DEMERSAL ASSEMBLAGES OF TROPICAL CONTINENTAL SHELVES

A study based on the data collected through the surveys of the R/V 'Dr. Fridtjof Nansen'

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Department of Fisheries and Marine Biology
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Thesis for the fulfillment of the Dr. Scient. degree

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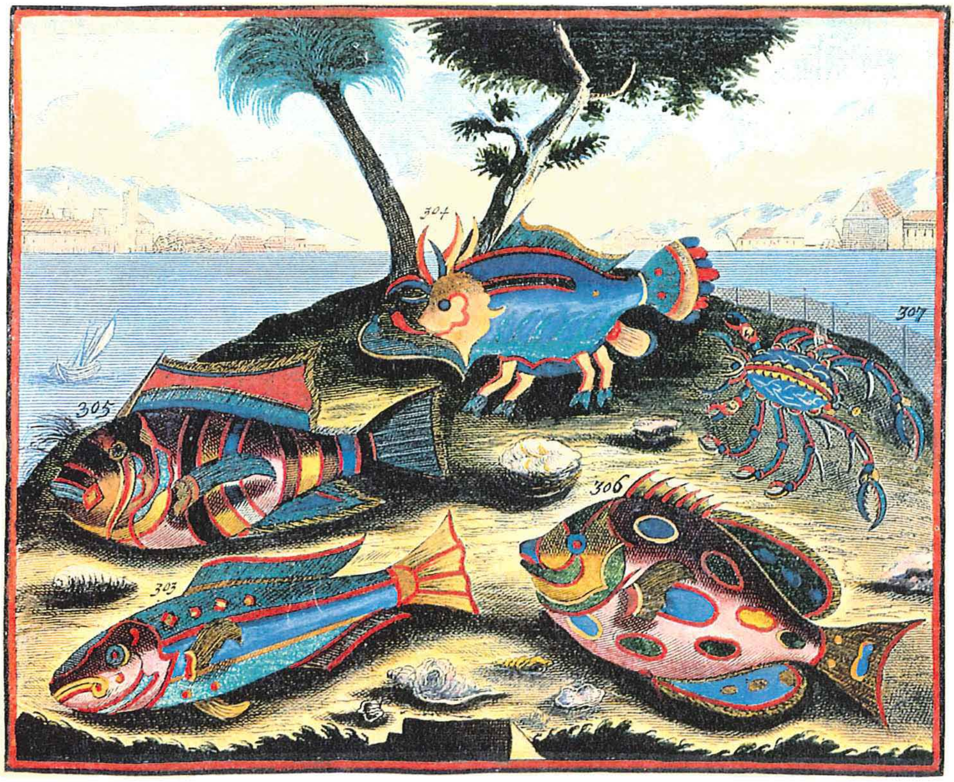

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Illustration by Samuel Fallours, part of the collection 'L'Inde orientale ancienne et nouvelle' (Published by Valentijn, 1726). Dr. M.L. Bauchot has kindly provided the illustration and its sources. See also Bauchot, M.L., Dajet, J. & Bauchot, R. (1990) 'L'ichtyologie en France au début du XIX^{e} siècle. L'histoire naturelle des poissons de Cuvier & Valenciennes'. Bull. Mus. natn. Hist. nat., Paris, 12 (1).

PREFACE

This thesis was financed by the Norwegian Research Council for Science and the Humanities from 1987 to 1991. Additional support for its completion was provided by the 'Dr. Fridtjof Nansen' Project.

I wish to thank Gunnar Sætersdal for his support throughout the project. His wide experience in tropical fisheries and fishery research has been a necessary directing element in the development of this work. The help received from Tore Høisæter has been manyfold. Apart from critically reviewing each paper he has introduced me to a number of ecological concepts, analytical methods and he has often kindly put at my disposal his vast literature collection. H. J. B. Birks has directed me in the choice of the multivariate analysis techniques used in this study and has kindly provided a more powerful version of the program TWINSPAN. Tore Strømme has been especially supportive through his programming abilities. Mari Sætersdal has kindly taken care of layout and page composition of this thesis.

Bergen, April 1992

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INTRODUCTION

Scope of this work

The main objectives of this work have been to detect recurring patterns of species associations in the demersal trawl catches from various tropical shelf areas, relate these to the main environmental parameters and thus infer the presence of different 'communities' or 'assemblages'.

Although the amount of literature on tropical fish, their population dynamics and fisheries is rapidly growing, knowledge on species interactions and responses of different assemblages to environmental gradients is still very limited. Major contributions to this field have covered the Gulf of Guinea (Fager & Longhurst 1968) and Guyana shelf (Lowe-McConnell 1962). Furthermore, the identification of subsystems within the marine tropical environment appears as a prerequisite for ecosystem and fishery modelling in these regions.

There is a general trend, both in tropical and temperate areas, to develop a more general framework for management of the resources. The realization that species are highly interacting and dependent on the physical environment and climate, on the one hand, and the necessity to develop more manageable units, on the other, has lead, for example, to the proposal of LME (Large Marine Ecosystems, Sherman & Alexander 1986) as units for conservation and management of the resources. Furthermore, tools to construct models and evaluate the relationships between various elements of an ecosystem are being developed (i.e. ECOPATH, Pauly & Christiansen 1991). In this context, the effort to identify recurrent species groups seems worthwhile, as it might help in better defining basic operational units both for ecological studies as well as for management purposes.

The data on which this work is based were obtained through bottom trawl sampling by the R/V Dr. Fridtjof Nansen on tropical continental shelves and slopes, within the framework of projects sponsored by UNDP/FAO and NORAD. Large areas of the Indian Ocean and of the tropical Atlantic and Pacific Oceans were covered in the period 1975- to date. These activities have produced the most comprehensive database on tropical demersal resources, unique for including data collected with the same type of gear throughout and for being readily available to for further analyses. Survey reports and data files are issued by the Institute of Marine Research, Bergen (Norway). Subsets of the above data set were selected, in the present work, to represent different geographical areas (Table 1 and Fig. 1)

Table 1. General overview of the surveys by the R/V 'Dr. Fridtjof Nansen' included in this study

Location	Date	Number of stations
INDIAN OCEAN		
Pakistan	5/ 9 to 16/ 9 1983	43
	20/ 1 to 2/ 2 1984	84
Oman	1/ 3 to 19/ 3 1983	37
	7/11 to 11/12 1983	52
	29/ 4 to 17/ 5 1984	37
Ethiopia	11/ 3 to 19/ 3 1984	25
Yemen	14/ 2 to 28/ 2 1984	47
	12/ 8 to 4/ 9 1984	35
Somalia	28/ 2 to 4/ 3 1984	18
	24/ 8 to 30/ 8 1984	21
Kenya	12/ 8 to 24/ 8 1982	53
	7/12 to 15/12 1982	27
Tanzania	16/ 6 to 8/ 7 1982	79
	12/11 to 3/12 1982	81
Mozambique	1/ 9 to 30/ 9 1982	61
Madagascar	16/ 6 to 28/ 6 1983	31
EASTERN ATLANTIC		
Congo-Gabon	28/ 1 to 8/ 2 1989	96
Angola	13/ 2 to 16/ 3 1989	163
WESTERN ATLANTIC		
Suriname-Orinoco	5/ 5 to 22/ 5 1988	94
	12/ 8 to 22/ 8 1988	72
EASTERN CENTRAL PACIFIC		
Nicaragua-Mexico	28/ 8 to 21/ 9 1987	191
	17/11 to 7/12 1987	157
TOTAL		1 504

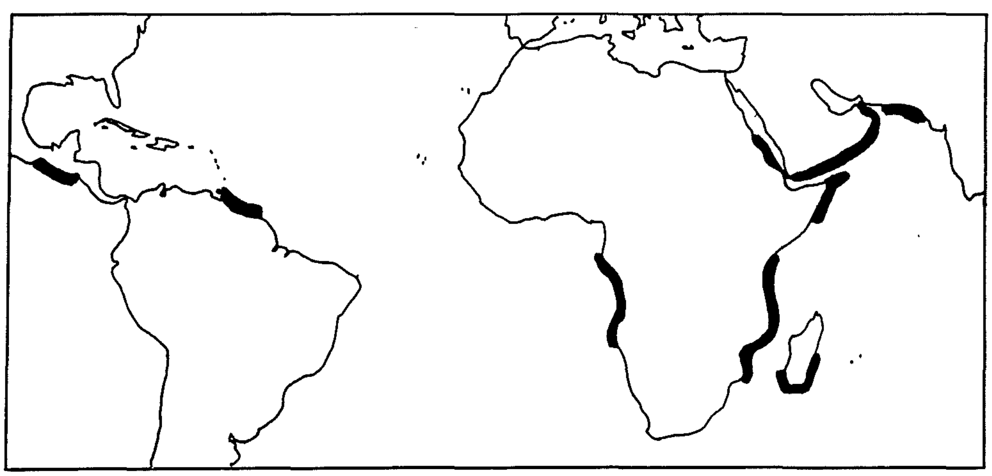


Fig. 1. Shelf areas covered by this study

The results from this work may have applications in:

- inferring unknown assemblages
- inferring catch composition in unknown areas
- stratification of fisheries by ecological regimes
- ecological regimes as basis for holistic and multispecies modelling

'Community', 'assemblage', 'ecosystem': a clarification

The problem of identifying boundaries in community ecology and hence the definition of 'community' and 'assemblage' is a common subject of discussion. The view of a community as a 'super organism' (Clements 1916, as cited by Begon et al. 1990) is largely abandoned while the 'individualistic' concept, according to which species co-exist because of their similar responses to environmental gradients, becomes more accepted. The word 'ecosystem' is used in the ecological literature in a most wide range of meanings and Loehle (1987) mentions this term as an example of 'error of abstraction' in ecology where a number of attributes are given to 'ecosystems' without operationally defining them.

Attempts to operational definitions of ecosystems may be found in the literature (Sherman & Alexander 1989) '.. LME are regions with unique hydrographic regimes, submarine topography, productivity and trophically dependent populations'. There seems to be a contradiction in this definition between 'large' and the defining criteria (according to which most marine ecosystems would not be very large). The definition of 'large' is given by Sherman, 1989, as an area equal to or larger than 200 000 km^2. This definition may well be applicable to areas characterized by pronounced oceanographic features (like those of the east boundary currents) or geographically well-delimited (Gulf of Thailand, North Sea, Adriatic Sea etc.). I find it difficult however to extend it to most of the tropical regions where, as I hope to have demonstrated in this work for those areas covered, there are clear signs of zonation and indications of different life strategies on a much smaller scale than presented by the above definition.

It is outside the scope of this work to review the various definitions of the above concepts, but I would like here to clarify the use made of these designations in this work. I have used 'community' and 'assemblage' as synonyms, to indicate an association of coexisting species with similar environmental tolerances, possibly trophic relationships, but not totally interdependent. Quasi-discrete boundaries between species assemblages usually appear in connection with sharp changes in the physical environment and, conversely, gradual changes in species associations reflect gradual changes in the environmental conditions.

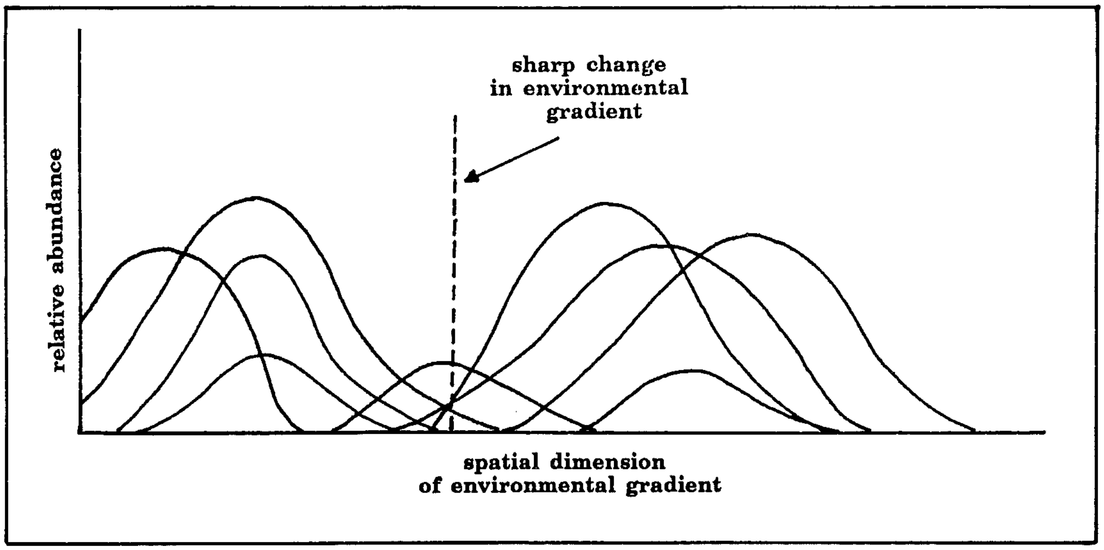


Fig. 2. Unimodal distribution of various species showing the presence of quasi-discrete assemblages as a result of a sharp change along an environmental gradient

The word 'ecosystem' has been used here either to indicate the biological community together with its physical environment or to describe areas of the ocean influenced by a given major oceanographic process (which might actually result in different biological communities).

Description of the way groupings of species are distributed in nature and the way these groupings are the result of the physical environment as well as of the interactions between species constitutes one of the first objectives in community ecology. A better definition of operational units on tropical continental shelves appears as a prerequisite for the further development of fields within ecological theory or of holistic methods for resources management.

Data analysis

The data set used includes a total of about 1 500 trawl stations and almost 2 000 species. The number of species and stations in each geographical area varied but in all cases it appeared necessary to take recourse to multivariate analytical methods to help in revealing the presence of structure in the data. The methods chosen, among a wide variety of possibilities, are based on Correspondence Analysis: a classification technique TWIA (Two-Way Indicator Analysis), implemented by the computer program TWINSPAN and an ordination technique DCA (Detrended Correspondence Analysis) implemented by the computer program DECORANA. In Paper 1 I explain the reasons for this choice, the main characteristics of the above methods and cite relevant literature.

I would like here to add that the detrending by segments has been restored and was used in all analyses except in Paper 1, where detrending by second order polynomials was used (ter Braak 1991). Furthermore, evidence has been presented by Jackson & Somers (1991) that the heuristic compensation for the arch effect in DCA by the 'detrending' procedure may affect the ordination at higher dimensions. The choice of the number of segments was shown to be particularly critical. However, this seems to be true when the number of samples is small as compared to the chosen number of segments and for short gradients. In the case of long gradients this effect is smaller and, conversely, the arch effect and compression of the extremes becomes stronger when using CA without detrending. Therefore, it was still found more appropriate to use DCA in this study. Furthermore, the definition of species groups is derived from a classification technique as well (viz TWIA) and in the light of environmental variables.

The ordination method used (DCA) is part of the class of methods of 'indirect gradient analysis' i.e. ecological regimes are inferred from species compositions only. The ordination obtained reflects the distribution of species along the main axes which, in turn, represent theoretical environmental gradients. After ordination, correlations with observed environmental parameters, may indicate the role they play in determining the observed species patterns. The program package used in this study (CANOCO, ter Braak 1991) allows a variety of analyses to relate species associations to environmental variables. This programme package, developed for floristic studies, is now being more and more used also in faunistic studies and I believe it will become rather popular also in fish community studies.

What was also found particularly advantageous with the above methods is the underlying unimodal model, i.e. reflecting the fact that species show bell-shaped response curves with respect to environmental gradients (Fig. 2) which appears more realistic than linear models (as for example in PCA - Principal Component Analysis).

A 'pseudo-F' test was performed in Papers 1 and 2 but later abandoned because considered redundant as the key or indicator species of each group can also be identified through TWIA.

Sampling errors and limitations

In Paper 1, under 'Discussion' I present some comments on sampling errors, mostly related to the gear used. A further comment regards the limited time-span represented by each observation in each of the studied areas, which partly reflects the type of data available, i.e. covering large areas but none of the area covered with consistent survey patterns over long periods of time.

Seek simplicity, but distrust it

The patterns of species associations found in this study will contribute to parsimony in the study of faunistic communities of tropical continental shelves. On the other hand, the descriptions presented obviously represent an oversimplification of reality. Apart from the sampling drawbacks, there is some degree of subjectivity at several stages of the analyses performed which are difficult to evaluate statistically. The options related to data transformation, detrending procedure, number of segments in the DCA analyses are, for example, quite crucial and different results may be obtained by choosing different options. The choice of pseudospecies cutlevels in TWIA is another example of options that may give different results. Furthermore, the recognition of 'meaningful' assemblages is mainly heuristic and not based on a totally objective discrimination. In choosing 'meaningful' assemblages I have combined environmental parameters in direct ways (i.e. correlation with DCA axes) and indirect ways (for example bottom type and biology of various species as provided in the literature).

The balance between finding general patterns without theoretically moving too far from reality is the most difficult task when trying to interpret the processes inherent to the biological world. The urge of 'making things simple' to be able to understand, or believe that we understand, might make us only search for the 'basic laws and patterns' governing biological complexity. On the other hand, the puzzling amount of species forms, the intricacy of the interactions between individuals and taxa, between communities and environment are there as a result of a long evolutionary process and a thorough understanding of reality cannot bypass these factors.

'Pelagic', 'semi-pelagic' and 'demersal'

Although the title of this work refers to demersal taxa, the analyses actually include species with intermediate type of behaviour. In fact, a large part of the catches consisted of species whose habits are semi-pelagic (sometimes referred to as bentho-pelagic). On the other hand, a number of species usually included in either category showed indeed an intermediate type of behaviour. The definition 'demersal' in fisheries usually includes species caught near the bottom (i.e. in bottom trawl fisheries) but this concept is obviously also used in ecological terms (Longhurst & Pauly 1987). A more ecological definition would encompass only truly benthos-feeding animals. To be consistent with the latter definition, I would have to exclude most of the species caught in the bottom trawl. Instead, I decided to include all species because of the difficulty in choosing 'real' demersal species and because the relative abundance of pelagic/semipelagic forms would reflect different environments notwithstanding the fact that they are not quantitatively representative of the relative species abundances in that community. Furthermore, is it appropriate to define demersal fish communities as operational units, in the sense of communities trophically separated from the upper water layers? Some of the findings of this work as well as available literature indicate that most dominating species in the various marine ecosystems show a great flexibility in their habits i.e. they are observed both pelagically and near the bottom and may have a wide range of feeding habits. Even species that are believed to be 'typical pelagic' as for example older juveniles of Sardinella aurita, may temporarily feed on benthic microorganisms as a major food item, possibly in the case of shortage of zooplankton. This is also observed in a number of other clupeoids (Van Thielen 1976).

