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Impact of fishing on size composition and diversity of demersal fish communities

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By analysing data sets from different world regions we add evidence to documented changes in demersal fish community structure that may be related to fishing. Changes are analysed by community properties that might be expected to capture relevant overall changes – size spectra slopes and intercepts, Shannon-Wiener diversity, and dominance. Cross-system differences in the shape of the integrated community size spectra appear to be related to ecosystem productivity. The slope of size spectra appears to respond in a consistent way to changes in exploitation levels. In most areas studied, but particularly in high-latitude regions, we observe a decreasing trend in the slope, reflecting changes in size composition toward a relative decline in larger fish. The results from tropical regions are less conclusive, partly owing to the difficulty in obtaining consistent data series, but probably also because the generally higher growth rates of the constituent species make the slope less sensitive to changes in fishing. No evidence was found of any decline in species richness, while changes in diversity (richness and evenness) were caused either by changes in patterns of dominance or by changes in the number of species identified resulting from improved survey protocols.

Key words: cross-system comparisons, diversity, fish community structure, size spectrum.

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Introduction

Fishing affects demersal fish communities through selective removal of target species, through the by-catch of non-target species, and through habitat modification, resulting in changes in overall biomass, in species composition and in size structure. The extent of the response depends on life-history characteristics of the individual species, trophic interactions among species, and on the type of changes generated in the physical habitat.

Documented changes in the structure of demersal fish communities include Pauly (1979), Gulland and Garcia (1984), Greenstreet and Hall (1996), Sharp and Csirke (1984), Sainsbury *et al.* (1997), Haedrich and Barnes (1997). In the Gulf of Thailand, wide-ranging changes in the demersal fish community were linked to the rapid expansion of the trawl fishery after 1961 (Pauly, 1988). The changes involved a severe decrease in the abundance of large, long-lived fish (e.g. rays) as well as of several families of smaller fish (e.g. Leiognathidae, Gerreidae, and Mullidae) and an increase in shrimps and squid.

Overall catch rates in the trawl fishery declined from about 300 kg h^{-1} in 1961 to 54 kg h^{-1} in 1983 (Suvapepun, 1991). Harris and Poiner (1991) studied a similar tropical community in the south-eastern Gulf of Carpentaria. In a comparison between scientific surveys before the start of the prawn fishery and surveys made 20 years later, 63% of the 82 taxa examined (including Leiognathidae) showed no change in abundance. The modest levels of prawn trawling (Blaber *et al.*, 1990) compared with the Gulf of Thailand may explain the different response.

On the shelf off north-western Australia, the fish community changed as the trawl fishery developed. The abundance of the main target species *Lutjanus* and *Lethrinus* declined, while *Saurida* and *Nemipterus* increased over the period 1962–1983 (Sainsbury, 1988). When part of the shelf was closed to trawling within the framework of an experimental management strategy, the abundance of *Lutjanus* and *Lethrinus* increased again. Several possible explanations were suggested, but subsequent analysis showed that a model relating species abundance to habitat structure best explained the trends (Sainsbury *et al.*, 1997). The change in fish community structure seems most likely to be related to the destruction of large epibenthic organisms (mostly sponges, alcyonarians, and gorgonians) by the trawl gear.

On Georges Bank, total fish biomass more than halved during the 1960s as a result of increasing exploitation by distant-water fleets (Fogarty and Murawski, 1998). Exploitation declined in 1977 after the establishment of the EEZ, but then increased again owing to increases in the domestic fleet. Fish community structure changed substantially in the 1970s with an apparent replacement of gadoids and flounders by small elasmobranchs. The increase in dogfish and skates was interpreted as a second-order effect of reducing the abundance of gadoids and flounders, mediated through reduced competition.

Rijnsdorp *et al.* (1996) compared trawl survey data collected in the southern North Sea in 1906–1909 and 1990–1995 and found lower species diversity and evenness in the latter period as well as a shift in the size distributions of flatfish and roundfish towards smaller fish. Changes in the survey gear between the periods hampered comparisons of overall abundance, but the data did suggest a large reduction. Greenstreet and Hall (1996) and Greenstreet *et al.* (1999) studied the fish community in the North-western North Sea from trawl survey data collected during 1925–1996. Overall, only minor changes had taken place, but their analyses revealed a modest decrease in diversity over time, an increase in dominance, and a shift in size composition towards smaller fish. Jennings *et al.* (1999) used the same data set to study whether the response of individual species was linked to their life histories and observed, among phylogenetically related species, a relative decrease in the abundance of the slower-growing, late-maturing species.

Pope and Knights (1982) observed a linear relationship between log numbers per size class and fish size in the North Sea and the Faroe Islands. Subsequent studies in various areas have confirmed the linearity of the relationship and suggested that the slope of the size spectrum might be used as a broad indicator of exploitation (Pope *et al.*, 1987; Murawski and Idoine, 1992; Gobert, 1994; Rice and Gislason, 1996; Gislason and Rice, 1998). For instance, Rice and Gislason (1996) found a significant decrease in slope and an increase in the intercept of the overall community size spectrum of North Sea fish from 1973 to 1993.

Several summary metrics have been proposed to capture changes in demersal fish communities in relation to fishing (Rice, this volume). We focus on changes in species diversity and size structure in response to fishing, using bottom-trawl survey data for different marine ecosystems from all over the world, in an attempt to answer the following questions:

- Are there cross-system differences in the slope and intercept of size spectra of fish communities from different habitats/ecosystems?
- Is there general evidence that increased exploitation results in a steepening of the slope of the size spectrum?
- Can size spectra be used to indicate the broad level of exploitation in poorly studied areas?
- Can changes in diversity and dominance be related to fishing?

Materials and methods

The data sets used (Table 1) were from highly productive boreal systems (Scotian Shelf, North Sea), eastern boundary currents (Humboldt, Benguela, and Canary Current), high-latitude systems on the Southern Hemisphere (Argentina and South East Australia), tropical areas (Ghana shelf, south-western Gulf of Mexico, Mozambique), and a shallow temperate and strongly fluctuating system (Bohai Sea). A series of bottom-trawl surveys –carried out by the Norwegian RV "Dr Fridtjof Nansen" on shelf and upper slope areas all over the world was used for cross-system comparisons (Table 2). Data comprised catch in numbers and weight by species and length frequency measurements from scientific bottom-trawl surveys. Efforts were made to select time series so as to avoid serious inconsistencies in survey protocols (species identification, measurements), gear used (type of trawl, codend mesh size) and geographic coverage.

Consistent time series that would cover both pristine or lightly exploited situations and periods of intensive exploitation were generally not available. The data from

Table 1. Specifications of local data sets analysed (depth: range in m; mesh: codend mesh size in mm).

