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ON THE DYNAMICS OF DEMERSAL FISH ASSEMBLAGES OFF NAMIBIA IN THE 1990s

G. BIANCHI, H. HAMUKUAYA† and O. ALVHEIM**

Demersal fish surveys carried out off Namibia from 1990 to 2000 were used to study the dynamics of demersal fish assemblages on the shelf and upper slope. The study was performed on each major assemblage, i.e. over the shelf (100–300 m deep) and the slope (300–600 m). Changes in size spectrum, diversity, species composition and trends in abundance of the dominating species were analysed. The most evident changes were those related to overall abundance and diversity of the slope assemblage.

Key words: community dynamics, diversity, Namibia, size spectrum, species composition

The shelf and upper slope demersal assemblages of Namibia were subject to heavy fishing by bottom trawlers from the 1960s. The Cape hake *Merluccius capensis* and *M. paradoxus* were the major component of the catch; they were seriously overexploited already by the mid 1970s and remained in that state despite the efforts of ICSEAF (International Commission for the Southeast Atlantic Fisheries) member countries to manage the resource better. By Independence in 1990, hake stocks were considered to be severely overexploited (Anon. 1988, Sætersdal *et al.* 1999). The Namibian government immediately implemented a rebuilding strategy by reducing the fishing capacity from some 300 vessels to just 55 in 1991 (Hamukuaya 1999). Landings, that had averaged >500 000 tons in the 1970s, and >300 000 tons in the 1980s, dropped to just over 100 000 tons in the early 1990s (Fig. 1). Fishing pressure remained well below earlier levels throughout the 1990s, although there has since been a steady increase in the number of vessels operating, to 105 in 2000.

It is reasonable to assume that the heavy fishing effort of bottom trawlers prior to 1990, for such a long period of time, had an impact on the marine environment and particularly on fish community structure. Fishing may impact community diversity, size composition and the life history traits of component species.

Efforts have recently been made by various authors to evaluate the extent to which fishing affects non-target species or, more generally, community structure. Jennings and Kaiser (1998) and Kaiser and de Groot (2000) reviewed several aspects of the effects of fishing on non-target species and habitats. Greenstreet and Hall (1996) recorded significant changes in species relative abundance and a reduction of species diversity in three regions of the north-western North Sea, when comparing data for the period 1929–1953 to that for the period 1980–1993; they concluded that these changes could constitute a fishing effect. In another study, of the English side of the southern North Sea, Rogers and Ellis (2000) compared research survey data from the period 1901–1907 with data from the period 1989–1997. Their data revealed increased diversity in the more recent period that could be explained by decreased dominance.

Another metric that has been explored and used to evaluate the effects of fishing on community structure is integrated community size composition (size spectrum). Rice and Gislason (1996) found a significant decrease in the slopes, and a concurrent increase in the intercepts, of the overall community size spectrum of North Sea fish over the period 1973–1993. Gislason and Rice (1998) demonstrated how slopes and intercepts of size spectra of a fish assemblage are linear functions of fishing. Zwanenburg (2000) showed that the integrated community size spectrum had been declining on the Scotian Shelf over a period of 20 years, a decline that corresponded to a decline in individual body weight of about 50% and was paralleled by an increase in fishing effort. The decrease in body weight was concurrent with changes in bottom temperature that may have affected the growth rates of individual species. Although the relative importance of fishing and bottom temperature on size composition seemed difficult to evaluate, Zwanenburg (2000) noticed that both the western and eastern Scotian Shelf had experienced a continuing reduction in mean size, despite the fact that trends in bottom temperature were contrasting in the two areas. He concluded that fishing had had an impact on community size composition.

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* Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway. E-mail: gabri@imr.no and oddgeir.alvheim@imr.no
† Ministry of Fisheries and Marine Resources, Private Bag 13355, Windhoek, Namibia. E-mail: hamukuaya@mfmr.gov.na

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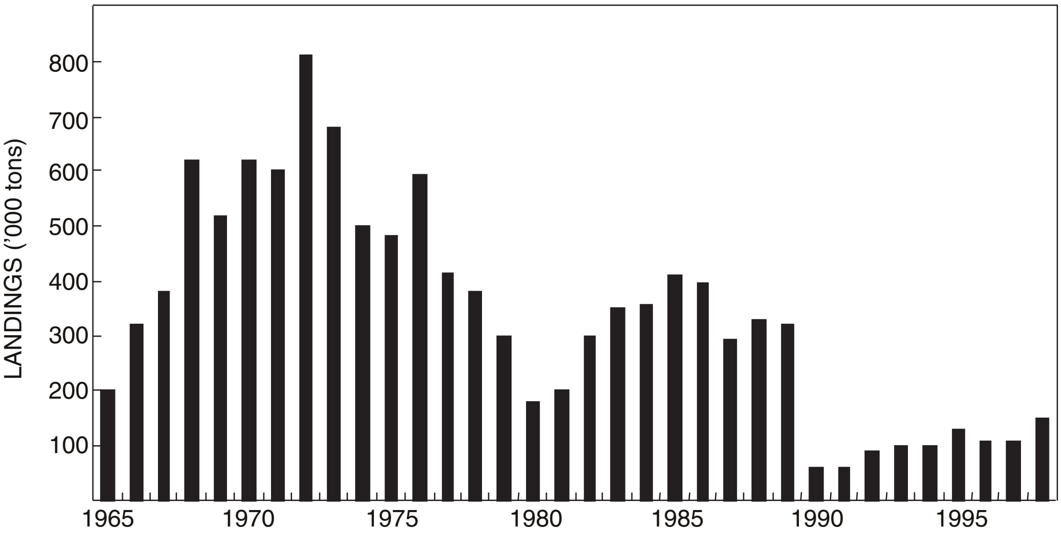

