

## Temporal Changes in the Diversity of Shelf-sea Fish Communities

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### Abstract

The North Sea and Georges Bank fish communities have lost species and size diversity over the past several decades. Hypotheses that may explain these changes include climate change that may induce shifts in the food web, historical and contemporary fishing pressure and selective fishing of certain species or sizes. We use a comparative approach to examine the support for these different hypotheses. Using standardized trawl-survey data, we identify the useful indicators of species diversity, and functional diversity as measured by changes in size structure and changes in functional groups. The North Sea and Georges Bank fish communities have much in common, including shared species and congeneric species. However, the communities are subject to different fishing regimes and the North Sea has relatively less fish biomass in the larger size classes. We use a length-based multispecies model to investigate the role of fishing in causing and maintaining these differences in size distribution.

Key words: biodiversity, fish community, North Sea, Georges Bank, selective fishing, multispecies model

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## Introduction

Biodiversity has been a dominant theme of the first decade of the 21st century. The Census of Marine Life sought to catalogue the existing marine biodiversity, to measure historical changes in the abundance of marine animals, and to project these trends into the future (O’Dor 2004). The Convention on Biological Diversity aims to protect existing biodiversity and to prevent further losses at the global, regional, and national scale ([www.cbd.int/convention](http://www.cbd.int/convention)). Maintaining biodiversity is one of the descriptors of “good environmental status” in the Marine Strategy Framework Directive for EC waters (European Union. 2008a). Biodiversity has also gained prominence in ICES as priorities have evolved from single species, to multispecies, to communities and ecosystems (Wilson 2009). The maintenance of biodiversity has been linked to a number of ecosystem services, including the long-term sustainability of fisheries. Thus the goals of maintaining biodiversity and maintaining fisheries are largely aligned, even though fisheries yields may be maximized at levels that incur considerable biodiversity loss compared with unfished conditions (Jennings 2007). Fishing affects marine biodiversity in various direct and indirect ways (Fogarty and Murawski 1998), and it is increasingly suggested that the selectivity of fishing, in addition to its intensity, shapes fishing effects on marine communities (Hall et al. 2000, Zhou et al. 2010). Recent modelling work suggests that both species-selectivity and size-selectivity interact with fishing intensity to determine the responses of various biodiversity indices to fishing (Andersen and Pedersen 2010, Rochet and Benoît Submitted, Rochet et al. Submitted).

To examine the effects of fishing on biodiversity, fishing selectivity needs to be characterized at the community level, which has seldom been done (Rochet et al. 2010a); average fishing mortality across species has been used (Blanchard et al. 2005), but when it comes to size-selectivity across several species, novel estimation methods need to be developed. Environmental fluctuations are also known to affect fish communities, *e.g.* decadal shifts in productivity (Beaugrand 2004), and the more gradual effects of global warming (Genner et al. 2004). Therefore a study of changes in marine community diversity should incorporate the related information. Because these drivers are temporally confounded, a comparative ecosystem approach provides informative contrasts, reduces confounding, and provides a degree of “replication” (Murawski 2010).

Standardized bottom-trawl surveys are one of the few comprehensive sources of data to assess temporal changes in diversity of marine communities and assemblages. Their strengths include relatively long duration, standardized sampling and species identification over many decades. These surveys were designed to capture commercially important fish species, such that there is a direct link between the biological diversity and the ecosystem service provided by the fisheries. This strength is also a weakness in that the trawls capture only a slice of the ecosystem, and even of the fish community. Any analysis of these data, and especially comparisons between surveys, must keep in mind the selectivity of bottom trawls.

In this study, we investigate changes in the diversity of the fish communities on Georges Bank and in the North Sea, two shelf-sea communities that have much in common, including shared species and congeneric species. To determine the main drivers of community change, we develop measures of overall fishing mortality and the degree of species and size selection at the

community level from stock assessments. Documentation on the changes in fishing regulations helps to explain the changes in exploitation patterns. Likewise, we compile the main changes in the physical environment and ecosystem, which could, in turn, influence the food web. Based on this information, we identify time periods with major changes in both fishing and environmental drivers. Then we use trawl-survey data from the North Sea and Georges Bank to examine the changes in biodiversity within each of these periods. Changes in biodiversity are investigated both by an analysis of relevant diversity metrics at the community level (*e.g.* evenness and size diversity), and by examining the relative fluctuations of functional groups. Finally, we use a multi-species, size-based model to predict if we could turn each community into the other just by fishing with intensity and selectivity patterns corresponding to the other community. This numerical experiment is meant as an additional element to determine if fishing is, or is not, the major driver of biodiversity in exploited marine communities.

## Methods

### Fishing selectivity at the community level

Fishing is widely considered the most pervasive threat to marine biodiversity (NRC 1995); however measuring fishing pressure at the community level continues to be difficult. Not all species in the community are fished, some are taken as bycatch, and others are affected indirectly by fishing-induced changes in the ecosystem. Our approach in this study was to extract estimates of fishing mortality ( $F$ ) by age for assessed species and to convert these estimates to  $F$  at length with growth curves for each species.

To convert  $F$  at age from stock assessments to  $F$  at length within stocks, we use formulas from Jones' length cohort analysis where the instantaneous numbers of fish entering a length class  $l_a$  can be derived from the number in a smaller length class  $l_0$  by  $N_{l_a} = N_{l_0} e^{-(M+F_{l_0})\tau_{l_a l_0}}$  (1) where  $\tau_{l_a l_0}$  is the time to grow from  $l_0$  to  $l_a$

$$\tau_{l_a l_0} = \frac{1}{k} \ln \frac{L_\infty - l_0}{L_\infty - l_a} \quad (1).$$

The  $F$  for each length class was calculated as a weighted average of the  $F$ -at-age falling within that length class, where the weights are based on the proportion of each age class ( $\tau$ ) within the length interval. These proportions were normalized to sum to one, so that the  $F$ -at-length retain units of inverse time and not inverse length. The plus group is treated as a terminal age as there is no information on older age/length groups in stock assessment results. The average number of

fish in length class  $l_1 l_2$  over the year is given by  $\bar{N}_{l_2 l_1} = \frac{N_{l_1} - N_{l_2}}{(M + F_{l_1})\tau_{l_2 l_1}}$ . Once the  $F$  and  $N$  at

length  $l$  were available for each species  $s$  they were combined into the weighted community average by

$$\bar{F}_l = \frac{\sum_s N_{s,l} F_{s,l}}{\sum_s N_{s,l}} \quad (2).$$

Each year  $F_{max}$  was calculated as  $\max_l(\bar{F}_l)$ . The proportion of fishing mortality inflicted on ‘large’ fish was used as an index to track changes in size selectivity. A reasonable size threshold common to both areas is 70 cm. Ranked species maximum  $F$ -at-age was plotted by year as a first look at species selection. Species ranks were also plotted against years to track the changes in the species bearing the highest fishing mortality. These ranks are the outcome of variations in targeting by fishermen, resource abundance and catchability; below we summarize this by ‘targeting.’ These calculations were performed with all species for which we could find stock assessments: cod, haddock, herring, mackerel, summer flounder, winter flounder, silver hake, witch flounder, and yellowtail flounder on Georges Bank; and cod, haddock, herring, plaice, saithe, sandeel, sole, and whiting in the North Sea.

## Bottom-trawl surveys

Data for the North Sea are from quarter one of the International Bottom Trawl Survey, which is conducted with a standardized GOV trawl with 2-cm mesh in the cod end (ICES 1996). The survey covers the entire North Sea, with an approximate area of 575,300 km<sup>2</sup> and 211 to 362 stations each year. We used the abundance data by species for the period 1982-2009 and aggregated by 5-cm length classes. Biomass was estimated from abundance with length-weight relationships for each species. To facilitate comparisons, both the North Sea and Georges Bank data were standardized per km<sup>2</sup>. The data were not corrected for catchability because the catchability conversions are uncertain and not available for all species (Fraser et al. 2007).

The Georges Bank data are from the Northeast Fisheries Science Center fall bottom trawl survey. For the years included in this study (1963-2007) this survey used a #36 Yankee trawl with a 1.25-cm liner. We used the data from 13 strata on Georges Bank, which cover an area of approximately 40,000 km<sup>2</sup>. We used the stratified mean abundance and biomass by species, classified by 5-cm length groups. For some species, a fairly high proportion of the records were not attributed to size class. However these unmeasured fish accounted for a very small percentage of the overall biomass (at most 1.5%), which suggests that they were all in the smallest size classes.

Subsets of the species were selected to exclude rare species for which high sampling variability would dominate their abundance patterns and which would make negligible contributions to most community metrics. The mean abundance of each species over the survey timeframe was plotted against persistence—the number of years the species was observed in the survey (Genner et al. 2004). A third-order polynomial was fit to these data and the inflection point calculated. We retained species to the right of the inflection point, which corresponds to high persistence and abundance. A second criterion was that the aggregate abundance of the selected species should account for >99% of the total abundance. Invertebrate species were only recorded in the IBTS survey during the most recent 10 years and were therefore not used in this study. Because the North Sea has a higher intensity of sampling, which translates to higher persistence, we

applied a third filter to the North Sea only, selecting those species with mean density  $>1 \text{ km}^{-2}$ , and persistence  $>13$  years. For the North Sea, this resulted in 47 species, which accounted for 99.9% of the total abundance. On Georges Bank we selected 46 species with persistence above the inflection point (24 years) of the abundance-persistence plot; these 46 species constituted 99.3% of the overall abundance (see species lists in Appendix).

## Community metrics

The trawl-survey data were used to calculate a suite of community metrics related to the distribution of individuals among species and size classes. The metrics include total abundance, mean length in the community, total biomass, and mean weight in the community. Geometric mean abundance across species was calculated relative to the first year of the survey (Rochet et al. 2010b). Each species was classified as commercial or non commercial and the proportional abundance of non-commercial species was calculated each year (Rochet and Trenkel 2003).