COMPARISONS OF SPECIES ASSEMBLAGES FROM DIFFERENT CONTINENTAL SHELVES

A classification of communities, based on their predictability in time and space, describes the existence of a spectrum of community types ranging from deterministic to stochastic, the former found in relatively undisturbed habitats, the latter in environments that are so variable as not to allow predictable communities to develop. The food webs will reflect this situation, with specialized feeders in the deterministic communities and non-specialized feeders in the stochastic communities.

'Tropical' communities have generally been ascribed to the deterministic type because of the stable conditions found in tropical areas (see for example Pauly 1979). As it will be shown in the following papers, large areas of tropical shelves are subject to important seasonal fluctuations of different type. For example, estuarine areas are flooded on a seasonal basis (during the rainy season); shallow waters of the tropical western coast of Africa and America, where the shallow and sharp thermocline is subject to vertical displacement due to ebb and flow, internal waves, seasonal upwelling (in some areas) etc., are exposed to different water masses; shelf areas are seasonally exposed to low-oxygen waters, like in the North-Western Indian Ocean. In these areas, according to ecological theory, we should expect more stochastic type of communities, while the shelf waters off, for example Tanzania, with rather stable conditions throughout the year, should show the existence of more deterministic-type of communities. The intervention by man on these communities, in the form of massive fishing and high mortality rates, should be considered in many cases more as an environmental disturbance than predation and thus eventually result in more stochastic communities. Thus tropical areas subject to intensive fishing may be looked upon as highly disturbed systems with density-independent reductions in biomass. These systems will, over time, loose their properties of stable ecosystems with K-selectionist species and acquire features of unstable, perturbed systems where r-selection will be the most successful way of life. This is shown in Fig. 3

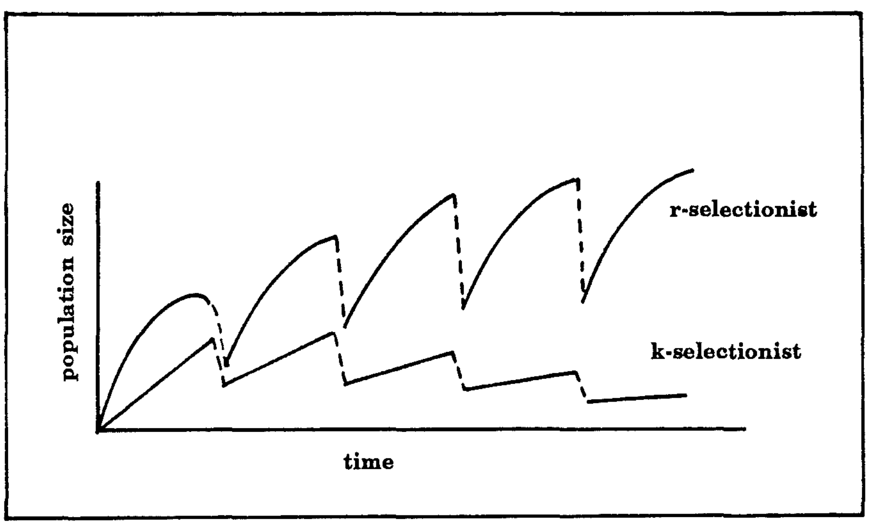


Fig. 3. Different responses to drastic reductions in population sizes (modified from Begon et al. 1990)

The following is an overview of the major assemblages identified in the course of this study and will focus on which species and which 'trophic guilds' dominate the various assemblages. This, in turn, reflects the life strategy of the various groups.

The species selected to represent the assemblages are those derived from the various analyses performed through this study. A more detailed description of these can be found in the various papers following this introduction. Here they are represented in terms of their percentage biomass, percentage numerical abundance and percentage frequency in each assemblage. The order of species was determined by the Index of Relative Importance i.e.

$$IRI = (\%W + \%N)\ \%F$$

and only species with an IRI > (or equal) 100 were included.

The above index was actually developed for stomach content studies (Olson 1982 as cited by Caddy & Sharp 1986), but was found useful also in this context for integrating different abundance indices.

Trophic guilds are defined as major classes of species sharing prey preferences, based on information derived from various literature sources (Lowe-McConnell 1962, for the northern coast of South America, Longhurst 1960, for West Africa, Fischer & Bianchi 1984 for the Indian Ocean), in the attempt of comparing different adaptive strategies in the various assemblages identified:

- **detritus feeders**: mainly benthic crustaceans, the shallow water representatives characterized by very fast turnover rate;

- **benthos feeders**: species feeding predominantly on bottom invertebrates (catfishes genus Arius), bathoid fishes (Raja, Dasyatis etc), several sciaenid species (Johnius, Micropogonias), seabreams and sweetlips (Sparus, Diagramma etc.). This group includes many K-selectionists species.

- **zooplankton feeders**: mostly clupeoids (except Anchoa spinifer, a well-known ichthyophagous species) some carangids (Decapterus). This group represents, 'par-excellence', species with rapid turn-over (r-selectionists). Most clupeiforms are restricted to shallow waters where they may have a semi-pelagic type of behaviour (this would be more difficult in deeper waters because of their physostomous type of swim-bladder).

- **generalists (small prey, mainly fish and invertebrates)**: this group includes several species, able to feed on a wide variety of small fishes and invertebrates both on the bottom and pelagically. This feeding habits are also reflected in the life style, usually bentho-pelagic. i.e. found both close to the bottom and in mid-waters. Representatives of this group come both from more typically pelagic groups (Carangidae, Chloroscombrus, Selar, Selene, in shallow waters and Trachurus, in deeper shelf waters), and from more typically demersal groups: Pomadasyidae (Brachydeuterus auritus), Balistidae (Balistes capriscus), Sparidae (Pagellus bellottii and Dentex macrophthalmus), Nemipteridae (Nemipterus japonicus) etc.

Many of the above species are described in the literature as demersal but they were observed both in mid waters and close to the bottom through acoustic registrations and sampling (this information is not yet published).

- **generalists (larger prey, mostly fish)**: larger sciaenids (Pseudotolithus typus and senegalensis, Cynoscion, Otolithus) Trichiurus lepturus, various species of snappers and seabreams (Lutjanus, Sparus, Dentex) sharks (Paragaleus, Rhizoprionodon, Carcharhinus etc.).

- **omnivorous, close to reef areas**: this category had to be defined for one group of stations off Tanzania with typically reef species.

Figs. 4 to 8 include assemblages found at increasing depths respectively, including the shelf and upper slope areas. Each group can be identified by the geographical area and its average depth, temperature, oxygen and salinity. The assemblages were chosen to reflect similar seasons (dry).

Shallow-water assemblages

Fig. 4 shows three assemblages found at depths < 20 m and Fig. 5 includes assemblages at average depths > than 20 m and < 30 m.

The top and bottom assemblages of Fig. 4 are from shallow waters under the influence of large river runoffs, of the northern coast of south America and Mozambique respectively. While off Mozambique clupeoids are largely dominating, off the northern coast of south America the commercially important shrimp Xiphopenaeus kroyeri and its main predator, the sciaenid Macrodon ancylodon (Isaak 1988) are typifying this assemblage. The very short food chain (with the shrimp as detritus feeder) and its short life-span must have made these species very strong and resistant even to the intensive fishing by trawlers and fixed nets that has been going on since the fifties (Willmann & Garcia 1985). Furthermore, their presence indicates that the main energy flow must come from detritus while the higher percentage of pelagic species off Mozambique indicates an important flow through the pelagic environment as well. The shallow waters off Suriname and Guyana are particularly charged with suspended mud. The extremely high turbidity might be responsible for lower productivity in the water column and thus explain the lower percentage of clupeoids

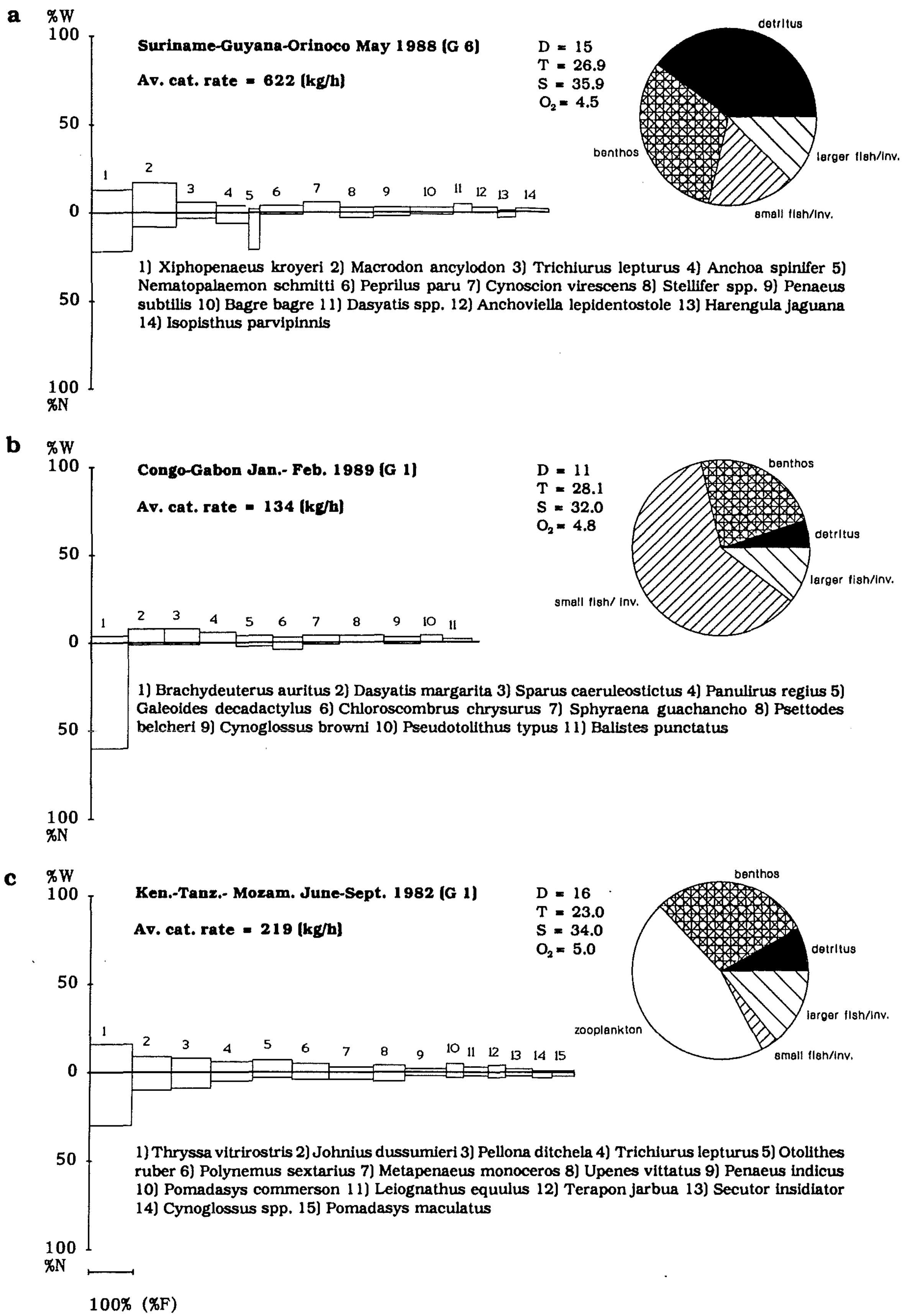


Fig. 4. Examples, from different regions, of shallow-water assemblages (depth < 20 m) where the main species are arranged according to their Index of Relative Importance (IRI). Pie charts represent the same species grouped according to their food preferences

observed here (also confr. Lowe-McConnell 1962). Off Gabon, where the shallow waters are not associated with any major river system, the catches were dominated by juveniles of Brachydeuterus auritus and a few demersal groups, mostly juveniles, with large Psettodes erumei probably preying on them.

Moving to slightly deeper waters (Fig. 5) we have representatives for all the areas covered. The two assemblages of the Eastern Central Pacific (a, b) and the corresponding assemblage off the northern coast of South America (c) are largely dominated by clupeoids (Anchoa and Pliosteostoma in the Pacific and Chirocentrodon and Pellona in the Western Atlantic, carangids (Chloroscombrus and Selene) and pelagic predators as for example Sphyraena. Trichiurus lepturus, a circumtropical as well as eurybathic and benthopelagic species, appears important off the northern coast of South America but does not appear in the Pacific where this species has a deeper depth range. It is interesting that about 70% of the species belong to Neotropical endemic taxa i.e. found only on either side of Central America, including both fish and invertebrates. Moving to the Eastern Atlantic (Fig. 5 d, e), both shallow water assemblages off Congo and Angola are dominated by the tropical Eastern Atlantic endemic Brachydeuterus auritus, a member of the family Haemulidae (=Pomadasyidae) that, contrary to the habits of the other members of the family, moves to intermediate waters and has been defined in various literature as eurybathic and eurythermic, having its greatest abundance in the zone occupied by the thermocline and thus characterized by a rapid change in the characteristic of the water (see Paper 2). Clupeoids, represented by Ilisha and Engraulis, do not appear as dominating as in the Pacific/Western Atlantic. Chloroscombrus and Selene are also important elements. Off East Africa (Fig. 3 f) the dominating taxa at this depth range are completely different and three species of Leiognathidae dominate both in biomass and numerical abundance, with Sphyraena as main predator. Clupeoids are represented by Pellona and Sardinella. The species association off Pakistan consists mainly of real demersal species, except for Trichiurus lepturus, with the highest IRI. In this region however the ecological conditions are quite peculiar, since the shelf species are pushed to shallow waters by the presence of oxygen-depleted waters and the oxygen levels are the lowest at this depth range than in any of the other regions. It is possible that the presence of the small, shallow-water clupeoids depends, among other things, on the presence of higher oxygen concentrations.

What I find striking is the dominance in all the regions, except for Pakistan and the shallowest group off South America, of species of pelagic semi-pelagic type. In the New World, the shallow water assemblages are dominated by a rich clupeoid fauna of mainly zooplanktivorous fishes. They are mostly small (< 10 cm) and characterized by a rapid turnover. Now the question is whether this is the result of intensive fishing for shrimp, by bottom trawl with fine meshes or an ecological adaptation to an environment that can be