Fig. 1: Landings of hake off Namibia, 1965–1998

Haedrich and Barnes (1997) analysed scientific survey data from the shelf off Newfoundland and Labrador for the period 1978–1993 and found that mean size of both target and non-target species had decreased over time. They concluded that overfishing seemed to be the main factor implicated in the changes.

Bianchi *et al*. (2000) analysed datasets from different areas of the world to study temporal and spatial cross-system patterns in size spectra and diversity. They also used these metrics to evaluate the effects of fishing on demersal fish community structure and concluded that size spectra seemed to respond to different levels of fishing intensity, but that there were also clear ecosystem patterns. Rice (2000) concluded that size spectra and k-dominance curves emerged as promising metrics of aggregated community properties to evaluate fishery impacts.

The present study aims to evaluate whether and in what manner the main demersal assemblages of Namibia have responded to lighter levels of exploitation during the past decade by analysing community metrics that have been shown to summarize community properties best, i.e. community size spectrum and diversity, including k-dominance. Abundance of non-target species is also analysed. It is assumed that the demersal fish assemblages off Namibia had been dramatically impacted by lengthy, continuous heavy fishing effort, and the hypothesis was therefore that

Table I: Surveys and the number of trawls used in the analysis. Project codes and station numbers used in the database from which the data were extracted are also included

Year	Start date	End date	Project code	Station number	Number of stations
1990	26/01	18/03	NA	2 – 242	241
1991	27/01	20/03	NA	501 – 710	210
1992	24/04	19/05	NA	1061 – 1225	165
1993	21/01	23/02	NA	1566 – 1759	194
1994	21/01	21/02	N1	1 – 152	152
1995	22/04	28/05	N1	920 – 1104	185
1996	14/01	17/02	N1	1185 – 1427	243
1997	12/01	19/02	N1	1857 – 2124	267
1998	13/01	20/02	N1	2229 – 2442	214
1999	13/01	18/02	NC	2600 – 2814	215
2000	17/01	22/02	NC	2815 – 3037	223

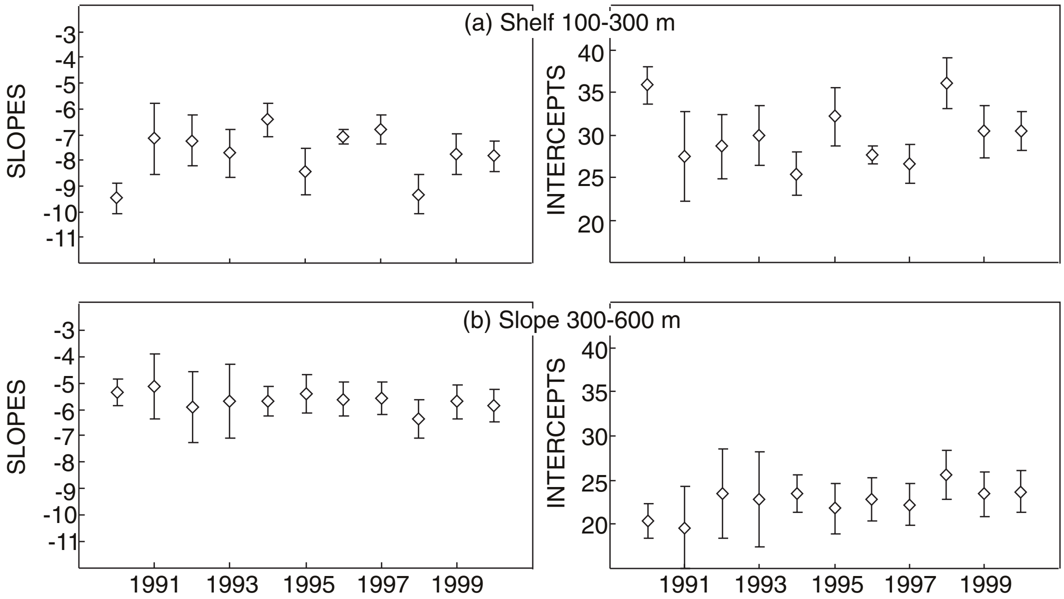

Fig. 2: Trends in slopes (left panels) and intercepts (right panels) with 1 *SE* of size spectra, 1990–2000, for (a) the shelf assemblage, (b) the slope assemblage

they had responded to the lighter fishing levels of the past decade. The expected direction of change was expected to be increased size spectrum slopes (relatively greater abundance of large fish), change in dominance and diversity, and an increase in species abundance and biomass.