We do not consider species richness here because the measures of richness depend on the geographic extent of the survey, the sampling intensity, and the consistency in identifying and naming rare species. The three diversity metrics we calculated are all based on Simpson diversity,  $D$ , which measures the probability that two individuals chosen at random belong to different species. Simpson's reciprocal evenness is  $1/(DS)$ , where  $S$  is the number of species. This index is independent of richness. Taxonomic distinctness,  $\Delta^*$ , is an extension of Simpson diversity, which accounts for the taxonomic distance ( $\omega_{ij}$ ) between species  $i$  and  $j$ , while removing the dominating effect of the species abundance distribution ( $x_i x_j$ ):

$$\Delta^* = \frac{\sum \sum_{i < j} \omega_{ij} x_i x_j}{\sum \sum_{i < j} x_i x_j}$$

(Warwick and Clarke 1995). In this application the species were classified by genus, family, order, class, and phylum. We used the PRIMER routine DIVERSE to calculate taxonomic distinctness.

Size diversity,  $\Delta$ , is another extension of Simpson's diversity based on the distribution of individuals across size classes (Rochet et al. 2009). Size diversity is the average size difference between two individuals chosen at random from the community. Finally, we calculated each year a size spectrum of log abundance by 5-cm length class. Because the spectra exhibited marked curvilinearity, we fit them with second-order polynomials and summarized them by their intercepts, slopes, and curvature. We tested for significant time trends in these metrics over the entire time series and for subsets of the time series, as identified below.

The full set of species was divided into four functional groups following Greenstreet et al. (1997) and Heath (2005): planktivores, pelagic piscivores, demersal piscivores, and benthivores (see species lists in Appendix). The purpose of this analysis was to determine to what extent the overall changes in abundance were explained by changes in the functional groups and also to test for compensation within functional groups. We therefore tested for significant time trends in functional group abundance over the entire time series and for the same subintervals as for the

community metrics. A test statistic for compensation is the ratio of the overall abundance of a group divided by the sum of variance of species in that group (Fischer et al. 2001). A ratio  $<1$  indicates compensation, whereas a ratio  $>1$  indicates that the species fluctuated in synchrony.

Analysis of covariance was performed to test for and to remove common time trends in functional group abundance, because the variance ratio test is easy to interpret on stationary data. A model with a common slope for all species in the group was fit; the estimated common slope was used to detrend the abundance of each species. Variance-ratio tests were performed on both the raw and detrended data and at both the community and functional group levels.

## Length-based model

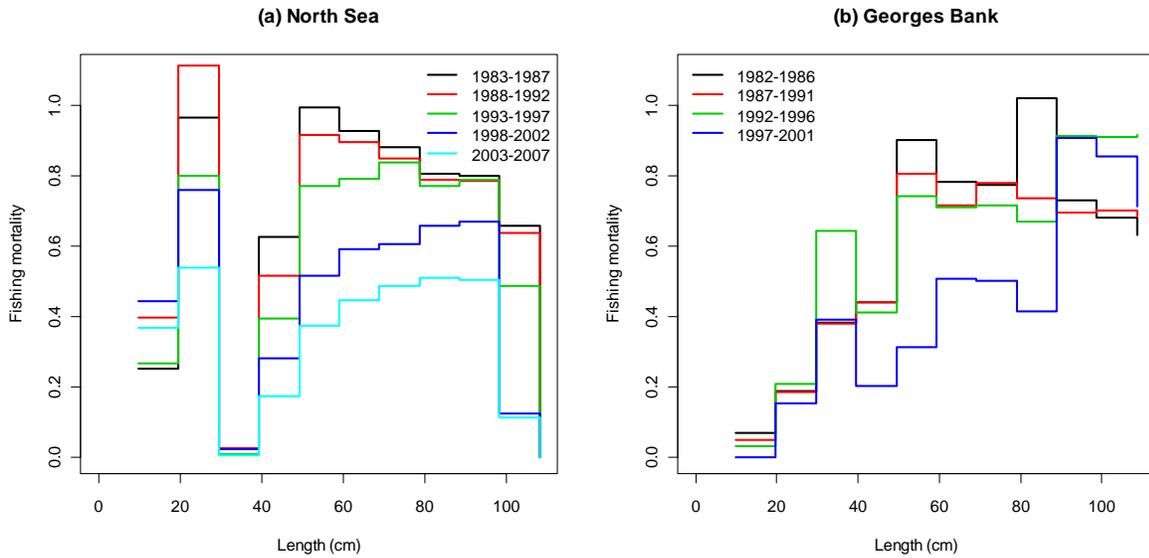
To better understand how changes in fishing pressure affect the community metrics, we used the length-based model LeMans, which has been parameterized for the North Sea and Georges Bank (Hall et al. 2006, Rochet et al. 2010a). LeMans simulates the dynamics of 21 species, divided into 10-cm length categories. Fishing, predation, and residual natural mortality are all functions of length. Because LeMans does not include food-dependent growth, it was not intended to investigate bottom-up forcing, but instead, top-down forcing of the community by predation and fishing. In this application, LeMans was used for three main purposes:

- (1) To measure the delay between change in fishing mortality and community metrics as they move toward a new equilibrium. The model was started with each species at its unfished equilibrium; then a new level of fishing mortality was imposed and we tracked the rate of change of community metrics.
- (2) In previous studies, LeMans was run with fishing mortality at length described with smooth functions—either logistic or sigmoid (Rochet et al. 2010a). In this application we used the empirically derived vectors of  $F$  at length to determine the sensitivity of the community metrics to the observed fishing patterns. In addition, we applied the  $F$  at length for the North Sea to Georges Bank and vice versa.
- (3) Finally, we used the observed changes in fishing selectivity, combined with the results of model simulations to make qualitative predictions of changes in community metrics to compare with the observed changes. These trials tested the extent to which changes in community metrics can be explained by fishing as opposed to changes in the environment or other causes.

## Results

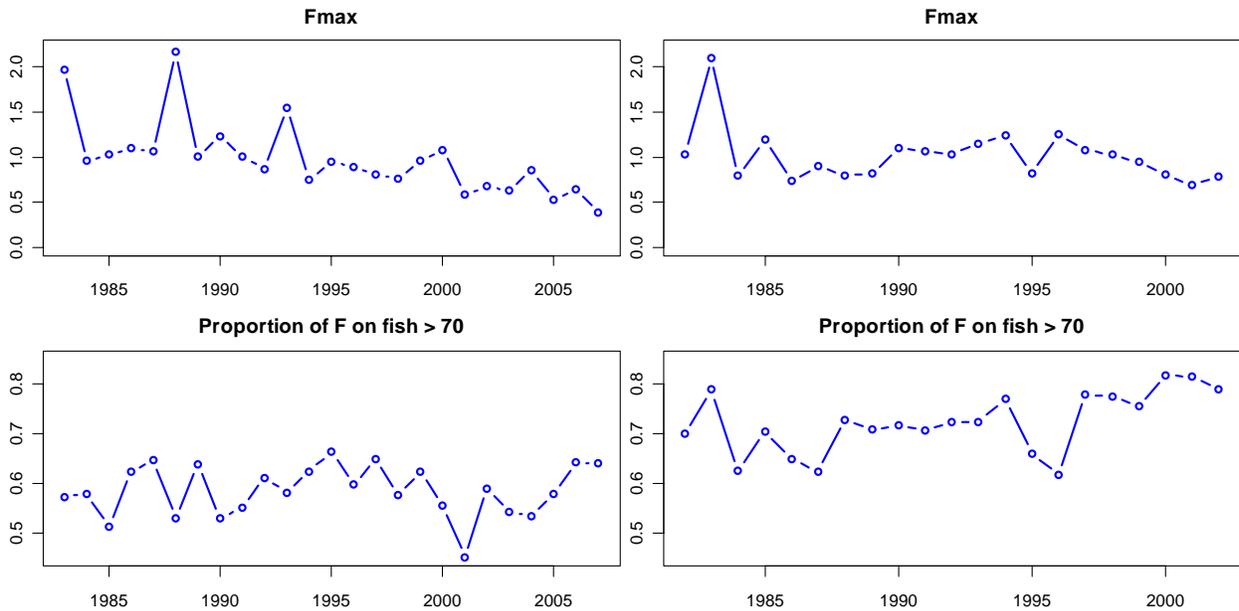
### Fishing selectivity at the community level

In both regions fishing mortality decreased over time, especially in the most recent time block. In the North Sea the resulting community fishing mortality is strongly bimodal (Fig. 1a). The first mode consists mainly of sandeel, for which numbers and fishing mortality fluctuate widely. Community selectivity on Georges Bank was somewhat bimodal as well, with the mode at 30 cm consisting of herring and mackerel (Fig. 1b). During the most recent time block (1997-2001) fishing became more selective toward larger sizes.