Area	Latitude/longitude	Years	Depth	Mesh	Assemblages
Scotian Shelf	41°07′–47°02′N 57°02′–67°03′W	70–97	100–400	32	Western/eastern
Portugal	36°30′–41°90′N	82, 90–98	20–700	40	Shallow (20–100 m)/ deep (100–400 m)
Argentina	45°–54°S 62°–68°W	87, 95, 97	100–200	20	Northern (<50°S)/ southern (>50°S)
Chile	30°–40°S	68/95	30–500	50/35	—
Bohai Sea (China)	32°–40°S 119°–124°′E	59, 82, 93, 98	10–40	20	—
Campeche Bank (Mexico)	18°–20°N 91°–93°W	51, 78–92, 97	20–100	35–38	—
Ghana	3°W–1°30′E	63–64, 79–82, 88–90	10–150	40	Shallow (10–50 m)/ deep (50–100 m)
Sofala Bank (Mozambique)	16°–21°S	77–78, 82–83, 90	10–50	20	—
New South Wales (Australia)	33°–38°S	77, 97	200–500	89	Sydney/Ulladulla/Eden

Table 2. Specifications of data sets from areas covered by surveys with RV "Dr Fridtjof Nansen" (depth: range in m; N: number of stations).

Area	Latitude/longitude	Years	Depth	N
Eastern Central Pacific	16°–01°30′N 95°–79°E	87	10–400	976
Northern South America	11°–04°30′N 75°–54°E	88	10–400	1055
Angola	05°–13°S	89, 91, 92	20–700	1086
Northern Benguela	17°30′–29°30′S	90–98	20–400	1528
East Africa	01°30′–21°S	82, 83	20–400	437
Western Arabian Sea	23°–16°30′N	83, 84	20–400	189

Australia are an exception, although they only represent two points in time. The data from Ghana, Bohai Sea, and Campeche Bank also include surveys during the early stages of the fisheries in these areas but their usefulness is limited owing to changes in survey protocols. The long time series of Scotian Shelf data does not include pristine or lightly exploited conditions. Results for the North Sea (ICES, 1996; Rijnsdorp *et al.*, 1996) are included for comparison.

Only bony fish and elasmobranchs were included in the analyses. Pelagic species were only included for the shallow-water tropical communities, where they are an important component and where pelagic-demersal coupling is expected to be substantial. For other areas, only demersal species were included.

Multivariate analysis was used initially to subdivide the data from each region into different assemblages and habitats, because species composition and community properties were expected to depend on habitat type. A classification of assemblages was already available for Portugal (ICES, 1998), Mozambique (Bianchi, 1992), and the Scotian Shelf (Mahon and Smith, 1989). For the other areas, two-way indicator species analysis (TWIA) as implemented by TWINSPAN (Hill, 1979) and detrended correspondence analysis (DCA; Hill and Gauch, 1980) was used. The version in CANOCO (ter Braak, 1991) allows the ordination axes from DCA to be correlated with environmental variables. The habitat stratification adopted is presented in Table 1.

For the Portuguese Shelf, integrated community size spectra were constructed by plotting the natural logarithm of the total number of individuals caught per hectare by 5 cm size group against the natural logarithm of the midpoint of each length interval, in line with the analysis available for the North Sea (ICES, 1996). For the other case studies, length frequencies were not available for all species. However, weights and numbers for each species in each haul were used to construct the size spectrum. Given species i and haul j, the average individual weight was calculated by dividing the catch in weight (W_{ij}) by the number of individuals caught (N_{ij}). Size categories were determined to correspond to 5 cm length intervals and by calculating the corresponding theoretical weight intervals, assuming isometric growth ($W=0.01L^3$). The number of individuals in each size category k (N_k) was then calculated by distributing all N_{ij} over the weight classes according to their W_{ij}. The natural logarithm of N_k was then plotted against the log of the midpoint of each size class. Slopes and intercepts, and their statistics, were calculated for the descending limb of the size-frequency distribution.

Weight-based spectra will differ from size spectra constructed from length measurements. Differences may result from the allocation of numbers to length-converted weight categories and from the bias introduced by using the average weight to represent the entire size distribution of a given species in a given haul. This bias is most severe when the size range of a species in the

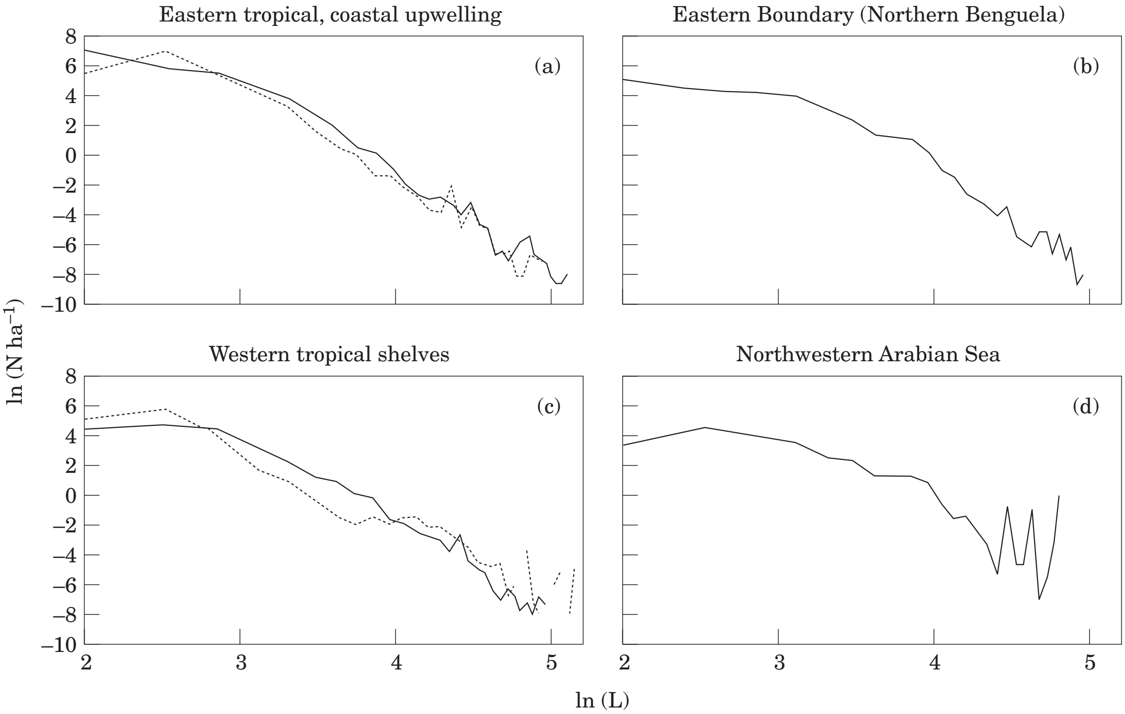

Figure 1. Cross-system comparisons, based on surveys of RV "Dr Fridtjof Nansen", of size spectra (L: length in cm) of demersal fish communities grouped by system type: (a) Eastern tropical, coastal upwelling (drawn line: Angola; dashed line: eastern Central Pacific). (b) Eastern boundary (Northern Benguela). (c) Western tropical shelves (drawn line: northern South America; dashed line: East Africa).

catch of a haul is large. Nonetheless, size spectra based on average weight should reflect changes in overall size composition.

