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THE STRUCTURE OF DEMERSAL ASSEMBLAGES OFF NAMIBIA IN RELATION TO ABIOTIC FACTORS

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Groundfish surveys carried out between October 1992 and October 1996 were used to describe the demersal assemblages of the northern Benguela along the Namibian coast. Multivariate analyses indicated a clear separation between shelf and slope habitats, which were divided into three and two assemblages respectively. These divisions were distinct, with clear distributional boundaries separating them. Species determining the structure of these divisions and subdivisions and their relative abundances were identified. Depth, bottom temperature, bottom salinity and dissolved oxygen were all significantly correlated with the spatial distribution of the assemblages. Minor changes or shifts in the distribution of assemblages were observed over the study period, although patterns of species associations remained relatively constant.

Key words: community, demersal, environment, fishery, Namibia, trawling

A major focus of contemporary ecological and evolutionary research has been on the relationships and structure of assemblages and their biotic and abiotic characteristics. The term assemblage is used in this study to indicate an association of coexisting species, with similar environmental tolerances, but not necessarily interdependent.

Fishing activities may affect assemblage structure by altering the relative abundance of species. Fishing effort, usually tuned to the most abundant and commercially important species, may bring about dramatic changes in the less abundant bycatch species. This may subsequently alter assemblage diversity, structure and productivity.

Knowledge of the intrinsic characteristics of fish communities and of the factors most important in structuring their composition are, therefore, important prerequisites for sustainable fishery management. Tyler (1999) emphasized the present practical conflict between the goals of maintaining biodiversity and maximizing long-term fishery yields, and advocated an "assemblage maintenance approach" as the only method of achieving multispecies persistence. This study is a step towards increasing understanding of the structure and spatial distribution of demersal assemblages off Namibia and may allow for more holistic fisheries management.

A quantitative analysis of the structure of demersal assemblages along the entire Namibian shelf over an extended period has not been attempted before. Previous studies on demersal assemblage structure off Namibia have been limited by either a spatial or a temporal scale (Lleonart and Roel 1984, Olivar and Shelton 1993, Macpherson and Roel 1987, Macpherson and Gordoa 1992, Bianchi *et al*. 1993). The present study also includes all demersal macrofauna caught (including invertebrates), and relates distribution of assemblages to environmental characteristics. The study is based on more than 500 samples collected from a series of extensive trawl surveys undertaken to monitor and assess the status of demersal species along the Namibian coast during the years 1992–1996. The aims of the study were to:

- analyse trawl-survey data from samples collected along the Namibian coast from 1992 to 1996 with multivariate analysis, and to describe the structure, diversity and distribution of demersal assemblages in Namibian waters;
- assess the environmental variables at sampling stations and to determine which ones relate to the spatial distribution of demersal assemblages.

THE STUDY AREA

The study area encompasses the Namibian continental shelf and upper slope, to 600 m depth, from the Orange River (29°S) in the south to the Kunene River (17°S) in the north. This area is part of the Benguela Current ecosystem, the main characteristics of which are well

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documented (Shannon *et al*. 1984, Shannon 1985).

The Benguela Current flows in a north to north-westerly direction, roughly following the isobaths or contours of the seabed. Upwelling is strongest in late winter (August) and spring (September–November), when the south-east trades and south-west coastal winds become more variable.

There are several water masses present off southern Africa's west coast including, among others, tropical and subtropical surface waters, South Atlantic Central, Antarctic Intermediate, deep and bottom waters (Shannon 1985). The characteristics of the water masses that upwell to the surface and subsurface along the coast of Namibia have salinity ranges from 34.5 to 35.5 and temperatures of 6–16°C. During winter and spring when upwelling is most intense, cold (11–15°C), low salinity (34.8–35.3) water is widely distributed along the coast. This water originates from Atlantic Central Water (Shannon and Pillar 1986). In contrast, warmer (16–23°C) more saline water (35.3–35.6) is found during summer and autumn, when upwelling relaxes.

During events such as Benguela *Niño*s, warm Angola Current water moves farther south than usual, giving rise to sea surface temperatures in the northern Benguela as high as 24°C. Such events can last for up to six weeks. Surface salinity usually ranges from 35.2 to 35.8, with highest values during summer and autumn, associated with warmer oceanic and Angolan water.

The water above the thermocline in the south-east Atlantic Ocean commonly contains 4.8–5.2 $m\ell\ O_2\ \ell^{-1}$ (Shannon and Hampton 1997). In contrast, shelf bottom waters of the central and northern Namibian coast frequently contain lower levels ($<3\ m\ell\ O_2\ \ell^{-1}$) and are at times anoxic (Bailey 1991, Dingle and Nelson 1993). Persistent oxygen deficiency is usually restricted to waters within the 100 m isobath, over inner-shelf areas in the central region (Dingle and Nelson 1993).

The main source of low oxygen water in the northern Benguela is the Angolan Basin, from where it is transported by means of the poleward undercurrent. The second source of low dissolved oxygen in the northern Benguela is of local origin. The Benguela Current upwelling system is a nutrient-enriched region of intense biological productivity. However, ungrazed phytoplankton dies and sinks, leading to eutrophication (Bailey 1991). High organic loadings, microbial breakdown of organics in which excess oxygen is stripped from the water, lead to anoxic bottom waters over large areas of the shelf (Hart and Currie 1960, Calvert and Price 1971, Chapman and Shannon 1985, Bailey 1991). During the oceanographic perturbations off the Namibian coast between 1993 and 1995, extensive areas of low oxygen water were found over the entire northern and central shelf, with the vertical extent of the anoxic layer being more than 250 m thick along parts of the shelf edge (O'Toole and Bartholomae 1994, Woodhead *et al*. 1997).

The shelf seabed of the northern Benguela consists mainly of fine sands, biogenic and opal-rich diatomaceous muds with high organic content (4–12% carbon by weight), which smells strongly of hydrogen sulphide (Rogers and Bremner 1991). Areas of highly organic sediments are found on the inner shelf, especially between Conception Bay and Palgrave Point. This area has been termed the "azoic zone" for its lack of bottom fish and absence of macrobenthic invertebrates (Marchand 1928, Von Bonde 1928). The azoic zone is persistently oxygen-depleted (Dingle and Nelson 1993). There, circulation patterns are favourable for retention of high inputs of organic decaying materials resulting from phytoplankton blooms in surface waters.

MATERIAL AND METHODS

Trawl data

The relative abundance of demersal fish was usually assessed three times per year (in January/February, April/May and October/November) from bottom trawl surveys conducted by the Norwegian research vessel *Dr Fridtjof Nansen*. The survey consisted of trawl transects at approximately 1° latitude intervals perpendicular to the coast. For the current analysis, the seven surveys used were those in October 1992, January 1993, January 1994, October 1994, May 1995, January 1996 and October 1996. The results of each survey were analysed separately.

The demersal sampling gear used was a high-opening shrimp and bottom fish trawl with a headline of 31 m and a footrope of 47 m, with roller discs 12 cm in diameter. This trawl has an estimated headline height of 5 m during towing and the distance between the wings is about 20 m. A technique of restraining (strapping) the warps was routinely used to maintain a constant swept area (Engås and Ona 1991). The warps were restrained about 140 m in front of the doors. The codend was lined with fine mesh (20 mm). Each trawl sample consisted of a tow on the seabed of 30 minutes at 3 knots, so sweeping about 1.5 nautical miles.

The bottom trawl stations were based on a semi-random distribution of hauls intended to cover the