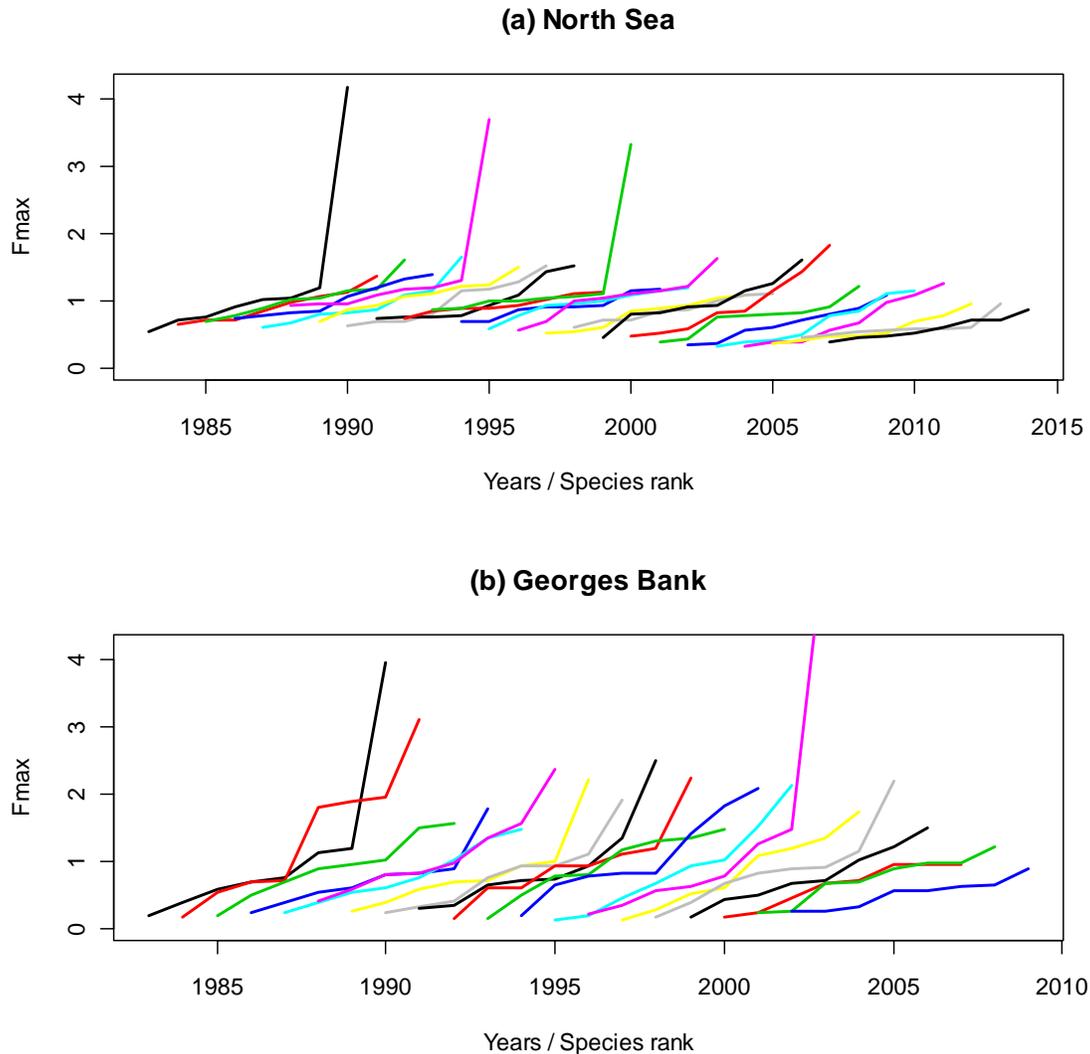
**Figure 1.** Community fishing selectivity averaged by 5-year time blocks. a) North Sea and b) Georges Bank.

In the North Sea  $F_{max}$  tended to decline (Fig. 2a); size selectivity varied with no clear trend, except an increase since 2001. On Georges Bank  $F_{max}$  peaked in the 1983 and remained around one until 1996, then decreased (Fig. 2b). Size selectivity was higher than in the North Sea and it increased starting in 1996.



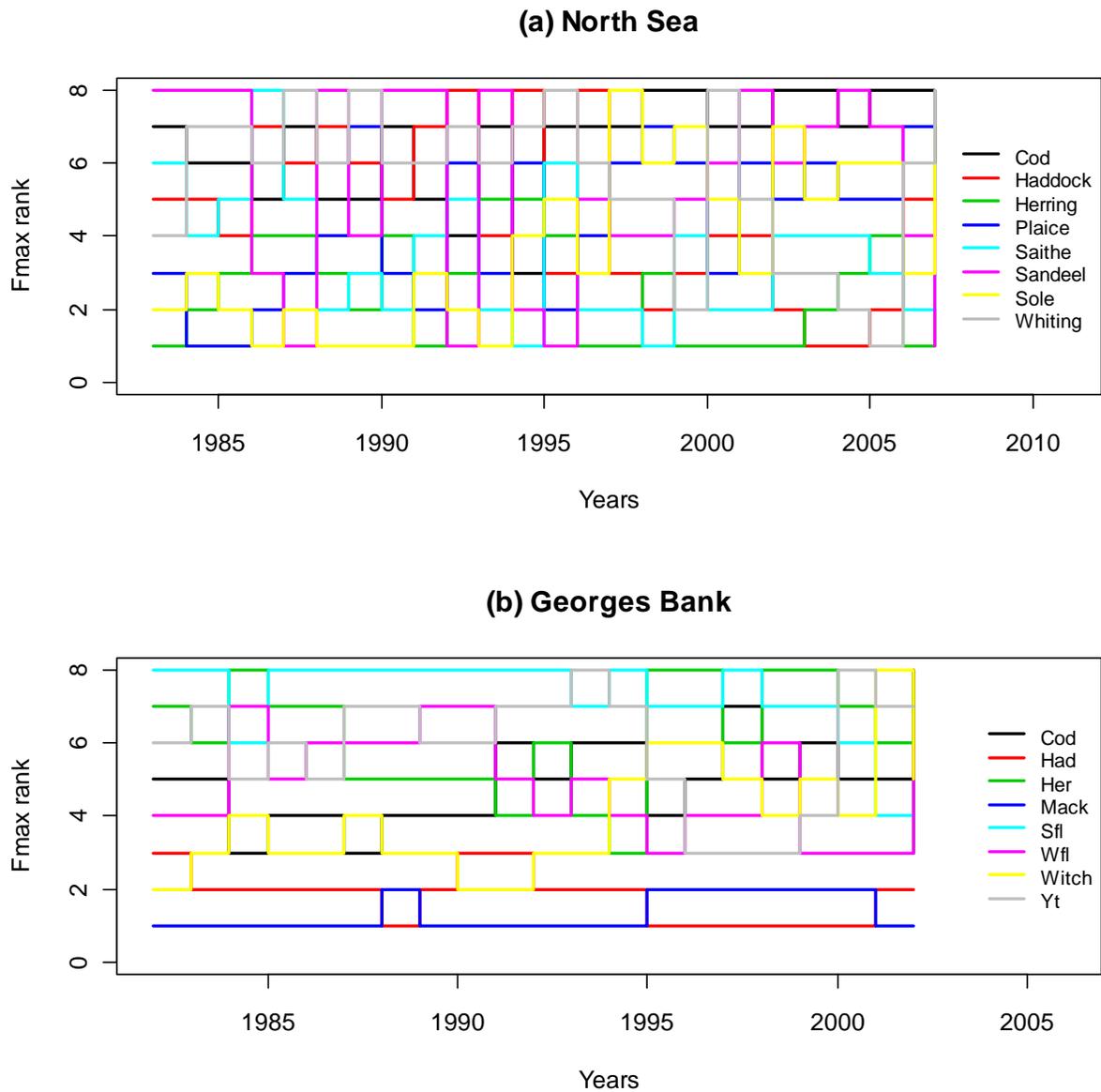
**Figure 2.** Changes in maximum fishing mortality and the proportion of fishing mortality on large fish (>70 cm) over the time periods for which assessments were available for all eight stocks. Left: North Sea over 1983-2007; Right: Georges Bank over 1982-2002.

Plots of maximum  $F_{max}$  across species indicate the degree of species selectivity (Fig. 3). In the North Sea maximum  $F_{max}$  across species decreased over the study time-period (Fig. 3a). Very high  $F_{max}$  on sandeel occurred only in the XX<sup>th</sup> century. The  $F_{max}$  curves tended to be more flat at the end of the period (after 2000). On Georges Bank the  $F_{max}$  curves were generally steeper than in the North Sea, which indicates greater species selection (Fig. 3b). Maximum  $F_{max}$  decreased over 1982-2002, except in 1996. The  $F_{max}$  curves also tended to be more flat at the end of the period.



**Figure 3.** Ranked species  $F_{max}$ . The x-axis spans both species rank (from 1 to 8) and years, each curve shows the ranked  $F_{max}$  for the year of its first point. a) North Sea; b) Georges Bank.

The  $F_{max}$  ranked by species indicates how species targeting changed over time (Fig. 4). In the North Sea species ranks tended to fluctuate, with cod generally at high rank, herring at low rank, plaice and sole increasing, saithe decreasing and sandeel fluctuating widely (Fig. 4a). On Georges Bank, species ranks were more stable than in the North Sea (Fig. 4b). Silver hake and yellowtail flounder had consistently high ranks, while haddock and mackerel were consistently low.



**Figure 4.** Species ranks for maximum fishing mortality at age. a) North Sea, 1983-2007; b) Georges Bank, 1982-2002. The highest Fmax is at the top of each subplot.

### Factors affecting community metrics and biodiversity

This section reviews the main drivers of community dynamics in the North Sea and on Georges Bank. Information on North Sea fisheries during the early part of the time series is from the OSPAR Commission (2000). Important management measures over the last decade are listed in ICES (2008). The main events in the North Sea were:

- Fishing effort and landings rose rapidly after WW II, and the increase accelerated in the 60s.
- Small-mesh industrial fisheries targeting sandeel, sprat and Norway pout started in the early 80s.
- EU fisheries are managed by TACs since the inception of the Common Fisheries Policy in 1983. Fishing effort in the entire North Sea further rose between 1983 and 1995, attributable largely to increased beam trawl effort in the southern and central North Sea.
- A climatologic regime shift in the 1980s (Beaugrand 2004) resulted in a change in the zooplankton community (especially calanoid species) and consequently to an increase in flatfish recruitment and decrease in gadoid recruitment.
- Another regime shift in occurred in 2000, which caused again changes in the plankton community that led to recruitment failure in herring and sand eel (Payne et al. 2009, van Deus et al. 2009).
- The EU reformed the Common Fisheries Policy in 2002, aiming to ensure the sustainable development of fishing activities (European Union 2002). The most obvious effect of the 2002 CFP has been a steady reduction in fishing effort in most European waters, especially the North Sea, over the last decade.
- In the North Sea, the most important management plan was the one for the recovery of cod stocks, launched in 2004, then revised in 2008 (European Union, 2004; European Union, 2008b). However, because cod is primarily taken in multi-species fisheries, it has been difficult to reduce fishing mortality on cod in the North Sea (ICES 2008; Rochet et al. 2010c).
- Another plan was put in force in 2007 for the management of plaice and sole in the North Sea (European Union 2007). This plan did not succeed in reducing fishing mortality on sole, and its effects are unlikely to be detectable in the community metrics until 2009.
- Another important driver is the constant increase in the fuel price since 2000 (ICES 2008). This increase has resulted in a diversification of target species in the North Sea fisheries. Much research has been devoted to improving gear selectivity to let non-target species escape, which could have balanced the diversification of targets. However, for lack of incentives these selective devices have only very recently started to be used by fishermen (ICES 2008), so that their effect on the community is likely not yet detectable.
- Regulations on mesh sizes have changed towards larger meshes in various North Sea fisheries over the decade.