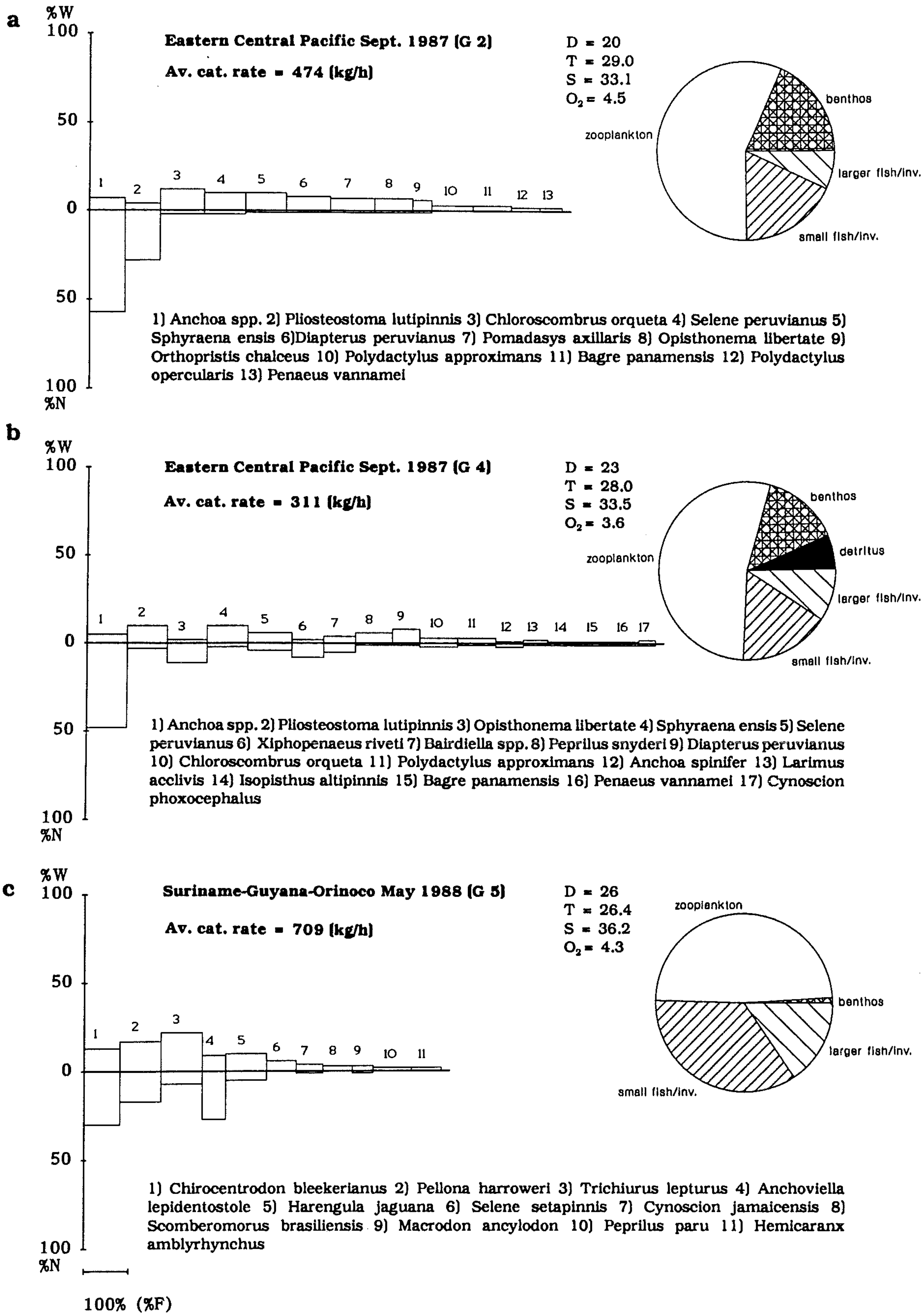
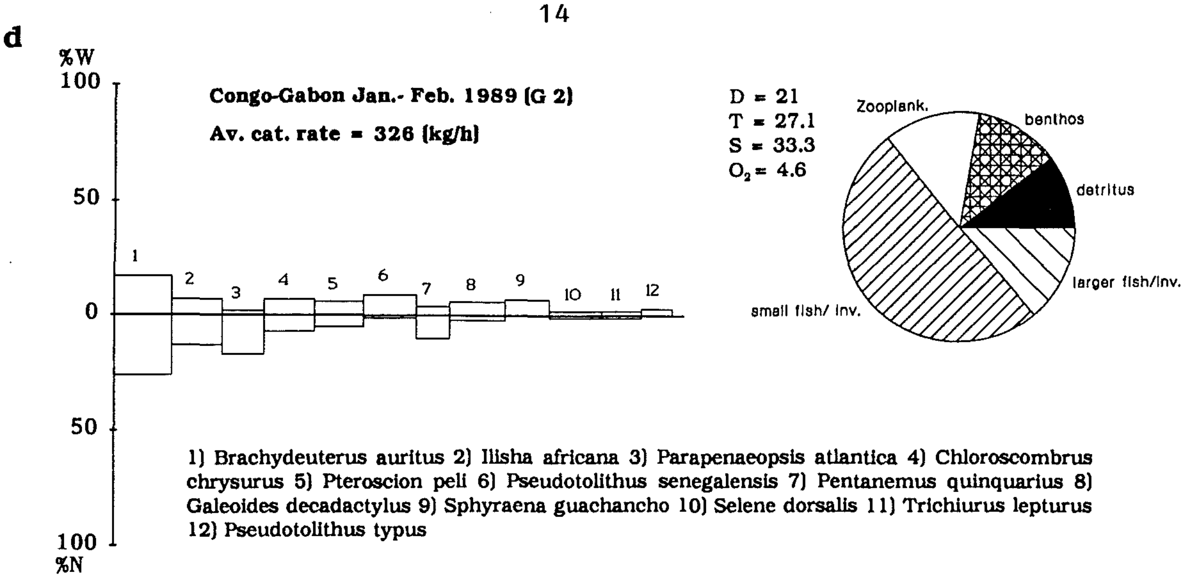
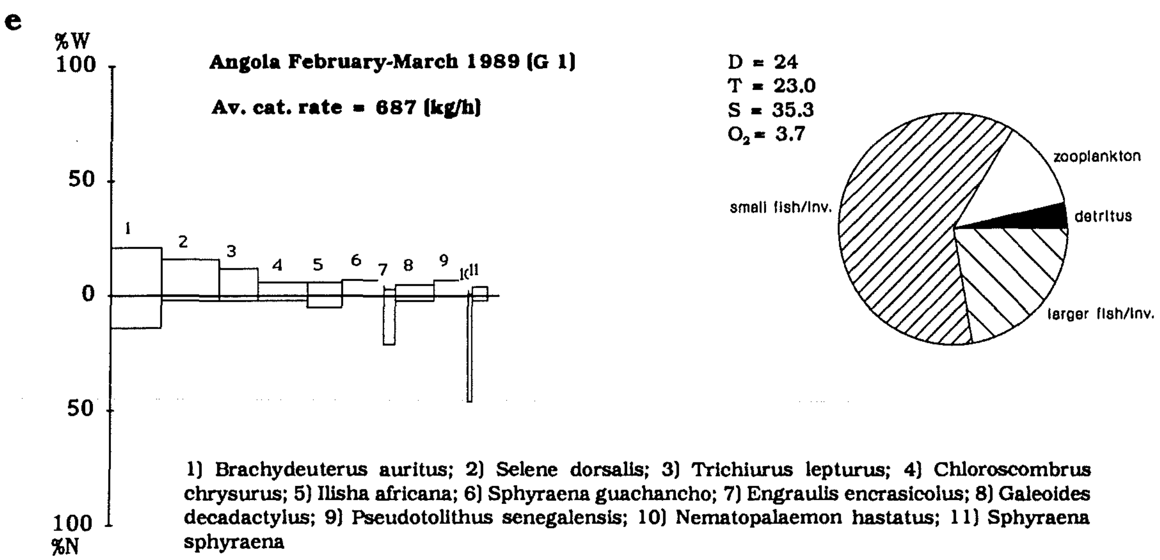


Fig. 5. Examples, from different regions, of shallow-water assemblages (20 < depth < 30 m) where the main species are arranged according to their Index of Relative Importance (IRI). Pie charts represent the same species grouped according to their food preferences





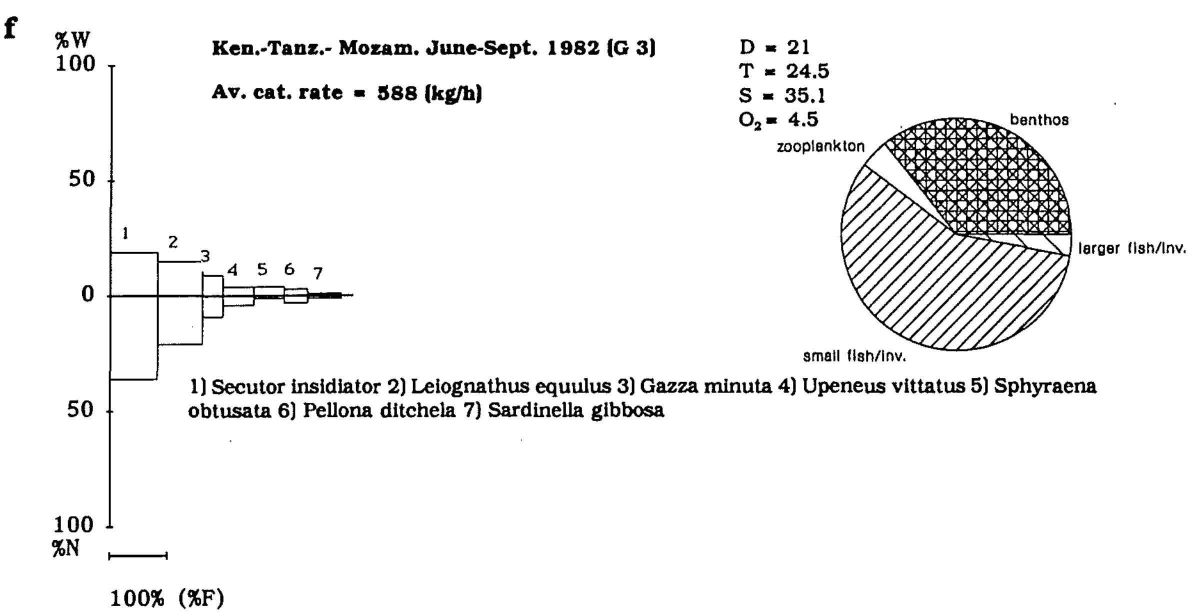


Fig. 5. Continued

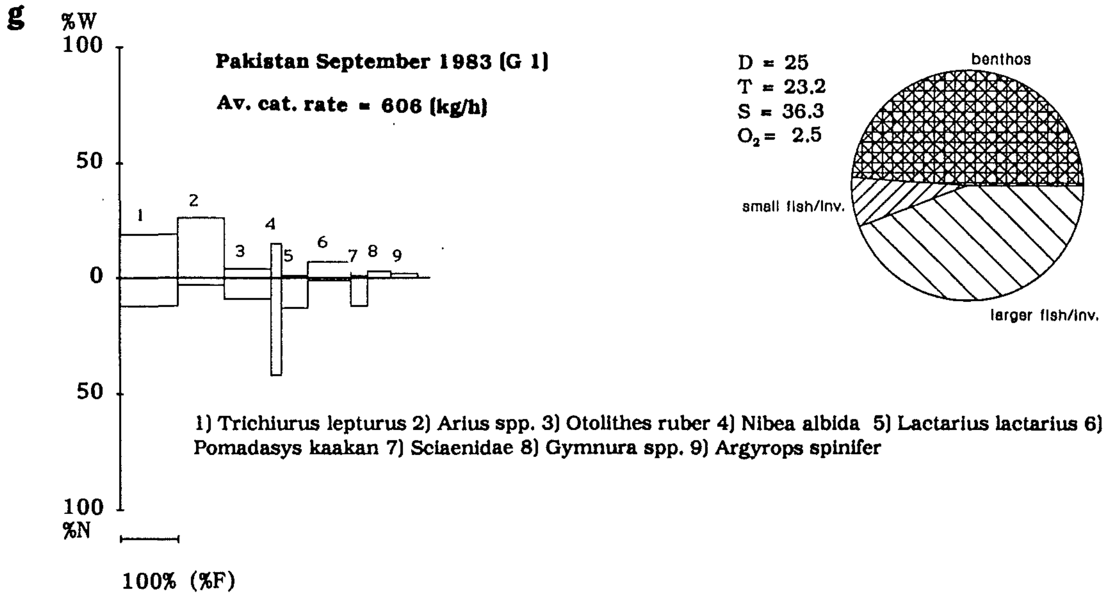


Fig. 5. Continued

rather unstable because of tidal movements, changes in turbidity ect. (Gines & Cervigon 1968). The continuous variation would prevent this system from reaching a climax and would favour phylogenetically primitive taxa (clupeoids). On the other hand, intensive fishing with bottom trawl and fine trawl meshes must lead to a selection of small clupeoids as compared to other, larger, longer-lived demersal fishes. The pattern that these communities possibly have undergone is presented in Fig. 3 where it is evident that when k-selectionists and r-selectionists are subject to the same type of disturbance (in this case reduction in population size by fishing pressure) the k-selectionists (usually larger demersal fishes) are more vulnerable. Furthermore, larger demersal fishes are probably more easily caught and are more available to bottom trawling than the small pelagics. The present situation probably reflects both mechanisms.

In the Eastern Atlantic there is a clear dominance of Brachydeuterus auritus. This species was described as dominating in the Gulf of Guinea already in the fifties. Off Congo-Gabon and Angola this species largely dominates. The reasons of its dominance must reside in its ecological flexibility, consisting in a eurybathic and eurythermic behaviour, entailing the capability of adjusting to environmental changes and in a semi-pelagic behaviour, which probably makes it less available to bottom trawling. This species reaches its highest abundances in areas with seasonal upwelling off Congo and Northern and Central Angola.

Intermediate shelf

Under this category I have included all assemblages around 40 m depth (Fig. 6). Zonation at around 30 m depth seems to be present in all the areas studied, independent of the structure of the water column, i.e. independent of the depth of the thermocline (see for example Paper 5 and Paper 7). Evidence for zonation at this depth was also found by McManus (1986) in the Samar Sea. The reason for the presence of this faunal boundary may indicate the separation between the shallow-water environment and the intermediate shelf environment and related differences in energy sources and flows. In shallow waters the relationship to the bottom must be stronger and primary production is enhanced both by nutrients brought by the rivers and through the stirring of the waters by local winds.

Fig. 6 shows the similarity between the two assemblages identified in the Eastern Central Pacific and two off the northern coast of South America (a and c, b and d). The interpretation of the presence of two different assemblages at a similar depth range in each of these areas was interpreted as depending on bottom substratum. Group 1 of the ECP and Group 3 of Suriname-Guyana are both dominated by Chloroscombrus (orqueta in the

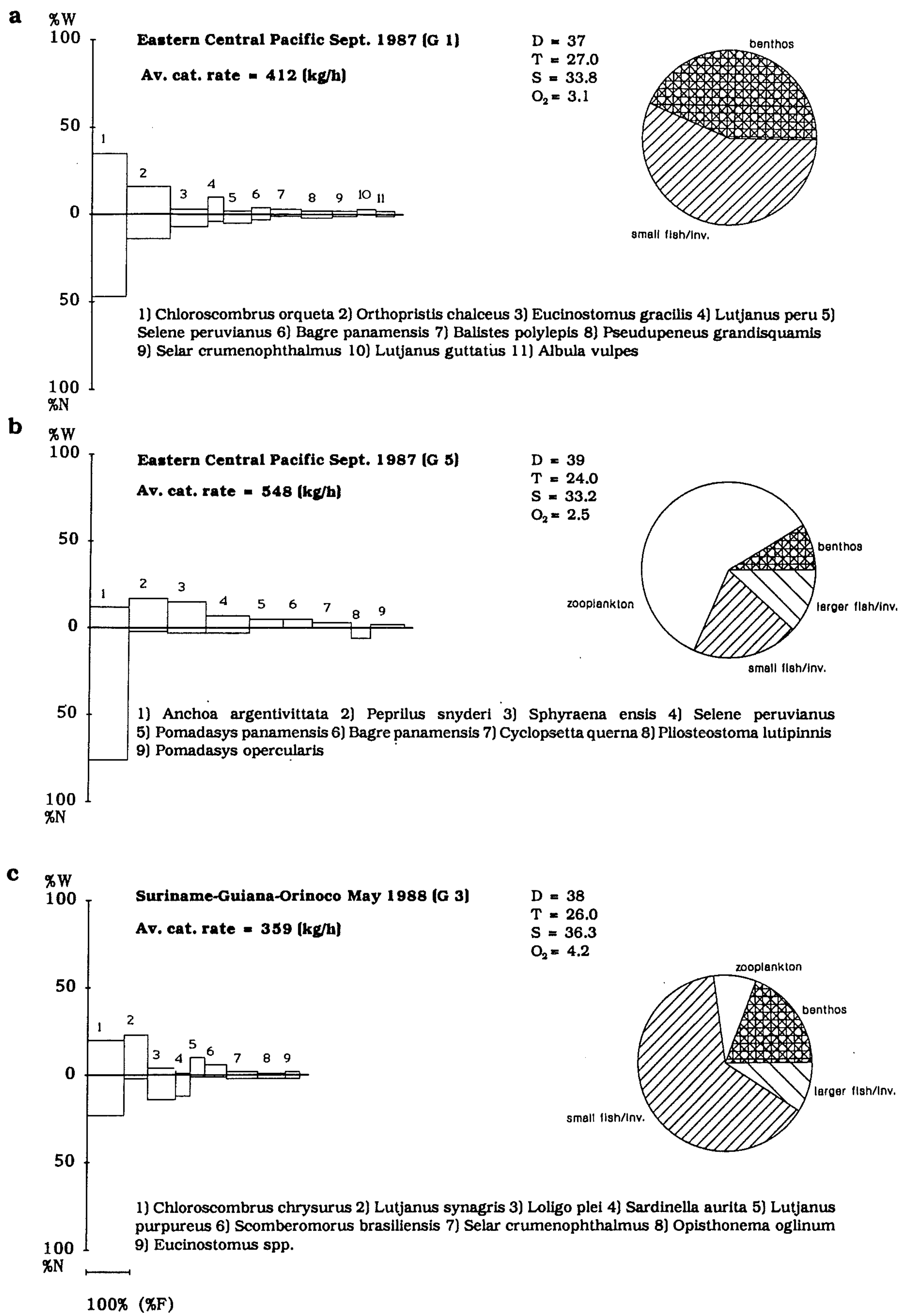


Fig. 6. Examples, from different regions, of intermediate-shelf assemblages (30 m < depth < 50 m) where the main species are arranged according to their Index of Relative Importance (IRI). Pie charts represent the same species grouped according to their food preferences