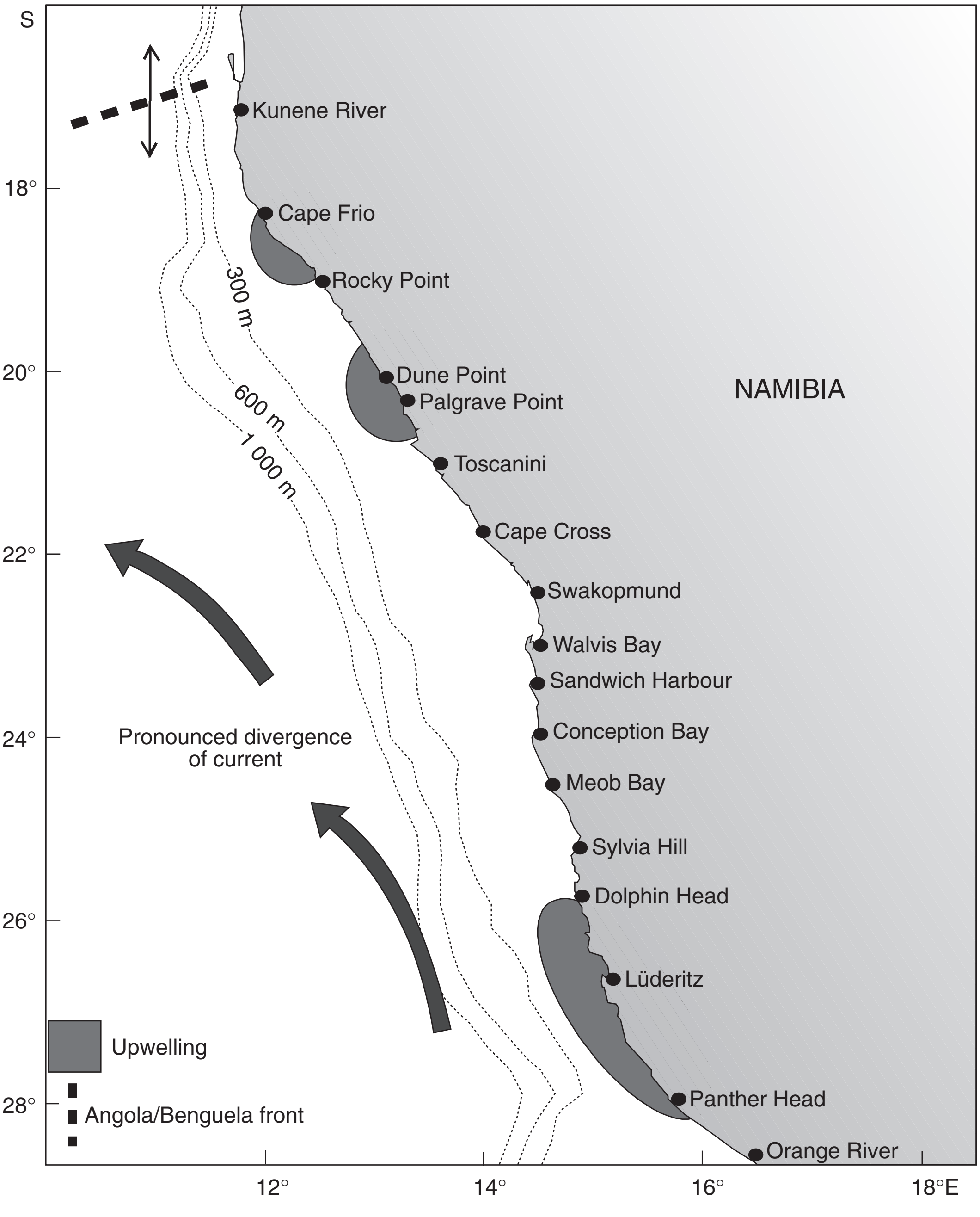

Fig. 1: The northern Benguela study area off the Namibian coast, showing the bathymetry, the Angolan-Benguela front, the main upwelling cell in the vicinity of Lüderitz and two smaller cells in the north, and the direction of flow of the Benguela Current

depth ranges 50–600 m. Further descriptions of the methodology, catch data and preliminary results are given in Sætersdal and Strømme (1990–1993), Strømme (1994–1995) and Strømme and Hamukuaya (1996). Small catches (<100 kg) were sorted in their entirety, but larger catches were weighed, a randomly selected subsample weighed and sorted, and the results raised to total catch weight. Species caught were identified on the basis of existing literature (Fischer *et al*. 1981, Smith and Heemstra 1991, Bianchi *et al*. 1993). Congeneric species that were difficult to separate were pooled. All station and raw species data were entered and stored in a microcomputer using *Nansis: Software for Fishery Survey Data Logging and Analysis* (Strømme 1992), to produce summary statistics of species and stations.

Environmental data

During the October 1992 and January 1993 surveys, just five environmental variables were recorded (bottom depth, bottom salinity, bottom temperature, sea surface temperature, and grain size of the bottom sediment). Hydrographic transects were made perpendicular to the coast at Panther Head, Dolphin Head, Conception Bay, Cape Cross, Dune Point and Cape Frio (Fig. 1). Environmental variables were extrapolated for stations between hydrographic transects. Standard hydrographic variables were recorded at each trawl station, including measurements of bottom oxygen concentration, from January 1994 onwards.

Water column profiles were made for the determination of temperature, salinity and dissolved oxygen using a CTD profiler fitted with a calibrated Beckman oxygen electrode to measure dissolved oxygen *in situ.* At most stations, water samples were collected in Niskin bottles and analysed for oxygen content by the Winkler titration method (Carpenter 1965).

Seabed characteristics at each trawl station were derived from the textural sediment survey maps of Bremner *et al*. (1988). The characterization was simplified to five substratum types: 1 – mud, 2 – sandy mud, 3 – muddy sand, 4 – sand, 5 – gravel. Gravel included gravelly sand and sandy gravel, although the latter is scarce off the Namibian coast.

Data analysis

Multivariate analyses were used to study joint relationships among the biota, which included teleosts, chondrichthyans, cephalopods and crustaceans (Appendix). These data were also used to determine correlations between the biotic components and the measured environmental variables.

A classification technique based on agglomerative hierarchical algorithms was first used to establish the main groupings and to determine whether there was spatial consistency. Dendrograms were produced by hierarchical agglomerative clustering (using group average linkage) of all samples, based on the Bray-Curtis dissimilarity measure (Bray and Curtis 1957) calculated on root-root transformed abundance data (Field *et al*. 1982).

To study the relationships between species data and abiotic variables, the data were subjected to canonical correspondence analysis (CCA), using the CANOCO software (Ter Braak 1987a). CCA selects the linear combination of environmental variables that maximizes the dispersion of the species scores. It chooses the best weights for the environmental variables in the first CCA axis. The second and further axes also select linear combinations of environmental variables that maximize the dispersion of the species scores, but subject to the constraint of being uncorrelated with previous CCA axes (Ter Braak 1987b). A multiple-regression-derived forward selection technique was used to identify the minimum set of variables that best explained the species data. Significance of the environmental variables and canonical axes was tested using an unrestricted Monte Carlo permutation test. Multicolinearity among all five environmental variables was examined with a correlation matrix and variance inflation factors (Ter Braak 1987b).

Following the recommendation in Field *et al*. (1982), the species abundance data were reduced by omitting all the "rare" species, i.e. those accounting for <4% of the total biomass of the sample at any given site. This was done for the multivariate analyses. The justification for deleting rare species is partly theoretical and partly pragmatic:

(a) catches of "rare" species are usually more a matter of chance than an indication of ecological conditions;
(b) most multivariate techniques are affected very little by "rare" species that carry only a small percentage of the overall information;
(c) ordination techniques tend to perceive rare species as outliers, so obscuring the analysis of the dataset as a whole (Gauch 1982).

As some species were very abundant and the results of multivariate analyses can be unduly influenced by a few extremely high values (Clifford and Stephenson 1975, Field *et al*. 1982), abundance data were trans-

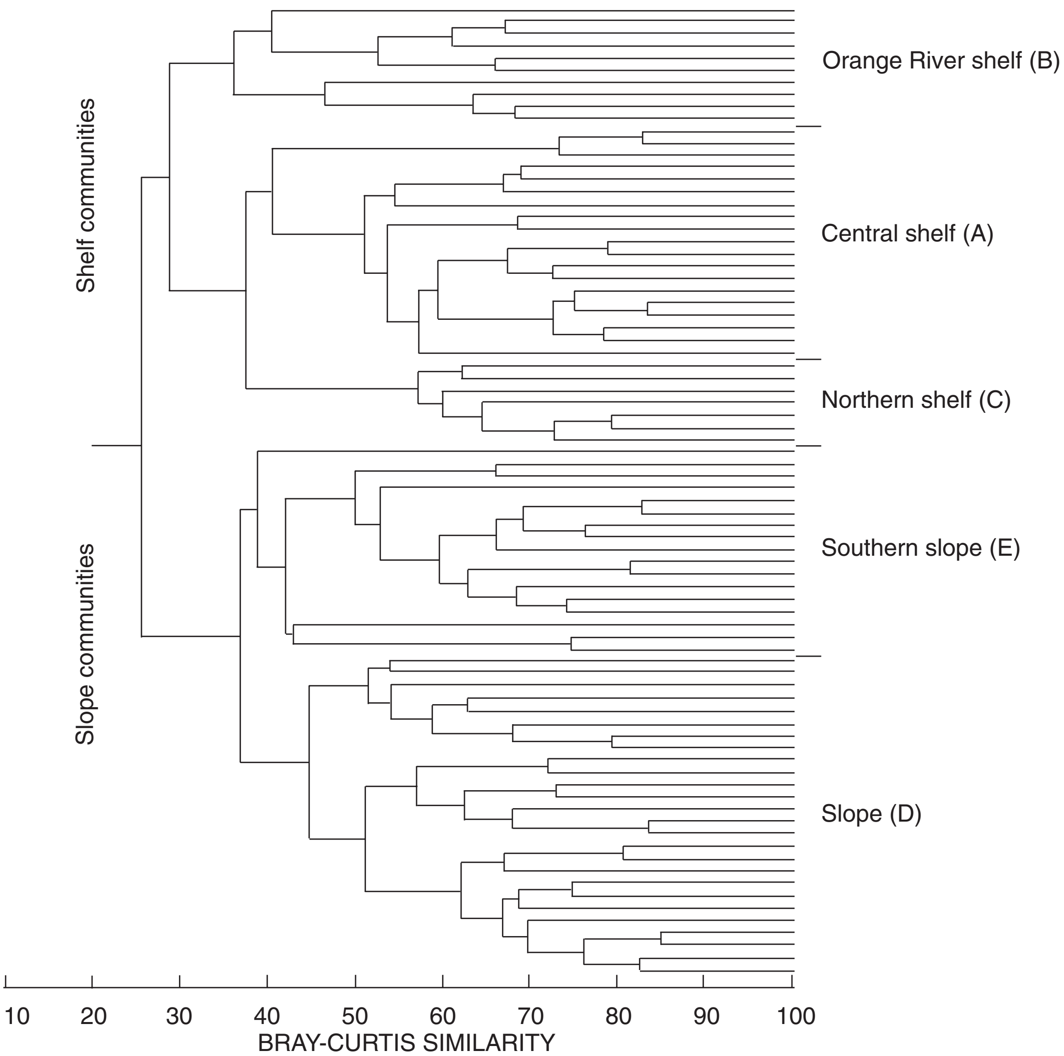

Fig. 2: Dendrogram resulting from hierarchical clustering of 79 site samples to illustrate the groupings of sites, using group-average linking of Bray-Curtis similarities calculated on √√-transformed species abundance data

formed by √√-transformation.