In summary, fisheries management appears to have been quite constant from 1983 to the late 1990s. During this period, fishing effort increased and there was a climatological regime shift. A significant decrease in fishing mortality on all sizes is observed since 2000. Major changes in fisheries regulations were introduced in the 21<sup>st</sup> century, but for various reasons these regulations have not fully met their objectives and their effects on community metrics may not yet be detectable. The fisheries have been unselective for size until recently when regulations have changed toward larger meshes. Species-selectivity has always been low and might have decreased further over the latter time period.

The important management measures on Georges Bank were listed by Fogarty and Murawski (1998). Physical regimes were described in the GB GLOBEC program:

- 1949: International Commission for the Northwest Atlantic Fisheries (ICNAF) established;
- 1953: Minimum otter trawl mesh size first established at 11.4 cm.
- 1960s to early 1970s: cold water, low nutrients; high catches by distant water fleets; abundant groundfish. Fisheries regulated by ICNAF. Management measures include seasonal spawning area closures for haddock and TACs.
- 1972-1976: TACs for all regulated stocks established. “Second-tier” TACs are less than the sum of national species TACs to allow for species interactions and by-catch of fisheries.
- 1977-1982: 12.7-cm minimum trawl mesh size.
- 1982-1985: All direct controls on fishing mortality eliminated by the US, replaced by minimum mesh sizes (14.0 cm) and landing sizes; seasonal closed areas retained.
- 1985-1995: average water temperature; overfishing of principal groundfish; peak in elasmobranch species;
- 1994: Amendment 5 to the Northeast Fishery Management Plan implemented in order to reduce overfishing of groundfish; measures include: effort reductions, closed areas expanded, trip limits, and mesh size increases to 15.2 cm.
- 1996: Amendment 7 to the FMP accelerates reductions in days at sea, establishes “target” TACs for cod, haddock, yellowtail flounder and other stocks.
- 1996-present: warmer water temperatures; low salinity; fishing mortality reduced; groundfish rebuild, elasmobranchs decline, and pelagics peak.

In summary, the environmental changes seem to be less pronounced than in the North Sea. There was a shift in species composition from demersal to pelagic in the early 1980s but it was in not a regime shift in the strict sense. There were important management changes, which are perhaps the dominant drivers. Fishing mortality increased after 1981 and was not substantially reduced until Amendment 5 was implemented in 1995. The otter trawl fishery has become increasingly more size selective. With respect to species selection, the fisheries are generally more selective than in the North Sea. Species selection appears to have been highest during the middle period and declined in the latter period as the fisheries diversified.

The compilation of these main events was used to divide the survey time periods into three temporal stanzas. For the North Sea, the resulting time periods are:

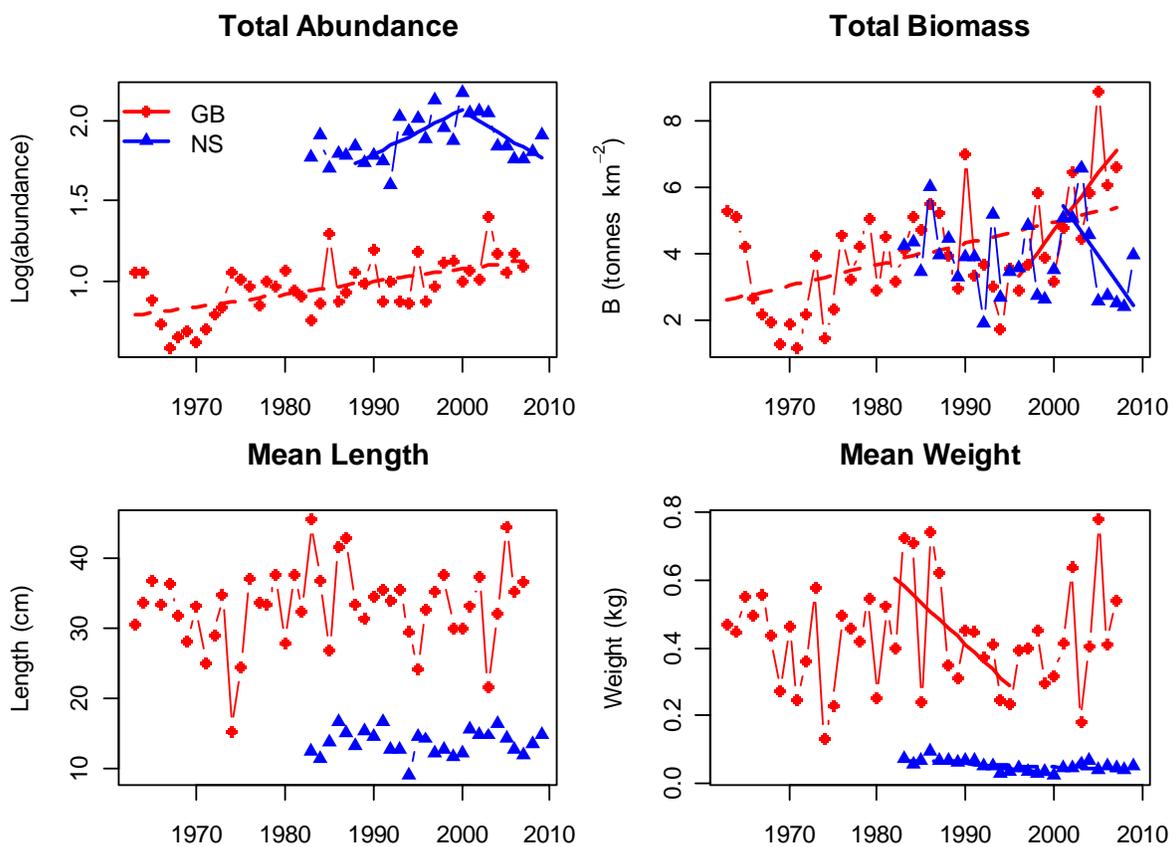
- 1983-1987: this was a period of high and increasing fishing pressure on many species, including small-sized individuals / species;
- 1988-2000: fishing pressure remained high on all community components, but we expect to see the effects of a climatologic regime shift that happened in 1988;
- 2001-2009: there were changes in several drivers as another regime shift seems to have taken place in 2000, but we also see a decrease in fishing effort, a diversification of target species and increase in size selectivity.

For Georges Bank the periods are:

- 1963-1981: management was primarily by ICNAF with low selectivity for species and size;
- 1982-1995: no quotas and high fishing mortality;
- 1996-2007: effective management measures were introduced and fishing mortality declined.

## Community metrics

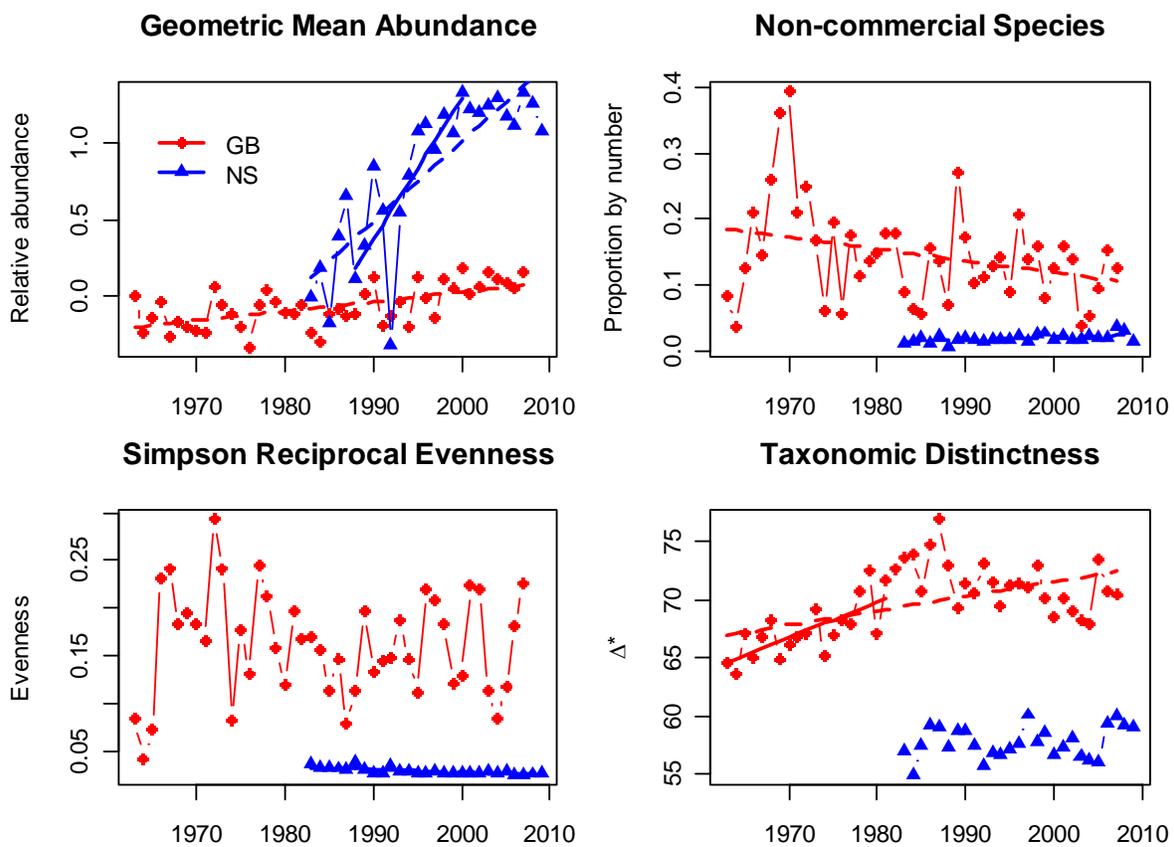
Total abundance was 10 times higher in the North Sea than on Georges Bank, even when the data were standardized by area (Fig. 5a). In the North Sea, abundance increased during the second time period and decreased during the most recent period. On Georges Bank total abundance increased over the entire time period but there were no significant changes during any of the subperiods. In marked contrast to abundance, total biomass had similar magnitudes in the two communities (Fig. 5b). The temporal patterns in biomass were similar between 1983 and



**Figure 5.** Community metrics for Georges Bank (GB) and the North Sea (NS). Broken lines show significant ( $\alpha=0.05$ ) linear trends for the entire time period. Solid lines are significant trends for sub-periods.