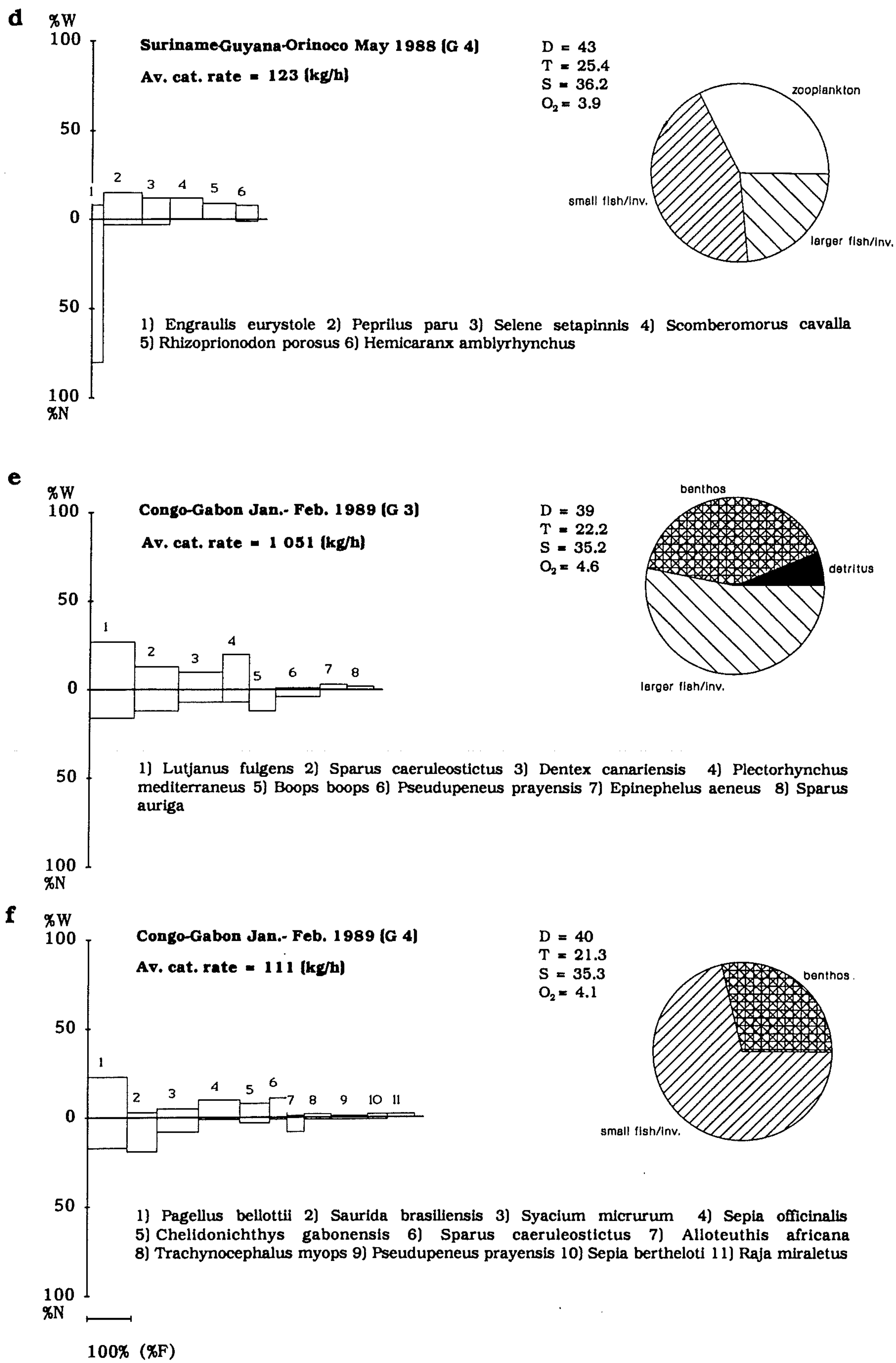


Fig. 6. Continued

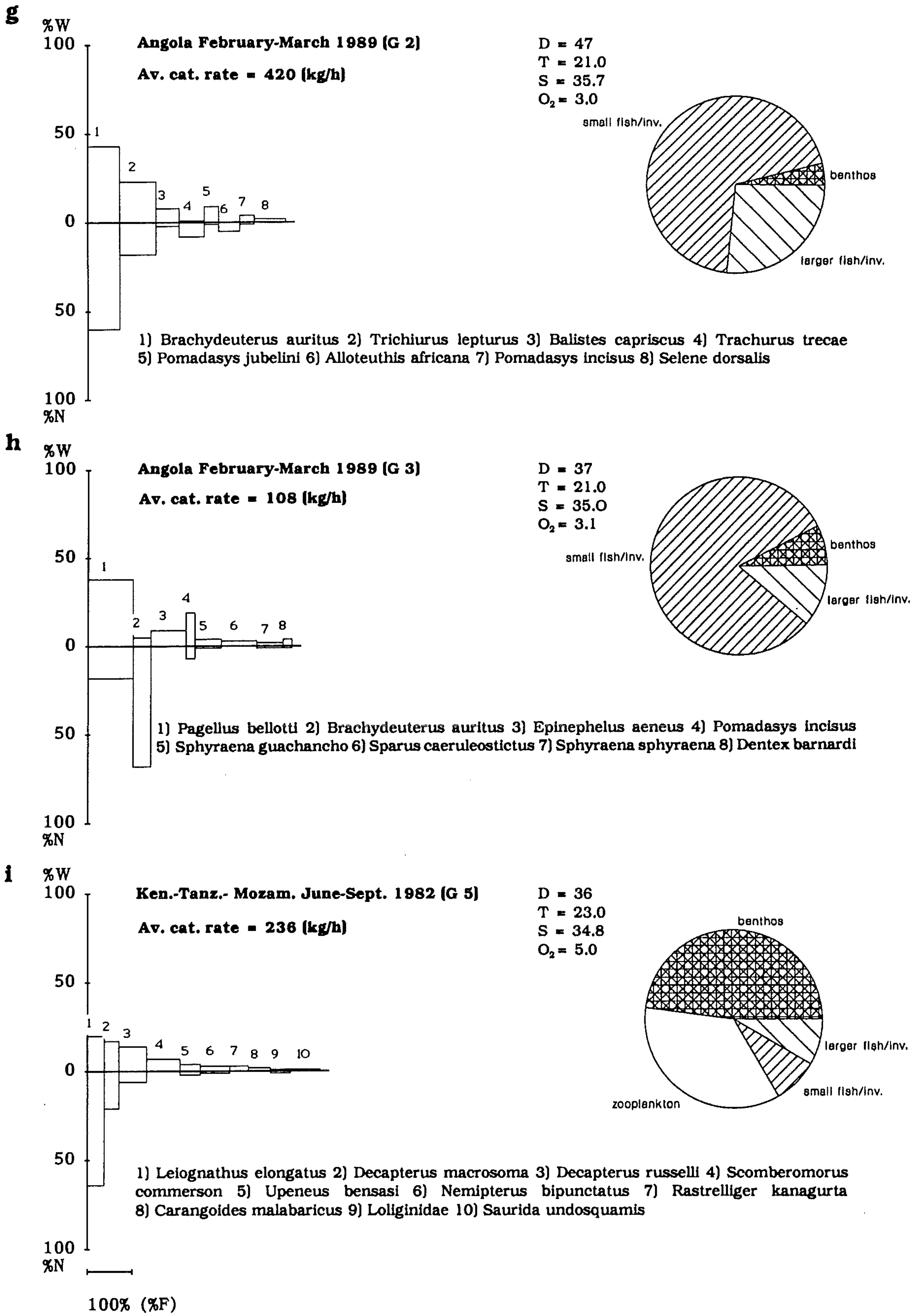


Fig. 6. Continued

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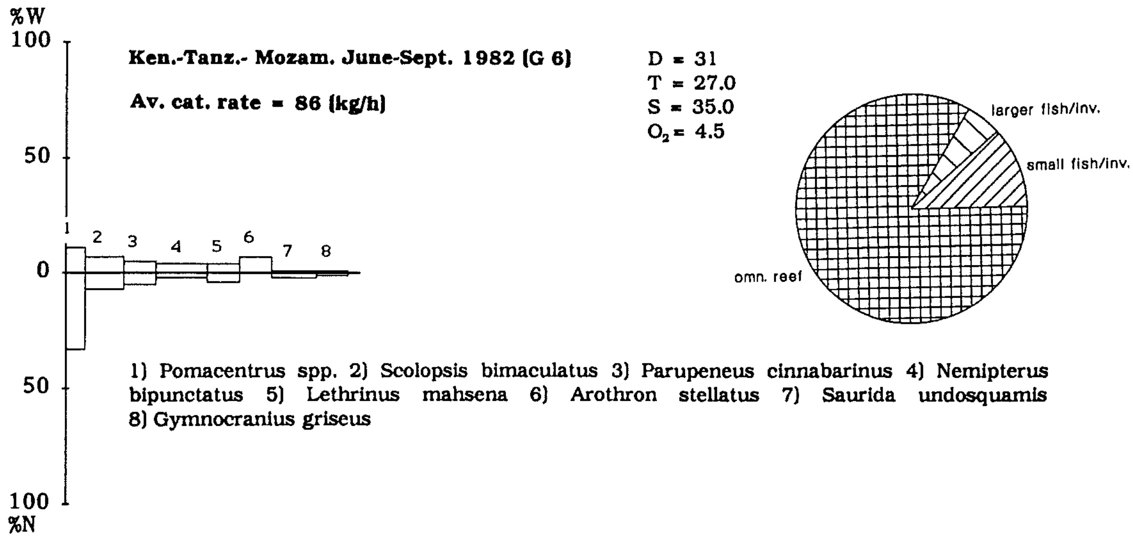

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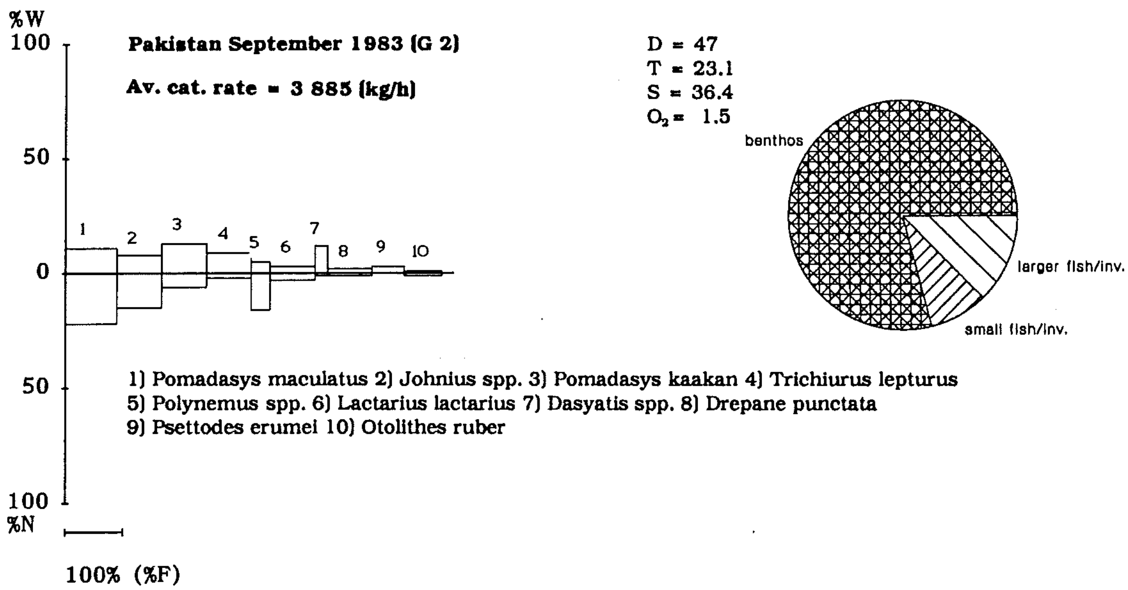


Fig. 6. Continued

ECP and chrysurus in the Atlantic) followed by a number of typically demersal species with preference for sandy bottoms and Selar crumenophthalmus. The demersal species include various species but in both the assemblages there are two Lutjanus species. The other type of assemblage includes an engraulid dominating in numbers, followed by the Peprilus snyderi, Sphyraena ensis and Selene peruvianus in the ECP and Peprilus paru, Selene setapinnis and Scomberomorus cavalla in the Atlantic. In this second type of assemblage there is a clear dominance, in the catch composition, of pelagic forms occupying various trophic levels, with the anchovies as planktivorous elements and predators of increasingly larger size.

In the Eastern Atlantic, on fine sand bottoms the sparid Pagellus bellottii was found to dominate this depth range both off Congo (Fig. 6 f) and off northern Angola (Fig. 6 h). However, where seasonal upwelling is stronger or because of softer type of bottom the eurythermic and eurybathic species Brachydeuterus auritus, Trichiurus lepturus and Balistes capriscus dominate totally.

Off East Africa, especially off Tanzania (Fig. 6 i), Leiognathus and a number of semi-pelagic species (Decapterus and Scomberomorus) constitute more than 60 % of the biomass in the catches and almost 100 % in numbers. Demersal species are represented by the goatfish Upeneus bensasi and the threadfin Nemipterus bipunctatus. However, in areas very close to coral reefs, a number of reef genera appear while Leiognathus disappear (Fig. 6 j).

Off Pakistan (Fig. 6 k), real demersal species are dominating the bottom trawl catches and small pelagics, semipelagics are practically missing. Again, this might be due to the particular environmental conditions found here, leading to the concentration of benthic fishes to the intermediate and shallow parts of the shelf to avoid oxygen-depleted waters.

Deeper shelf (Assemblages with average depths greater than 40 m)

The shelf edge is rather deep off the ECP, it reaches to about 100 m depth off the Northern Coast of South America, about 150 m off Congo-Gabon Angola. In the Indian Ocean it is extremely shallow off east Africa where the shelf shows a break already at 60-70 m. In the North Western Indian Ocean the shelf edge is at about 100 m throughout. Therefore, the average depths of the assemblages under 'deeper shelf' include a large depth range (Fig. 7).

In the ECP an intermediate type of assemblage (Fig. 7 a), separating the well oxygenated waters from those with extremely low concentrations found on the deeper shelf, appears numerically dominated by the small cephalopod Loliolopsis diomedeae. Of the few demersal species present, the small toadfish Porichthys nautopaedium was consistently present and was the indicator species of the group. Possibly its oxygen requirements are very low considering its body shape which suggest a rather stationary way of life. Where oxygen levels are below 1 ml l^{-1} (Fig. 7 b), most shelf species disappear and diversity becomes extremely low. The galatheid crustacean Pleuroncodes monodon largely dominates in biomass and numbers. The separation of this species from P. planiceps (rather famous for having partially occupied the anchovy niche off California, (Walsh et al. 1977) is taxonomically unresolved and possibly more studies are required to ascertain whether two species are really present. There appears to be a different behaviour in the two species but I am more inclined to believe that it is one species with different types of feeding behaviour. The great abundance of this species may be explained in the light of lack of predation and the fact that it is a detritus feeder.

Off Suriname and Guyana (Fig. 7 c) oxygen concentrations and temperature are still quite high at the shelf edge. Furthermore, the bottom is sandy with rocky/coral outcrops and this explains the occurrence of several species of Lutjanidae. These are however represented by the smaller Rhomboplites aurorubens and Pristipomoides macrophthalmus and to a lesser extent by larger representatives of the family (Lutjanus purpureus). The larger lutjanids might however be confined to the rocky areas not sampled with the bottom trawl. There is also a massive presence of semipelagic species represented by Trachurus lathami, Selar crumenophthalmus and Decapterus punctatus, mostly feeding on small fishes, invertebrates and fish larvae.

Off Gabon (Fig. 7 e) a sparid community may be identified, with Dentex congoensis and other species usually ascribed to the Eastern Central Atlantic sparid community of Fager & Longhurst (1968). Boops boops is another representative of the family though with a more semi-pelagic behaviour as well as Pagellus bellotti. Trachurus trecae is the second most important species in the catches. Off Congo (Fig. 7 d) Brachydeuterus auritus has no competitors and the sparid community appears rather depauperate in terms of what are known to be its typical species (Fager & Longhurst 1968). Dentex angolensis, which was reported by Durand (1967) as dominating the edge of the shelf, appears only at the end of the diagram. Off northern Angola (Fig. 7 f), although the sparid fauna is well represented, the bulk of the species caught are of semi-pelagic type. At the edge of the shelf the catches consist almost exclusively of bentho-pelagic forms found both close to the bottom and in mid-waters (Fig. 7 g). Southern Angola (Fig. 7 h) displays a lower diversity, with dominance of three species: Dentex macrophthalmus, Trachurus trecae and Trachurus

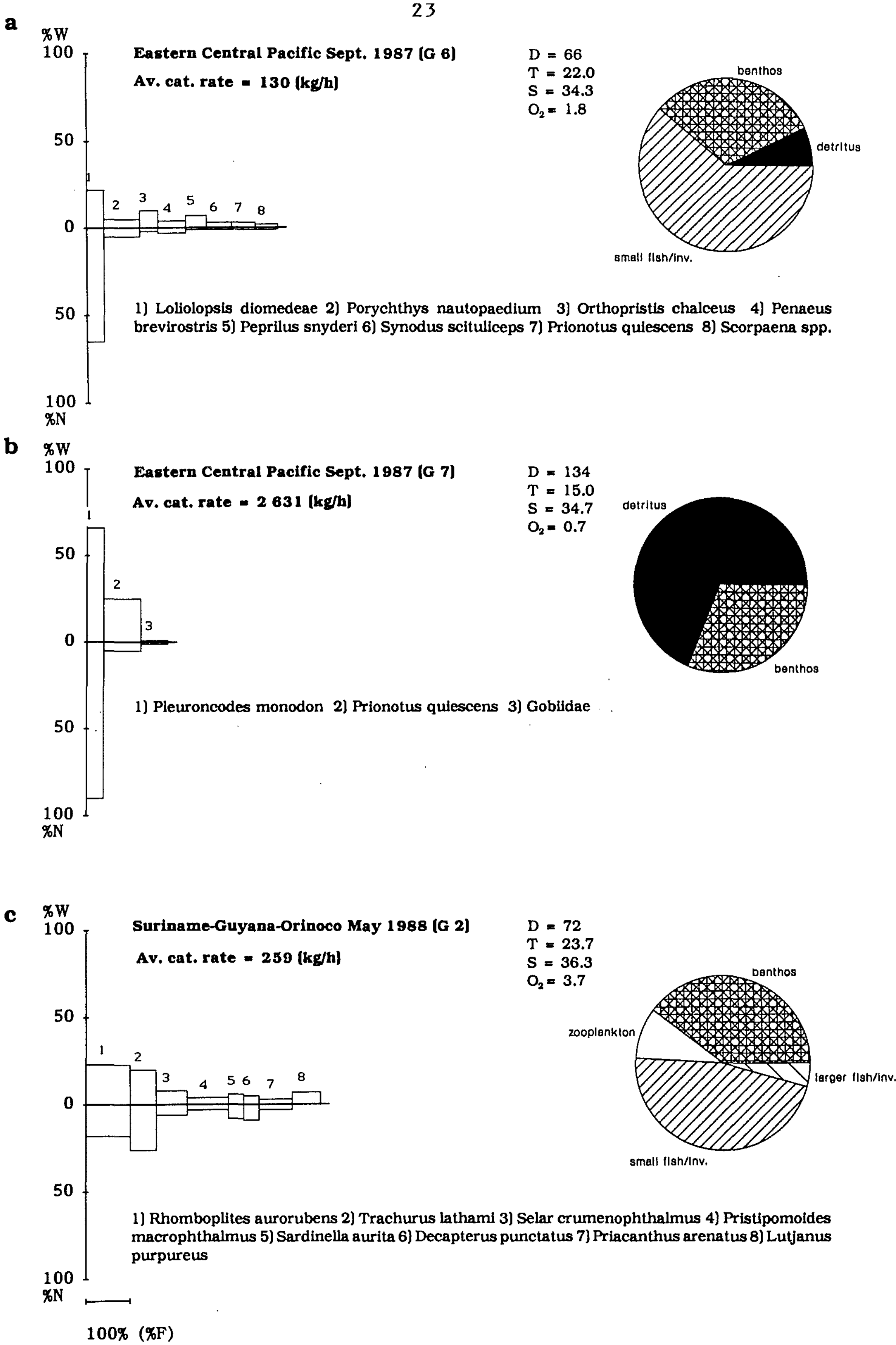
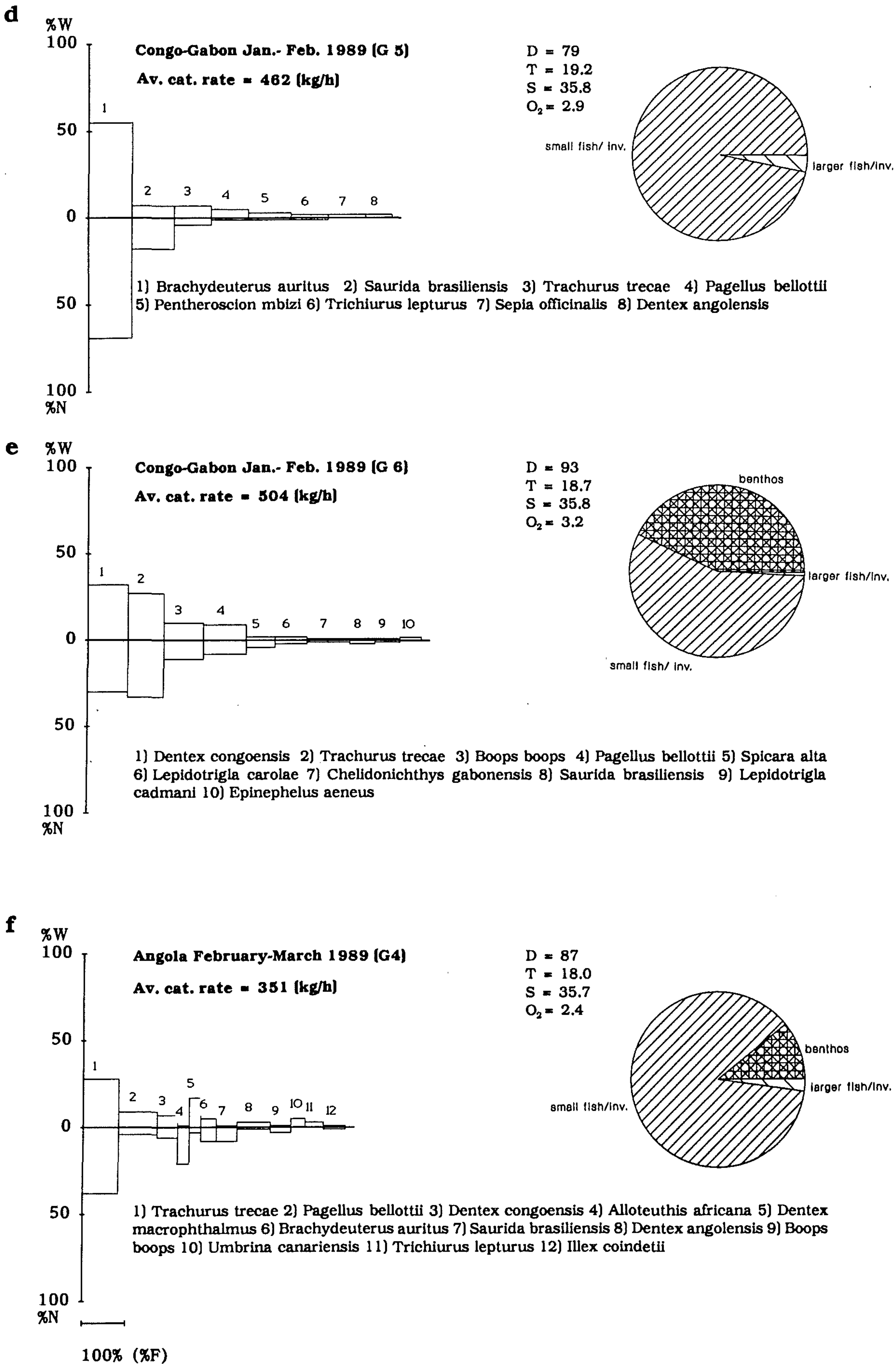