Species that characterized the observed assemblages were identified by a SIMPER (similarity percentages) procedure implemented in the PRIMER software package (Warwick and Clarke 1991, 1994, Clarke 1993). The procedure determined the contribution of each species to the average similarity measure S_i within sample groups. In a SIMPER routine, the contribution of each species to the Bray-Curtis similarity measure is calculated after √√-transformation of abundance data. Species are then ranked in order of their contribution to within-group similarity. The more abundant a species within a group, the more it will contribute to intra-group similarity. A species typifies the group if it has a consistent abundance in the samples classified within the group, so that the

Table I: Percentage composition by weight of the main demersal taxa by survey (1992–1996)

Survey	Teleosts	Chondrichthyans	Invertebrates*
October 1992	96.2	2.3	1.5
January 1993	96.3	2.6	1.1
January 1994	91.8	5.4	2.8
October 1994	92.6	5.5	1.9
May 1995	93.9	3.3	2.8
January 1996	95.6	2.9	1.5
October 1996	95.3	3.3	1.4

*Including cephalopods, crabs, stomatopods, shrimps and lobsters

$SD(S_i)$ is small and the ratio $\overline{S}_i/SD(S_i)$ is high. An abundant species that is not consistently found in the group would contribute little to intra-group similarity.

Diversity indices

Hill's diversity measures (Hill 1973) were used in this study because they are easier to interpret ecologically than other diversity indices, because they are based on units of species numbers (Ludwig and Reynolds 1988, Krebs 1989). However, they have sometimes been criticized for their inherent tendency either to include or to ignore rare species (Alatalo and Alatalo 1977). Krebs (1989) provided further justification for this particular choice of measure. In equation form, these diversity numbers are

$$N0 = s$$

$$N2 = \frac{1}{\lambda}$$

where s is the total number of species and λ is the Simpson index:

$$\lambda = \sum_i p_i^2$$

As λ increases, diversity decreases and therefore the diversity can be expressed as $1/\lambda$. These indices emphasize the two components of diversity, i.e. the richness ($N0$) and the evenness ($N2$).

RESULTS

A list of species from major taxonomic groups collected and used for the analyses is given in the Appendix. Frequency of occurrence was used for categorization. Any species that appeared four or more times in any of the samples during any of the R.V. *Dr Fridtjof Nansen* surveys considered here, is placed into the "frequent" category and the rest in the "rare" category.

Teleosts dominated catches to the tune of 92–96% of faunal biomass. Chondrichthyans contributed another 2–6%. Other taxa caught included cephalopods, crabs, stomatopods, shrimps and lobsters, but their biomass was low compared to fish groups (Table I). The relative abundance of teleosts declined between January 1994 and May 1995 and, conversely, the relative abundance of chondrichthyans increased.

Agglomerative hierarchical classification

Throughout the study period (October 1992 to October 1996) consistency was observed in the pattern of clusters, with a major division between shelf (50–350 m water depth), and slope (350–600 m) habitats. An example of a typical dendrogram (for October 1992) is given in Figure 2. The shelf habitat comprised three assemblages and the slope habitat two. The assemblages were therefore denominated according to their geographical distributions as follows:

- central shelf assemblage (Group A)
- Orange River shelf assemblage (Group B)
- northern shelf assemblage (Group C)
- slope assemblage (Group D)
- southern slope assemblage (Group E).

There was a high degree of consistency in the groups represented by the dendrograms from each survey.

Assemblage composition

The average abundances, ratios and cumulative percentage similarities contributed by species occurring in all assemblage groups are presented in Tables II–V for a selection of surveys throughout the study period. Species are listed according to decreasing values as to their contribution to within-group similarity. *Merluccius capensis* occurred at a high level of within-group similarity and had a high ratio in all surveys and all groups, except for the southern slope assemblage (Group E), in which *M. paradoxus* dominated.

It is of note that, in the slope assemblage dominated by *M. capensis* at the beginning of the study period (Tables II, III), *M. paradoxus* became progressively the dominant species (Tables IV, V). This result is considered indicative of an expansion of the latter species northwards during the study period. The southern slope assemblage was further characterized by the presence of *Todarodes sagittatus*, *Coelorinchus fasciatus* and *Helicolenus dactylopterus*.

Table II: Average abundance of demersal fish species and their contribution to within-group similarity measures during the October 1992 survey. Species are listed in order of their contribution. The top four species or at least those contributing to at least 80% cumulative similarity are included. S = average similarity; S_i = average similarity of species i; SD = standard deviation of S_i

Species	Average abundance	S_i	$S_i/SD(S_i)$	%	Cumulative %
Group A ($\bar{S}$ = 52.97)					
Merluccius capensis	1 237	33.0	3.9	61.9	61.9
Trachurus trachurus capensis	121	9.0	1.1	16.3	78.2
Sufflogobius bibarbatus	65	7.0	0.8	12.6	90.8
Chelidonichthys capensis	17	2.0	0.5	4.4	95.3
Group B ($\bar{S}$ = 43.94)					
Merluccius capensis	124.7	13.2	1.9	30.0	30.0
Sepia australis	10.7	5.4	1.4	12.2	42.1
Chelidonichthys capensis	11.6	4.7	1.1	10.8	52.9
Merluccius paradoxus	86.4	2.9	0.6	6.5	59.5
Galeorhinus galeus	14.1	2.6	0.5	5.8	65.3
Helicolenus dactylopterus	1.7	2.6	0.9	5.8	71.1
Trachurus trachurus capensis	17.2	2.2	0.7	5.0	76.1
Lophius vomerinus	2.8	2.1	0.7	5.0	80.8
Group C ($\bar{S}$ = 61.59)					
Merluccius capensis	370.0	15.8	5.1	25.6	25.6
Trachurus trachurus capensis	441.4	10.2	3.2	16.6	42.2
Dentex macrophthalmus	236.0	10.2	1.4	16.6	58.9
Pterothrissus belloci	61.7	8.0	2.5	13.0	71.8
Synagrops microlepis	16.6	4.1	1.4	6.7	78.5
Chlorophthalmus atlanticus	44.1	3.9	1.4	6.3	84.8
Group D ($\bar{S}$ = 52.10)					
Merluccius capensis	499.9	17.0	4.5	32.6	32.6
Helicolenus dactylopterus	46.9	8.7	3.1	16.7	49.6
Merluccius paradoxus	79.2	5.6	0.9	10.8	60.1
Todarodes sagittatus	6.7	3.3	1.0	6.4	66.4
Galeus polli	7.2	3.1	1.0	6.0	72.4
Trachurus trachurus capensis	40.4	3.0	0.7	5.6	78.0
Lophius vomerinus	3.5	1.6	0.6	3.0	81.0
Group E ($\bar{S}$ = 51.34)					
Merluccius paradoxus	560.1	22.9	5.1	44.6	44.6
Todarodes sagittatus	31.0	9.3	5.5	18.2	62.8
Nezumia sp.	15.7	5.1	1.2	9.9	72.7
Coelorinchus fasciatus	17.3	3.5	0.7	6.8	79.6
Helicolenus dactylopterus	6.6	3.0	0.8	5.6	85.1

Sufflogobius bibarbatus was consistently among the species most contributing to within-group similarity in the central shelf assemblage. The other two shelf assemblages, i.e. the Orange River shelf assemblage, Group B, and the northern shelf assemblage, Group C, were characterized, besides *M. capensis*, by species with preference for temperate (e.g. *Chelidonichthys capensis* and *M. paradoxus*) and tropical/subtropical waters (e.g. *Dentex macrophthalmus, Synagrops microlepis* and *Pterothrissus belloci*) respectively. *Trachurus capensis* was a common feature of the three shelf assemblages.

Spatial distribution

A summary of spatial distributions in terms of latitudinal limits is presented in Table VI. The spatial distributions of each assemblage identified by multivariate analyses, for the surveys at the beginning (October 1992 and January/February 1993) and the end (January/February 1996 and October 1996) of the study period, are shown in Figure 3. Table VII lists the results of the test for significant interannual difference (for data from the same season) in mean depth of groups between different years but the same season.