The Shannon-Wiener diversity index, which combines information on species richness (number of species) and how individuals are distributed among species (Magurran, 1996), was calculated. Changes in evenness (or dominance) were graphically represented by k-dominance curves (Lambshead *et al.*, 1983).

A crude index of exploitation was derived by dividing total landings of target species by their biomass. For the North Sea and Scotian Shelf, biomass estimates were based on stock assessment. For the other areas, the standing biomass was estimated from the bottom-trawl surveys. The latter usually represent a fraction of the true standing biomass and the indices must therefore be treated as relative: they are not comparable across systems but may be used to analyse trends within each region.

Results

Size spectra

The size spectra of the RV "Dr Fridtjof Nansen" data (Fig. 1) were grouped according to broad ecosystem similarities. When slopes are plotted against intercepts (Fig. 2), the points representing the different regions fall on an almost straight line, indicating a correlation between the respective values of the two parameters. However, the most productive systems (Northern Benguela, Angola, and the eastern Central Pacific) are grouped in the upper left of the diagram, whereas the lowest values of the intercepts are found off East Africa (13.4, SE 1.8) and in the western Arabian Sea (18.6, SE 1. 8). Thus, the intercepts seem to reflect the level of productivity.

In the boreal systems represented by the North Sea (ICES, 1996) and Scotian Shelf (Fig. 3a), the slopes tend to decrease and the intercepts increase correspondingly. On the eastern Scotian Shelf, there may be a reversal of the trend from about 1994 onwards.

Time series for upwelling systems (Fig. 3b) are less comprehensive and they either consist of few points or cover a short time span. Off Portugal, the shallow assemblage shows a clear decrease in slopes while no clear trend is obvious for the deep assemblage. Data for Namibia cover the period after its independence. The slopes increase gradually, and the intercepts decrease, until 1995 and the trends reverse afterwards.

Among the cold-water, upper-slope systems of the Southern Hemisphere (Fig. 3c), the three New South

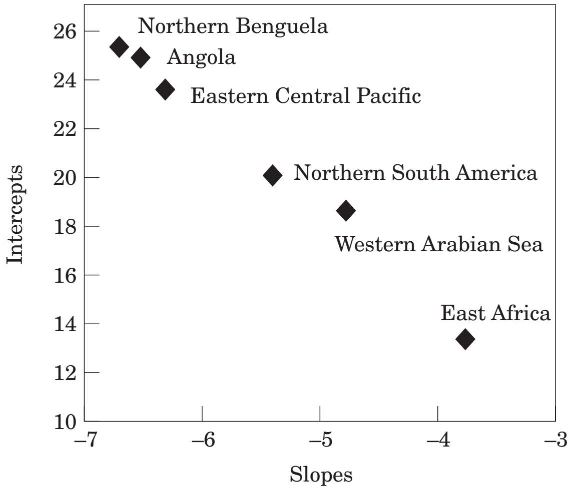

Figure 2. Cross-system comparisons of the relationship between slopes and intercepts of size spectra of demersal fish communities (size range used in regressions: 20–70 cm).

Wales assemblages show drastic changes in slopes and intercepts, reflecting a significant shift in the size spectrum toward smaller sizes.

No significant changes are evident for the shelves off Ghana, Mexico, and Mozambique (Fig. 3d). Also, no great change seems to have occurred in the Bohai Sea between 1959, when the fisheries were hardly developed, and 1992. However, the results for 1998 indicate a sharp decrease in slope and thus a shift in the size composition towards smaller sizes.

Exploitation indices

Time series of slopes and exploitation indices are presented in Figure 4. In the North Sea, the exploitation indices have been fluctuating over the past 20 years around a fixed value, in contrast to the clear decreasing trend in the slope of the size spectrum.

On the eastern Scotian Shelf, the history of fishing during the past 30 years can be split into three periods: high exploitation until the establishment of Canada's EEZ in 1977 (maximum catch of 450 000 t), lower and stable exploitation until 1992, and a strong reduction after the introduction of the moratorium in 1993 (catches of about 30 000 t). The slopes oscillate, with a period similar to that of the catches, around a declining trend, indicating an increasing proportion of smaller fish. Trawlable biomass has also declined from 1982 to 1998. However, since the moratorium was imposed, the trend has been reversed and the annual slopes of the integrated community size spectrum show an increasing trend. On the western shelf, the exploitation index has been variable, with an apparent increase over the past 8–10 years. The corresponding slopes exhibit a decreasing trend throughout the period.

The data for the northern Benguela follow 20 years of heavy exploitation. After independence in 1990, the Namibian Government implemented a stock-rebuilding policy. As a consequence, effort was drastically reduced and hake catches dropped from around 350 000 t in the 1980s to 50 000 t in 1990. Thus, the slopes for 1990 and 1991 represent the result of two decades of heavy exploitation and the start of a period of lighter exploitation. In 1993 the slopes already seem to have responded to the more conservative exploitation rate and they increase further until 1995. However, the exploitation index has been increasing again, although not at the same rates as in the 1980s. This seems to coincide with a new downward trend in the slopes. However, hake stocks dominate the demersal biomass (about 60% of the total) and fluctuations in year-class strength, which may be related to the environment (Strømme and Hamukuaya, 1998), also affect the slope.

On the shrimp grounds of the Campeche Bank (Mexico), slopes are at the same level as in the 1980s, while exploitation rate has been much lower since about 1982. Size spectra on the Sofala Bank (Mozambique) do not show a significant change, despite a threefold increase in fishing effort (Gammelsrød, 1992). In the Bohai Sea, the drastic change in the slope in 1998 followed an increase in exploitation index between 1982 and 1992. Also, bottom trawling was forbidden in 1998 and the introduction of gillnets may have increased fishing pressure on large fish (Jin, 1996). In Ghana, the size spectrum has apparently fluctuated around a constant level, despite a doubling of the exploitation index between 1980 and 1990 (K. Koranteng, pers. obs.).

Diversity

The Shannon-Wiener (SW) index of diversity, its equitability (evenness) component and the number of species recorded for the two assemblages of the Scotian Shelf (top) and the two off Portugal (bottom) are presented in Figure 5. On the western Scotian Shelf, the SW index has fluctuated without clear trend in the past 20 years. The minimum was around 1972, coinciding with a decrease in evenness. Species richness has increased slightly over time. On the eastern shelf the pattern is similar, but the lowest value of SW was observed in 1989 and seems also associated with reduced evenness. Species richness appears to have increased markedly from around 40 in the 1970s to 60 in 1994.

Off Portugal, the SW index fluctuates much more than on the Scotian Shelf and seems to be largely synchronized with fluctuations in species evenness. However, the high level of diversity in the shallow assemblage of 1982 is due to the high number of species identified. The system seems to be highly dynamic in terms of relative abundance of species and year-to-year differences within assemblages are larger than the between assemblages.

