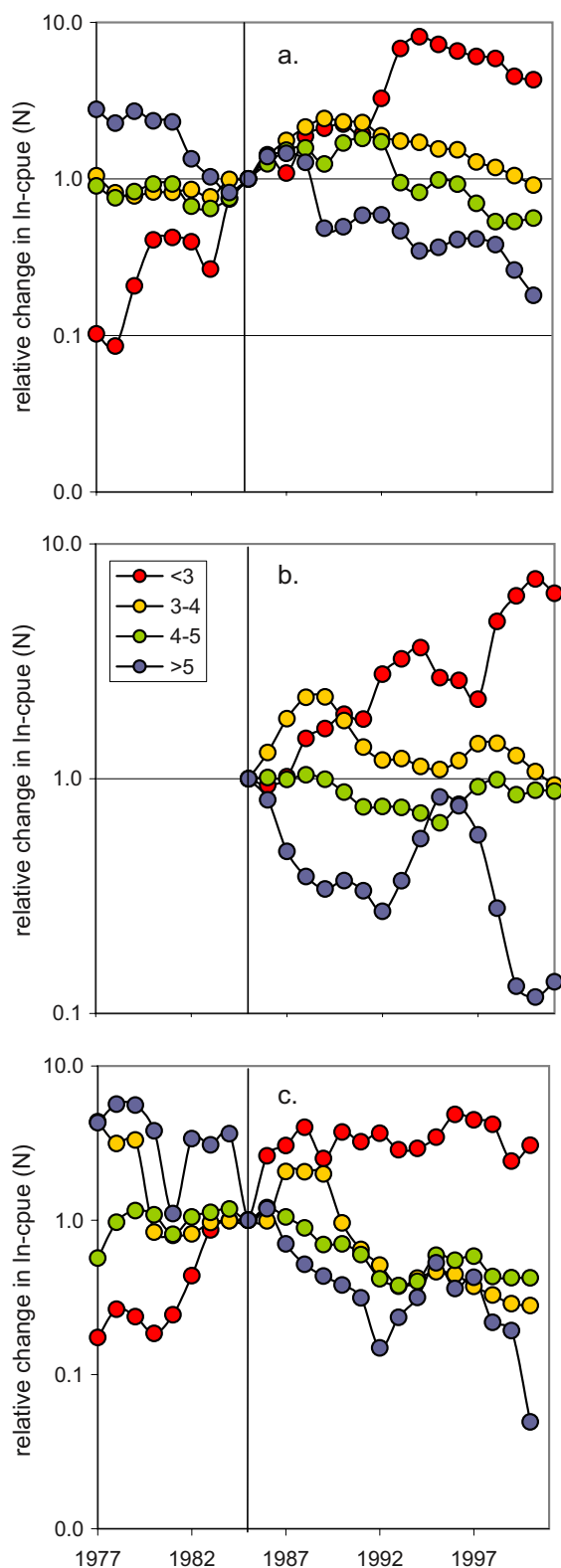


Figure 7. Trends in $\ln$ -cpue by $\ln$ -Lmax class for demersal fish in RFA 6 by survey.

Table 2. Estimated slopes of the regression of $\ln\text{-cpue}$ (in numbers) on year by $\ln\text{-Lmax}$ class (IBTS and DYFS: 1977–2001 – $n = 24$; BTS: 1985–2001 – $n = 16$) by roundfish area (RFA; bold: $p < 0.01$; regular: $p < 0.05$; n.s.: not significant).

Survey	Subset	$\ln\text{-Lmax}$ class					
		<3	3–3.5	3.5–4	4–4.5	4.5–5	>5
IBTS	Total North Sea	0.157	0.025	0.050	0.045	0.030	n.s.
	RFA 1	0.188	n.s.	0.111	0.042	n.s.	n.s.
	RFA 2	0.069	n.s.	0.044	0.050	0.045	n.s.
	RFA 3	0.273	0.183	0.127	0.042	0.025	n.s.
	RFS 4	0.195	n.s.	0.106	0.066	n.s.	n.s.
	RFA 5	0.177	0.133	n.s.	n.s.	n.s.	n.s.
	RFA 6	0.197	0.101	0.028	n.s.	n.s.	–0.105
	RFA 7	0.235	0.122	0.051	n.s.	0.059	n.s.
	RFA 8	0.210	0.111	0.101	0.065	0.104	n.s.
BTS	RFA 6	0.116	0.045	–0.027	0.048	–0.022	–0.086
DYFS	RFA 6	0.160	–0.012	–0.078	–0.042	–0.037	–0.165

slope (negative) and the three size classes (positive for <30 cm and 30–50 cm; negative >50 cm) were highly significant for lags >6 years. This was also the case for $\ln\text{-Lmax}$ classes <3 and 3–5 (positive), whereas for spectrum height and $\ln\text{-Lmax}$ class >5, only lag 6 yielded a negative correlation at $p < 0.05$.