Table III: Average abundance of demersal fish species and their contribution to within-group similarity measures during the January 1993 survey. Species are listed in order of their contribution. The top four species or at least those contributing to at least 80% cumulative similarity are included. S = average similarity; S_i = average similarity of species i; SD = standard deviation of S_i

Species	Average abundance	S_i	$S_i/SD(S_i)$	%	Cumulative %
Group A ($\bar{S}$ = 60.55)					
Merluccius capensis	656.3	40.0	4.0	69.8	69.8
Sufflogobius bibarbatus	75.1	11.0	1.2	19.6	89.4
Trachurus trachurus capensis	452.7	4.2	0.5	7.5	96.8
Austroglossus microlepis	3.0	1.6	0.5	2.8	99.6
Group B ($\bar{S}$ = 39.45)					
Merluccius capensis	452.0	16.1	7.0	35.2	35.2
Callorhinchus capensis	156.7	6.5	1.3	14.2	49.4
Chelidonichthys capensis	191.8	6.0	4.0	13.1	62.5
Austroglossus microlepis	17.9	5.0	1.3	10.7	73.2
Trachurus trachurus capensis	462.7	3.0	0.5	6.2	79.4
Genypterus capensis	11.3	2.2	0.7	4.7	84.2
Group C ($\bar{S}$ = 57.45)					
Merluccius capensis	387.2	24.2	3.9	43.9	43.9
Dentex macrophthalmus	128.0	9.8	3.8	17.8	61.7
Trachurus trachurus capensis	77.0	8.0	1.2	14.4	76.1
Pterothrissus belloci	62.0	4.2	0.8	7.7	83.8
Group D ($\bar{S}$ = 56.87)					
Merluccius capensis	581.5	22.7	4.1	42.0	42.0
Helicolenus dactylopterus	72.7	13.4	2.6	24.7	66.7
Galeus polli	6.6	3.6	1.1	6.7	73.4
Merluccius paradoxus	14.9	2.5	0.6	4.7	78.1
Nezumia sp.	3.2	2.4	0.9	4.5	82.6
Group E ($\bar{S}$ = 51.34)					
Merluccius paradoxus	2 324.5	18.2	5.1	30.2	30.2
Todarodes sagittatus	20.1	11.8	3.7	19.7	49.9
Coelorinchus fasciatus	22.8	7.6	1.6	12.6	62.5
Helicolenus dactylopterus	17.3	6.9	1.5	11.5	74.1
Genypterus capensis	19.3	6.3	1.5	10.5	84.5

The central shelf assemblage (Group A) was usually found between 19 and 27°S (Table VI). However, there was a major change in depth distribution in October 1996, confirmed by the significant p value of the comparisons between the depths for all October surveys (Table VII, $p = 0.009$), indicating expansion offshore. This trend was not found for summer surveys.

The distribution of the Orange River shelf assemblage (Group B) in the northern Benguela was spatially limited. From 1992 to 1995, it extended no more than 2° north of the Orange River mouth (Table VI), but in 1996 it reached 23°S (Fig. 3c). Depth distribution was rather stable, except in January 1996 when it extended farther offshore (Table VII).

The north-south distribution of the northern shelf assemblage (Group C) was variable (Table V). During October 1992, October 1994 and in May 1995, the southern border of this assemblage was at about 21°S. However, in January 1993, January 1994 and January 1996, it extended farther south, to 26°S, indicating seasonal displacement. There were also significant differences in depth distribution, particularly for the summer months of 1993, 1994 and 1996 (p = 0.002, Table IV).

Both the slope and southern slope assemblages had average depths >300 m in all seasons and years. The spatial distribution of the slope assemblage (Group D) essentially encompassed the deep-water zone from the southern to the northern borders of Namibia. During May 1995, however, the slope assemblage (Group D) terminated at about 19°S (Table VI). This assemblage moved progressively deeper and offshore during the study period, and the difference

Table IV: Average abundance of demersal fish species and their contribution to within-group similarity measures during the May 1995 survey. Species are listed in order of their contribution. The top four species or at least those contributing to at least 80% cumulative similarity are included. S = average similarity; S_i = average similarity of species i; SD = standard deviation of S_i

Species	Average abundance	S_i	$S_i/SD(S_i)$	%	Cumulative %
Group A ($\bar{S}$ = 47.98)					
Merluccius capensis	824.4	29.6	2.6	60.6	60.6
Trachurus trachurus capensis	621.0	8.0	0.9	16.3	76.8
Sufflogobius bibarbatus	7.5	7.6	0.9	15.5	92.3
Todarodes sagittatus	2.9	1.4	0.3	2.8	95.2
Group B ($\bar{S}$ = 50.12)					
Merluccius capensis	123.8	14.3	5.0	28.7	28.7
Sepia australis	39.5	7.8	2.9	15.5	44.3
Etrumeus whiteheadi	85.4	3.9	0.7	7.8	52.2
Lepidopus caudatus	14.5	3.7	1.7	7.5	59.7
Lophius vomerinus	5.9	3.5	1.8	7.1	66.8
Chelidonichthys capensis	15.4	3.1	1.0	6.1	72.9
Thyrsites atun	10.6	2.9	1.0	5.8	78.7
Merluccius paradoxus	79.1	2.3	0.4	4.6	83.4
Group C ($\bar{S}$ = 53.23)					
Merluccius capensis	1 110.3	12.6	6.2	23.6	23.6
Dentex macrophthalmus	166.1	7.8	1.3	14.6	38.3
Trachurus trachurus capensis	159.7	5.5	0.8	10.3	48.5
Lophius vomerinus	32.1	5.3	1.3	9.9	58.5
Hedlicolenus dactylopterus	178.3	4.5	1.1	8.4	66.9
Chlorophthalmus atlanticus	138.2	4.2	1.4	7.9	74.9
Synagrops microlepis	41.0	4.1	1.2	7.8	82.7
Group D ($\bar{S}$ = 55.66)					
Merluccius paradoxus	332.9	11.4	1.5	20.5	20.5
Todarodes sagittatus	34.2	7.7	1.8	13.8	34.3
Trachyrinchus scabrus	80.2	7.4	1.2	13.3	47.6
Nezumia sp.	39.9	6.4	3.3	11.6	59.2
Hoplostethus cadenati	77.8	4.8	1.4	8.7	67.8
Shrimps	6.8	3.6	1.7	6.5	74.4
Selacophidium guentheri	6.9	3.1	1.2	5.5	79.9
Group ($\bar{S}$ = 54.76)					
Merluccius paradoxus	243.6	11.3	1.9	20.7	20.7
Helicolenus dactylopterus	71.4	9.1	3.7	16.7	37.4
Todarodes sagittatus	19.1	6.9	2.3	12.6	50.0
Merluccius capensis	125.5	5.9	1.1	10.8	60.8
Coelorinchus fasciatus	30.3	4.5	1.4	8.1	69.0
Lophius vomerinus	14.8	3.8	1.4	7.0	76.0
Nezumia sp.	17.1	3.3	1.3	6.1	82.1

in mean depth was highly significant (Table VII), irrespective of season.

The southern slope assemblage (Group E) varied in its distribution during the study period. It is worth noting that, although at the beginning of the study period it was found only south of about 25°S, it expanded to reach 19°S thereafter (Fig. 3). This geographic expansion of the assemblage coincides with the increase in biomass of deep-water Cape hake *Merluccius paradoxus* reported from the surveys of the R.V. *Dr Fridtjof Nansen* (Strømme *et al*. 1997). Nevertheless, the main area of distribution of this assemblage appeared to be in the south, close to the border between Namibia and South Africa (Table VI). The assemblage experienced offshore-inshore shifts, and the difference in mean depths was significantly different from season to season over the study period.

Table V: Average abundance of demersal fish species and their contribution to within-group similarity measures during the October 1996 survey. Species are listed in order of their contribution. The top four species or at least those contributing to at least 80% cumulative similarity are included. S = average similarity; S_i = average similarity of species i; SD = standard deviation of S_i