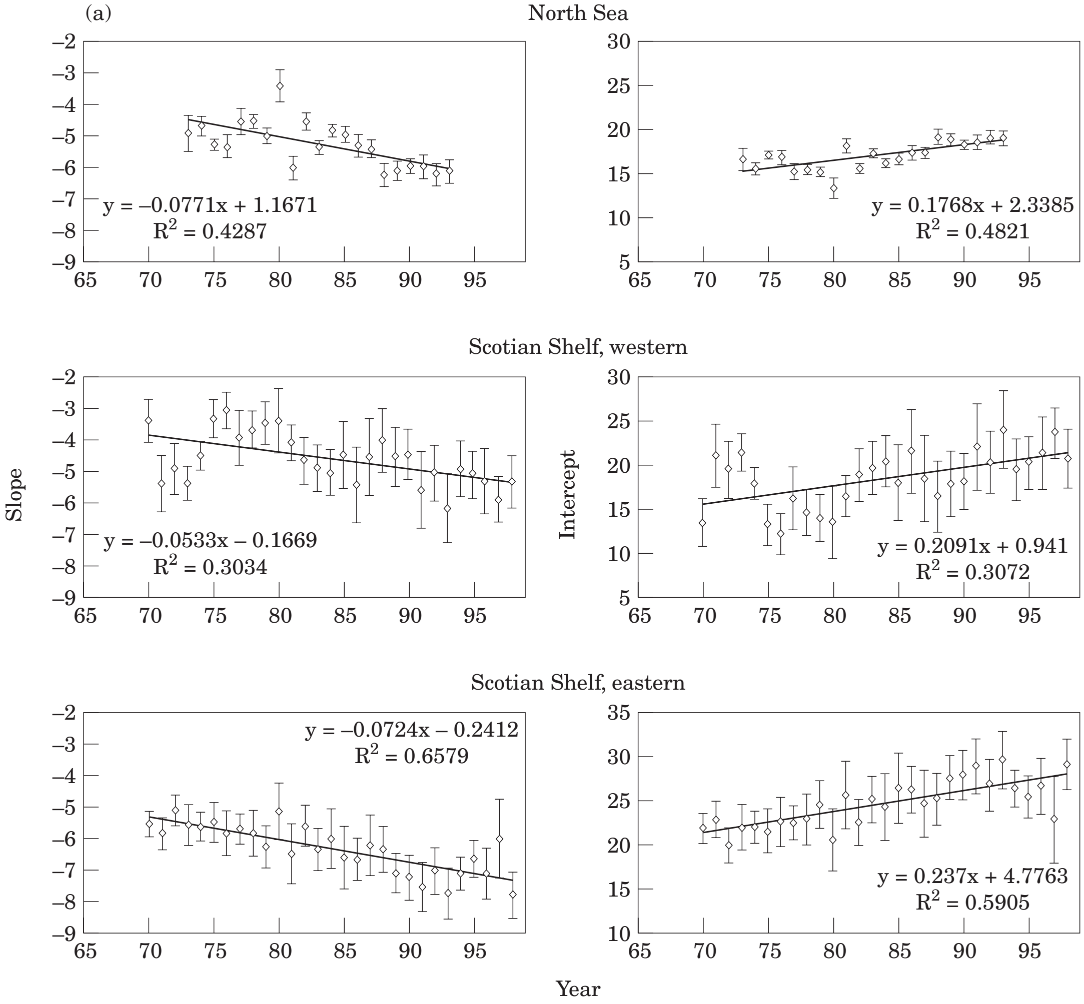

Figure 3 (a)

Figure 6 shows a plot of the SW index in relation to evenness and species richness for some tropical and temperate regions, for which time series are too short to reveal clear trends. The SW index is influenced both by evenness and richness and the different regions seem to be characterized by specific combinations of the values of the three parameters. Thus, besides year-to-year fluctuations within each region, Chile and Argentina fall on the side with lowest diversity indices, whereas diversity is highest in the tropical regions, both because of higher species richness and because of higher evenness.

Figure 7 shows the k-dominance curves for different areas and years. On the Scotian Shelf, dominance curves fluctuate more strongly in the eastern part (with a marked shift upwards in 1998), while the pattern is more consistent and at a lower level on the western shelf. The shallow assemblage off Portugal seems to have moved to a high dominance regime, with snipefish (*Macrorhamphosus scolopax*) representing 80% of the catch, compared to the early 1980s, when blue whiting (*Micromesistius poutassou*) represented 30% of the catch. The snipefish is small (about 8 cm), covered by hard scales, and with strong spines at the fins. It has recently been joined by boarfish (*Capros aper*), a closely related species with similar body structure and habitat.

Tropical systems (Fig. 7) appear to be characterized by higher evenness, and trends over time seem to go in the opposite direction to those observed for higher-latitude systems (i.e. evenness increases; Ghana, Campeche Bank, and Sofala Bank).

Discussion

Size spectra

The question whether cross-system differences can be detected in the size spectra from different ecosystems