Fig. 7. Examples, from different regions, of deep-shelf assemblages, where the main species are arranged according to their Index of Relative Importance (IRI). Pie charts represent the same species grouped according to their food preferences



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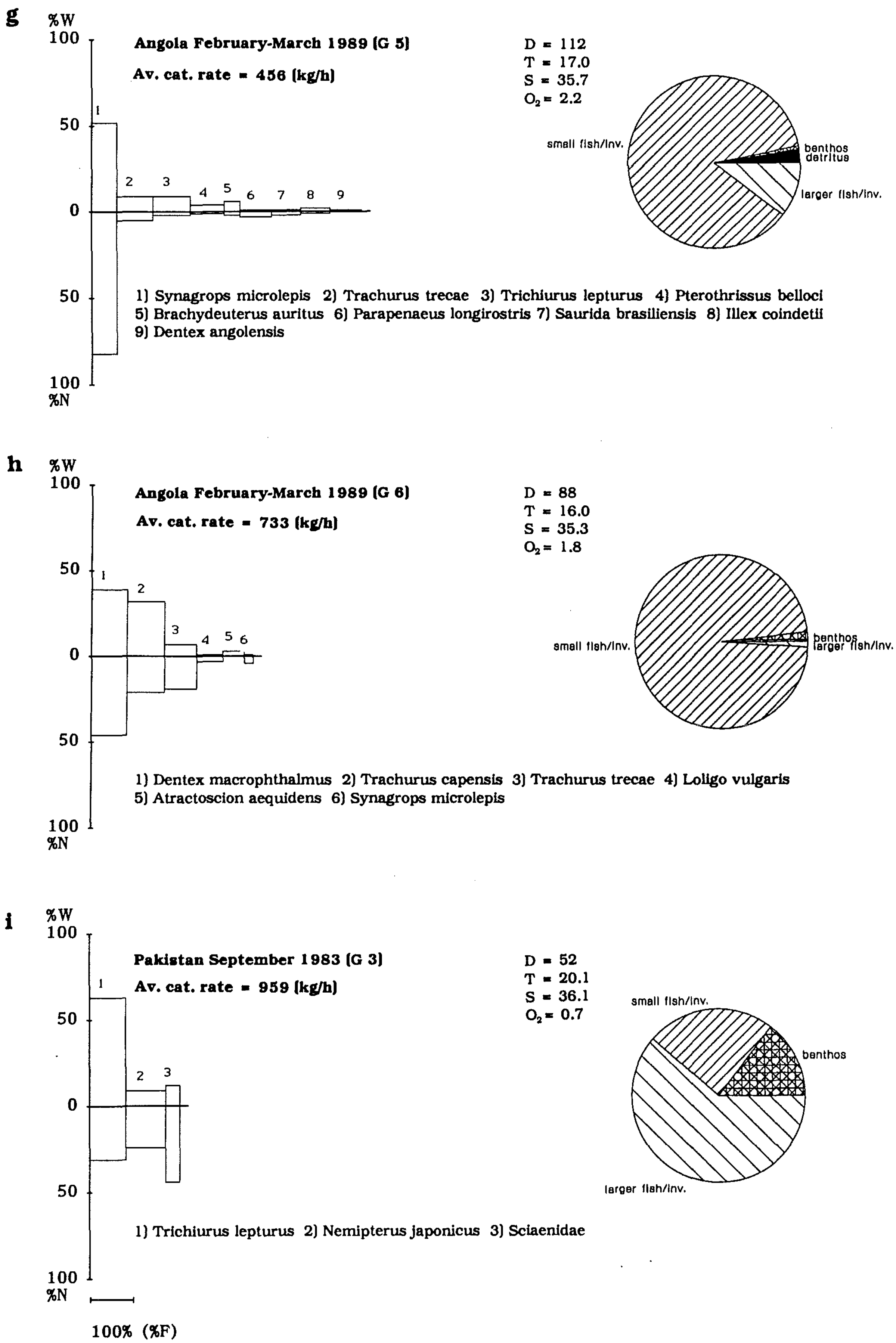

Fig. 7. Continued

capensis, all with bentho-pelagic habits and feeding on smaller prey.

Off Pakistan (Fig. 7 i), at average depths of about 50 m, the low oxygen concentrations encountered in the south-west monsoon period, show the extremely low diversity and two absolutely dominating species i.e. Trichiurus lepturus and Nemipterus japonicus. As discussed in Paper 6, these species show the ability to avoid, by vertical migrations and possibly on a periodical basis, the oxygen depleted waters present on the bottom.

Also in the deeper part of the shelf the dominating groups are species with a semi-pelagic behaviour. The two areas exposed to oxygen-depleted waters show two different strategies: in the more stable environment of the ECP the galatheid crustacean Pleuroncodes monodon, apparently undisturbed by any predation or competition and not depending on any larger prey to make a living, being a detritus feeder, is of undisputable dominance. Off Pakistan the presence of water with low-oxygen concentrations is seasonal and the species adapted to live there are otherwise rather ubiquitous.

Shelf-edge / upper-slope area

Fig. 8 shows three examples from the Eastern Central Pacific (a) Congo (b) and Angola (c). with the overwhelming dominance of Pleuroncodes in the Pacific, explained by presence of oxygen-depleted waters. Off West Africa the bentho-pelagic Synagrops microlepis was the dominant species. The very high catch rates off Angola and the ECP are indicative of enrichment processes probably related to falling of unutilized primary production (on a seasonal base) and/or other phenomena as shelf-edge upwelling (Longhurst & Pauly 1987).

The review above shows that the marine assemblages found in the tropical region cannot be classified under a common denomination as it can be found in various literature (Pauly 1979, Ursin 1984). Generalization like 'tropical seas' (Ursin 1984) and 'tropical communities' cannot be used to cover the marine environment or the fish communities in geographically tropical regions. I argue that generalizations that may be valid to the Gulf of Thailand not necessarily apply to regions of the Atlantic, Western Indian Ocean or Eastern Central Pacific, at similar latitudes. Tropical seas (at least the areas covered) display a wide variety of combinations of oceanographic conditions, type of bottom and zoogeography and the type of fauna reflects these conditions with a wide variety of forms and life strategies.

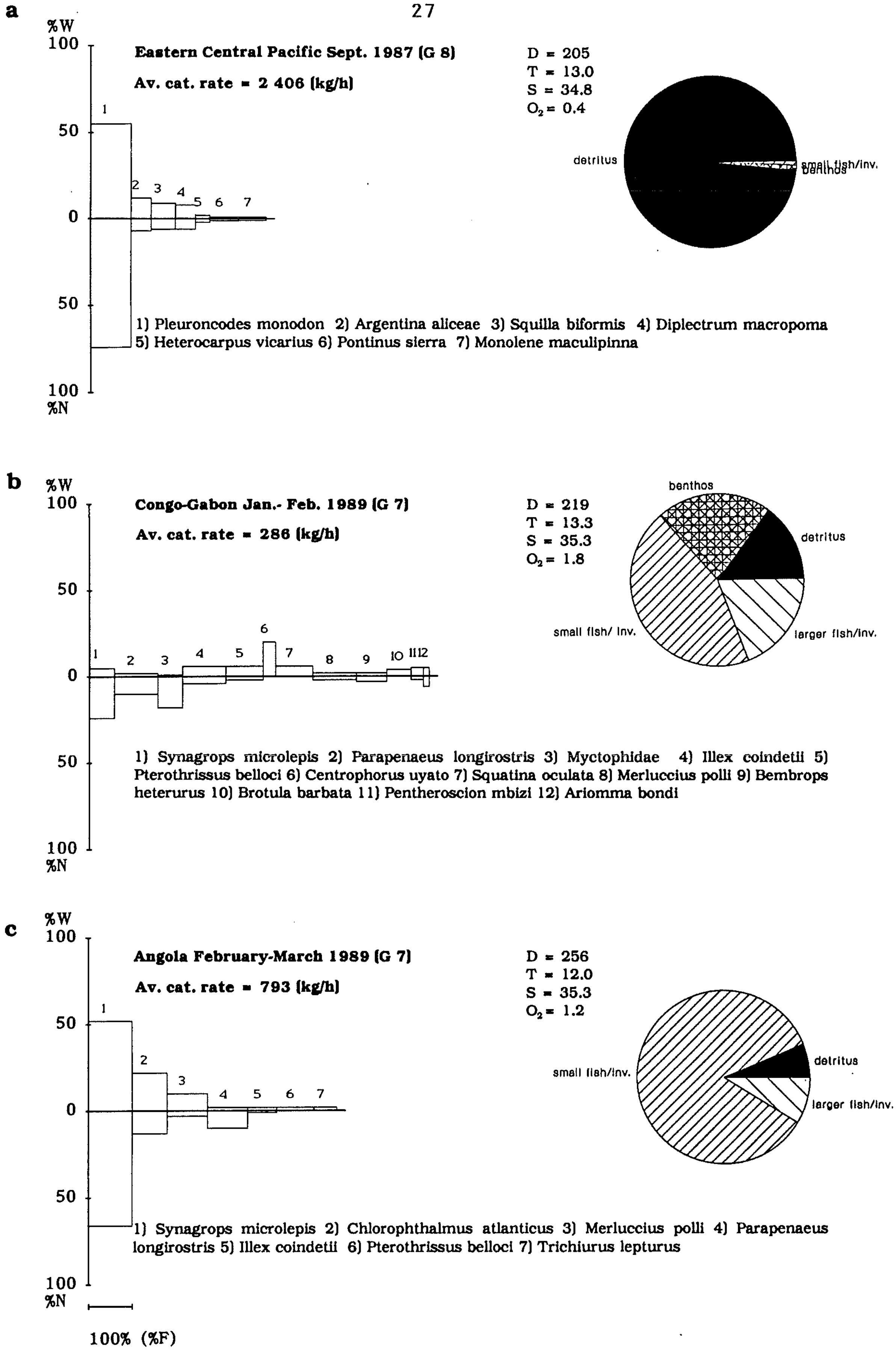

Fig. 8. Examples, from different regions, of upper slope assemblages, where the main species are arranged according to their Index of Relative Importance (IRI). Pie charts represent the same species grouped according to their food preferences

Tentative definition of continental shelf ecological regimes

Below is an attempt to define the main ecological regimes found in the areas covered by this study, as inferred from the observed species compositions. 'Expected trend' indicates which groups are likely to dominate a given 'ecosystem' under the present conditions. More than a realistic description, this is meant to be a line of thinking in working toward predictability of species assemblages.

Shallow, turbid waters influenced by major river runoffs

Ex: Fig 4 a

Type of environment: unstable, on a seasonal base
Dominant species: detritus feeders/ demersal predators
Main energy source:detritus
Fisheries: intensive
Expected trend: short-lived detritus feeders/short-lived predators

Shallow waters (often still under the influence of river runoffs)

Ex: Fig. 5

Type of environment: unstable
Dominant species: clupeoids/ opportunists/ larger bottom and pelagic feeders
Main energy source: zooplankton, but also feeding on the bottom
Fisheries: intensive
Expected trend: clupeoids/ different opportunistic species

Shelf region, where a sharp thermocline meets the shelf

Ex: Fig. 6 a,b,f,g,h

Type of environment: unstable
Dominant species: eurybathic/ eurythermic, opportunists
Main energy source: zooplankton, but also feeding on the bottom
Fisheries: locally intensive
Expected trend: possibility of alternation of different opportunistic species

Deeper shelf areas subject to seasonal upwelling

Ex: Fig 7 a, d-h

Type of environment: unstable on a seasonal base
Dominant species: eurybathic/ opportunists (Trachurus), demersal (K-sel.) fish
Main energy source: zooplankton/ bottom invert.
Fisheries: locally intensive
Expected trend: reduction of demersal fish and possibility of alternation of different opportunistic species

Shelf areas subject to stressful conditions (hypoxic waters) on a seasonal basis Ex: Fig. 7 i	**Type of environment**: unstable on a seasonal base **Dominant species**: opportunists **Main energy source**: pelagic vert./ invert. **Fisheries**: Light **Expected trend**: alternation of different opportunists
Deeper shelf and upper slope areas with persistent stressful conditions (hypoxic waters) Ex: Fig. 7 b, 6 a	**Type of environment**: stable **Dominant species**: species adapted to live in oxygen-depleted waters (various crustaceans) or able to carry out vertical migrations (various bony fishes, cephalopods) **Main energy source**: detritus, zooplankton **Fisheries**: None **Expected trend**: Stable
Intermediate shelf with stable conditions (typically tropical hydrography) Ex: Fig. 4 i, j	**Type of environment**: Stable **Dominant species**: k-selectionists **Main energy source**: zooplankton, but also feeding on the bottom **Fisheries**: locally intensive **Expected trend**: reduction of K-selectionists and invasion of unpredictable r-selectionists

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PAPER 1

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Demersal assemblages of the continental shelf and slope edge between the Gulf of Tehuantepec (Mexico) and the Gulf of Papagayo (Costa Rica)

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ABSTRACT: The structure of demersal assemblages (fish, crustaceans and cephalopods) of the continental shelf and upper slope between the Gulf of Tehuantepec and the Gulf of Papagayo was studied from data obtained in the course of surveys carried out by the RV 'Dr. F. Nansen' in 1987, by means of an ordination technique, Detrended Correspondence Analysis (DCA) implemented by the program DECORANA, and a classification technique, Two-Way Indicator Species Analysis (TWIA) implemented by the program TWINSPAN. Three major groups of species were identified: those distributed above the thermocline, those within the range of the thermocline and a third group below the thermocline, where oxygen content is extremely low. Highest biomass densities were found below the thermocline, consisting mainly of the galatheid crustacean *Pleuroncodes monodon* (H. Milne Edwards, 1837). Correlation of DCA Axis 1 with depth, temperature, salinity and oxygen showed that depth is the main gradient along which faunal changes occur.

INTRODUCTION

Since 1975 the Norwegian RV 'Dr. F. Nansen' has carried out acoustic and trawl surveys of the continental shelves and upper slopes of many tropical countries. The present study is the first of a series based on material from these surveys, investigating the structure of demersal assemblages in relation to principal environmental variables and geographical location. The taxa included in the analysis are bony and cartilaginous fishes, stomatopods, decapod crustaceans and cephalopods.

As pointed out by Caddy & Sharp (1986), this type of study is a necessary step toward understanding of multispecies stocks. Such work can then be extended to 'descriptive community dynamics' (McManus 1985) in order to find general patterns of which species compositions can be expected under given environmental conditions and fishing effort. Comparison of assemblages from similar ecosystems in different areas might also reveal general trends in the community dynamics of tropical shelves.

In addition, this work could be useful in fisheries management. For example, species composition of trawl catches from a given study area may be roughly anticipated from assemblage maps derived from the analysis, especially for those areas most recently investigated.