Species	Average abundance	S_i	$S_i / SD(S_i)$	%	Cumulative %
Group A ($\bar{S}$ = 51.75)					
Merluccius capensis	360.4	14.1	4.0	27.2	27.2
Sufflogobius bibarbatus	98.8	5.7	1.18	11.1	51.4
Coelorinchus fasciatus	20.0	6.8	1.8	13.2	40.3
Merluccius paradoxus	278.5	5.4	0.7	10.5	62.0
Myctophidae	31.9	4.2	1.5	8.1	70.1
Lophius vomerinus	15.4	4.0	1.7	7.8	77.9
Todarodes sagittatus	12.7	3.6	0.9	7.0	84.8
Group B ($\bar{S}$ = 46.45)					
Merluccius capensis	238.4	13.3	5.5	28.6	28.6
Trachurus trachurus capensis	37.4	5.4	1.7	11.6	40.2
Chelidonichthys capensis	27.6	4.8	1.4	10.3	50.5
Lepidopus caudatus	9.1	2.7	1.0	5.8	56.2
Callorhinchus capensis	21.9	2.4	0.7	5.2	61.5
Sufflogobius bibarbatus	12.5	2.1	0.7	4.6	66.1
Sepia australis	5.8	2.0	1.0	4.3	70.4
Lophius vomerinus	3.9	1.7	0.7	3.7	74.2
Thyrsites atun	136.8	1.6	0.5	3.5	77.7
Holohalaelurus regani	2.9	1.4	0.7	3.0	80.7
Group C ($\bar{S}$ = 41.04)					
Merluccius capensis	415.2	12.3	3.1	29.4	29.4
Trachurus trachurus capensis	2 222.9	9.3	0.9	22.3	51.7
Pterothrissus belloci	80.5	5.0	1.3	11.9	63.6
Synagrops microlepis	59.7	3.0	1.0	7.2	70.9
Chlorophthalmus atlanticus	198.6	2.6	0.6	6.2	77.04
Dentex macrophthalmus	167.7	2.4	0.7	5.7	82.7
Group D ($\bar{S}$ = 52.45)					
Merluccius paradoxus	377.1	12.7	5.2	24.2	24.2
Nezumia sp.	77.0	8.1	5.1	15.5	39.7
Trachyrhinchus scabrus	204.9	6.3	1.2	11.9	51.6
Hoplostethus cadenati	30.2	5.0	3.8	9.6	61.2
Todarodes sagittatus	9.5	3.0	1.1	5.6	66.8
Lophius vomerinus	8.4	2.9	1.1	5.5	72.3
Selacophidium guentheri	11.4	2.9	1.2	5.5	77.8
Group E ($\bar{S}$ = 42.74)					
Merluccius paradoxus	176.5	8.1	1.9	19.0	19.0
Helicolenus dactylopterus	123.6	7.2	5.0	16.8	35.8
Coelorinchus fasciatus	103.4	4.1	1.0	9.5	45.3
Lophius vomerinus	21.3	4.0	1.5	9.5	54.7
Merluccius capensis	156.8	2.9	0.6	6.7	61.4
Nezumia sp.	19.6	2.6	1.0	6.0	67.4
Galeus polli	10.2	2.2	1.1	5.1	72.4
Todarodes sagittatus	8.8	1.9	0.8	4.6	77.0
Epigonus denticulata	7.6	1.5	1.0	3.5	80.5

Diversity

A most striking feature of the surveys was the low diversity of the central shelf assemblage compared to that of all other assemblages (Fig. 4). Both *N*0 and *N*2 diversities were low, with values fluctuating between 3.8 and 10.9 for *N*0 (average number of species caught in trawl hauls) and between 1.4 and

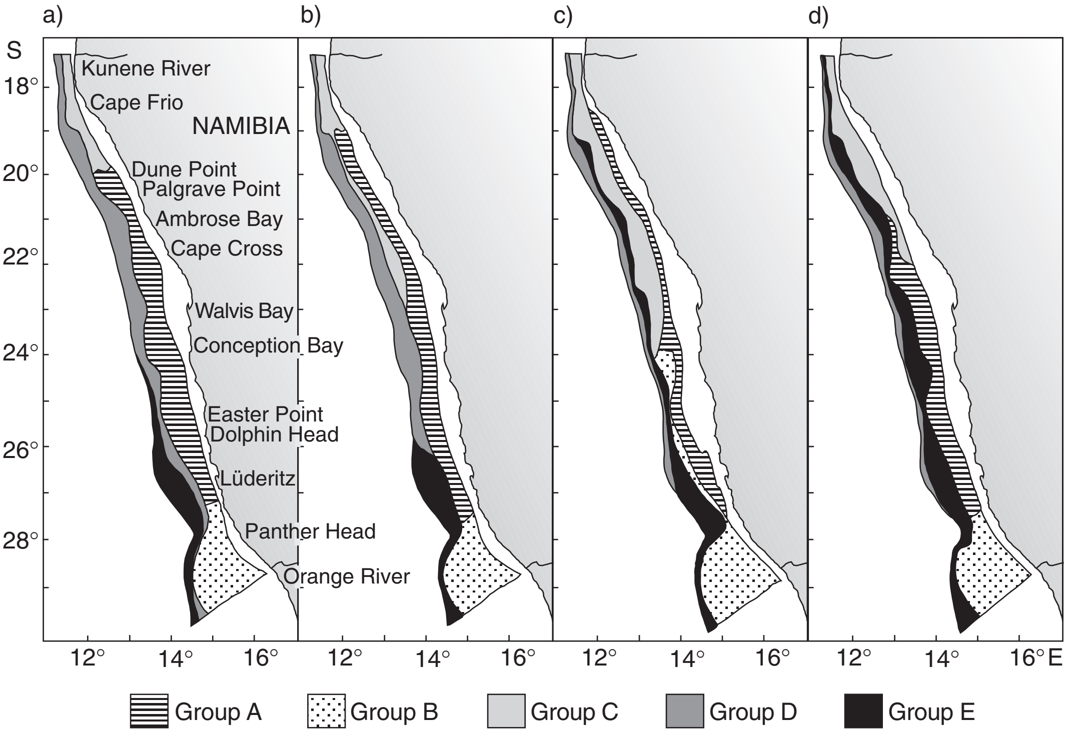

Fig. 3: Distributional patterns of five demersal assemblages identified by classification and ordination techniques – (a) October 1992; (b) January 1993; (c) January 1996; (d) October 1996

2.1 for *N*2. The low value of *N*2 reflected the dominance of a few species. The other assemblages showed distinctively greater diversity, with the average number of species >10. Notwithstanding the results, such a general increase in diversity indices should be interpreted with caution, because diversity indices are directly related to the number of samples. The number of samples was low during January 1993 when diversity was least, and high in October 1996 when diversity was greatest.

The average number of species per survey and assemblage is plotted as a function of temperature,

Table VI: Summary of spatial distribution of assemblages by latitude (Ang – border with Angola; SA – border with South Africa). Groups A, B, C, D and E represent the central shelf, Orange River shelf, northern shelf, slope and southern slope assemblages respectively

Survey	Spatial distribution of assemblage				
	Group A	Group B	Group C	Group D	Group E
October 1992	20°–27°S	27°S–SA	Ang–20°S	Ang–SA	24°S–SA
January 1993	19°–27°S	27°S–SA	Ang–23°S	Ang–26°S	26°S–SA
January 1994	19°–27°S	27°S–SA	Ang–26°S	Ang–28°S	26°S–SA
October 1994	19°–27°S	27°S–SA	Ang–20°S	Ang–SA	18°S–SA
May 1995	20°–27°S	27°S–SA	Ang–21°S	19°S–SA	19°S–SA
January 1996	19°–27°S	23°S–SA	Ang–26°S	Ang–SA	19°S–SA
October 1996	21°–27°S	23°S–SA	Ang–22°S	19°–27°S	17°S–SA

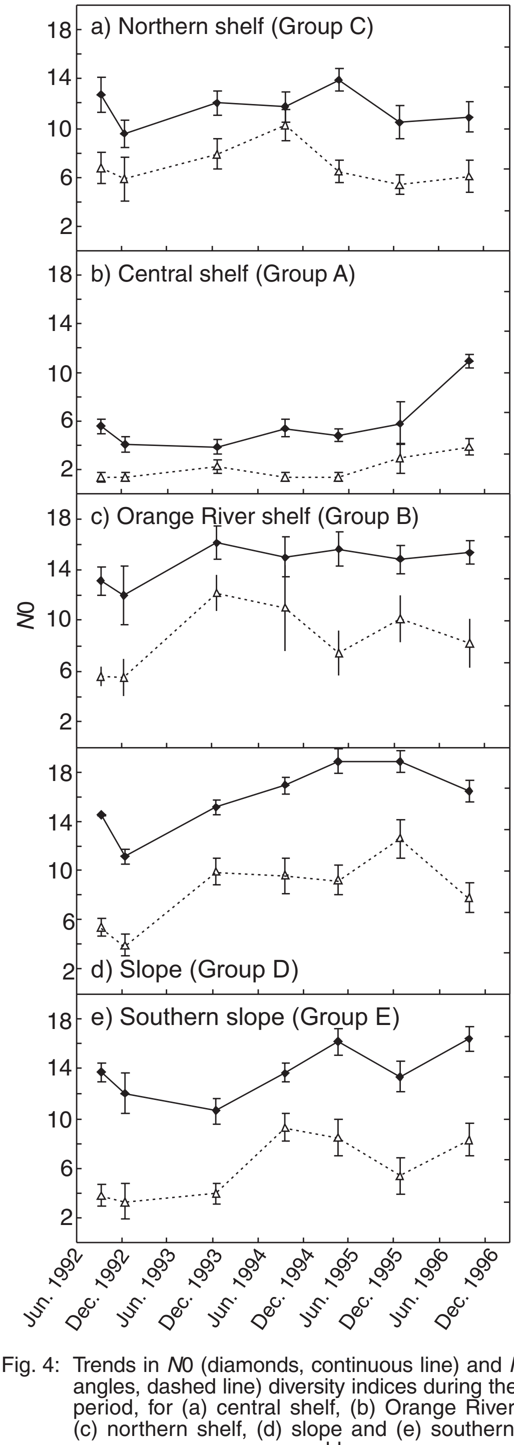

Fig. 4: Trends in *N*0 (diamonds, continuous line) and *N*2 (triangles, dashed line) diversity indices during the study period, for (a) central shelf, (b) Orange River shelf, (c) northern shelf, (d) slope and (e) southern slope assemblages