MATERIAL AND METHODS

In all, 11 surveys, comprising 2 309 trawls, were carried out between 1990 and 2000 by the F.R.V. *Dr Fridtjof Nansen* and a commercial trawler off Namibia (Table I). All surveys used for the analysis took place in January or February, except for 1992 and 1995 when they took place in April/May. A description of the demersal sampling gear used can be found in Hamukuaya *et al.* (2001); it was constant throughout the study period.

A size spectrum was constructed for the shelf and upper slope assemblages, as in Bianchi *et al.* (2000), by plotting the natural logarithm of the total number of individuals per hectare, by 5 cm length-class, for all species in the assemblage, against the natural logarithm of the mid-length (weight) of each size-class. As length frequency distributions were not available for all species, though weight and numbers for each species at each trawl were available, the size spectrum was constructed in the following manner. For given species i, trawl j and K weight categories, the average individual weight of species i in trawl j was calculated by dividing the catch biomass of species i in trawl j (W_{ij}) by the number of individuals of species i caught in trawl j (N_{ij}). N_K was then calculated by cumulating all the N_{ij} corresponding to a given K weight-class. The natural logarithm of N_K was then plotted against each size-class. Size categories were determined to correspond to 5-cm length intervals and by calculating the corresponding theoretical weight, assuming isometric growth ($W = 0.01L^3$).

Slopes and intercepts of the integrated community size spectrum were calculated for the descending limb of the size frequency distribution. The size range 20–80 cm was used for calculating the regression coefficients. Furthermore, pelagic species of the families Carangidae and Clupeidae were excluded from the analyses. Intercepts and slopes, and their statistics, obtained for each dataset were used to study changes of these parameters over time.

The Shannon-Wiener diversity index, its evenness component and the number of species were used to explore differences in species diversity over time

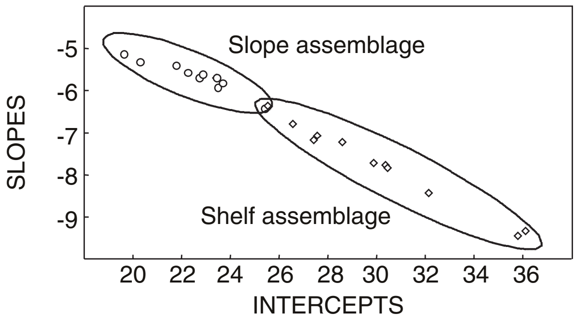

Fig. 3: Comparisons of the relationship between slopes and intercepts of size spectra for the shelf and slope assemblages off Namibia, 1990–2000

Table II: Results from the regressions of size spectra slopes and intercepts and significance of the test H_0: $b = 0$ (b is the regression slope)

Parameter	b	Upper 95%	Lower 95%	p
Shelf (100–300 m)				
Slopes	0.0054	-0.2175	0.2282	0.957
Intercepts	0.0272	-0.7690	0.8235	0.940
Slope (300–600 m)				
Slopes	-0.0519	-0.1143	0.0103	0.091
Intercepts	0.3325	0.0578	0.6072	0.023

(Magurran 1996). Changes in evenness (or dominance) were graphically represented by k-dominance curves (Lambshead *et al.* 1983). The distribution of the number of individuals and biomass among species were compared to determine the level of disturbance in the communities (ABC method; Warwick 1986). The idea is that, in environments subjected to limited disturbance, long-lived, k-selected species dominate biomass. These usually have large body size and long lifespan. In the same community, smaller, r-selected species dominate numerically. The ABC method involves plotting separate biomass and abundance k-dominance curves on the same graph and comparing the two distributions among species. Species are ranked in order of importance in terms of abundance and biomass respectively along the *x*-axis (logarithmic scale), with percentage dominance on the *y*-axis (cumulative).

Catch rates (kg h^{-1}) for the dominant species in each community were calculated for each assemblage from the NANSIS database (Strømme 1992), as a simple average in the given stratum.

Analyses were performed for the shelf (100–300 m) and slope (300–600 m) assemblages separately. Other studies (Hamukuaya *et al.* 2001) have indicated that the 300 m isobath corresponds approximately to the main ecotone of Namibian demersal assemblages.