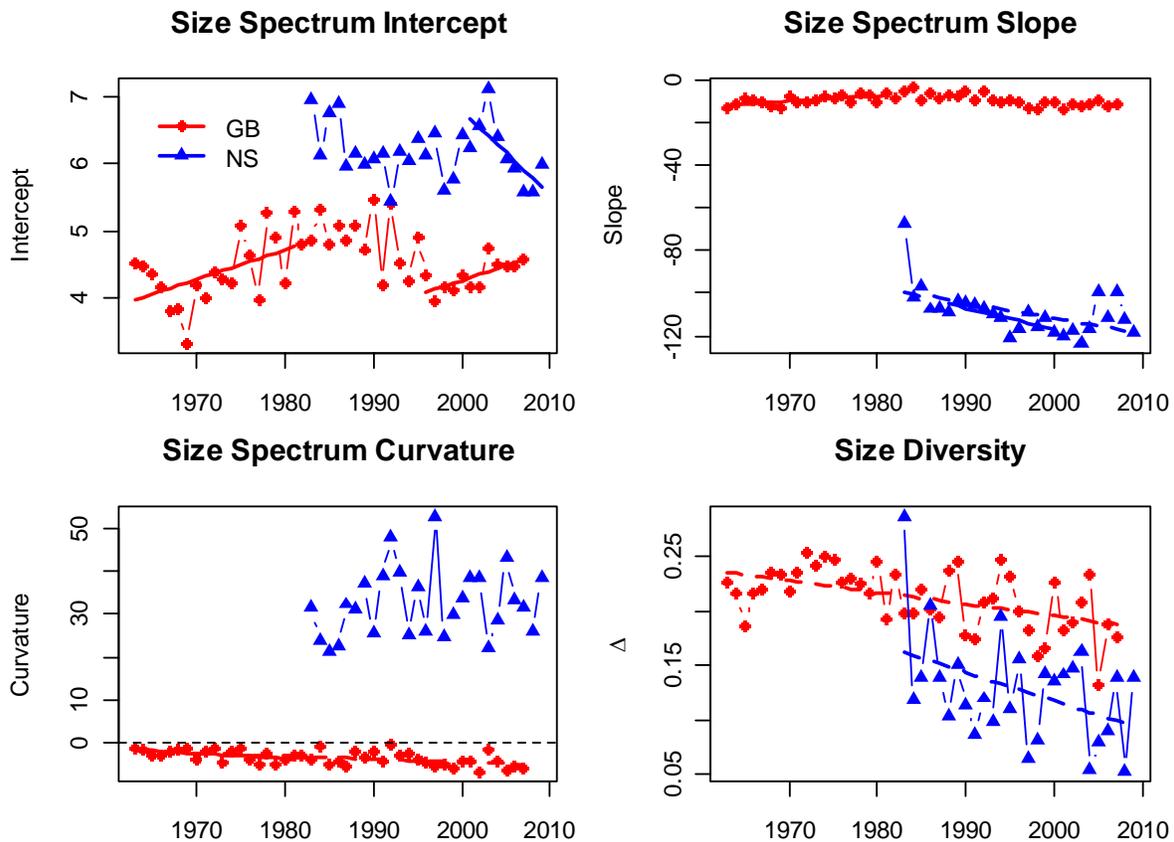
2000, after which biomass on Georges Bank increased while biomass decreased in the North Sea. On Georges Bank there was also a significant increase in biomass over the entire time period. Mean length in the community was about three times higher on Georges Bank than in the North Sea (Fig. 5c). There were no significant time trends in mean length, which implies that the changes in abundance occurred over all size classes. The difference in mean length between the communities is amplified in mean weight (Fig. 5d). In the North Sea, mean weight declined over the entire timeseries, whereas on Georges Bank, there was a significant decline only during the middle period. Mean weight can be decoupled from mean length if the condition factor changes or the species composition changes to fish with different weight at the same length.

Geometric mean abundance increased significantly in the North Sea, especially during the middle time period (Fig. 6a), which corresponds to increase in abundance of several species. Geometric mean abundance also increased gradually on Georges Bank over the entire time period. The proportion of non-commercial species was higher on Georges Bank and it declined over the entire survey time period (Fig. 6b). On Georges Bank 16 of the 46 species were non commercial, in contrast to 13 of 47 species in the North Sea. Evenness and taxonomic distinctness were consistently higher on Georges Bank than in the North Sea (Figs. 6c,d). Taxonomic distinctness increased on Georges Bank, especially during the first time period.



**Figure 6.** Community metrics for Georges Bank (GB) and the North Sea (NS). Symbols and lines are as in Fig. 5.

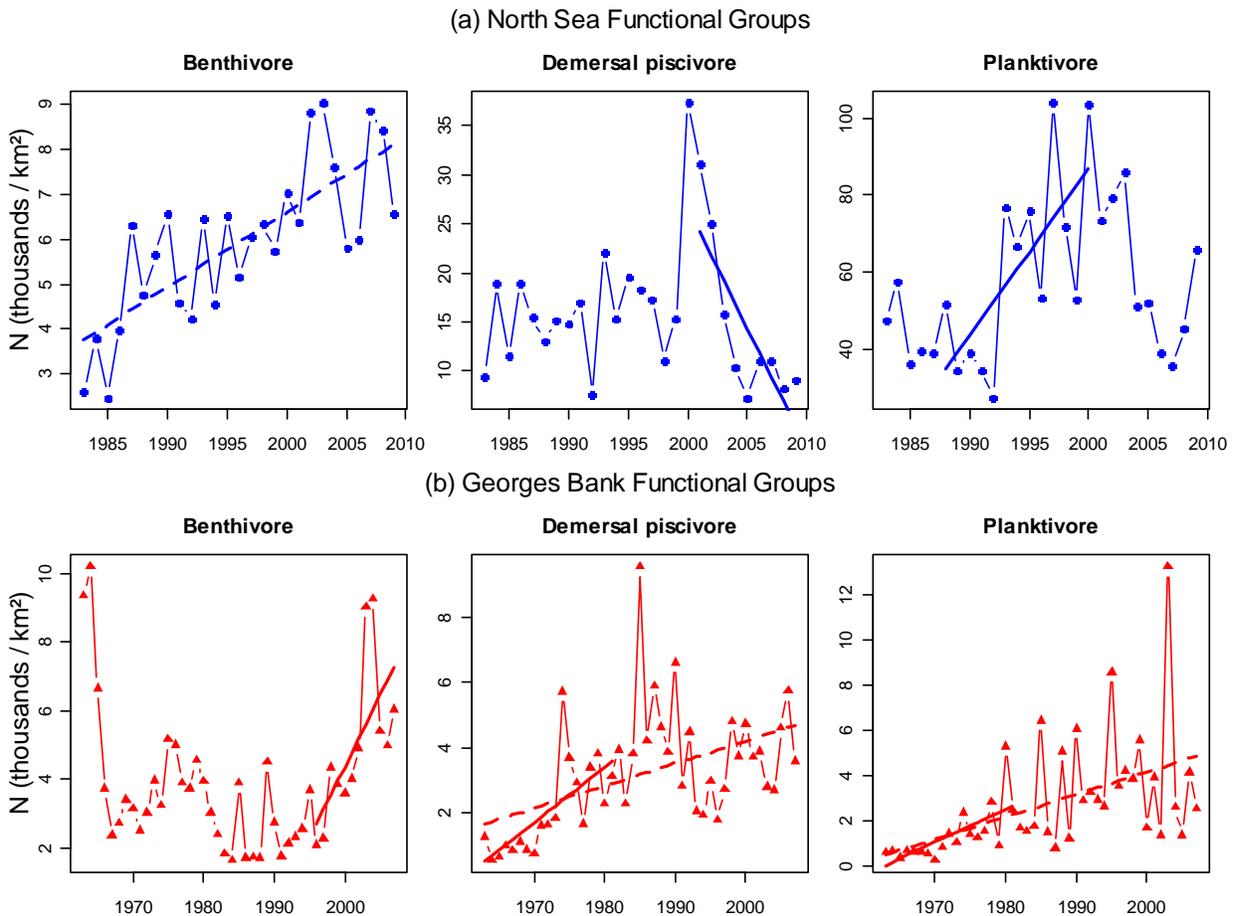
The intercept of the size spectrum was consistently higher in the North Sea than on Georges Bank (Fig. 7a), which reflects the greater abundance of small fish in the North Sea. In addition, the temporal changes in the intercepts reflect the changes in total abundance (Fig. 5a). The slopes of the size spectra were more negative in the North Sea (Fig. 7b), which indicates a steeper spectrum. The size spectrum curvature (Fig. 7c) was positive (convex upwards) in the North Sea and negative on Georges Bank (convex downwards). During the first time period on Georges Bank, the size spectrum intercept increased at the same time the slope increased and the curvature became more negative. These changes indicate a spectrum that shifted upward and became more curved. In the North Sea the curvature remained constant but the slope decreased over time, especially during the middle time period (Fig. 7b). Size diversity incorporates characteristics of the size spectra in a single index (Fig. 7d). Size diversity was higher on Georges Bank because the spectra are less steep. Over the entire time period there were declining trends in size diversity in both communities, because of increasing steepness of the size spectra in the North Sea (Fig. 7b) and increasing curvature on Georges Bank (Fig. 7c). Community metrics for the subset of species included in the length-based model (not shown) had patterns similar to those for the full community.



**Figure 7.** Community metrics for Georges Bank (GB) and the North Sea (NS). Symbols and lines are as in Fig. 5.

## Functional Groups

Results for the pelagic piscivore group are not shown because there were only two species in this group for the North Sea and only one on Georges Bank. In the North Sea benthivore group there is synchrony in the sense that the two dominant species, dab and long rough dab, showed a significant increase; when this trend is removed the two species instead show compensation in their year-to-year fluctuations (Table 1). In the two other groups there is no general trend and we rather see synchrony between species fluctuations within groups. Planktivores increased in the middle time period (Fig. 8a). Piscivores do not seem to have benefited from this increase in their prey apart from the pulse in 2000 (actually some species such as hake and small spotted catshark increased while others such as cod decreased; still we do not see compensation in that group). Piscivores decreased in the most recent time period (Fig. 8a).