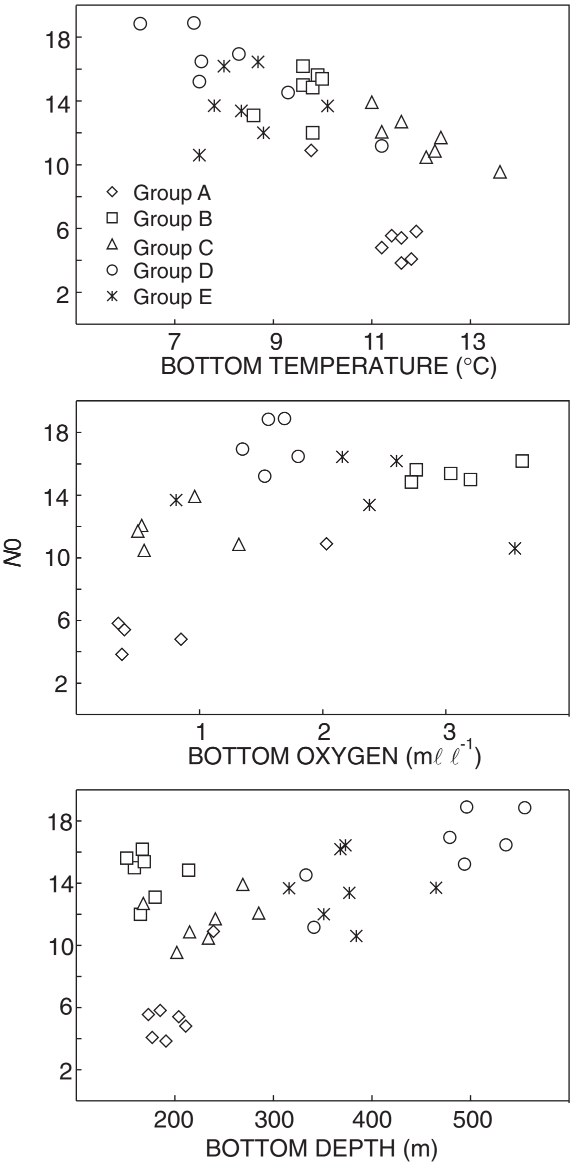

Fig. 5: Relationship between environmental parameters (bottom temperature, oxygen and depth) and *N*0 diversity for the five assemblages identified by cluster analysis over the study period off Namibia, 1992–1996

oxygen and depth on Figure 5. There was an inverse relationship between diversity (*N*0) and temperature. A similar plot of *N*0 as a function of oxygen saturation showed a positive relationship, *N*0 increasing at least to oxygen levels of about 1–1.5 mℓ ℓ^{-1}. Beyond this

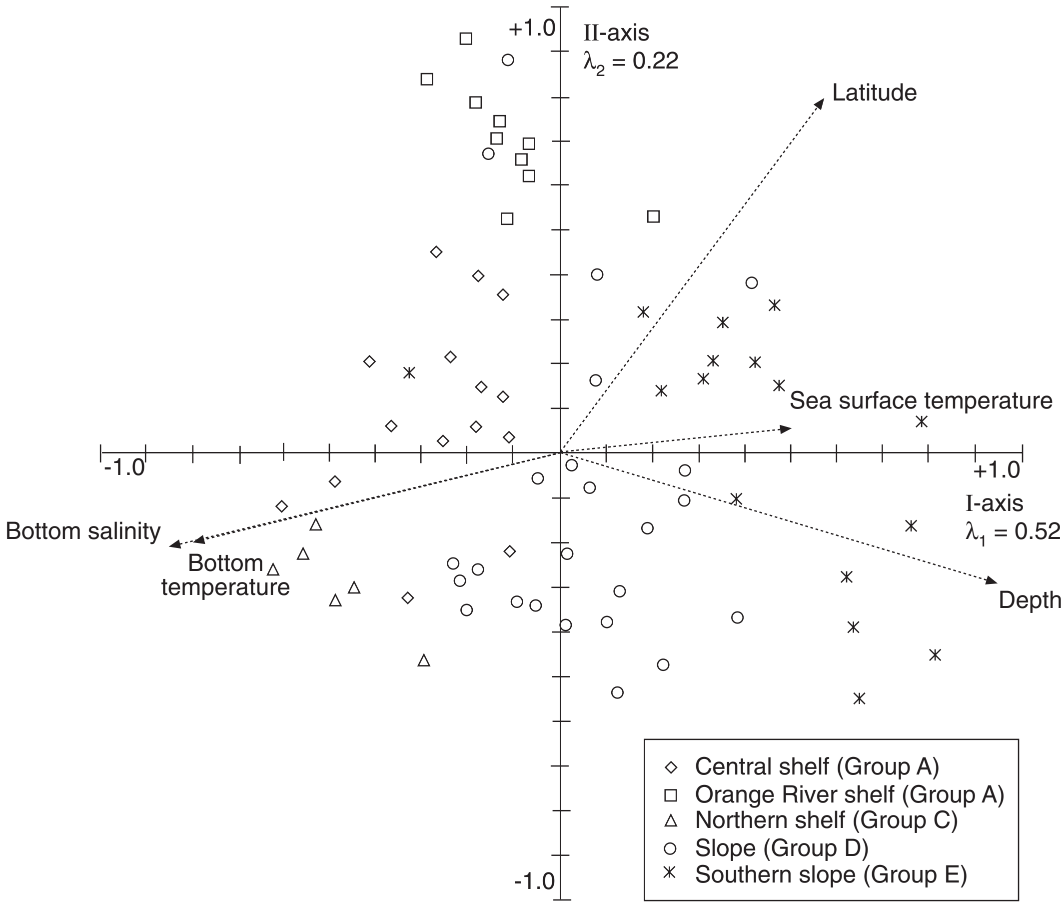

Fig. 6: CCA ordination diagrams (biplots). Sampling stations are represented by different symbols according to their relationship with groups identified by cluster analysis. Environmental variables are represented by arrows, their position depending on the eigenvalues and correlations with ordination axes (see Table IX)

level, higher oxygen levels did not seem to influence diversity. The plot of *N*0 diversity, as a function of bottom depth, showed that the greatest span in diversity values was independent of depth and was found among the shelf assemblages. Nevertheless, there was an overall positive relationship between depth and diversity.

Relationships between biological groups and their environment

Site-environment biplots produced by CCA display the assemblages and the environmental variables correlated with them (Fig. 6). The assemblages, as identified by cluster analysis, are denoted with different symbols on CCA plots. A Monte Carlo permutation test for the first canonical axis of CCA revealed that species composition was significantly correlated with environmental variables (Table VIII). The following scenarios emerged: the first axis separated shelf from slope assemblages along a depth gradient, whereas the second axis arranged the assemblages along a latitudinal gradient (Table IX). Both depth and latitude are spurious "environmental variables" because they indicate the spatial distribution of sampling sites. Nonetheless, depth and latitude may also be viewed as surrogates for temperature and productivity regimes. The information is also of interest because it indicates the spatial dimension along which major faunal

Table VII: Results of single factor ANOVA of significant differences in mean depths of assemblages between different years but of the same season

Group	Survey date	ANOVA *F*	*F*-crit	*p*	Significance*
A	Oct. 1992	5.16	3.21	0.009	S
	Oct. 1994				
	Oct. 1996				
	Jan. 1993	0.26	3.27	0.76	NS
	Jan. 1994				
	Jan. 1996				
B	Oct. 1992	0.64	3.29	0.52	NS
	Oct. 1994				
	Oct. 1996				
	Jan. 1993	4.31	3.27	0.002	S
	Jan. 1994				
	Jan. 1996				
C	Oct. 1992	2.47	3.35	0.10	NS
	Oct. 1994				
	Oct. 1996				
	Jan. 1993	7.12	3.22	0.002	S
	Jan. 1994				
	Jan. 1996				
D	Oct. 1992	41.32	3.14	0.001	S
	Oct. 1994				
	Oct. 1996				
	Jan. 1993	19.69	3.18	0.001	S
	Jan. 1994				
	Jan. 1996				
E	Oct. 1992	22.52	3.14	0.001	S
	Oct. 1994				
	Oct. 1996				
	Jan. 1993	10.84	3.35	0.001	S
	Jan. 1994				
	Jan. 1996				

*S = significant at the 5% level;
NS = not significant

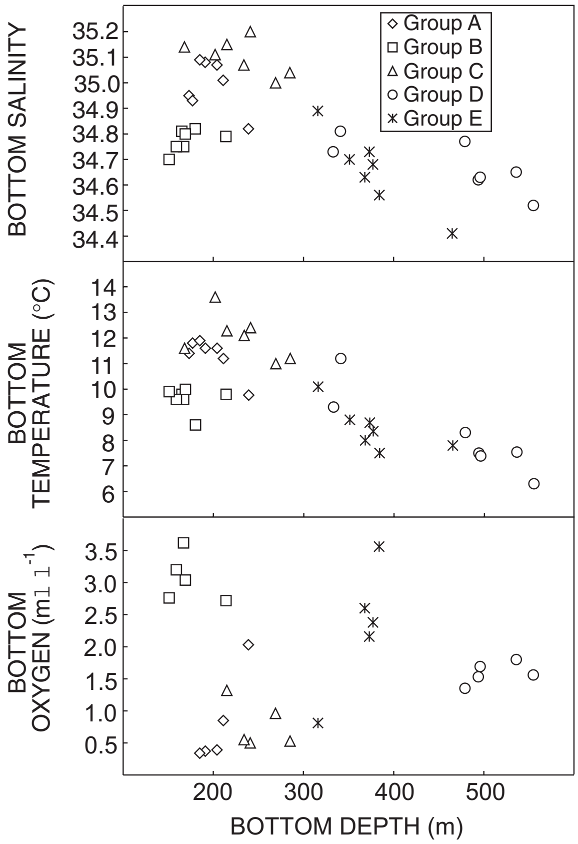

Fig. 7: Scatter plots of the main environmental variables by depth for the station groups identified by cluster analysis

changes take place. Temperature and salinity were also strongly correlated with the first axis, whereas bottom oxygen concentration was correlated with the second axis. This trend was consistent throughout the study period. In May 1995, however, dissolved oxygen contributed significantly to the separation between shelf and slope assemblages. Neither surface temperature nor sediment type seemed to be related to the observed groups.