RESULTS

Slopes and intercepts of the integrated community size spectrum for both shelf and slope assemblages are plotted as a function of survey year in Figure 2. The patterns differed in the two assemblages. The highly productive shelf was characterized by a relatively large proportion of small animals (values of the regression slope between -9.47 and -6.42), whereas the slope was characterized by a community with a higher percentage of larger animals (regression slopes between -5.94 and -5.14). The trends over time were also different in the two areas. The shelf assemblage was characterized by large fluctuation in the slopes from year to year, whereas the values were more stable for the slope assemblage. The results of regressions performed on the slopes and intercepts for each assemblage are presented in Table II, including the test of H_0: $b = 0$. In all cases, the slopes of the regression line were not significantly different from zero, indicating no linear trend in the values, except for the intercepts of the slope assemblage, where b was significantly greater that 0.

A scatter plot of slope and intercept values for both assemblages and for the whole period analysed is presented in Figure 3. Each point represents a given year for each assemblage. The fact that the points fall along an almost straight line is due to the correlation between the respective values of the two parameters. This seems to be a property of the size spectra present also when different ecosystems are compared (Bianchi *et al.* 2000). The points representing shelf and slope assemblages fall into specific parts of the diagram, despite the spread of values of slopes and intercepts, evidencing differences in size composition in the two subsystems.

The ABC plots confirmed the different nature of the two main assemblages (Figs 4, 5), with much stronger dominance over the shelf than over the slope. Furthermore, biomass and abundance curves were much closer to each other for the shelf community than for the slope community. The trends over time were not indicative of any major change in the shelf community, apart from a declining dominance (increasing evenness) over time. In the case of the slope community, there was a diverging trend of biomass