**Figure 8.** Abundance of functional groups in the North Sea and on Georges Bank. Symbols and lines are as in Fig. 5.

Georges Bank has more demersal benthivores and fewer Planktivore species (Table 1), which can be explained by the fact that Georges Bank is a shallow submarine plateau, while the North Sea has more pelagic habitat. There were general increases in the abundance of demersal piscivores and planktivores (Fig. 8a).

In the benthivore group there is no overall temporal trend in numbers or biomass (Fig. 8b). The biggest contributions to the mean and variance are from haddock (*Melanogrammus aeglefinus*), longhorn sculpin (*Myoxocephalus octodentatus*), yellowtail flounder (*Limanda ferruginea*), and red hake (*Urophycis chuss*). There is some evidence of compensation in biomass but not in numbers. In the piscivore group only two species have a significant increasing trend and contribute most to the variance components: silver hake (*Merluccius bilinearis*) and spiny dogfish (*Squalus acanthias*). There is some evidence of synchrony in biomass.

In the planktivore group only two species have an increasing trend: herring (*Clupea harengus*) and butterfish (*Peprilus triacanthus*), the other species have no trend in either direction. These two species also make the biggest contribution to the variance ratio denominator. There is some evidence of compensation in detrended biomass (Table 1). In the total community the variance ratios for numbers are >1 even when detrended. In biomass units there is evidence of compensation when the data are detrended.

Table 1. Results of functional group analyses. Note: variance ratios were not calculated for biomass in the North Sea.

North Sea			
Functional group	No species	Variance ratio Number	Variance ratio N (detrended series)
Demersal benthivores	19	1.61	0.73
Demersal piscivores	13	1.22	1.17
Planktivores	13	1.49	1.48
Whole community	47	1.85	1.72

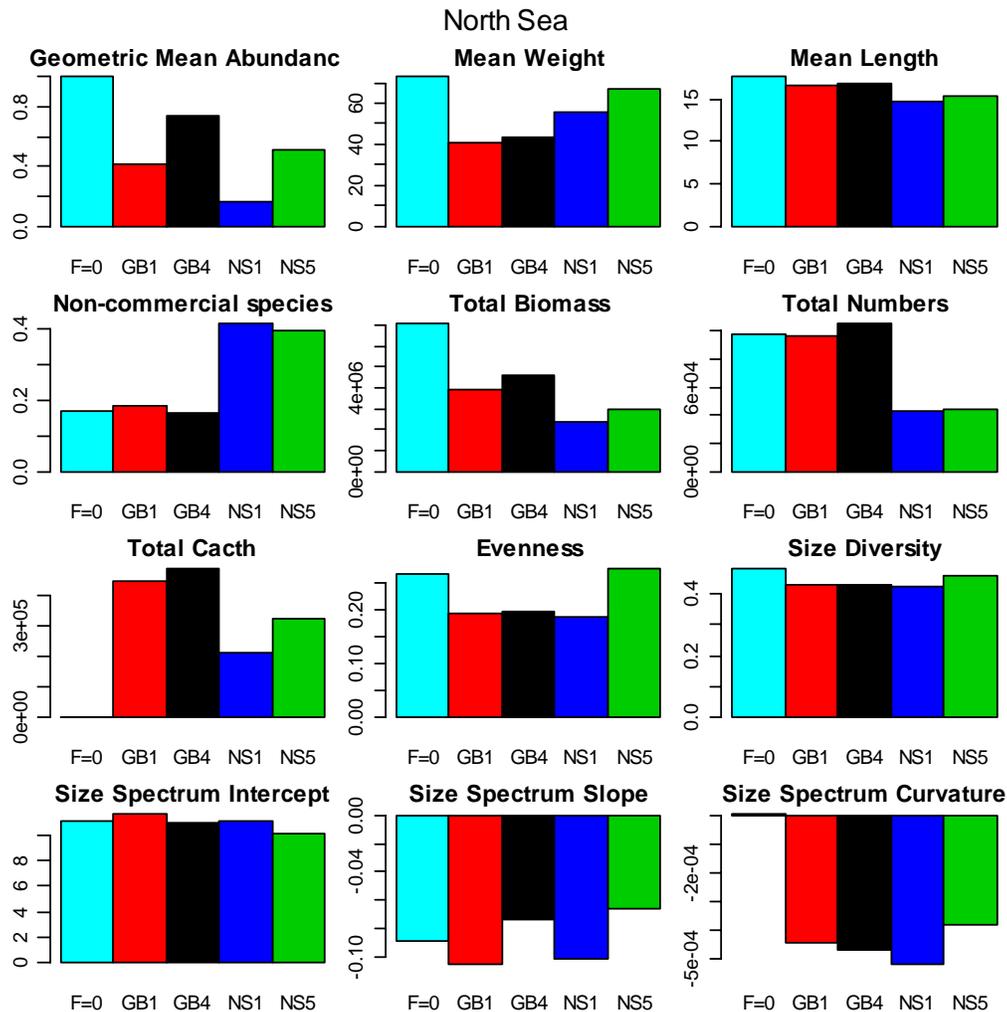
Georges Bank			
Functional group	No species	Variance ratio Number	Variance ratio N (detrended series)
Demersal benthivores	23	1.43	1.09
Demersal piscivores	14	1.03	1.05
Planktivores	8	1.30	1.02
Whole community	46	1.52	1.19

Functional group	No species	Variance ratio Biomass	Variance ratio B (detrended)
Demersal benthivores	23	1.09	0.81
Demersal piscivores	14	1.44	1.41
Planktivores	8	1.19	0.75
Whole community	46	1.10	0.82

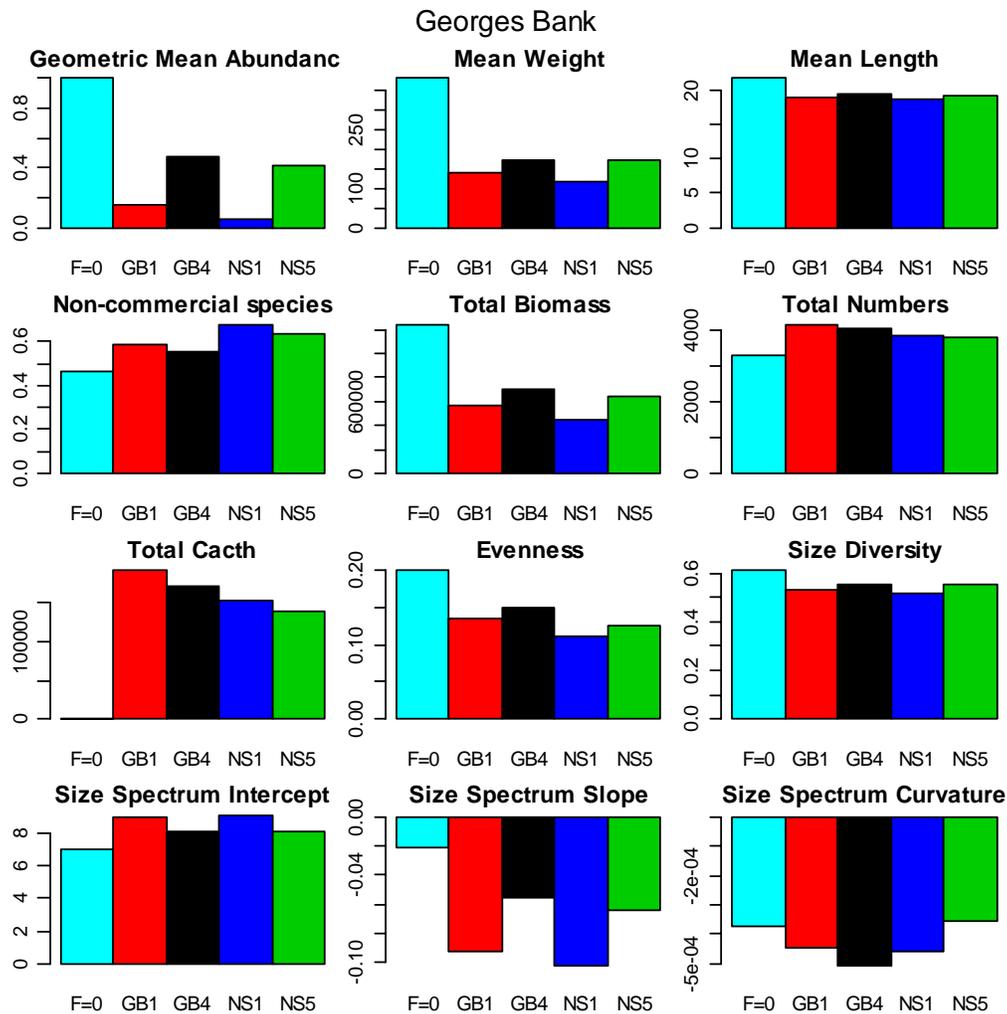
## Length-based model results

Some of the community metrics respond much more quickly than others to changes in fishing mortality, according to simulations made with LeMans. Metrics that incorporate mean size in the community (mean weight, mean length, total biomass) responded more rapidly, reaching their equilibrium after only two years. In contrast, metrics based on numbers and species composition (total numbers, evenness, proportion of non-commercial species) took about 10 years to re-equilibrate. Size diversity took about 5 years to respond, whereas the size-spectrum slope was still changing after 25 years. The patterns were similar regardless of the magnitude of the changes in fishing mortality.



**Figure 9.** Community metrics calculated for 21 species in the North Sea with LeMans. The fishing scenarios correspond with the blocks of community fishing selectivity in Fig. 1. F=0 is no fishing; GB1 is for Georges Bank empirical  $F$ -at-length 1982-1986; GB4 is for 1997-2001; NS1 is for 1982-1987; NS5 is for 2003-2007.