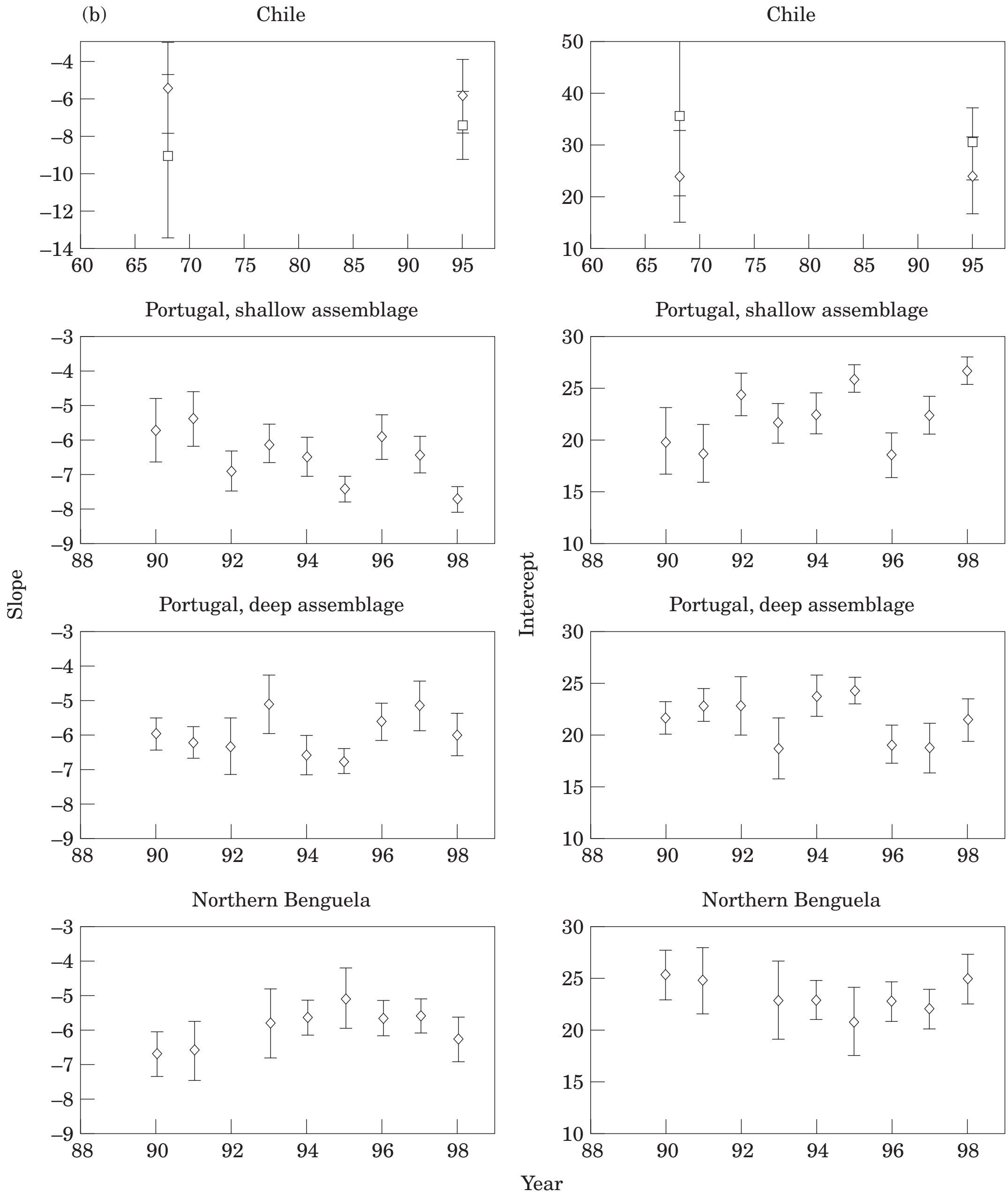

Figure 3 (b)

was first posed by Pope and Knights (1982) in relation to the differences between the size spectra of the North Sea and the Faroe Bank. They wondered whether these differences resulted from different fishing regimes or merely from system differences.

Cross-system comparisons of size spectra are difficult because not only do different regions have different environmental regimes, they also have different histories of exploitation. Also, available data have often been collected with different sampling gears and different levels of resolution. The data set based on RV "Dr Fridtjof Nansen" surveys has the advantage of having been collected with the same gear type. Major differences were found in the characteristics of the demersal community size spectra, which mainly appear to reflect different levels of productivity, with East Africa being the poorest among all areas investigated. The low value for the shelf off Oman is surprising, considering that the

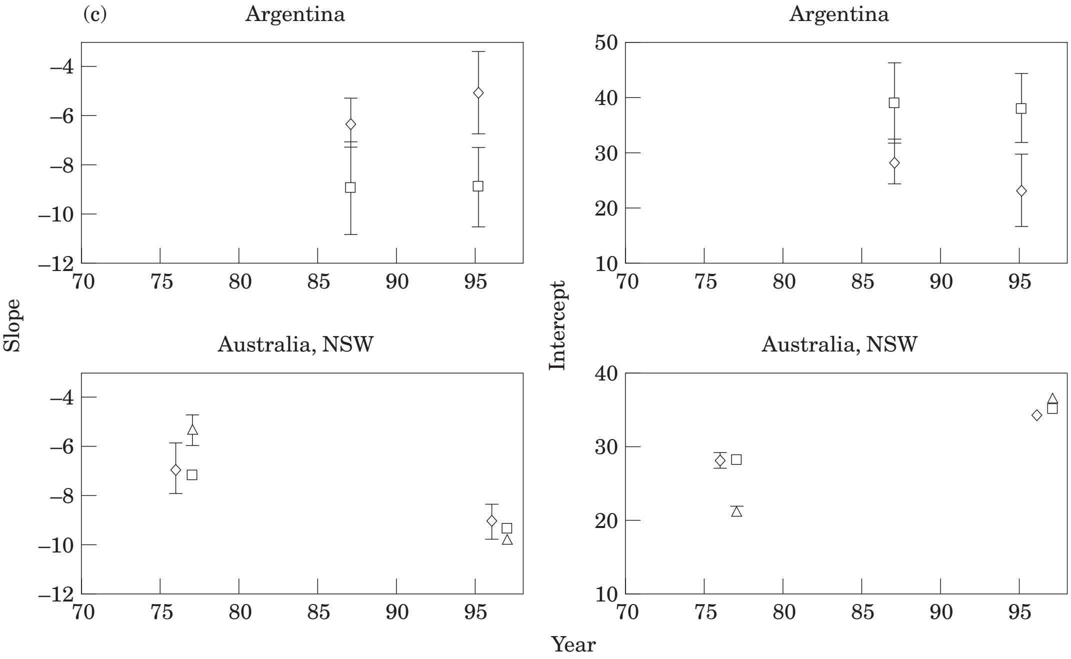

Figure 3 (c)

seasonal monsoon strongly enhances productivity and that demersal fish were practically unexploited at the time of the survey. This shelf seems to be more like the East African Shelf in terms of densities than like the other tropical upwelling regions (eastern Central Pacific and Angola). Sætersdal *et al.* (1999), in summarizing the results from the survey on the shelf off Oman, indicate that the low fish production compared with expectations on the basis of primary production measurements (Gulland, 1971) can be explained by strong offshore transport. The upwelling regions of the northern Benguela and the eastern Central Pacific are the richest according to the intercepts of the size spectra. Although intercepts are also influenced by exploitation level, and comparisons between ecosystems are therefore not straightforward, an overriding consistency appears to exist between system productivity and the intercepts. Boudreau and Dickie (1992) reached a similar conclusion from a comparison of biomass spectra from seven different aquatic environments.

The slopes are directly related to fishing. According to Gislason and Rice (1998), the slope of the integrated size spectrum is proportional to fishing mortality. Our findings would indicate that the level of exploitation is lowest off East Africa and Oman, intermediate off the northern coast of South America, and slightly higher in the other regions. However, the steep slope obtained for the eastern Central Pacific is surprising, considering that this shelf is virtually unexploited, except in the very shallow part, similar to the East African Shelf. The slopes for the shallow waters of the Sofala Bank off Mozambique, which is under heavy exploitation by shrimp trawlers, are indeed steeper than off East Africa and Oman, suggesting that indeed the slope may be related to the level of fishing rather than to type of environment.

Overall, our answer to the first question is that size spectra do differ in different ecosystems. Each profile reflects the integrated density of fish in an area and thus the overall productivity of fish. The intercepts seem to be related to system productivity while slopes depend on the level of exploitation. These features are, however, not always consistent. Despite general ecosystem differences, the size spectra are affected by different histories of fishing intensity, and therefore their interpretation within an area is not straightforward.

For areas where consistent time series are available, slopes and intercepts respond consistently to changes in level of exploitation: slopes become steeper following heavy exploitation (North Sea) and flatter after periods of less exploitation (recent years for the eastern Scotian Shelf and Northern Benguela). This adds evidence to the findings by Rice and Gislason (1996).