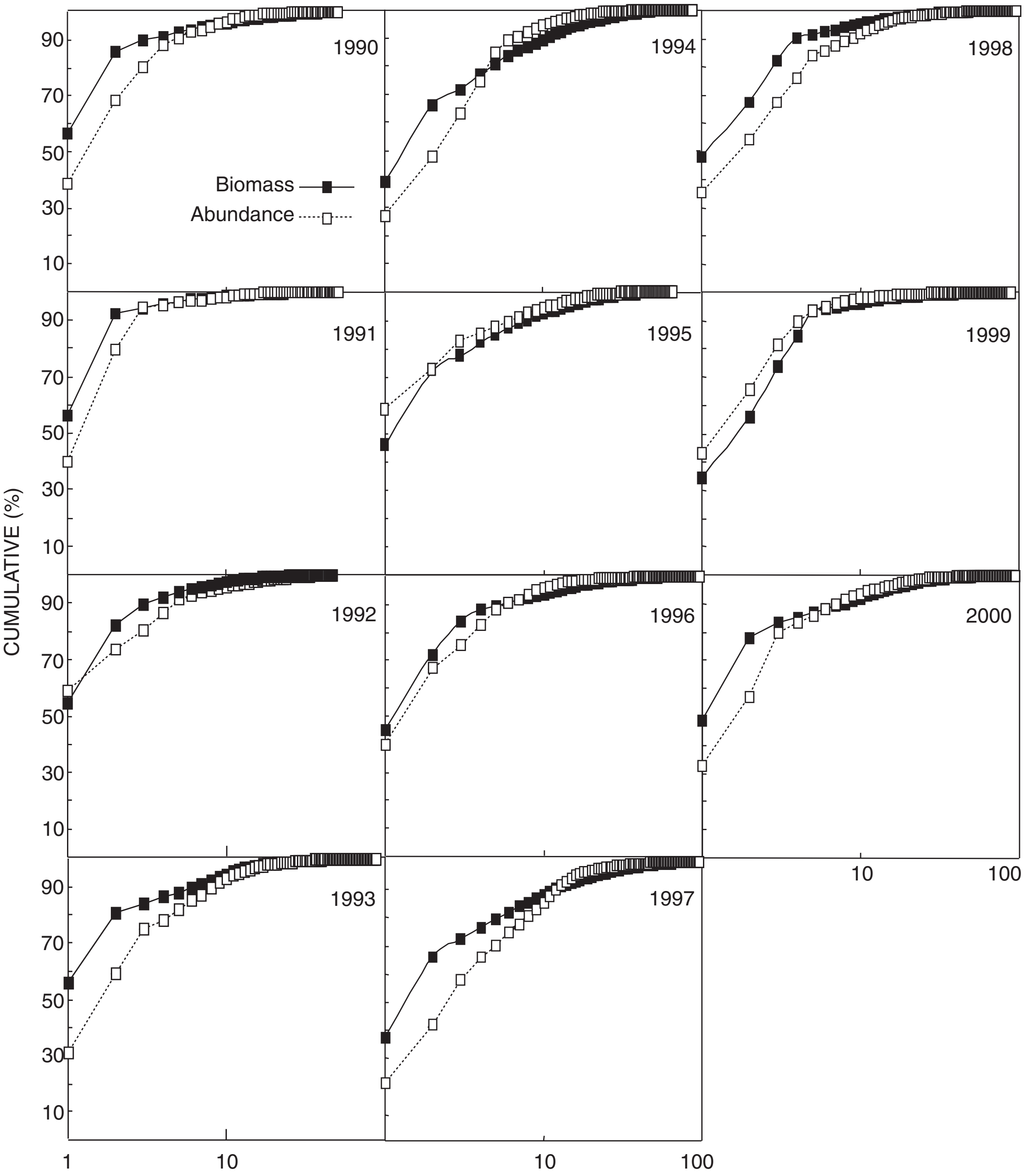

Fig. 4: Average k-dominance curves for abundance and biomass of the shelf assemblage off Namibia, 1990–2000

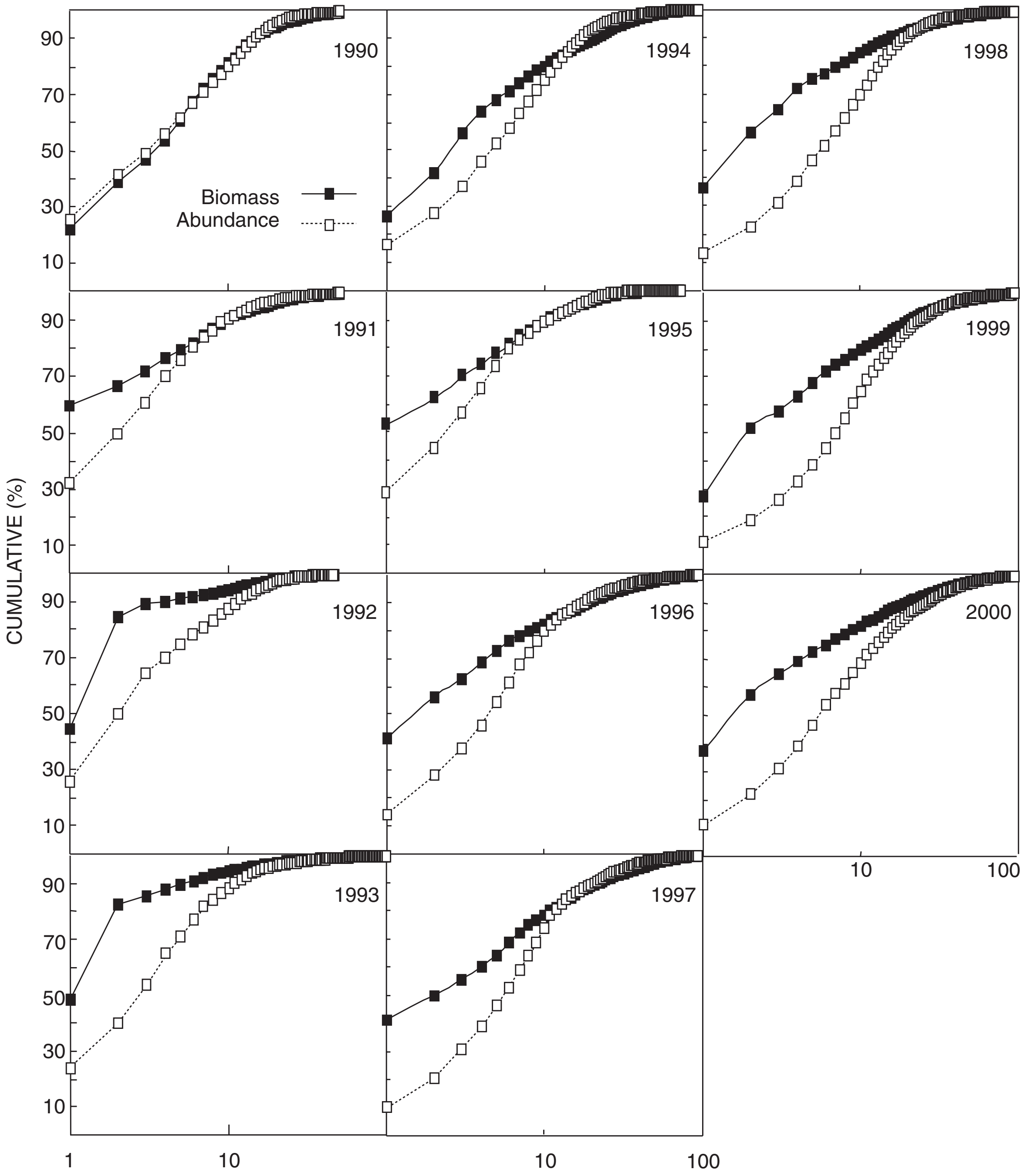

Fig. 5: Average k-dominance curves for abundance and biomass of the slope assemblage off Namibia, 1990–2000