Studies of tropical fish community structure by means of multivariate analysis (excluding coral reef areas and lagoon systems) have been carried out in the Gulf of Guinea (Fager & Longhurst 1968), Namibia (Lleonart & Roel 1984), upwelling areas of West Africa (Roel et al. 1985), the Gulf of Nicoya, Costa Rica (Bartels et al. 1983), the Samar Sea, Philippines (McManus 1985), Malaysia (Chan & Liew 1986), northern Australia (Rainer & Munro 1982 and Rainer 1984) and northwestern Australia (Sainsbury 1987).

To the author's knowledge, no other studies of shelf assemblages have covered the area considered in the present work, i.e. the shelf between the Gulf of Tehuantepec and the Gulf of Papagayo. Bartels et al. (1983) described the occurrence, distribution, abundance and diversity of fish assemblages in the Gulf of Nicoya, Costa Rica. Studies on fish community structure in coastal lagoon systems on the Pacific coast of Mexico were carried out by Warburton (1978), Yanez-Arancibia (1978 a, b) and Chavez (1979).

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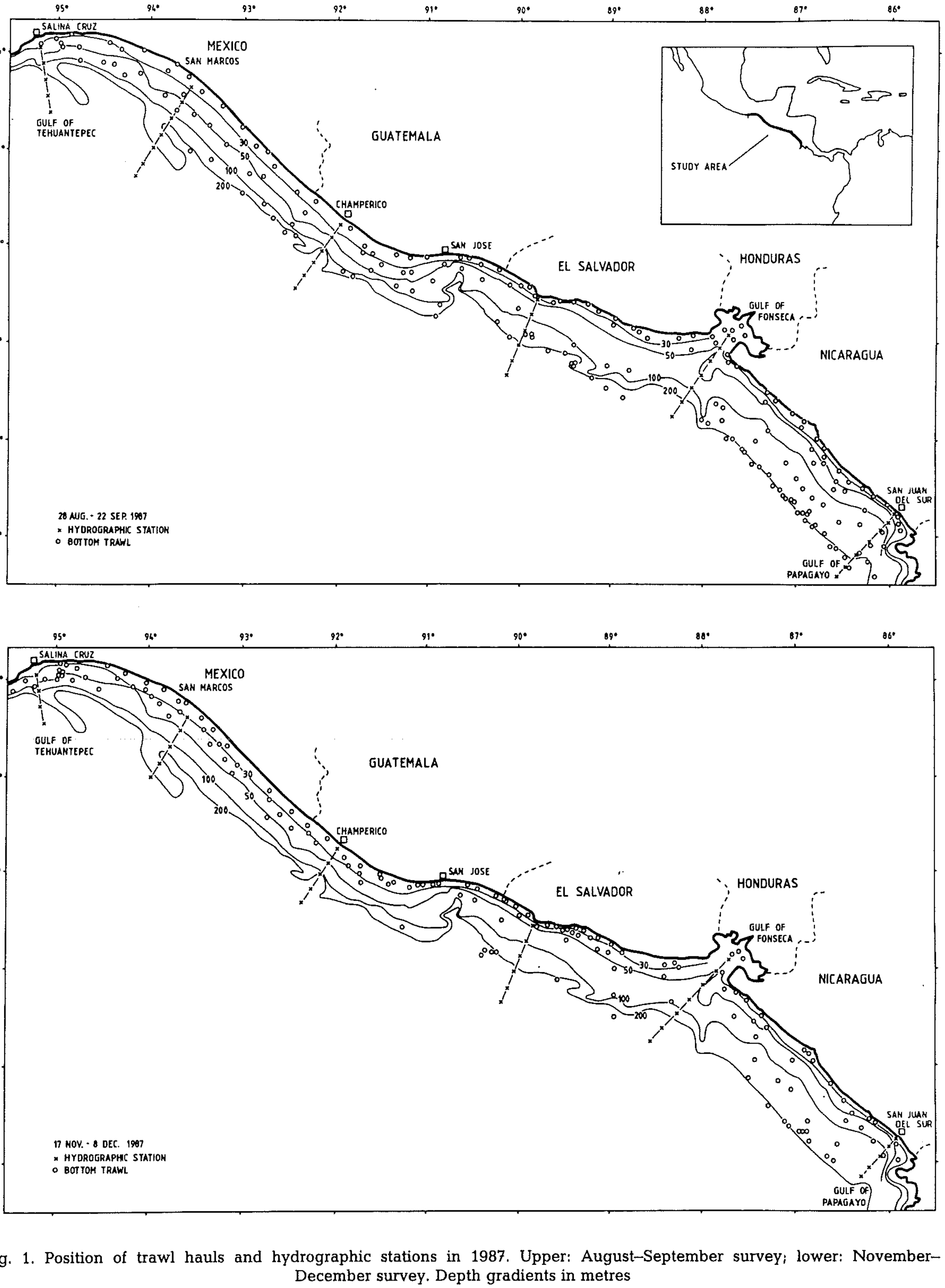

Fig. 1. Position of trawl hauls and hydrographic stations in 1987. Upper: August–September survey; lower: November–December survey. Depth gradients in metres

STUDY AREA

The study area (Fig. 1) included a coastline of about 685 nautical miles, from 95° 30′W (Mexico) to 85° 50′W (northern Costa Rica), and an area of about 28 300 square nautical miles (from about 10 to 500 m depth), of which 23 000 represent the shelf area to 200 m depth and about 5300 represent the upper slope (Strømme & Sætersdal 1988). Off Nicaragua and El Salvador the shelf is wide; it narrows off Guatemala and widens again off southern Mexico. The shelf bottom is muddy throughout, but sand and shells are dominant off southern Mexico (Anonymous 1977). The slope to 500 m depth is quite steep off Nicaragua and northwards to Guatemala. Off Mexico it is much wider, with steep and rough bottoms especially in the northwest.

Water masses of the eastern tropical Pacific are comprehensively described by Wyrtki (1967). Hydrographic conditions on the shelf area during the survey period are described in the survey report (Strømme and Sætersdal 1988). The biological oceanography of the eastern tropical Pacific has been reviewed by Blackburn (1966).

The surface offshore circulation of this area is characterized by the Costa Rica Current, i.e. the north branch of the Equatorial Counter Current which splits when approaching Costa Rica. Strongest from June to December, this current flows parallel to the coast and around the Costa Rica Dome and turns westward to feed the North Equatorial Current.

An oxygen-minimum layer more than 1200 m thick characterizes the intermediate water masses off Mexico to Costa Rica; its upper boundary is described as being shallower than 50 m in the coastal and offshore areas from about 9°N (Costa Rica) to 16°N (southern Mexico). This oxygen-minimum layer is a consequence of sluggish water movement in these areas where circulation of the subtropical anticyclones does not penetrate (Wyrtki 1967). In the course of our survey, oxygen levels of 1 ml l^{-1} were observed on the shelf bottom between 50 and 150 m depth, varying with geographical location and season and with a tendency to occur in shallower waters towards the north. In September this level was found between 75 m (Salina Cruz, Mexico) and 125 m (San Juan del Sur, Nicaragua), while in November/December it ascended and was located at about 50 and 75 m respectively. Below the 1 ml l^{-1} isoline, oxygen content decreased and levels of 0.5 ml l^{-1} were found at the edge of the continental shelf or upper slope throughout the year (Strømme & Sætersdal 1988). Fig. 2 shows oxygen profiles at selected stations, for both warm and cold seasons.

The thermocline is shallow, located between about 35 and 100 m and present all year round. It appears to be slightly shallower during the cold (upwelling) season (Fig. 3). Coastal upwelling occurs as a consequence of the strong northeast trade winds, from November to April, through the mountain gaps of southern Mexico and southern Nicaragua/northern Costa Rica. Upwelling in the Gulf of Tehuantepec is

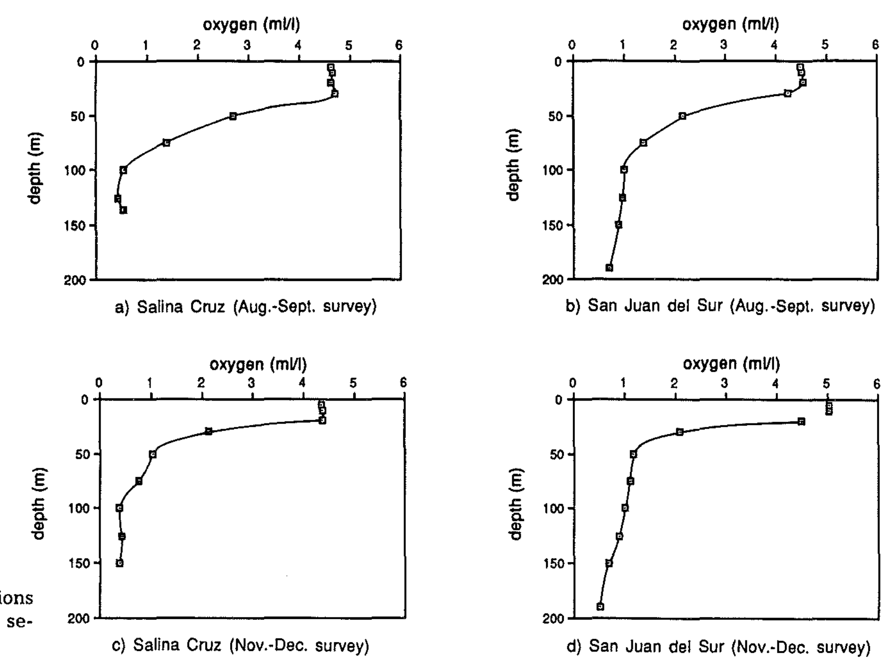

Fig. 2. Oxygen concentrations (ml l^{-1}) in relation to depth at selected stations in 1987

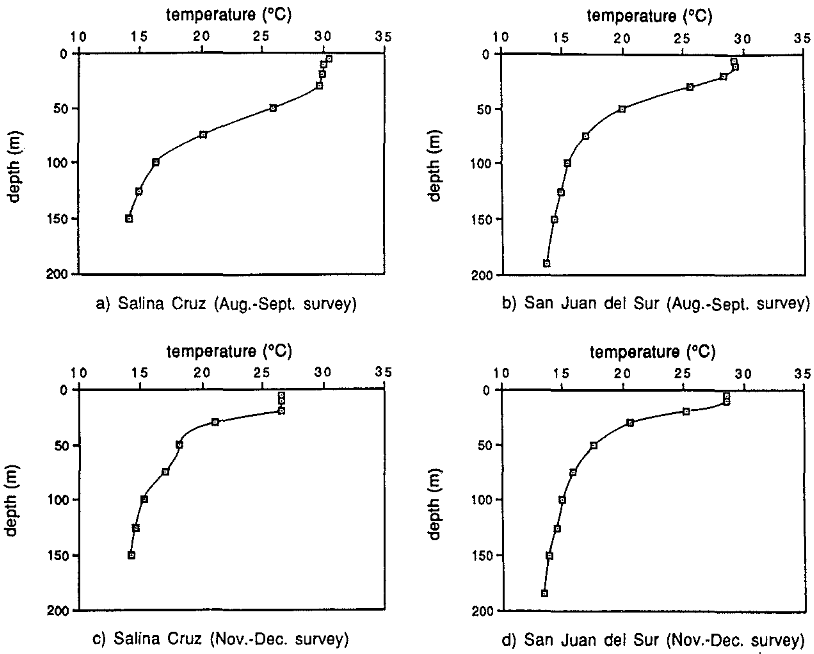

Fig. 3. Temperature in relation to depth at selected stations in 1987

described by Roden (1961). Upwelling in the Gulf of Papagayo is also a well-known event. Temperatures below 20 °C have been observed in the surface waters near San Juan del Sur (Nicaragua), lasting about 3 mo (January to March; Glynn et al. 1983). Hydrographic observations made with the RV 'Dr. F. Nansen' showed a clear upward trend in depth of the thermocline in the course of Survey 3 (in December 1987). Offshore upwelling has been described for the Costa Rica Dome by Wyrtki (1967), and the associated higher productivity by Blackburn (1966). More detailed studies on phytoplankton and copepod distribution in this area are presented by Sameoto (1986) and Subba-Rao & Sameoto (1988); the latter compared vertical distribution (0 to 1000 m) of phytoplankton inside and outside the Dome area and reported a much higher phytoplankton concentration inside the area, at all depths. Higher concentrations were also found in the aphotic zone originating from the overlying euphotic waters, and this probably plays an important role in the food web of the deep sea.

The shoal thermocline seems also to be a cause of high productivity. Brandhorst (1958) found that in areas of the eastern Pacific where the thermocline was close to the surface (20 to 50 m), standing stocks of chlorophyll and zooplankton were higher than in areas with a deeper thermocline. This is probably due to enrichment from below by wind-mixing and to the significantly higher productivity in the well-lit waters below the mixed layer (Blackburn 1966).

MATERIALS AND METHODS

Trawl data. Material was collected on 2 cruises in 1987 (28 August to 21 September and 17 November to 7 December, respectively). A shrimp and fish trawl was used, with a headline of 31 m, footrope of 47 m, and estimated headline height and distance between wings during towing of 6 and 18–20 m respectively. Mesh size was 2 cm, with double lining in the cod end. Each tow had a standard duration of 30 min. Other details on the gear used may be found in Strømme & Sætersdal (1988). The bottom-trawl stations used in this analysis were randomly set along the cruise track, but in the November–December survey higher effort was concentrated in the inshore areas and at the edge of the continental shelf and upper slope off Nicaragua. The present analysis is based mainly on the August–September survey, with a higher and better-distributed effort, while the November–December survey was used for comparison. A total of 191 and 157 stations were sampled in the course of the 2 surveys respectively (Fig. 1a, b).

Each specimen caught was counted and weighed separately. In cases where identification was possible only to genus or family, provisional names were given and specimens were retained and later identified by experts on the various groups. For the present analysis congeneric species which were difficult to separate were pooled together.

A large collection of bony fishes and crustaceans was deposited at the Senckenberg Museum (Frankfurt, Germany). All station and species data were stored using the B-trieve file system (data available in ASCII format upon request to the author).

Hydrographic data. Samples for temperature, salinity and oxygen measurements were taken with Nansen bottles at standard depths, along fixed transects (Fig. 3a, b). Surface temperature (4 m depth) was continuously recorded by a thermograph. Details on oceanographic data can be found in Strømme & Sætersdal (1988, Vol. 2: Data File).

Temperature, salinity and oxygen data were used in the present analysis to examine relationships of the different species assemblages to the physical environment. For the above variables, values were assigned to each trawl station from the nearest hydrographic station at a similar depth.

Data analysis. The primary objective was to identify major patterns of species associations based on the trawl data, to relate them to the more significant environmental factors and hence to explain the observed patterns. The method traditionally used in fish-community studies to identify groups of species/samples has been cluster analysis, usually using an agglomerative clustering algorithm. This method produces a classification diagram (dendrogram) which also shows the hierarchical relationships between groups. Drawbacks of this method are the production of miscellaneous clusters from 'left-overs' or chaining, i.e. adding objects one-by-one to groups to which they do not really belong. Also, it is quite difficult to relate the sample dendrogram to the species dendrogram and understand which species group corresponds to a given sample cluster.

Two-Way Indicator Species Analysis – TWIA (Hill 1979), implemented by the computer program TWINSPAN – was considered well suited to the main objectives of this work. This method involves a primary ordination of the samples by correspondence analysis (see below) and divisions near the midpoint of each principal axis from each successive analysis, so that each division serves to contrast the most dissimilar object types. The method '... constructs a classification of the samples, and then uses this classification to obtain a classification of the species according to their ecological preferences. The two classifications are then used together to obtain an ordered two-way table that expresses the species' synecological relations as succinctly as possible' (Hill 1979). In addition to a hierarchical classification of samples and species, TWIA produces a sorted community table in which stations and species are arranged along the major gradients within the data. Importance values are not used directly but are converted to a scale based on lower class limits (set at 0, 10, 100, 1000 and 10 000 kg in this study, according to catch size by species, which varied from 0 to ca 20 000 kg).

Detrended Correspondence Analysis (DCA; Hill & Gauch 1980), implemented by the computer program DECORANA, was used as a complementary ordination method. This method is particularly useful in ecological studies as it does not assume linear relationships between species abundances and environmental variables. It implicitly assumes a simple unimodal species-response model (ter Braak & Prentice 1988). DCA is a heuristic modification of Correspondence Analysis (CA), developed to eliminate the 'arch effect' and the distortion of relative distances in the ordination which are characteristic of CA. The particular version used in this study (from the program package CANOCO; ter Braak 1987) provides the option of detrending by second-order polynomials (ter Braak & Prentice 1988) instead of by segments as in the original version of the program DECORANA (Hill & Gauch 1980). Detrending by second-order polynomials seems to avoid the inconvenience of destruction of ecologically meaningful information which might occur when detrending by segments (Jongman et al. 1987) and was thus used in the present study.

The above methods are both based on correspondence analysis, which makes it possible to compare their results directly, i.e. the classification from TWINSPAN and the ordination along the first axis of DCA. Comparison is useful, as outliers can affect site classification and can be identified through the ordination results.

The relationship between station groups and environmental variables was analyzed using the DCA application in the program package CANOCO, which also provides the option of correlating the ordination axes with environmental variables (depth, temperature, salinity, and oxygen). This option also produces the mean and SD of the environmental variables for each group.

A table of 'pseudo-*F*' values (ratios of among-group to within-group variances) was constructed to evaluate the degree of conformity of a given species to a site group obtained from the above methods. A formal *F*-test cannot be performed in this case because it would be based on the same data previously used to establish the groups (Green & Vascotto 1978).

In this study biomass (wet weight) was used as a measure of abundance. Biomass is of more relevance to fisheries management and seems ecologically appropriate.

Each weight (x) was converted to $\ln(x+1)$ before DCA and the 'pseudo-*F*' test were performed. This transformation minimizes the dominant effect of anomalous catches. The addition of 1 unit is necessary to avoid problems derived by the presence of values $= 0$ or values < 1. Trials on a small sample of stations showed that this transformation did not affect the results. No transformation is necessary in the case of

TWIA, where abundances are converted to numbers corresponding to different abundance classes (so-called pseudospecies).