The rate at which the slope changes appears to be related to the growth rates of the species present. Gislason and Lassen (1997) show that the rate of change of the slope under a given fishing pressure is inversely proportional to a weighted average of the von Bertalanffy growth parameter K of the constituent

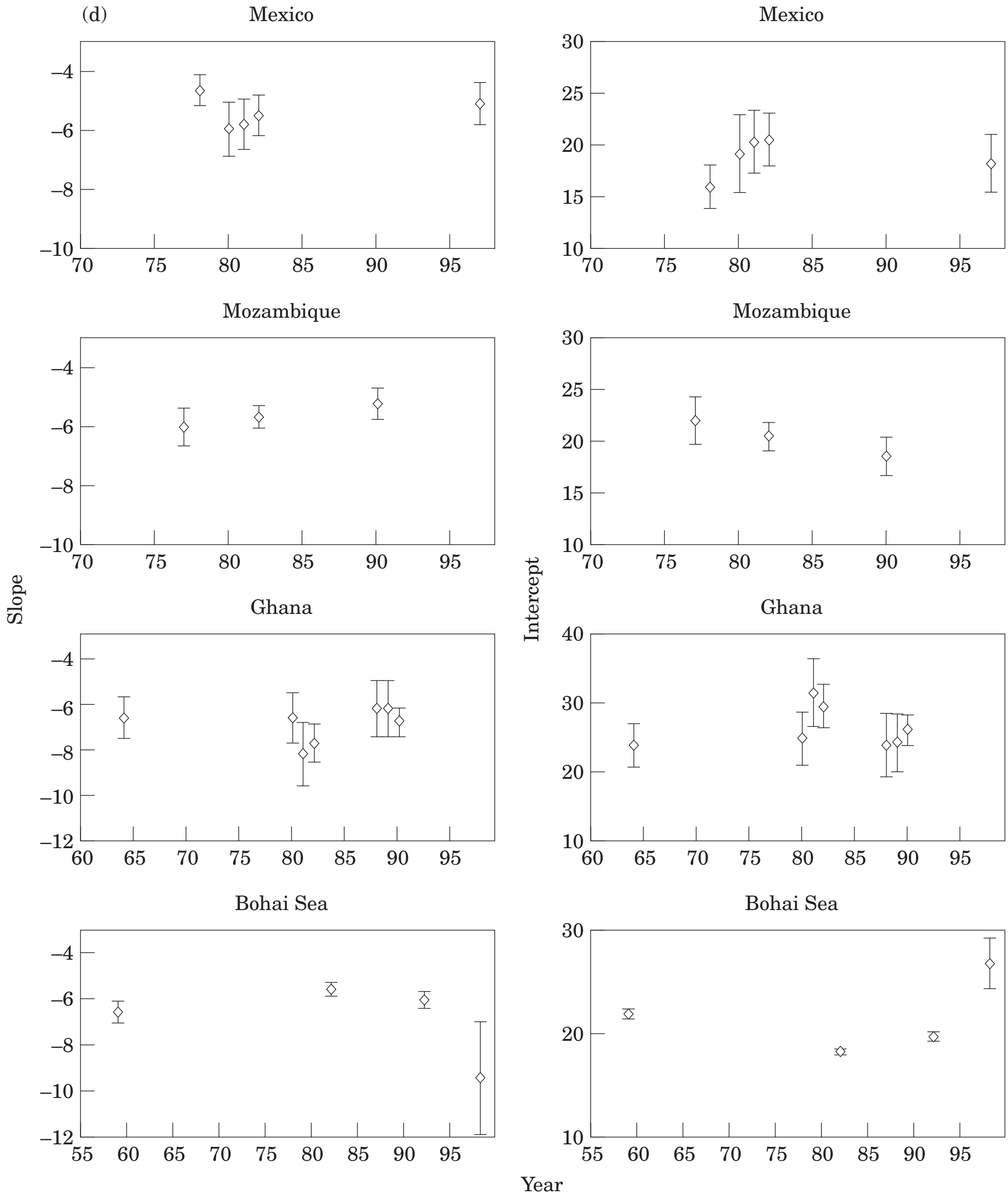

Figure 3 (d)

Figure 3. (a) Trends in slopes (left panels) and intercepts (right panels) with 1 SE over time for size spectra (range used in regressions in parentheses). (a) Boreal regions (20–80 cm): North Sea (data from ICES, 1996) and western and eastern Scotian Shelf. (b) Trends in slopes (left panels) and intercepts (right panels) with 1 SE over time for size spectra (range used in regressions in parentheses). (b) Upwelling regions: Chile (25–60/75 cm; diamonds: shallow assemblage; squares: deep assemblage), shallow and deep assemblage Portugal (5–60 cm), northern Benguela (20–70 cm). (c) Trends in slopes (left panels) and intercepts (right panels) with 1 SE over time for size spectra (range used in regressions in parentheses). (c) Cold waters of the Southern Hemisphere: Argentina (40–70 cm; diamonds: northern assemblage; squares: southern assemblage), North South Wales (Australia; 30–90 cm; diamonds: Ulladulla; squares: Sydney; triangles: Eden). (d) Trends in slopes (left panels) and intercepts (right panels) with 1 SE over time for size spectra (range used in regressions in parentheses). (d) Tropical regions: Mexico (12–48 cm), Mozambique (20–70 cm), Ghana (15–65 cm); and the Bohai Sea (10–70 cm).

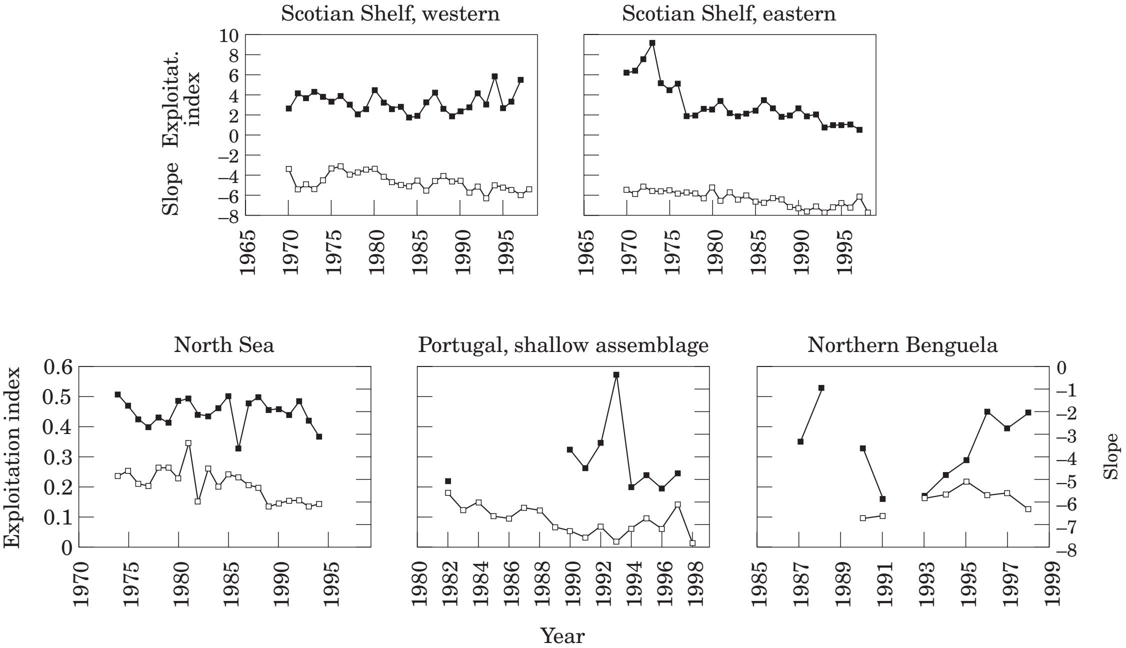

Figure 4. Time series of slopes (open squares) and exploitation indices (filled squares) for the western and eastern Scotian Shelf, North Sea, shallow-water assemblage Portugal and northern Benguela.