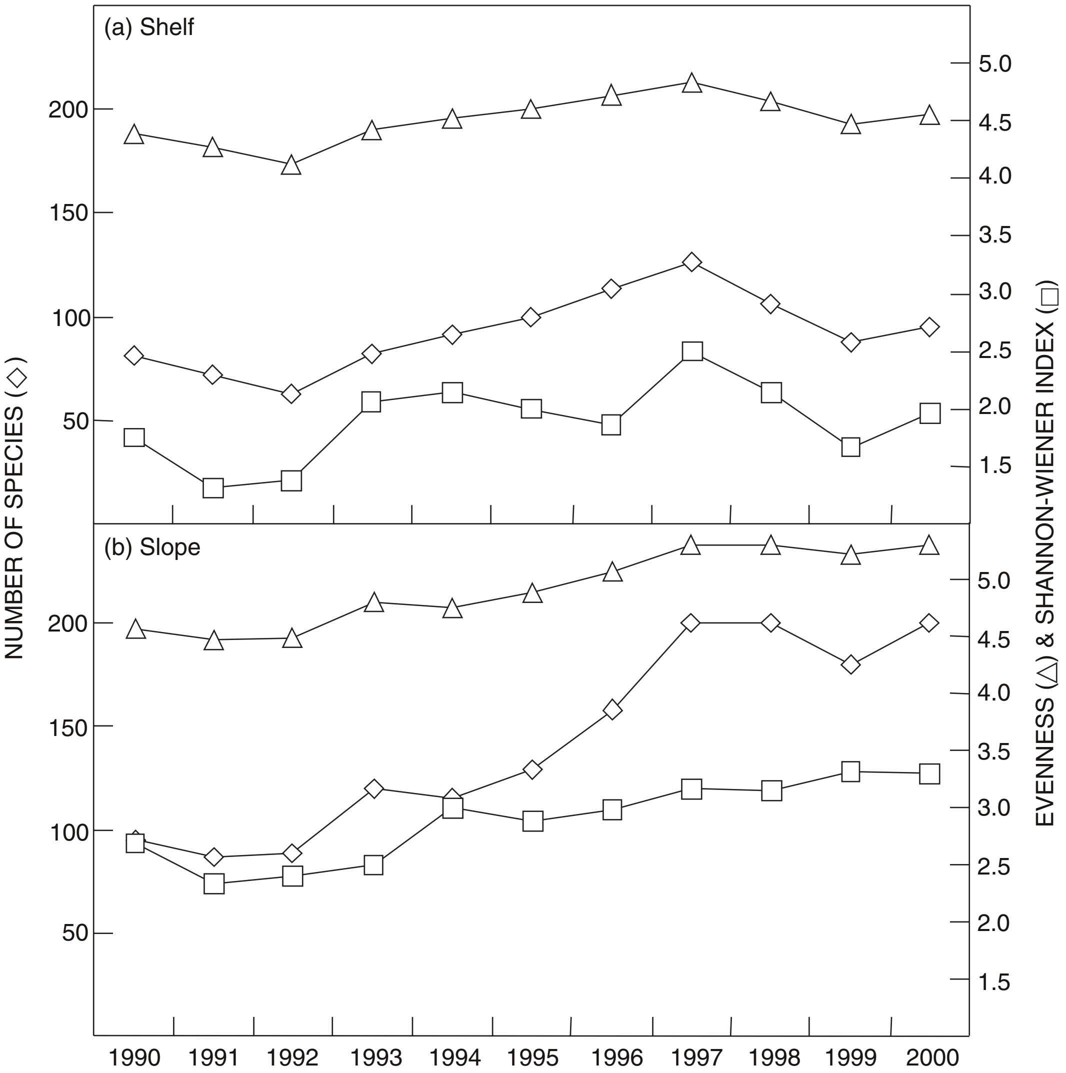

Fig. 6: Trends in the number of species, and in the evenness and Shannon-Wiener indices of diversity for (a) the shelf assemblage and (b) the slope assemblage, 1990–2000

and abundance curves over time, indicating a state of lower "disturbance". Also in this case, there is a trend of decreasing dominance in the community.

There was an increasing trend in the Shannon-Wiener index of diversity for both assemblages (Fig. 6), but it was stronger for the slope assemblage. This increase was caused by increases in both evenness and richness. The increase in richness, however, has to be interpreted with caution because it was most probably attributable to improved species identification.