The results of applying the empirical fishing mortality regimes (Fig. 1) to the communities simulated with LeMans are summarized with 12 community metrics (Figs. 9&10). Each metric is compared with its value with no fishing as a baseline. When  $F$ -at-length from the first time block in the North Sea was applied to the North Sea community, seven species were collapsed at the end of 25 years (i.e. biomass <10% of unfished biomass). The collapsed species were both large (e.g. monkfish, cod, saithe) and small (e.g. sandeel) due to high  $F$  at 20-30 cm (Fig. 1a). Compared with no fishing, total numbers and biomass were much reduced and the proportion of non-commercial species was higher (Fig. 9). The  $F$ -at-length corresponding to the recent time block in the North Sea (2003-2007) caused saithe and sandeel to be depleted but not monkfish or cod. Compared with block 1, mean weight and total catch increased more than total biomass and numbers. Evenness and size diversity were approximately the same in this fishing scenario as with no fishing. The size spectrum intercept, slope and curvature were all reduced.



**Figure 10.** Community metrics calculated for 21 species on Georges Bank with LeMans. The fishing scenarios are as described in the Fig. 9 caption.

The main difference in the fishing mortality rates for Georges Bank is the lower  $F$  between 20 and 40 cm (Fig. 1b). When applied to the North Sea community, the  $F$ -at-length for time block 1 caused the three largest species to collapse, but allowed the small species to match their unfished levels or to increase because of predator release. This change is reflected in the higher size-spectrum intercept and lower slope (Fig. 9). Total catch is higher with the fishing mortalities from Georges Bank, because the fishing mortality regime from the North Sea causes more species to be overfished. When the recent  $F$ -at-length from Georges Bank was applied to the North Sea, only one species collapsed (saithe) and the changes in metrics were relatively small compared with time block 1.

The Georges Bank community responded somewhat differently to fishing pressure (Fig. 10). The Georges Bank fishing mortalities in the first time block caused seven large species to collapse. Small species, such as sandeel, increased because of predator release. These changes are reflected in the size spectrum—the intercept increased, the slope decreased, and the spectrum became more curved (Fig. 10). With fishing, the mean weight and biomass decreased substantially while total numbers increased. Total catch was highest with the fishing mortalities from the first time block, which highlights the trade-offs between catch and measures of biodiversity. When the lower  $F$ -at-length for the recent time block on Georges Bank was applied, only four species collapsed. The metrics all changed in the direction of the unfished community, except that the size-spectrum became more curved (Fig. 10), possibly because of higher numbers at intermediate sizes.

When applied to the Georges Bank community, the fishing mortality rates from the first time block in the North Sea caused eight species to collapse. In contrast with the North Sea, sandeel increased to its highest level because it is unfished on Georges Bank and also released from predation. The higher fishing mortality rates caused larger decreases in several of the community metrics and an increase in the proportion of non-commercial species and size-spectrum intercept. The relaxation in  $F$ -at-length in the most recent time block of the North Sea again caused the community metrics to change in the expected directions (Fig. 10).

## Discussion

Is biodiversity in these shelf-sea fish communities being maintained or lost? The main diversity metrics that we calculated are size diversity, evenness, and taxonomic distinctness. We did not calculate species richness because of unequal sampling intensity. In the North Sea, size diversity declined over the entire survey time series. Evenness also declined over the time series and particularly during the middle time period, 1988-2000. There were no trends in taxonomic distinctness. On Georges Bank size diversity declined over the entire survey time series but there were no trends in evenness. Taxonomic distinctness increased, especially during the first time period, 1963-1981. Based on these metrics we conclude that biodiversity has been lost during the past decades of the trawl surveys. The same metrics calculated with a length-based model (LeMans) indicate that evenness and size diversity would be higher in an unfished community compared with the levels of community fishing we estimated in this paper.

Which drivers are primarily responsible for the observed changes in biodiversity and other community metrics? The main hypotheses that have been advanced to explain these changes are fishing, regime shifts in the food web, and the more gradual and directional shifts of climate change. In the North Sea the overall reduction in mean weight, evenness, size spectrum slope, and size diversity, and the increase in the proportion of non-commercial species are consistent with the effects of sustained or increasing fishing (Table 2). Likewise the reductions in mean weight, evenness, and size-spectrum slope during 1988-2000 can be explained by fishing because this was still a period of high fishing mortality. The time trends in the functional groups suggest changes within the food web that are not directly caused by fishing. Between 1988 and 2000 there was an increase in abundance and a decrease in size and evenness, because herring, dab, and sprat, three of the six most abundant species in the community, increased over this time-period. Two of these species are targeted by pelagic fisheries and bore sustained fishing mortalities over that time period, so their increase cannot be a consequence of a change in fishing pressure. During the recent period, 2001-2009, total numbers, biomass, and size-spectrum intercept all declined. Functional group analysis indicates that this loss occurred primarily in the piscivore group. These decreases are surprising because this was a period of reduced fishing mortality. LeMans predicts that numbers and biomass should increase with the community fishing mortality observed during this period, and that the size-spectrum intercept should decrease due to increased predation.

Table 2. Summaries of trends in community metrics and abundance of functional groups. The metrics are Ntot: Total numbers, Gtot: Geometric mean abundance, Btot: Total biomass, Wbar: Mean weight in the community, PNC: Proportion of non-commercial species; SRE: Simpson Reciprocal Evenness,  $\Delta^*$ : Taxonomic distinctness, SSsl: Size Spectrum slope, SSint: Size Spectrum intercept, SScur: Size Spectrum curvature,  $\Delta$ : Size diversity, Btv: Benthivores, DPis: Demersal Piscivores, Plv: Planktivores.

#### North Sea

Period	Ntot	Gtot	Btot	Wbar	PNC	SRE	$\Delta^*$	SSsl	SSint	SScur	$\Delta$	Btv	DPis	Plv
1983-1987	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1988-2000	↗	↗	—	↘	—	↘	—	↘	—	—	—	—	—	↗
2001-2009	↘	—	↘	—	—	—	—	—	↘	—	—	—	↘	—
1983-2009	—	↗	—	↘	↗	↘	—	↘	—	—	↘	↗	—	—

#### Georges Bank

Period	Ntot	Gtot	Btot	Wbar	PNC	SRE	$\Delta^*$	SSsl	SSint	SScur	$\Delta$	Btv	DPis	Plv
1963-1981	—	—	—	—	—	—	↗	↗	↗	↘	—	—	↗	↗
1982-1995	—	—	—	↘	—	—	—	—	—	—	—	—	—	—
1996-2007	—	—	↗	—	—	—	—	—	↗	—	—	↗	—	—
1963-2007	↗	↗	↗	—	↘	—	↗	—	—	↘	↘	—	↗	↗

On Georges Bank the overall increases in total numbers, biomass, and the reduction in the proportion of non-commercial species is consistent with the effects of reduced fishing intensity (Table 2). However, we would expect these fishing induced changes to be strongest in the most recent time period because fishing mortality was high until 1996. In 1997-2007 the increase in total biomass, primarily benthivores, can be attributed to lower fishing mortality but, based on LeMans results, the size spectrum intercept would be expected to decrease, not increase (Fig. 10). The overall increases in abundance, particularly in piscivores and planktivores during the first time period may be a bottom-up response to increased nutrient input (Steele et al. 2007), a trophic response to reduced benthivore abundance, or a response to reduced exploitation by foreign fleets. During the middle time period (1982-1995) the community was dominated by piscivores and planktivores. This shift may have been induced by the direct and indirect effects of fishing (Fogarty and Murawski 1998, Collie et al. 2009). The only significant trend during this period was a decrease in mean weight, which is consistent with high exploitation (Table 2). The increase in taxonomic distinctness reflects the increased importance of elasmobranchs, which are taxonomically distinct from teleost fish. In summary, climatic effects appear less pronounced on Georges Bank than in the North Sea. There have been shifts in species composition but they have been attributed primarily to the direct and indirect effects of fishing (Fogarty and Murawski 1998).

Despite their similar species composition, the North Sea and Georges Bank fish communities have very different levels of species and size diversity. The magnitude of biomass is strikingly similar in the two communities, which suggests a trophic similarity in the production of fish biomass. However, in the North Sea this biomass comes in much smaller packages. The density of fish the North Sea is 10 times higher but the mean length is  $\frac{1}{3}$  that on Georges Bank. The North Sea has a greater dominance of small pelagic species (sandeel, sprat, herring) than Georges Bank, which is reflected in lower evenness in the distribution of individuals among species. The North Sea also has consistently lower taxonomic distinctness of the fish community and lower size diversity. The preponderance of small fish in the North Sea causes the size spectra to have a higher intercept, more negative slope and convex upward shape.

These fundamental differences in community composition are not simply explained by the recent exploitation histories. The maximum fishing mortality ( $F$ ) has been quite similar in the two communities. However, the range of fishing mortality estimates from available stock assessments may be an insufficient descriptor of fishing pressure at the community level, which also depends on how many species are fished (and maybe discarded) but not assessed. Moreover, the distribution of  $F$  across lengths has been very different. The Georges Bank fisheries have been increasingly selective for large sizes, whereas the North Sea has had high  $F$  on the 20-to-30 cm size class. The Georges Bank fishery is also consistently more species selective, with a higher proportion of the community consisting of non-commercial species.

Results of the multispecies model (LeMans) suggest that elimination of fishing would increase evenness, size diversity, and mean size in both communities. A difference is that on Georges Bank, total number decreased with no fishing because of increased predation, whereas in the North Sea, total numbers more than doubled when the small species were no longer fished. Applying the  $F$ -at-age from Georges Bank to the North Sea would tend to accentuate this pattern

in that it would capture the predators and not the prey species. The opposite exploitation pattern—fish the small but not the large species—would probably be required to obtain greater evenness and size diversity in the North Sea (Rochet et al. 2010a). Conversely, the application of the North Sea-like fishing mortalities to Georges Bank had the general effect of increased fishing intensity without fundamentally changing the community composition.