Figure 7 shows the station groups plotted as a function of the environmental variable found to be of significance. The patterns that emerged indicated that the two slope assemblages (Groups D and E) were characterized by water of low salinity (<34.9), low bottom temperature (<10°C) and relatively high oxygen concentration (>1 mℓ $ℓ^{-1}$). These characteristics were also shared, except for the depth range, with the Orange River shelf assemblage (Group B). The latter was most closely related to the southern slope assemblage as regards the combination of environmental variables. However, there seems to be some irregularity in the pattern documented above. Two points of the slope assemblage (Group D), corresponding to October 1992 and January 1993 respectively, had a much shallower distribution and higher temperature and salinity than the other survey periods.

DISCUSSION

Spatial heterogeneity in demersal fish assemblages in relation to physical variables has been documented for many world shelf regions, including southern Africa (Fager and Longhurst 1968, Lleonart and Roel 1984, Macpherson and Roel 1987, Mas-Riera *et al*. 1990, Macpherson and Gordoa 1992, Bianchi 1992a, b, Smale *et al*. 1993). This study is the first to

Table VIII: Results of a Monte Carlo permutation test for the first canonical axis of CCA

Survey	Eigenvalue	*F*-ratio	*P*
October 1992	0.52	9.85	0.01
January 1993	0.45	6.24	0.01
January 1994	0.68	7.95	0.01
October 1994	0.63	10.54	0.01
May 1995	0.58	8.39	0.01
January 1996	0.62	9.70	0.01
October 1996	0.60	8.54	0.01

cover the whole Namibian shelf and upper slope and the first to relate demersal assemblages to abiotic factors.

Identification of fish assemblages is a first step towards a more holistic approach to fisheries management. Tyler *et al*. (1982) described the Assemblage Production Unit (APU) in these terms and proposed it as an operational unit for fisheries management. Ecological attributes can be described for each assemblage (species composition, diversity measures, size spectra, etc.) and monitored over time to understand, for example, how changes in climate or anthropogenic activity may impact marine assemblages. Tyler (1999) further discussed the limitations of reductionistic philosophies in fisheries science and management. He emphasized the present inadequacies of modelling the behaviour of individual species and their interactions with other species and the environment as a tool for management. He suggested a more holistic approach to fisheries management, i.e. one based on an "assemblage maintenance programme", with extensive surveys and fishery observer programmes, and with fishery regulation by area. In this context, assemblage classification provides an ecologically based stratification for research or management purposes.

Fish assemblages usually do not have sharp boundaries, and assemblage structure often changes gradually or corresponding with changes in environmental gradients. Quasi-discrete boundaries (ecotones) between assemblages may appear in connection with sharp gradients in the physical environment, e.g. boundaries between water masses with different characteristics. Shelf/slope configuration (e.g. physical available space for a given depth stratum) also plays a key role in determining faunal complexity and assemblage structure in a given area.

This study identified two primary habitats, viz. the shelf and the slope, with a faunal boundary about 300–350 m deep. Shelf and slope habitats were consistently arranged along the first ordination axis, and this was strongly correlated with depth, temperature and salinity. These habitats were further distinguished into assemblages, three on the shelf and two on the slope. The three shelf assemblages followed a

Table IX: Interset correlations (*r*) of environmental variables with ordination axes

Variable	Sea surface temperature	Bottom temperature	Bottom salinity	Dissolved oxygen	Depth	Sediment type	Latitude
October 1992							
Axis 1	0.47	-0.73*	-0.79*	No data	0.82**	0.18	0.59*
Axis 2	-0.03	-0.04	-0.01	No data	-0.33	0.04	0.61*
January 1993							
Axis 1	0.19	-0.59*	-0.47	No data	0.73*	0.25	0.45
Axis 2	0.00	-0.42	-0.10	No data	-0.46	0.10	0.67*
January 1994							
Axis 1	0.27	-0.82**	-0.68*	0.08	0.96**	0.18	-0.28
Axis 2	-0.34	0.37	-0.47	0.89**	-0.09	0.08	0.75*
October 1994							
Axis 1	0.01	-0.83**	No data	0.01	0.90**	0.30	0.24
Axis 2	-0.35	-0.29	No data	0.72*	-0.24	-0.10	0.84**
May 1995							
Axis 1	0.14	-0.88**	No data	0.62*	0.80**	0.30	0.43
Axis 2	-0.32	0.04	No data	0.51*	-0.43	0.54*	0.76*
January 1996							
Axis 1	0.12	-0.82**	No data	0.29	0.90**	-0.57*	0.18
Axis 2	-0.29	-0.30	No data	0.63*	-0.17	-0.10	0.90**
October 1996							
Axis 1	0.44	-0.83**	No data	0.05	0.93**	No data	0.06
Axis 2	0.49	0.46	No data	-0.58*	0.19	No data	-0.89**

**Strong correlation (r >0.80);
*Good correlation (r >0.50)

latitudinal pattern, whereas the slope assemblages were affected by depth and latitude. Large-scale patterns of demersal fish assemblages off Namibia track the pattern of different water masses impinging on the bottom, and each assemblage was associated with a specific range of values of the environmental variables considered. This association did not seem to be disrupted by the *El Niño* event that took place during the study period. In particular, the northern and central shelf assemblages seemed to move deeper to avoid the more extended anoxic conditions found in that period.

Studies of demersal assemblages of the neighbouring waters off Angola (Bianchi 1992a) and South Africa (Roel 1987) also reported an important ecological boundary between shelf and slope areas. Off Angola, this boundary is shallower, between 100 and 150 m deep. On the shelf off northern and central Angola, shelf assemblages are further separated by the sharp temperature gradient found where the thermocline impinges on the bottom (Bianchi 1992a). The shelf assemblage off southern Angola is associated with the northern Benguela regime, is quite different from the northern tropical shelf assemblages, and more closely resembles the northern shelf assemblage (Group C) of this study, with species such as *Dentex macrophthalmus* and *Trachurus* spp. (*T. t. capensis* and *T. trecae*) dominating the catches. The shelf-slope assemblage boundary off the western coast of South Africa is at a depth of about 380 m (Roel 1987). She identified five assemblages over the shelf, including an Agulhas Bank shelf assemblage that features a number of species not found in the Benguela system *per se*. Species composition by sample association was not provided by that study, although the shelf assemblages off the coast of northwestern South Africa seem to continue into Namibia as assemblage B (Orange River shelf assemblage) of this study.

Curiously, sediment grain size did not appear to influence the spatial distribution of demersal assemblages off Namibia. The correlation of sediment to the fish assemblages may emerge at finer scales, once an in-depth study has been carried out. On the other hand, this result may also indicate a low trophic interaction between sediment infauna and epifauna and demersal fish. Most species of fish and invertebrates dominating the demersal catches off Namibia feed largely, at least for part of their life cycle, on the rich zooplankton fauna or are piscivorous.

Diversity seemed to be affected by oxygen concentration, with lowest levels of diversity in the central shelf assemblage (Group A), followed by the northern shelf assemblage (Group C). The central shelf, associated with an area very low in oxygen, was characterized by an extremely low diversity. Other studies have shown dramatic declines in diversity (or number of species) where oxygen concentrations drop below about 1.0 $m\ell\ \ell^{-1}$ (Bianchi 1991, 1992a). Shelf/upper slope areas with low oxygen concentrations are often associated with high primary productivity. The few species adapted to live in almost anoxic conditions are, therefore, found in large concentrations. Shallow-water Cape hake *Merluccius capensis*, horse mackerel *Trachurus t. capensis* and goby *Sufflogobius bibarbatus* dominate the demersal environment. The negative relationship displayed between temperature and diversity, apparently contradicting general zoogeographic trends of increasing diversity with increasing water temperature, should be interpreted with caution. The relationship is most probably not one of cause and effect but rather attributable to the fact that, in this region, water masses with higher oxygen concentration are those from deeper and therefore low-temperature waters.