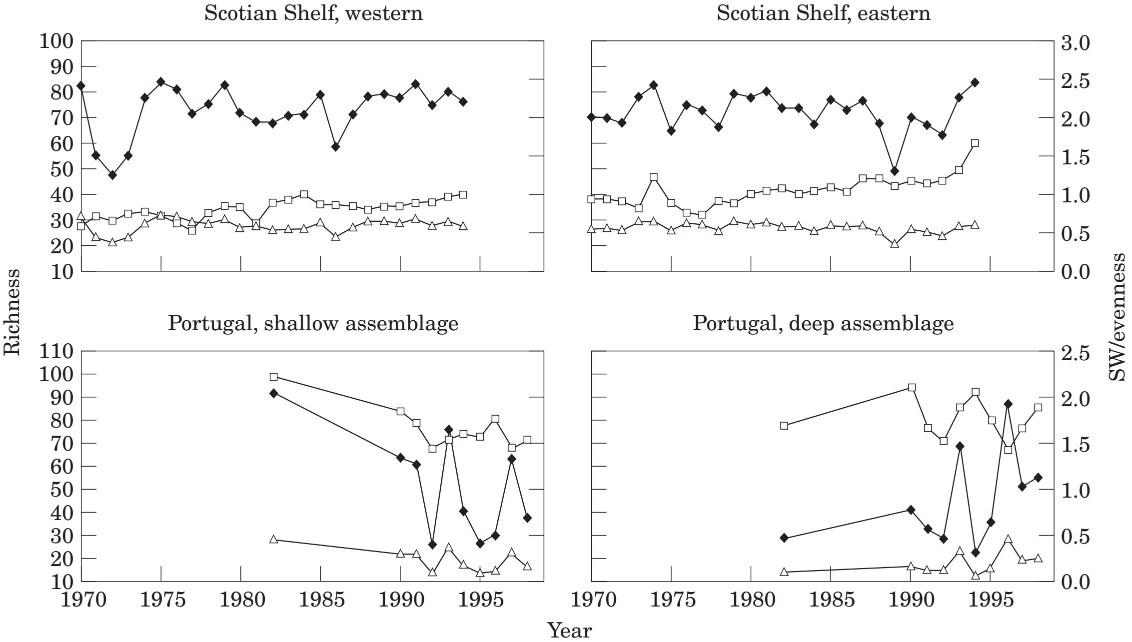

Figure 5. Time series of Shannon-Wiener diversity index (diamonds), richness (squares), and evenness (triangles) for the western and eastern Scotian Shelf and the shallow-water and deep-water Portugal.

species. Differences in K between warm- and cold-water demersal species have been reported by Pauly (1980), higher values being expected in species of warm tropical regions. Higher K-values are also related to smaller size at first maturity and would mean, other things being equal, a lower rate of change of the slope of the spectrum for a given fishing pressure. The opposite would be true for species living in cold, deep water,

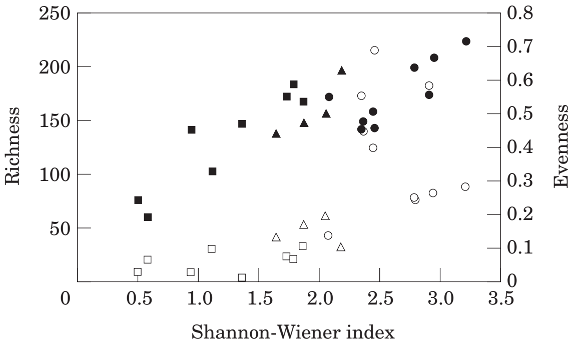

Figure 6. The relationship between annual Shannon-Wiener indices and annual evenness (filled symbols) and richness (open symbols) for Chile and Argentina (squares), Bohai Sea (triangles), and Mozambique, Oman and Mexico (circles).

and/or high-latitude environments. This might explain the drastic change observed in deep waters off Australia as opposed to the lack of change observed off Ghana or Mozambique after a steep increase in fishing effort (Gammelsrød, 1992). The relationship between growth characteristics of species within a given community, their vulnerability to fishing, and how this affects the rate of change in the slopes of the integrated community size spectrum all seems worth further investigation.

The most complete data series (North Sea and Scotian Shelf) show important year-to-year fluctuations. In systems dominated by a few species, fluctuations may be expected to be strong and related to variations in recruitment. A very strong year class will make the slope steeper as it recruits to the community, but will have the opposite effect as it moves through the larger size classes until it disappears from the community. Thus, in systems characterized by large recruitment variation, a snapshot of the community size spectrum might not be informative in respect of state of exploitation. Aside from annual fluctuations, however, the overall steepening of the slopes is probably caused by fishing, consistent with findings by Haedrich and Barnes (1997) for the Labrador Shelf and by Rice and Gislason (1996) for the North Sea. Neither of these studies covers the time before heavy fishing. Steepening of the slope may reflect two effects: a stronger reduction in k-selected species (large maximum size and slow growth) and disappearance of older age classes from the population. These effects appear to be stronger than the homeostatic properties hypothesized by Murawski and Idoine (1992), by which the community would tend to maintain its size structure.

Construction of size spectra entails a number of subjective choices that may lead to different results. Size spectra always show a tail of points departing from the linear model, representing rare, large specimens. The selection of the length range or data points to include in the regression is critical to the slope estimate. More theoretical work appears to be necessary for standardization of the results.

As regards the question whether size spectra can be used as an indicator of level of exploitation in poorly known areas, it seems that the slope does provide some indication, but only at a coarse level.

Diversity and dominance

We have looked at possible changes in diversity in terms of species composition and dominance. Overall, there is no evidence in any of the data sets analysed that fishing has changed community structure in the direction of lower diversity. The Shannon-Wiener index suffers, however, from combining two distinct facets of diversity – species richness and the way individuals are distributed among species (evenness). These two facets may work in opposite directions and their effects are confounding, so that major changes in a community may result in similar diversity indices. For some data sets, the diversity index increased (e.g. eastern Scotian Shelf) following many years of high exploitation. In all cases, higher diversities were related to a higher number of species identified, to increased evenness or to both. In the eastern Scotian Shelf there is a gradual, overall increase in number of species identified. Whether this increase is caused by an influx of new species, increased abundance of formerly rare species, or by an improved survey protocol remains to be ascertained.