Demersal biomass densities (weight per unit area) were calculated using the 'swept area' method, by depth stratum:

$$D_j = C_j / q\, a_j$$

where D_j = density in Stratum j (tonnes per nautical mile), C_j = catch taken in hauls in Stratum j (tonnes), a_j = area of the bottom 'swept' by the trawl hauls in Stratum j (square nautical miles), q = catchability coefficient (= 1, i.e. all fish in the path of the trawl were caught).

Sampling errors and limitations. The research vessel could only operate in waters deeper than 10 to 15 m. Therefore, shallow-water communities were insufficiently sampled.

Bottom trawls are both species- and size-selective, and it was impossible to adjust for this type of selectivity without knowing the behaviour of most species or the real age/size structure of populations. Also, in the case of long tows, the trawl might have artificially blended different assemblages occurring within the path of the trawl.

Species identification often poses serious problems in tropical areas. Unfortunately, no guides such as the F.A.O. Species Identification Sheets for fishery purposes were available for the eastern central Pacific. Although taxonomic work was carried out with the participation of well-trained taxonomists, errors in identification may have occurred because of the participation of less-trained personnel.

Effort (i.e. number of stations) was not uniformly distributed in space or time, and this might have led to biased results. In fact many species, both demersal and pelagic, show important day/night variations in behaviour pattern, but a comparison between day and night catches was not possible because most of the deep-water stations were sampled at night, while stations in shallower water were sampled during the day. This choice was deliberate, based on patterns observed with the echo-integration system indicating that bottom fish tend to be closer to the bottom during daytime while a large number of species move to upper water layers at night. This phenomenon appears to be less pronounced in the deeper part of the shelf and upper slope.

Many typically pelagic species are often caught in bottom trawls. In shallow waters (10 to 20 m), it is quite difficult to differentiate between these 2 groups: small pelagic fish of this zone are also found quite close to the bottom, as some of them feed on bottom detritus and are preyed upon by both demersal and pelagic predators. It seems that in these very shallow waters, demersal and pelagic groups have a much closer relationship than in more offshore waters. For this reason, although this analysis is mainly aimed at demersal communities, pelagic species were included in the analysis whenever they occurred in the bottom trawl. In the deeper part of the shelf and upper slope, some pelagic and mesopelagic species which perform diurnal vertical migrations were caught in bottom trawls during daytime. Even when this occurred the species were included in the analysis, although the results were interpreted in the light of this information.

RESULTS

A total of 230 species comprising 16 004 372 specimens (203 155 kg) were sampled. Table 1 gives a list of the most important species collected and used in the analysis.

Appendix 1 shows the 2-way classification of species and stations obtained with TWINSPAN, while Fig. 4 shows the TWIA dendrogram for station groups. The first dichotomy separates all the stations shallower than 100 m (Groups 1 to 6) from those on the deeper part of the shelf and upper slope (Groups 7 and 8), where oxygen levels are well below 1 ml l^{-1}. At the second division level Group 6 (the intermediate shelf-dwellers, at depths between 50 and 100 m) is separated from Groups 1 to 5, and Group 7 from Group 8. Further divisions of the deeper stations were not considered as they seemed to be mainly due to day/night variations in the catches. At the third division level Group 1 (stations at about 30 to 40 m depth, on sandy/shell bottoms off Guatemala and Mexico) is separated from the very shallow stations (Groups 2 to 4) and from the corresponding depth range in the southern part, off Nicaragua and El Salvador (Group 5). Finally, Group 4, including the Gulf of Fonseca and the adjacent shallow waters, is separated from the remaining shallow coastal waters (Groups 2 and 3) in the fifth division.

Fig. 5 shows the ordination of the stations from the August–September survey on DCA Axes 1 and 2. The eigenvalues of the first 4 axes were 0.92, 0.43, 0.28 and 0.24 respectively. This shows that the gradient represented by the first axis is by far the most important. The 2 largest discontinuities along the first axis (0.42 and 0.63 SD, respectively) produce 3 groups: a first group including stations usually shallower than 50 m, a second group of stations between 50 and 100 m, and a third group in which most stations were deeper than 150 m.

Results from the correlation of DCA Axes 1 and 2 with the environmental variables are presented in Table 2. The first axis was highly correlated with depth, temperature and oxygen, while there was no significant correlation of these variables with Axis 2.

Table 1. Main species collected in 1987 between the Gulf of Tehuantepec (Mexico) and the Gulf of Papagayo (Costa Rica), by major taxonomic groups and families

Cephalopods

Loliginidae
- *Loliolopsis diomedeae* (Hoyle)
- *Lolliguncula panamensis* Berry

Stomatopods

Squillidae
- *Squilla biformis* Bigelow
- *Squilla panamensis* Bigelow

Decapod crustaceans

Solenoceridae
- *Solenocera agassizii* Faxon

Penaeidae
- *Penaeus brevirostris* Kingsley
- *Penaeus californiensis* Holmes
- *Penaeus vannamei* Boone
- *Xiphopenaeus riveti* Bouvier

Pandalidae
- *Heterocarpus* sp.

Galatheidae
- *Pleuroncodes monodon* (H. Milne Edwards)

Calappidae
- *Mursia gaudichaudii* (H. Milne Edwards)

Portunidae
- *Portunus acuminatus* (Stimpson)
- *Portunus asper* (A. Milne Edwards)

Sharks

Carcharhinidae
- *Carcharhinus porosus* (Ranzani)
- *Nasolamia velox* Gilbert

Sphyrnidae
- *Sphyrna lewini* (Cuvier, Griffith & Smith)

Bony fishes

Albulidae
- *Albula vulpes* (Linnaeus)

Muraenidae

Ophichthidae

Clupeidae
- *Neoopisthopterus tropicus* (Hildebrand)
- *Opisthonema libertate* (Günther)
- *Opisthopterus dovii* (Günther)
- *Opisthopterus equitorialis* (Hildebrand)
- *Pliosteostoma lutipinnis* (Jordan & Gilbert)

Engraulididae
- *Anchoa* sp.
- *Anchoa argentivittata* (Meek & Hildebrand)
- *Anchoa spinifer* (Valenciennes)
- *Lycengraulis poeyi* (Kner & Steindachner)

Ariidae
- *Arius* spp.
- *Bagre panamensis* (Gill)
- *Galeichthys peruvianus* Lütken

Argentinidae
- *Argentina aliceae* Cohen

Synodontidae
- *Synodus evermanni* Jordan & Bollman
- *Synodus scituliceps* Jordan & Gilbert

Myctophidae

Moridae

Merlucciidae
- *Merluccius angustimanus* Garman

Ophidiidae
- *Lepophidium pardale* (Gilbert)

Batrachoididae
- *Porichthys nautopaedium* Jordan

Lophiidae
- *Lophiodes caulinaris* (Garman)

Ogcocephalidae
- *Zalieutes elater* (Jordan & Gilbert)

Scorpaenidae
- *Pontinus sierra* (Gilbert)
- *Scorpaena* spp.

Triglidae
- *Prionotus horrens* Richardson
- *Prionotus quiescens* Jordan & Bollman

Serranidae
- *Diplectrum euryplectrum* Jordan & Bollman
- *Diplectrum labarum* Rosenblatt & Johnson
- *Diplectrum macropoma* (Günther)
- *Hemanthias signifer* (Garman)
- *Pronotogrammus eos* Gilbert

Carangidae
- *Caranx caballus* Günther
- *Caranx caninus* Günther
- *Chloroscombrus orqueta* Jordan & Gilbert
- *Carangoides ortrynter* (Jordan & Gilbert)
- *Hemicaranx* spp.
- *Oligoplites refulgens* Gilbert & Starks
- *Selar crumenophthalmus* (Bloch)
- *Selene peruvianus* (Guichenot)

Lutjanidae
- *Lutjanus guttatus* (Steindachner)
- *Lutjanus peru* Nichols & Murphy

Gerreidae
- *Diapterus aureolus* (Jordan & Gilbert)
- *Diapterus peruvianus* (Cuvier)
- *Eucinostomus gracilis* (Gill)

Haemulidae
- *Conodon macrops* Hildebrand
- *Orthopristis chalceus* (Günther)
- *Pomadasys axillaris* (Steindachner)
- *Pomadasys leuciscus* (Günther)
- *Pomadasys panamensis* (Steindachner)
- *Xenichthys xanti* (Gill)

Sciaenidae
- *Bairdiella* spp.
- *Cynoscion phoxocephalus* Jordan & Gilbert
- *Cynoscion reticulatus* (Günther)
- *Cynoscion stolzmanni* (Steindachner)
- *Isopisthus altipinnis* (Steindachner)
- *Larimus acclivis* Jordan & Bristol
- *Larimus effulgens* Gilbert
- *Larimus gulosus* Hildebrand
- *Micropogonias altipinnis* (Günther)
- *Stellifer* spp.

Mullidae
- *Pseudupeneus grandisquamis* (Gill)

Ephippididae
- *Chaetodipterus zonatus* (Girard)
- *Parapsettus panamensis* (Steindachner)

Sphyraenidae
- *Sphyraena ensis* Jordan & Gilbert

Polynemidae
- *Polydactylus approximans* (Lay & Bennet)
- *Polydactylus opercularis* (Gill)

Gobiidae

Trichiuridae
- *Trichiurus nitens* Garman

Scombridae
- *Scomberomorus sierra* Jordan & Starks

Stromateidae
- *Peprilus snyderi* Gilbert & Starks

Bothidae
- *Citharichthys platophrys* Gilbert
- *Cyclopsetta querna* (Jordan & Bollman)
- *Monolene maculipinna* Garman

Cynoglossidae
- *Symphurus* spp.
- *Symphurus atramentatus* Jordan & Bollman
- *Symphurus elongatus* (Günther)

Balistidae
- *Pseudobalistes polylepis* Steindachner

Tetraodontidae
- *Sphoeroides annulatus* (Jordan)
- *Sphoeroides lobatus* (Steindachner)

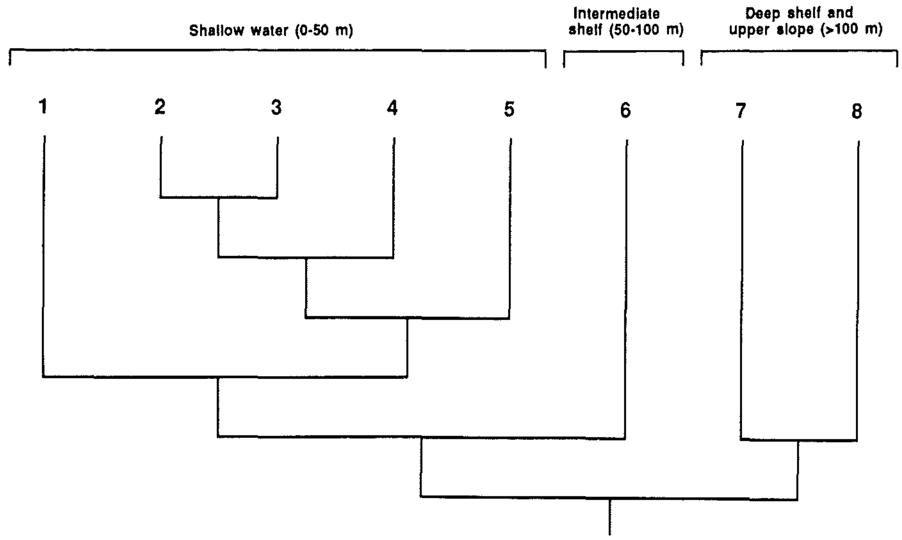

Fig. 4. Dendrogram of station groups (1 to 8) derived from classification with the program TWINSPAN (Hill 1979). See 'Results' for description of each station group

Fig. 6 shows a plot of the station scores on DCA Axis 1 against depth. Although there was a strong correlation between Axis 1 and depth, this correlation was not significant for stations shallower than 50 m and deeper than 150 m.

In order to improve the resolution of the shallow-water stations, these were further analysed using DCA. Fig. 7 shows the results after extraction of Group 1, which was better separated from the other shallow-water groups. The first 4 eigenvalues were 0.24, 0.17, 0.13 and 0.10 respectively, showing a low degree of separation of these stations, which were indeed very similar in species composition. Results from the correlation of Axes 1 and 2 with depth, temperature, salinity and oxygen are shown in Table 3. These values clearly show that faunal changes in shallow-water areas must depend on other factors, such as bottom type, connection to river estuaries, etc.

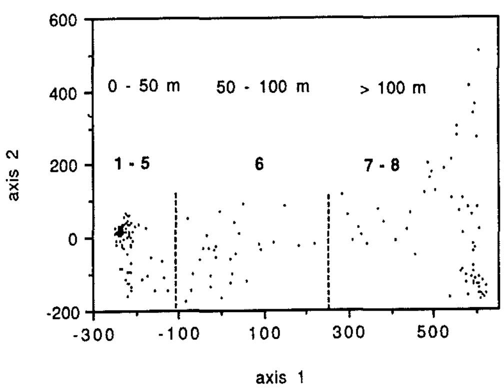

Fig. 5. Detrended correspondence analysis for the August–September survey (SD units × 100). Corresponding TWIA (Two-Way Indicator Species Analysis) groups (1 to 8) and depth ranges also indicated

Comparison of the results from classification analysis (TWIA) to those from ordination analysis (DCA) shows that TWIA Groups 1 to 5 correspond to the first group of

Table 2. Pearson product-moment correlation coefficients between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations

Variable	Axis 1	Axis 2
Depth	0.96	−0.10
Temp.	−0.93	0.02
Salinity	0.57	−0.05
Oxygen	−0.85	0.05

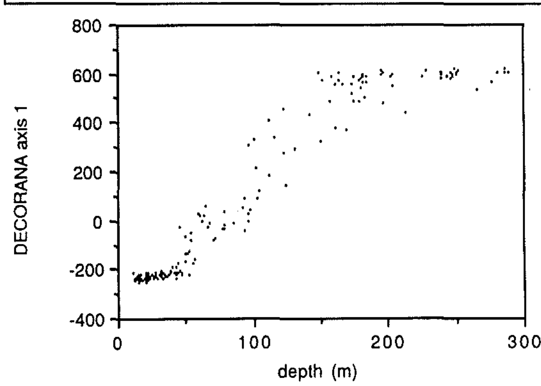

Fig. 6. Plot of station scores on DCA (Detrended Correspondence Analysis) Axis 1 against depth

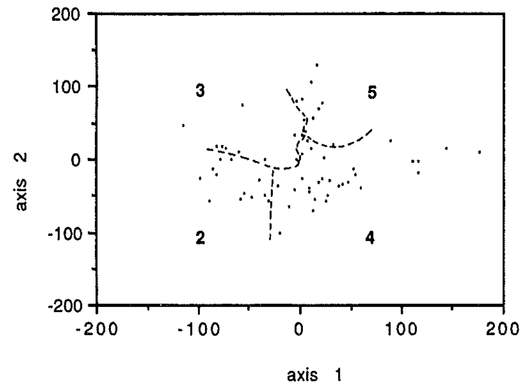

Fig. 7. Detrended correspondence analysis for station Groups 2 to 5 (indicated by numbers) of the August–September survey (SD units × 100)

Table 3. Pearson product-moment correlation coefficients between DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for shallow-water stations (Groups 1 to 5)

Variable	Axis 1	Axis 2
Depth	0.13	0.70
Temp.	−0.15	−0.66
Salinity	0.07	0.09
Oxygen	−0.41	−0.56

DCA, TWIA Groups 6 and (partly) 7 correspond to the second DCA group, and TWIA Group 8 coincides with the third DCA group.

Table 4 presents results from the 'pseudo-*F*' test applied to the above groups, together with the average values and standard deviations of the environmental variables. Each station/species group also corresponds to distinct geographical areas, as shown in Fig. 8. Table 5 gives the total weight, numbers and frequency of the main species from each station group.

Fig. 9 shows values of biomass densities obtained with the swept-area method, plotted against depth, for both surveys.