Cape hake (*M. capensis* and *M. paradoxus*) dominated both shelf and slope assemblages. A study carried out by Macpherson and Gordoa (1992) on the trends in fish assemblages off Namibia from 1983 to 1990, including the area from south of Walvis Bay to the Orange River, described the main assemblages in the area. They identified four main associations, two on the shelf and two on the slope. The former largely correspond to Groups A and B of the current study, and the latter with Groups D and E. Biomass and species composition appeared stable in the period considered and it was concluded that the demersal assemblages were at equilibrium. Neither the high levels of fishing effort then, nor the warming events observed in the summers of 1984, 1989 and 1990 had any strong effect on species composition and abundance. A similar conclusion seems to emerge from the data series used in this study where, despite the warming event of summer 1995, there was no major disruption of the faunal assemblages. The fish assemblages off Namibia may therefore be well adapted to a variable environment.

Management of the central shelf assemblage deserves special attention, given the extremely low diversity and anomalous environmental conditions found in the area where it is found. Cape hake is a key species in this assemblage, both ecologically and economically. Its special adaptations to conditions of low oxygen concentration and its ability to access the high productivity of the system at lower trophic levels through its cannibalistic behaviour (Roel and Macpherson 1988), makes it unique to this ecosystem. Therefore, the need for a precautionary approach in the management of this ecosystem seems to be particularly relevant in this case.

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APPENDIX

Species included in the analyses

Families listed in systematic order, asterisks indicating frequently encountered species (see text for definition)

Stomatopods
SQUILLIDAE
Squilla acuelata calmani

Shrimps and Prawns
SOLENOCERIDAE
*Solenocera africana
ARISTEIDAE
*Aristeus varidens
Plesiopenaeus edwardsianus
PENAEIDAE
Parapenaeus longirostris
PANDALIDAE
Heterocarpus grimaldii
Plesionika martia
**Plesionika* sp.

Lobsters
PALINURIDAE
Jasus lalandii
NEPHROPIDAE
Nephropsis atlantica
POLYCHELIDAE
Stereomastis grimaldi
Stereomastis sculpta

Crabs
LITHODIDAE
*Lithodes ferox
Neolithodes asperrimus
GALATHEIDAE
Munida sp.
GERYONIDAE
*Chaceon maritae
PORTUNIDAE
*Bathynectes piperitus

Cephalopods
SEPIIDAE
*Sepia australis
Sepia bertheloti
Sepia orbignyana
SEPIOLIDAE
Rossia enigmatica
LOLIGINIDAE
*Lolliguncula mercatoris
Loligo vulgaris
Loligo reynaudi
LYCOTEUTHIDAE
Lycotheuthis diadema
ONYCHOTEUTHIDAE
Moroteuthis robsoni
HISTIOTEUTHIDAE
Histioteuthis reversa
OMMASTREPHIDAE
Illex coindetii
Ommastrephes pteropus
*Todarodes sagittatus
*Todaropsis eblanae
THYSANOTEUTHIDAE
Thysanoteuthis rhombus
VITRELEDONELLIDAE
Vitreledonella
OPISTHOTEUTHIDAE
OCTOPODIDAE
Octopus sp.
Octopus vulgaris

Hagfish
MYXINIDAE
*Myxine capensis

Sharks
HEXANCHIDAE
Heptranchias perlo
Hexanchus griseus
LAMNIDAE
Isurus oxyrinchus
SCYLIORHINIDAE
*Galeus polli
*Holohalaelurus regani
*Scyliorhinus capensis
TRIAKIDAE
*Galeorhinus galeus
Mustelus mustelus
Mustelus palumbes
CARCHARHINIDAE
Prionace glauca
SQUALIDAE
*Centroscymnus crepidater
*Centroscyllium fabricii
Centrophorus granulosus
*Centrophorus squamosus
*Deania calcea
Deania quadrispinosum
*Deania profundorum

**Etmopterus brachyurus*
**Etmopterus lucifer*
**Etmopterus pusillus*
Scymnodon squamulosus
Squalus acanthias
Squalus blainvillei
**Squalus megalops*
Squalus mitsukurii
OXYNOTIDAE
Oxynotus centrina

Rays
TORPEDINIDAE
Torpedo nobiliana
RAJIDAE
**Bathyraja smithii*
**Cruriraja parcomaculata*
Raja alba
Raja clavata
**Raja caudaspinosa*
**Raja confundens*
Raja doutrei
**Raja leopardus*
Raja miraletus
Raja pullopunctata
**Raja straeleni*
Raja wallacei

Chimaeras
CALLORHINCHIDAE
**Callorhinchus capensis*
Hydrolagus sp.
RHINOCHIMAERIDAE
**Neoharriotta pinnata*

Bony fish
ALBULIDAE
**Pterothrissus belloci*
HALOSAURIDAE
Halosaurus ovenii
NOTACANTHIDAE
**Notacanthus sexspinis*
OPHICHTHIDAE
Mystriophis rostellatus
CONGRIDAE
**Bassanago albescens*
**Bathyuroconger vicinus*
NEMICHTHYIDAE
Nemichthys curvirostris
**Nemichthys scolopaceus*
CLUPEIDAE
**Etrumeus whiteheadi*
Sardinops sagax
ENGRAULIDAE
Engraulis capensis
ARIIDAE
Galeichthys feliceps
ALEPOCEPHALIDAE
**Alepocephalus* sp.
BATHYLAGIDAE
Bathylagus glacialis
PLATYROCTIDAE
Maulisia microlepis
STERNOPTYCHIDAE
Argyropelecus sp.
**Maurolicus muelleri*
GONOSTOMATIDAE
Triplophus sp.
PHOTICHTHYIDAE
**Photichthys argenteus*
**Yarella blackfordi*
CHAULIODONTIDAE
Chauliodus sloani
STOMIIDAE
Stomias boa boa
ASTRONESTHIDAE
CHLOROPHTHALMIDAE
**Chlorophthalmus atlanticus*
**Chlorophthalmus punctatus*
PARALEPIDIDAE
Macroparalepis macrogeneion
NEOSCOPELIDAE
Neoscopelus macrolepidotus
MYCTOPHIDAE
Diaphus sp.
MERLUCCIIDAE
**Merluccius capensis*
**Merluccius paradoxus*
**Merluccius polli*
OPHIDIIDAE
Dicrolene intronigra
**Genypterus capensis*
**Lampogrammus exutus*
**Selacophidium guentheri*
MORIDAE
Gadella imberbis
**Laemonema laureysi*
Physiculus capensis
Tripterophysis gilchristi
MACROURIDAE
**Coelorinchus braueri*
**Coelorinchus fasciatus*
**Coelorinchus matamua*
**Coelorinchus polli*
Hymenocephalus italicus
**Malacocephalus laevis*
Malacocephalus occidentalis
**Nezumia* sp.
Nezumia leonis

**Trachyrinchus scabrus*
BATRACHOIDIDAE
Chatrabus melanurus
Perulibatrachus rossignoli
LOPHIIDAE
**Lophius vaillanti*
**Lophius vomerinus*
OGCOCEPHALIDAE
Dibranchus atlanticus
MELANOCETIDAE
Melanocetus johnsoni
DICERATIIDAE
Phrynichthys wedli
SCOMBERESOCIDAE
Scomberesox saurus
ATELEOPODIDAE
Guentherus altivela
BERYCIDAE
**Beryx splendens*
TRACHICHTHYIDAE
Hoplostethus atlanticus
**Hoplostethus cadenati*
Hoplostethus mediterraneus
**Hoplostethus melanopus*
ZEIDAE
Allocyttus verrucosus
**Zeus capensis*
**Zeus faber*
OREOSOMATIDAE
Oreosoma atlanticum
CONGIOPODIDAE
**Congiopodus spinifer*
Congiopodus torvus
MACRORAMPHOSIDAE
Notopogon macrosolen
SCORPAENIDAE
**Helicolenus dactylopterus*
Trachyscorpia capensis
TRIGLIDAE
**Chelidonichthys capensis*
Chelidonichthys queketti
**Trigla lyra*
PSYCHROLUTIDAE
**Ibinania costaecanarie*
ACROPOMATIDAE
**Synagrops microlepis*
POLYPRIONIDAE
Polyprion americanus
CALLANTHIDAE
Callanthias legras
SERRANIDAE
Anthias anthias
EPIGONIDAE
**Epigonus dendiculata*
Epigonus pandionis
**Epigonus telescopus*
CARANGIDAE
**Trachurus trachurus capensis*
Trachurus trecae
BRAMIDAE
**Brama brama*
EMMELICHTHYIDAE
**Emmelichthys nitidus*
SPARIDAE
**Dentex macrophthalmus*
SCIAENIDAE
Atractoscion aequidens
SPHYRAENIDAE
Sphyraena guachancho
CALLIONYMIDAE
**Paracallionymus costatus*
GOBIIDAE
**Sufflogobius bibarbatus*
GEMPYLIDAE
Paradiplospinus gracilis
Ruvettus pretiosus
**Thyrsites atun*
TRICHIURIDAE
Aphanopus sp.
Benthodesmus tenuis
**Lepidopus caudatus*
SCOMBRIDAE
Scomber japonicus
CENTROLOPHIDAE
Centrolophus sp.
**Centrolophus niger*
Hyperoglyphe moselii
**Schedophilus huttoni*
NOMEIDAE
Cubiceps caeruleus
BOTHIDAE
Arnoglossus capensis
SOLEIDAE
**Austroglossus microlepis*
Austroglossus pectoralis
CYNOGLOSSIDAE
**Cynoglossus capensis*
Cynoglossus zanzibarensis