Discussion

Size spectra analyses generally reduce the fish community to a two-parameter model (slope and intercept/height). This simplification is only sensible if the two parameters characterize the community sufficiently well that trends in their values can be associated with effects of changes in

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 largely the pattern in average exploitation rate over all species routinely assessed (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 in exploitation, 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 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 consider 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 dropped subsequently. A similar pattern is seen in the shorter BTS data series. Thus, height shows a different trend from those shown by slopes and exploitation rate, suggesting that heights and slopes capture two different effects of exploitation. The highest correlation coefficients between slope and the (smoothed) exploitation index were found if the latter was lagged by 12 years, whereas the correlation with height was just significant only after a delay of 6 years. Similar results were obtained for the correlations between $\ln\text{-cpue}$ by size class and E_{all} and between $\ln\text{-Lmax}$ class and E_{demersal} . All these results strongly suggest that considerable time lags may be involved in the responses

Table 3. Correlation coefficients between abundance metrics (y ; IBTS only) and exploitation indices (x ; cf. Figure 3) for various time lags ($y_t = x_{t-\text{lag}}$; italics: negative coefficients; bold: significant; *: $p < 0.05$; **: $p < 0.01$).

Lag	0	3	6	9	12
Size spectrum vs. E_{all}					
Slope	0.03	–0.10	–0.65**	–0.80**	–0.93**
Height	–0.25	0.19	–0.44*	–0.35	–0.39
Abundance by size class vs. E_{all}					
<30 cm	0.03	0.23	0.42*	0.60**	0.87**
30–50 cm	0.26	0.19	0.72**	0.75**	0.78**
>50 cm	0.34	0.07	–0.50**	–0.65**	–0.90**
Abundance by $\ln\text{-Lmax}$ class vs. E_{demersal}					
<3	–0.36	–0.13	0.25	0.68**	0.75**
3–5	–0.37	–0.07	0.18	0.40*	0.49*
>5	–0.01	–0.10	–0.46*	0.00	0.11

of the fish community to fishing, but the interpretation remains complicated.

If the responses of the small and medium size classes reflect increased survivorship owing to reduced predation, the delays suggest that the effects accumulate for several years. Because fish with a low L_{max} may spend several years in the smallest size classes experiencing reduced predation, their abundance may keep increasing for a few years after the abundance of large fish has been reduced. Moreover, expanding exploitation rates may continue to reduce the number of large fish for several years thereafter, and thus have delayed effects. Nevertheless, it seems hard to account for time lags of up to 12 years if release from predation is the only cause of the response in small fish, because reduced predation should immediately cause increased survival, and the effect would compound most strongly in the years immediately after predator removal. Additional time might be needed for the community to adjust to the new size-specific mortality schedule, but although not proven, a longer-term stock-recruit response may be implicated as well.

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 changes in competition or reduced predation by large fish provides a more likely explanation than local trawling impacts, 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 by differential fishing effort in different regions, because slopes in RFA 6 (where an extensive beam trawl fishery operates) are shallower than anywhere else. Also, the squares with steep slopes in the German Bight lie within the plaice box and are not likely to be heavily exploited in recent years. Thus, regional differences in size spectra are presumably partly related to fundamental differences in overall abundance, size, and species composition of local fish communities, as has been concluded also by Rogers *et al.* (1998) with specific reference to coastal nursery areas.

The hypothesis addressed 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. The patterns based on individual size classes clearly allow distinction between potential direct and indirect effects. The IBTS data provide strong support for an increase in small fish 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 surveys, the trend in the smallest size class in the BTS was not significant, and abundance of small fish even declined slightly in the DYFS. Differences in the assemblage sampled by the survey gears may contribute to these differences across surveys. Nevertheless, the patterns observed in the IBTS data are consistent over large areas, and are not restricted to particular species groups. These common patterns point to a common causal factor and fishing serves as a prime candidate that may explain the observed patterns adequately.

The abundance by size class 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 species composition of the fish community. The L_{max} analysis revealed significant changes in RFA 6, which were supported by all three surveys: total abundance (over all sizes) of low- L_{max} species have significantly increased, those with medium L_{max} have remained stable, and those with high L_{max} have declined. This result supports the hypothesis that high- L_{max} species (as a proxy for high M) are more sensitive to exploitation than low- L_{max} species. However, the reduction of high- L_{max} species has apparently been restricted to the southeastern North Sea and at a total North Sea scale there is no indication of an apparent sensitivity of high- L_{max} species to exploitation: if changes in the abundance of small species are a universal response to variations in fishing pressure, changes in "large" species apparently are not. The increase in the proportion of fish with an $L_{max} < 30$ cm in research vessel catches around the British Isles between the start of the twentieth century and the 1990s observed by Rogers and Ellis (2000) points in the same direction. In conclusion, the generalization that fishing appears to favour small species is strongly supported by survey data over large areas of the North Sea. Reduced predation pressure owing to the removal of large predators as indicated by the size spectra analysis provides a simple explanation for these observations.

These correlation analyses cannot prove that the observed increases in small fish and in low- L_{max} 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 events 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, particularly when augmented by possible stock-recruit responses over longer time periods. However, 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.

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 generating information on annual recruitment of commercially important fish species. As a consequence, most countries involved paid initially more attention to exploited species than to non-target species and for this reason all years before 1977 had to be excluded. 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, the different surveys revealed similar main trends, and trends in the IBTS are consistent over large areas sampled by different countries. Therefore, it seems unlikely that a common bias would apply to all.

Despite showing similar patterns, the actual values of the metrics used vary considerably among surveys. This suggests that the values have no absolute meaning because they refer to the assemblage typically sampled by the gear, but can only be interpreted in a relative sense. The true values of such metrics for “the North Sea fish community” may never be known, which complicates the issue when trying to use metrics 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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