The LeMans results suggest that the fundamental differences between the North Sea and Georges Bank communities are not the consequences of their recent exploitation histories or the selective nature of their fisheries. On the contrary, the exploitation patterns may be a response to the underlying community structure, not its cause. It should be remembered, however, that LeMans was parameterized with abundance from the trawl surveys such that the community composition is constrained by the model inputs (Rochet et al. 2010a). Even so, the fact that the differences in community structure existed at the start of the survey time series, persisted throughout, and were not reversed without fishing, suggest that they were “pre-existing conditions” for which a deeper explanation is needed.

These marine ecosystems do not differ much in the structure of the habitat. Georges Bank is a shallow, marine plateau defined by the 200-m isobath, with strong benthic-pelagic coupling. The North Sea also has important shelf habitats and is mostly less than 200 m deep, except the Skagerrak and a few holes in the central North Sea with depths more than 500 m <5% of area (Eisma 1987). North Sea fish production is more dependent on zooplankton production than on benthos (Heath 2005). Thus it is perhaps not surprising for the fish biomass in the North Sea to be dominated by small pelagic species.

Another potential explanation lies in the long-term exploitation of these communities, both of which have been fished for centuries and with motorized trawlers for the past 100 years. Reconstructions of unfished food webs suggest a greater dominance of large fish (Steele and Shumacher 2000) so it is possible that these large fish were selectively removed, leaving a community dominated by small fish. It is difficult to compare the fishing intensity of historic and contemporary fisheries because of gear changes. One approach is to examine the fishing mortality of the species with the longest stock assessments. Estimates of fishing mortality for Georges Bank haddock extend back to 1931. Fishing mortality was in the range 0.26 to 0.74 between 1932 and 1962, and on average was higher before 1963 than since. Fishing mortality of North Sea plaice steadily increased from ~0.15 in the 1950s to 0.7 in 2000. The pre-war fishing mortality might have been higher than post-war, around 0.3 (Bannister 1977). If these levels of fishing mortality extended across the community, these ecosystems would have been heavily exploited before the trawl surveys were initiated.

In summary, biodiversity has been lost from the North Sea and Georges Bank fishing communities during the past several decades, though other community metrics have been more stable over this time period. Unsurprisingly, the causes of these changes appear to be a combination of fishing and the environment. The theoretical effects of fishing selectivity are not detectable in the real communities, probably because they interact with multiple other drivers. The changes in fishing mortality during the most recent time periods are expected to increase biodiversity, but such increases have not yet been detected in the real communities.

## Acknowledgements

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## Appendix: lists of species used in the analysis

### a) North Sea

Common name	Latin name	Functional Group	LeMans species
Hooknose	<i>Agonus cataphractus</i>	Demersal benthivore	
Shad	<i>Alosa spp</i>	Planktivore	
Thorny skate	<i>Amblyraja radiata</i>	<sup>(1)</sup>	x
Sandeel	<i>Ammodytes</i>	Planktivore	x
Greater argentine	<i>Argentina silus</i>	Planktivore	
Lesser argentine	<i>Argentina sphyraena</i>	Planktivore	
Scaldfish	<i>Arnoglossus laterna</i>	Demersal benthivore	
Red gurnard	<i>Aspitrigla cuculus</i>	Demersal benthivore	
Solenette	<i>Buglossidium luteum</i>	Demersal benthivore	
Dragonet	<i>Callionymus lyra</i>	Demersal benthivore	
Dragonet	<i>Callionymus maculatus</i>	Demersal benthivore	
Herring	<i>Clupea harengus harengus</i>	Planktivore	x
Lesser weever	<i>Echiichthys vipera</i>	Demersal benthivore	
Four-bearded rockling	<i>Enchelyopus cimbrius</i>	Demersal piscivore	
Anchovy	<i>Engraulis encrasicolus</i>	Planktivore	
Grey gurnard	<i>Eutrigla gurnardus</i>	Demersal piscivore	x
Silvery pout	<i>Gadiculus argenteus</i>	Planktivore	
Cod	<i>Gadus morhua</i>	Demersal piscivore	x
Witch	<i>Glyptocephalus cynoglossus</i>	Demersal benthivore	x
Gobies	<i>Gobius spp</i>	Demersal benthivore	
Long rough dab	<i>Hippoglossoides platessoides</i>	Demersal benthivore	x
Greater sandeel	<i>Hyperoplus lanceolatus</i>	Planktivore	
Megrim	<i>Lepidorhombus whiffiagonis</i>	Demersal piscivore	
Sandy ray	<i>Leucoraja naevus</i>	<sup>(1)</sup>	x
Dab	<i>Limanda limanda</i>	Demersal benthivore	x
Anglerfish	<i>Lophius piscatorius</i>	Demersal piscivore	x
Snake blenny	<i>Lumpenus lampretaeformis</i>	Demersal benthivore	
Checker eelpout	<i>Lycodes vahlii</i>	Demersal benthivore	
Pearl-side	<i>Maurollicus muelleri</i>	Planktivore	
Haddock	<i>Melanogrammus aeglefinus</i>	Demersal piscivore	x
Whiting	<i>Merlangius merlangus</i>	Demersal piscivore	
Hake	<i>Merluccius merluccius</i>	Demersal piscivore	x
Blue whiting	<i>Micromesistius poutassou</i>	Planktivore	

Lemon sole	<i>Microstomus kitt</i>	Demersal benthivore	x
Ling	<i>Molva molva</i>	Demersal piscivore	
Bull-rout	<i>Myoxocephalus scorpius</i>	Demersal benthivore	
Flounder	<i>Platichthys flesus</i>	Demersal benthivore	
Plaice	<i>Pleuronectes platessa</i>	Demersal benthivore	x
Saithe	<i>Pollachius virens</i>	Demersal piscivore	x
Pilchard	<i>Sardina pilchardus</i>	Planktivore	
Mackerel	<i>Scomber scombrus</i>	Pelagic piscivore	x
Lesser spotted dogfish	<i>Scyliorhinus canicula</i>	Demersal piscivore	
Sole	<i>Solea solea</i>	Demersal benthivore	x
Sprat	<i>Sprattus sprattus sprattus</i>	Planktivore	x
Greater weever	<i>Trachinus draco</i>	Demersal benthivore	
Horse mackerel	<i>Trachurus trachurus</i>	Pelagic piscivore	x
Norway pout	<i>Trisopterus esmarkii</i>	Planktivore	
Bib	<i>Trisopterus luscus</i>	Demersal piscivore	x
Poor cod	<i>Trisopterus minutus</i>	Demersal piscivore	x

<sup>(1)</sup>Those species were used in the simulation model but were not sufficiently well sampled by the survey to be included in the data analysis.

#### b) Georges Bank

Common Name	Latin name	Functional group	LeMans species
Blueback herring	<i>Alosa pseudoharengus</i>	Planktivore	
Alewife	<i>Alosa sapidissima</i>	Planktivore	
Thorny skate	<i>Amblyraja radiata</i>	Benthivore	
Northern sandlance	<i>Ammodytes dubius</i>	Planktivore	x
Atlantic wolffish	<i>Anarhichas lupus</i>	Benthivore	
Alligatorfish	<i>Aspidophoroides monopterygius</i>	Benthivore	
Cusk	<i>Brosme brosme</i>	Benthivore	
Black sea bass	<i>Centropristis striata</i>	Benthivore	
Gulfstream flounder	<i>Citharichthys arctifrons</i>	Benthivore	
Atlantic herring	<i>Clupea harengus</i>	Planktivore	x
Barndoor skate	<i>Dipturus laevis</i>	Benthivore	
Fourbeard rockling	<i>Enchelyopus cimbrius</i>	Benthivore	
Atlantic cod	<i>Gadus morhua</i>	Demersal piscivore	x
Witch flounder	<i>Glyptocephalus cynoglossus</i>	Benthivore	x
Blackbelly rosefish	<i>Helicolenus dactylopterus</i>	Benthivore	
Sea raven	<i>Hemitripterus americanus</i>	Demersal piscivore	x
American plaice	<i>Hippoglossoides platessoides</i>	Benthivore	
Atlantic halibut	<i>Hippoglossus hippoglossus</i>	Demersal piscivore	
Little skate	<i>Leucoraja erinacea</i>	Benthivore	x
Winter skate	<i>Leucoraja ocellata</i>	Demersal piscivore	x
Yellowtail flounder	<i>Limanda ferruginea</i>	Benthivore	x
Goosefish	<i>Lophius americanus</i>	Demersal piscivore	x
Ocean pout	<i>Macrozoarces americanus</i>	Benthivore	
Smooth skate	<i>Malacoraja senta</i>	Demersal piscivore	

Haddock	<i>Melanogrammus aeglefinus</i>	Benthivore	x
Offshore hake	<i>Merluccius albidus</i>	Demersal piscivore	
Silver hake	<i>Merluccius bilinearis</i>	Demersal piscivore	x
Smooth dogfish	<i>Mustelus canis</i>	Benthivore	
Longhorn sculpin	<i>Myoxocephalus octodecemspinosus</i>	Benthivore	x
Summer flounder	<i>Paralichthys dentatus</i>	Demersal piscivore	x
Fourspot flounder	<i>Paralichthys oblongus</i>	Benthivore	x
Butterfish	<i>Peprilus triacanthus</i>	Planktivore	
Pollock	<i>Pollachius virens</i>	Demersal piscivore	x
Bluefish	<i>Pomatomus saltatrix</i>	Pelagic piscivore	
Northern sea robin	<i>Prionotus carolinus</i>	Benthivore	
Winter flounder	<i>Pseudopleuronectes americanus</i>	Benthivore	x
Atlantic mackerel	<i>Scomber scombrus</i>	Planktivore	x
Windowpane	<i>Scophthalmus aquosus</i>	Planktivore	x
Acadian redfish	<i>Sebastes fasciatus</i>	Demersal piscivore	
Spiny dogfish	<i>Squalus acanthias</i>	Demersal piscivore	x
Scup	<i>Stenotomus chrysops</i>	Benthivore	
Moustache sculpin	<i>Triglops murrayi</i>	Benthivore	
Longfin hake	<i>Urophycis chesteri</i>	Planktivore	
Red hake	<i>Urophycis chuss</i>	Benthivore	x
Spotted hake	<i>Urophycis regia</i>	Demersal piscivore	
White hake	<i>Urophycis tenuis</i>	Demersal piscivore	x

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