Survey catch rates of dominant demersal species are presented in Figures 7 and 8 for the shelf and slope assemblages respectively. Catch rates on the shelf for all demersal species combined seemed to increase during the last part of the decade. Shallow-water Cape hake *M. capensis* and large-eye dentex *Dentex macroph-*

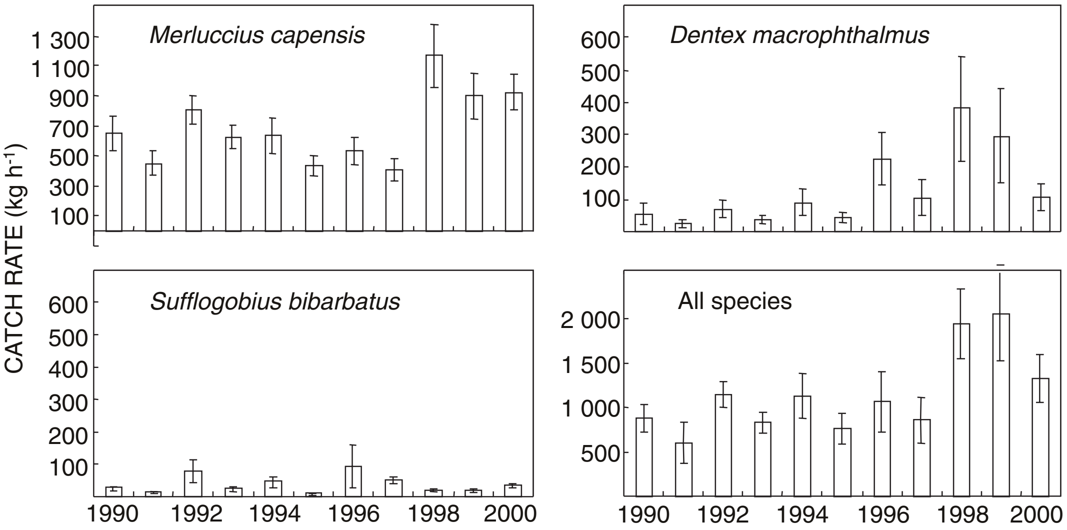

Fig. 7: Trends in average catch rates for the main species of the Namibian shelf assemblage, 1990–2000

thalmus account for most of this increase. Another dominant species, the pelagic goby *Sufflogobius bibarbatus*, appeared to be more variable, probably because of its semipelagic existence and its consequently variable availability to the sampling gear.

There was a notable increase in the catch rates of both target and non-target species for the slope assemblage, other than *M. capensis*, for which the catch rate fluctuated. Of the non-target species, increases were notable in members of the family Macrouridae (particularly *Coelorinchus fasciatus* and *Trachyrinchus scabrus*), sharks, mainly members of the family Squalidae, and jacopever *Helicolenus dactylopterus* (Fig. 8).

DISCUSSION

The results of the size spectrum analysis indicated differences in size composition between the two subsystems (shelf and slope) that can probably be attributed to differing ecosystem productivity. Differences in the dynamics of the two assemblages with regard to these metrics were also observed, the shelf assemblage showing greater variability in the overall size composition than the slope assemblage. No significant increase in the abundance of large size-classes relative to smaller ones was found for the period investigated, a surprising result given the fact that the study encompassed a decade of lighter fishing pressure. For the slope assemblage, there was a significant increase in the intercept which, combined with a lack of significant change in the slope, may be explained by an increase in number of animals of all size categories.

Macpherson and Gordoa (1996) analysed biomass spectra in the fish assemblages of the shelf and upper slope off Namibia over the three-year period 1987–1990, covering the area from just south of Walvis Bay to the Orange River; they related the patterns they observed to zonal productivity. They also concluded that there were no appreciable differences between northern and southern upper slope assemblages, which they stated were subject to higher and lower levels of fishing intensity respectively. This result is consistent with the current findings, showing some homeostatic properties of the slope communities in terms of relative abundance across size-classes.

The theory developed for the ABC curves has proven successful in determining levels of disturbance (pollution-induced or otherwise) on benthic macrofauna communities. Application to fish communities has been limited to the use of abundance k-dominance (e.g. Greenstreet and Hall 1996, Rijnsdorp *et al.* 1996). In this study, the ABC curves confirm the intrinsic differences between the two assemblages, with greater dominance of fewer species on the shelf compared to the slope, reflecting the different nature of the two biotopes. The greater dominance that characterizes the shelf assemblage may also largely explain the greater year-to-year fluctuations in size spec-