Rijnsdorp *et al.* (1996) and Greenstreet and Hall (1996) found that dominance increased (i.e. evenness decreased) in the southern and north-western North Sea, respectively, when comparing data from the first half of the century with data from the second half. We found similar trends in cold-water systems if available time series covered decadal periods (Scotian Shelf and Portugal).

Inconsistencies in species identifications over time effectively reduce the possibility of detecting real changes that may have occurred. Proper taxonomic classification of non-commercial species has not always been a priority, even in scientific surveys. The lack of proper and readily available taxonomic literature has aggravated this problem, particularly in the highly diverse, tropical regions. From the case studies available to us, we believe these difficulties are of global extent.

Conclusions

Our understanding of demersal fish communities, and how fishing activities affect them, is still in an exploratory phase. In the kaleidoscope of natural and man-induced fluctuations, we are trying to detect general patterns. Data collected from pre-fishery years represent

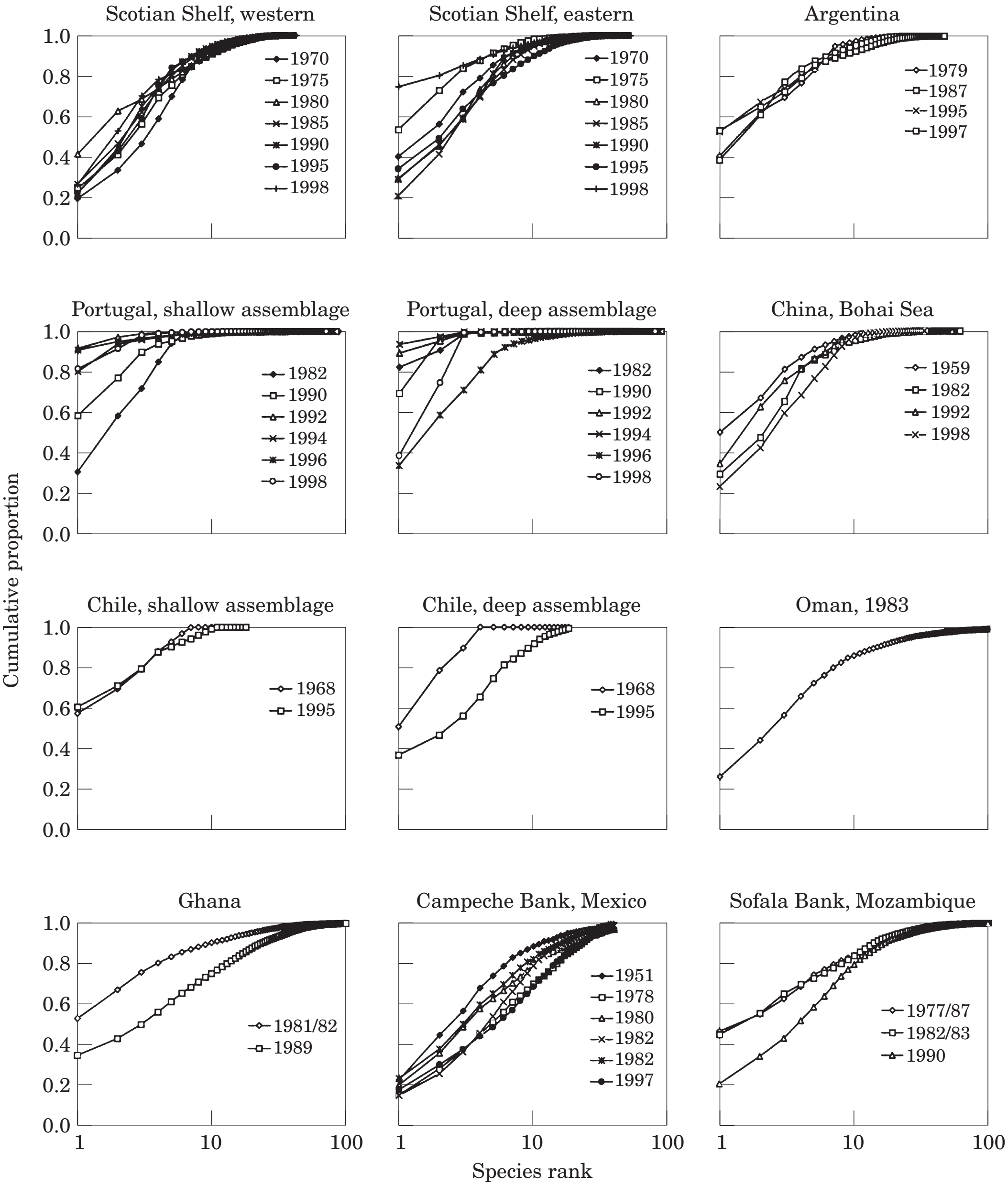

Figure 7. k-Dominance curves for different demersal fish communities for selected years.

an important reference for evaluating the relative importance of man-made disturbance, and such data should be further analysed. Data archaeology – recovery of data from early scientific surveys – should become a priority item on the scientific agenda world-wide. International legislation should ensure that coastal countries, and particularly developing countries, gain access to datasets collected before their EEZs were established. Only this will allow them to reconstruct the history of the fisheries and the impacts these have had on the environment.

However, utilization of scientific surveys has important limitations. Surveys are generally planned to estimate the abundance of main commercial species and little effort is devoted to systematically recording all species caught. Aware of past mistakes, worldwide efforts should be made to generate a baseline for future reference, even though this baseline will often represent a state already influenced by heavy exploitation.

Notwithstanding these problems, the following conclusions can be drawn:

(1) There is evidence that the size structure of demersal fish communities is affected by fishing and slopes of size spectra of communities subject to intensive exploitation tend to become steeper, indicating decreasing average length of the individuals caught. This is particularly evident if comparisons involve pre-fishery stages, but it is also true for time series that start during periods of high fishing pressure. The overall trend is one of a reduction in large fish and a relative increase in small fish.

(2) The rate of change in the size spectrum of communities in different ecosystems in response to fishing may be different, and further theoretical work is necessary to take into account differences in life history strategies of component species.

(3) The usefulness of size spectrum analysis for management purposes is still limited as there is not enough empirical and theoretical background for the interpretation of observed values of slopes and intercepts.

(4) The largest changes in diversity appear to be due to changes in evenness and/or species richness, often leading to an increase in diversity in response to heavy exploitation. In some cases, the increases in diversity may be caused by improved survey and identification protocols.

(5) Efforts should be made to recover and analyse data collected during early scientific surveys. These constitute important historical material and will be invaluable in determining the overall direction of change.

(6) Throughout their work, the authors have encountered difficulties because of inconsistencies in the available data sets. Effort should be put into standardizing data collection and developing appropriate sampling design to satisfy requirements of comparative studies. Long-term research, planned to provide consistent time series, is crucial for a proper monitoring, and understanding, of the marine environment. Efforts world-wide should acknowledge the long-term objective of ecosystem management in addition to short-term goals of obtaining information on the main commercial species.

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