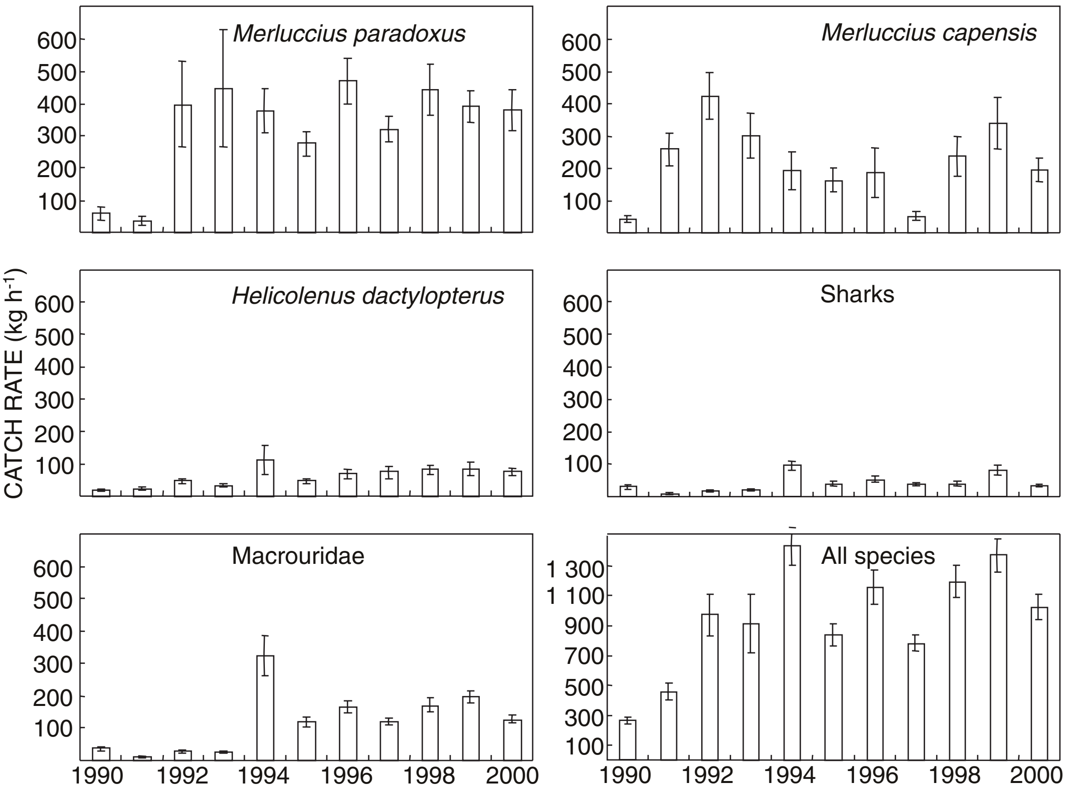

Fig. 8: Trends in average catch rates for the main species of the Namibian slope assemblage, 1990–2000

tra found in that assemblage. Given that *M. capensis* dominate the shelf assemblage, and that that species exhibits strong fluctuations in recruitment (Strømme and Voges in prep.), the overall assemblage spectrum will be largely determined by the abundance of young of that species. Strong recruitment fluctuations will introduce noise and make the detection of overall changes in size composition, attributable to different levels of fishing, more difficult. Long time-series, covering probably two or three decades, as for example shown by Zwanenburg (2000), have to be available in order to detect overall trends in community composition and to differentiate them from recruitment noise.

Changes in k-dominance over time are evident for the slope assemblage (Fig. 5), with an increase in evenness and diverging curves of biomass and abundance. These results are consistent with ecological theory, suggesting that in less "disturbed" systems, the biomass curve should be well above the abundance curve, the lower level of disturbance being in this case the significant lower level of fishing during the past decade. The results given here are also consistent with other studies where k-dominance has been used to study the effects of fishing. Greenstreet and Hall (1996) compared data for the periods 1929–1953 and 1980–1993 to study changes in fish community structure in the north-western North Sea. They showed that, in parallel with increasing fishing effort, diversity had decreased somewhat, and stated that k-dominance curves suggested increased dominance over the same period. A similar result was obtained for the southern North Sea when comparing k-dominance curves for the period 1906–1909 with those for the period 1990–1995 (Rijnsdorp *et al.* 1996).

A direct effect of fishing is the change in relative abundance of species in the assemblage. Jennings *et al.* (1999) showed how changes in the structure of the North Sea fish community could be explained by the differential effect of fishing on species with different life history parameters. They also demonstrated that fishing had more effect on slow-growing, larger species that mature late. Sharks are a typical example of such species. In the present study, this group, characteristic of the slope assemblage, showed clear indication of increasing catch rates in the past decade, a sign that the community could be responding to the changed fishing pressure in the same manner that ecological theory would predict. A systematic study of how all the main species have reacted to the revised fishing pressure in relation to their life history characteristics could be a worthwhile avenue of research for the assemblages considered in this study.

Documentation of the effects fishing is having on fish community structure is increasing, and patterns of response are emerging. These usually show how community structure changes as a consequence of increasing fishing pressure over a given period of time. This study is unique in showing how demersal assemblages react to a period of much reduced fishing pressure. Some of the patterns observed are consistent with what would be expected from ecological theory and from the results obtained from other studies and add evidence on the usefulness of the metrics used to evaluate fishery impacts. It should be recognized, however, that the phase of discovering and describing patterns is still in progress and that the processes involved are still largely unknown. Furthermore, the usefulness of the metrics used as an overall measure of community state is still limited by inadequate empirical and theoretical background for their interpretation. However, it is believed that description of patterns such as those presented here contributes to the creation of a useful basis for future theory developments.

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