The different groups identified are described as follows:

Group 1: Sandy/shell bottoms off Guatemala and Mexico. This group includes 14 stations and a total of 71 species, located between an area near Salina Cruz (Mexico) and San José (Guatemala), at an average depth of 36 m. This group exhibits a well-defined species composition: it lacks most of the species found in the other shallow-water groups, and is characterized by species whose primary distribution is within this area, including the brassy grunt *Orthopristis chalceus*, the goatfish *Pseudupeneus grandisquamis*, the triggerfish *Pseudobalistes polylepis*, the mojarra *Eucinostomus gracilis*, the jacks *Carangoides ortrynter* and *Caranx caballus*, and the snappers *Lutjanus peru* and

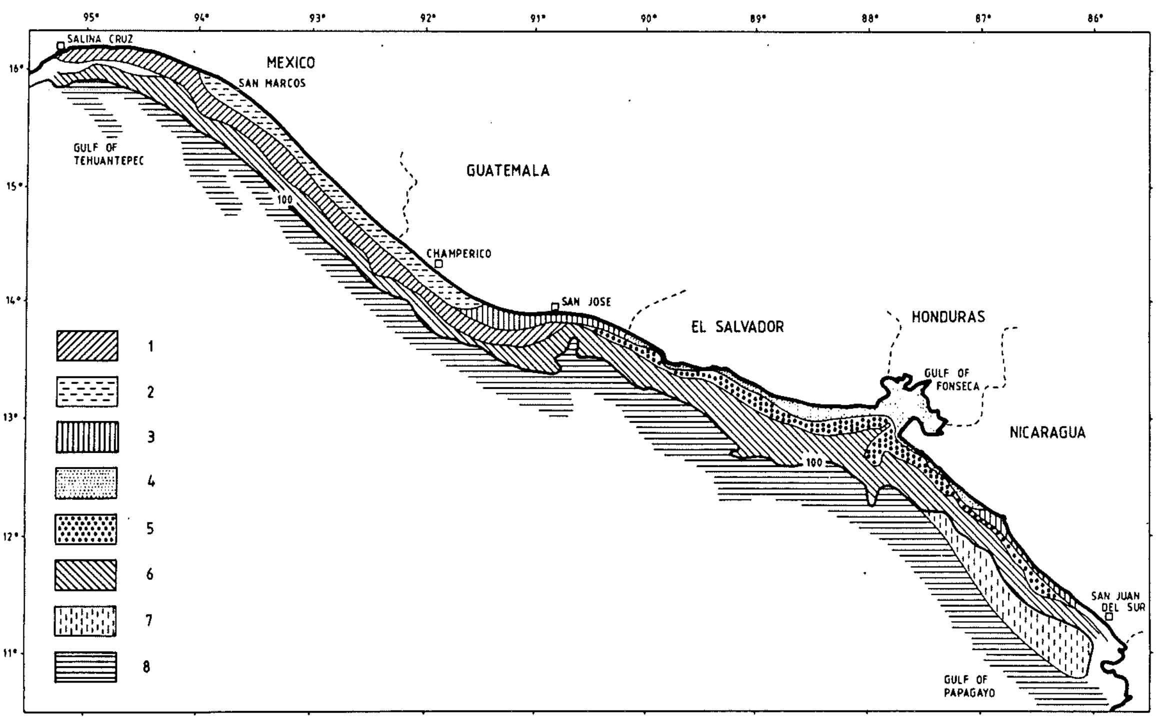

Fig. 8. Subareas corresponding to station groups. Depth gradient in metres

Table 4. Two-way table based on classification and ordination analyses, showing conforming species groups within site groups. Pseudo-*F* (P–*F*) values preceded by an asterisk indicate conformity at a significance of p = 0.05 or better. The average biomass value (kg) of a species within each group, converted to ln $(x+1)$, is preceded by an asterisk whenever the 95 % confidence interval for the mean is not overlapping. (****) Indicates that a species is found only in 1 group. Mean values of environmental variables are also shown for each group, with standard deviations in parentheses. Only the most important species are included

	Site groups								P–*F*
	2	3	4	5	1	6	7	8	
Environmental variables									
Depth (m)	20(5)	25(8)	23(8)	39(6)	37(8)	66(17)	134(33)	205(43)	
Temp. (°C)	29(1)	27(2)	28(2)	24(2)	27(2)	22(4)	15(1)	13(1)	
Salinity (‰)	33.1(0.3)	33.7(0.5)	33.5(0.5)	33.2(0.5)	33.8(0.4)	34.3(0.3)	34.7(0.2)	34.8(0.0)	
Oxygen (ml l^{-1})	4.5(0.4)	3.6(0.7)	3.6(0.7)	2.5(0.5)	3.1(1.0)	1.8(0.9)	0.7(0.1)	0.4(0.1)	
Species									
Anchoa spinifer			*0.836						****
Bairdiella spp.	0.191	0.228	*1.558	0.561					*17.5
Lycengraulis poeyi		0.279	*0.948	0.439					*17.4
Xiphopenaeus riveti	0.243		*1.376	0.203					*20.2
Polydactylus opercularis	1.449	1.382	0.994	1.685		0.022			*17.5
Penaeus vannamei	*1.520	0.474	0.800	0.611	0.174				*22.5
Sphyraena ensis	2.779	*4.326	2.745	2.934	0.591	0.066			*57.5
Hemicaranx spp.	0.872	1.193	1.073	0.244	0.026	0.011			*11.3
Opisthonema libertate	1.794	2.393	2.407	1.287	0.518	0.054			*26.0
Opisthopterus dovii	0.698	0.390	0.595	0.396					* 7.2
Pliosteostoma lutipinnis	1.991	0.473	1.563	0.937					*26.4
Polydactylus approximans	1.700	2.379	1.800	1.589	0.034	0.031			*33.8
Anchoa spp.	1.827	1.457	*2.210	0.331					*30.1
Isopisthus altipinnis	1.006	0.671	0.964	0.754					*14.2
Oligoplites refulgens	0.882	0.157	0.796	0.024					*14.0
Anchoa argentivittata	0.258	*1.349	0.384	*3.280	0.183	0.049			*22.6
Larimus acclivis	1.019	*1.791	0.863	0.325	0.087	0.052			*14.4
Scomberomorus sierra	1.462	*2.835	1.022	1.193	0.189	0.052			*31.7
Diapterus peruvianus	3.098	3.314	1.690	1.265	0.285				*32.6
Stellifer spp.	*1.207		0.111						*16.3
Selene peruvianus	2.083	*3.858	2.010	2.734	1.014	0.211		0.006	*32.6
Pomadasys panamensis	0.034	1.421	0.672	*2.420	0.631	0.136			*14.3
Chloroscombrus orqueta	3.537	4.390	1.592	0.513	2.299	0.019			*57.3
Pomadasys axillaris	*3.044	0.598			0.495				*50.8
Diapterus aureolus	0.342	*1.541	0.168	1.326	0.224	0.167			*13.1
Bagre panamensis	2.122	2.541	1.230	2.232	1.059	0.466			*20.5
Carangoides ortrynter			0.006	0.199	*1.099			0.043	*16.3
Selar crumenophthalmus		0.925	0.067	0.081	*1.184				*13.7
Caranx caballus	0.361	0.631	0.267	0.114	0.763	0.030			* 5.0
Eucinostomus gracilis	0.266	0.846	0.212	0.526	1.330	0.247			* 9.0
Pseudupeneus grandisquamis	0.283	0.497	0.176	0.454	*1.307	0.106			*11.4
Orthopristis chalceus	1.136	1.505			*3.150	0.979			*19.3
Cyclopsetta querna		0.563	0.166	*2.356	0.013	0.469			*24.1
Pseudobalistes polylepis					*1.614	0.244			*19.0
Scorpaena spp.						0.674			****
Peprilus snyderi	1.368	2.702	2.149	3.214	0.607	1.028	2.060	0.146	*13.4
Trichiurus nitens		0.079	0.535	0.071		0.191	*1.160	0.708	* 2.9
Loliolopsis diomedeae	0.069		0.166	0.334		0.806	0.383	0.033	* 3.8
Porichthys nautopaedium	0.004		0.083	0.077		*1.269	0.641	0.041	*14.3
Penaeus brevirostris						*1.035	0.125		*15.0
Lepophidium pardale						0.219	*0.624	0.070	* 3.8
Gobiidae				0.088		0.029	*1.764	0.020	*24.2
Citharichthys platophrys			0.034			0.272	*1.168		*14.3
Prionotus quiescens			0.051			*0.862	*3.426	0.134	*16.3
Synodus evermanni	0.139		0.078	0.045	0.259	0.625	*1.248	0.070	* 5.8
Zalieutes elater						0.301	0.329	0.184	1.9
Pontinus sierra						0.009	1.844	1.548	*14.9
Squilla biformis			0.056			0.024	0.655	*2.522	*12.3
Monolene maculipinna						0.015	0.264	*1.513	*14.7
Pleuroncodes monodon							*1.661	*5.721	*63.3
Merluccius angustimanus							0.442	*1.628	*10.9
Heterocarpus vicarius								*1.120	****
Argentina aliceae							0.868	*2.045	* 8.6
Diplectrum macropoma								*1.420	****

Table 5. Total weight (W, in kg), numbers (N) and frequency (F: no. of stations where found in the respective group) of main species from station Groups 1 to 8

Species	W	(%)	N	(%)	F
Group 1 (14 stations)					
Chloroscombrus orqueta	2 027	(35)	36 204	(47)	11
Orthopristis chalceus	897	(16)	10 550	(14)	14
Lutjanus peru	564	(10)	2 968	(4)	5
Bagre panamensis	247	(4)	2 008	(3)	6
Pseudobalistes polylepis	186	(3)	1 058	(1)	10
Eucinostomus gracilis	171	(3)	5 590	(7)	12
Lutjanus guttatus	158	(3)	204	(0)	6
Albula vulpes	140	(2)	372	(1)	6
Pseudupeneus grandisquamis	100	(2)	1 460	(2)	10
Selar crumenophthalmus	93	(2)	804	(1)	8
Selene peruvianus	87	(2)	4 042	(5)	9
Caranx caballus	47	(1)	274	(0)	7
Carangoides ortrynter	39	(1)	142	(0)	8
Pomadasys panamensis	18	(0)	130	(0)	7
Total	4 774	(83)	65 806	(85)	
Total (all species)	5 764		77 674		
Group 2 (14 stations)					
Chloroscombrus orqueta	830	(12)	14 754	(2)	14
Selene peruvianus	680	(10)	10 732	(2)	13
Sphyraena ensis	629	(10)	5 410	(1)	13
Diapterus peruvianus	527	(8)	7 726	(1)	14
Pomadasys axillaris	490	(7)	9 880	(1)	14
Opisthonema libertate	477	(7)	5 889	(1)	12
Anchoa spp.	443	(7)	402 400	(57)	11
Orthopristis chalceus	392	(6)	4 814	(1)	6
Pliosteostoma lutipinnis	275	(4)	198 282	(28)	11
Peprilus snyderi	209	(2)	1 130	(0)	7
Bagre panamensis	177	(3)	1 892	(0)	12
Polydactylus approximans	167	(3)	2 604	(0)	13
Polydactylus opercularis	106	(2)	866	(0)	9
Stellifer spp.	93	(1)	2 980	(0)	9
Scomberomorus sierra	76	(1)	262	(0)	10
Larimus acclivis	68	(1)	1 852	(0)	7
Penaeus vannamei	65	(1)	1 660	(0)	14
Isopisthus altipinnis	57	(1)	1 028	(0)	9
Total	5 761	(87)	674 161	(96)	
Total (all species)	6 640		704 308		
Group 3 (11 stations)					
Chloroscombrus orqueta	2 442	(22)	34 372	(16)	11
Sphyraena ensis	1 655	(15)	11 082	(5)	11
Selene peruvianus	1 075	(10)	26 290	(13)	11
Diapterus peruvianus	746	(7)	2 538	(1)	10
Peprilus snyderi	730	(7)	3 842	(2)	8
Opisthonema libertate	435	(4)	4 972	(2)	9
Bagre panamensis	338	(3)	1 000	(0)	10
Scomberomorus sierra	328	(3)	790	(0)	10
Anchoa argentivittata	254	(2)	71 376	(34)	6
Orthopristis chalceus	251	(2)	2 890	(1)	6
Polydactylus approximans	228	(2)	2 280	(1)	10
Hemicaranx spp.	209	(2)	1 348	(1)	5
Pomadasys panamensis	158	(1)	702	(0)	5
Diapterus aureolus	140	(1)	4 604	(2)	8
Anchoa spp.	97	(1)	32 333	(15)	6
Larimus acclivis	95	(1)	934	(0)	9
Polydactylus opercularis	86	(1)	438	(0)	6
Eucinostomus gracilis	25	(0)	292	(0)	6
Isopisthus altipinnis	23	(0)	182	(0)	5
Penaeus vannamei	13	(0)	192	(0)	4
Pseudupeneus grandisquamis	11	(0)	122	(0)	5
Total	9 349	(83)	202 579	(96)	
Total (all species)	11 205		210 926		

Table 5 (continued).

Species	W	(%)	N	(%)	F
Group 4 (29 stations)					
Sphyraena ensis	903	(10)	10 101	(2)	27
Opisthonema libertate	879	(10)	12 557	(3)	26
Diapterus peruvianus	722	(8)	2 729	(1)	18
Selene peruvianus	577	(6)	18 159	(4)	29
Peprilus snyderi	543	(6)	6 388	(1)	24
Anchoa spp.	468	(5)	234 000	(48)	26
Bairdiella spp.	383	(4)	23 164	(5)	21
Polydactylus approximans	254	(3)	4 310	(1)	25
Chloroscombrus orqueta	253	(3)	8 303	(2)	25
Xiphopenaeus riveti	207	(2)	40 795	(8)	21
Pliosteostoma lutipinnis	204	(2)	53 707	(11)	26
Larimus acclivis	204	(2)	4 382	(1)	16
Cynoscion phoxocephalus	202	(2)	2 880	(1)	11
Hemicaranx spp.	192	(2)	1 846	(0)	19
Pomadasys panamensis	138	(2)	2 575	(1)	9
Bagre panamensis	125	(1)	3 220	(1)	22
Scomberomorus sierra	125	(1)	306	(0)	17
Galeichthys peruvianus	120	(1)	453	(0)	11
Polydactylus opercularis	117	(1)	1 097	(0)	18
Parapsettus panamensis	116	(1)	1 480	(0)	10
Anchoa spinifer	101	(1)	8 565	(2)	18
Isopisthus altipinnis	95	(1)	4 450	(1)	20
Oligoplites refulgens	74	(1)	1 040	(0)	18
Lycengraulis poeyi	71	(1)	1 403	(0)	25
Penaeus vannamei	71	(1)	3 104	(1)	18
Trichiurus nitens	43	(1)	2 198	(0)	15
Total	7 187	(80)	452 789	(93)	
Total (all species)	9 040		487 172		
Group 5 (9 stations)					
Peprilus snyderi	838	(17)	5 943	(2)	8
Sphyraena ensis	722	(15)	7 567	(3)	8
Anchoa argentivittata	610	(12)	217 932	(76)	8
Selene peruvianus	354	(7)	9 321	(3)	9
Bagre panamensis	250	(5)	854	(0)	6
Pomadasys panamensis	246	(5)	1 004	(0)	7
Cyclopsetta querna	158	(3)	1 025	(0)	8
Diapterus peruvianus	111	(2)	320	(0)	4
Polydactylus opercularis	110	(2)	698	(0)	7
Polydactylus approximans	90	(0)	770	(0)	5
Pliosteostoma lutipinnis	62	(0)	18 088	(6)	4
Opisthonema libertate	56	(0)	1 014	(0)	7
Diapterus aureolus	47	(0)	2 078	(1)	6
Scomberomorus sierra	44	(0)	65	(0)	5
Isopisthus altipinnis	19	(0)	210	(0)	4
Penaeus vannamei	10	(0)	261	(0)	6
Total	3 727	(76)	267 150	(93)	
Total (all species)	4 935		287 095		
Group 6 (31 stations)					
Loliolopsis diomedeae	906	(22)	204 320	(65)	12
Orthopristis chalceus	412	(10)	7 281	(2)	13
Peprilus snyderi	281	(7)	2 651	(1)	15
Porichthys nautopaedium	182	(5)	16 644	(5)	26
Penaeus brevirostris	153	(4)	8 297	(3)	20
Cynoscion reticulatus	128	(3)	135	(0)	3
Prionotus quiescens	122	(3)	2 218	(1)	17
Synodus scituliceps	112	(3)	1 826	(1)	18
Prionotus horrens	88	(2)	422	(0)	6
Synodus evermanni	86	(2)	3 122	(1)	11
Squilla panamensis	85	(2)	6 612	(2)	8
Diplectrum labarum	68	(2)	1 926	(1)	11
Scorpaena spp.	64	(2)	4 380	(1)	16
Solenocera florea	39	(1)	12 708	(4)	5
Muraenidae	21	(1)	248	(0)	11
Zalieutes elater	20	(1)	1 472	(1)	11
Total	2 767	(69)	274 262	(87)	
Total (all species)	4 036		316 257		

Table 5 (continued)

Species	W	(%)	N	(%)	F
Group 7 (13 stations)					
Pleuroncodes monodon	22 583	(66)	2 935 558	(90)	5
Prionotus quiescens	8 480	(25)	170 114	(5)	11
Trichiurus nitens	285	(1)	8 036	(0)	8
Pontinus sierra	275	(1)	9 454	(0)	9
Gobiidae	256	(1)	27 357	(1)	8
Peprilus snyderi	219	(1)	6 844	(0)	11
Synodus evermanni	161	(1)	9 050	(0)	8
Lepophidium pardale	71	(0)	1 952	(0)	8
Argentina aliceae	59	(0)	2 778	(0)	5
Diplectrum euryplectrum	56	(0)	1 464	(0)	6
Citharichthys platophrys	56	(0)	5 792	(0)	11
Porichthys nautopaedium	35	(0)	3 970	(0)	8
Zalieutes elater	12	(0)	1 444	(0)	8
Monolene maculipinna	8	(0)	1 224	(0)	5
Penaeus brevirostris	2	(0)	72	(0)	5
Total	32 543	(95)	3 184 647	(98)	
Total (all species)	34 209		3 258 052		
Group 8 (55 stations)					
Pleuroncodes monodon	72 499	(55)	7 910 418	(74)	51
Argentina aliceae	15 406	(12)	780 158	(7)	25
Squilla biformis	12 235	(9)	661 894	(6)	31
Diplectrum macropoma	11 126	(8)	610 184	(6)	25
Heterocarpus vicarius	2 295	(2)	249 071	(2)	18
Merluccius angustimanus	1 339	(1)	45 308	(0)	29
Trichiurus nitens	1 101	(1)	38 273	(0)	16
Pontinus sierra	937	(1)	58 091	(1)	36
Monolene maculipinna	789	(1)	75 034	(1)	36
Total	117 727	(89)	10 428 431	(97)	
Total (all species)	132 326		10 736 293		

L. guttatus (see Appendix 1). The biomass of most of these species is also highest here, as shown in Table 4. The Pacific bumper *Chloroscombrus orqueta* and the Peruvian moonfish *Selene peruvianus*, the most widely distributed shallow-water species, are also found here, the former species accounting for 35 % in weight and 47 % in abundance of the total catches for this group (Table 5). Sea charts (Anonymous 1977) report mud/sand, sandy bottoms with shells and shingle in this area, and some of the above species, for example *L. peru* and *L. guttatus*, are in fact known to prefer hard bottoms (Allen 1985).

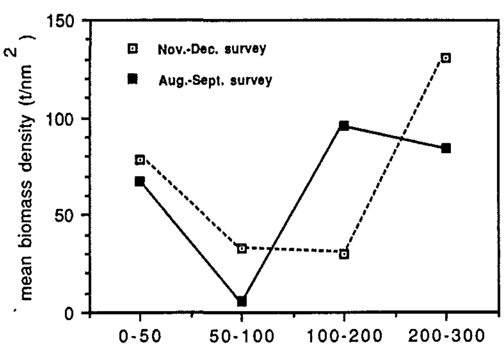

Fig. 9. Plot of mean biomass density (tonnes per square nautical mile) by depth stratum against depth for the August–September and November–December surveys. Both pelagic and demersal species included for the depth stratum 1–50 m

Groups 2, 3, 4 and 5 have several species in common: *Selene peruvianus*, *Chloroscombrus orqueta*, the threadfins *Polydactylus opercularis* and *P. approximans*, the whiteleg shrimp *Penaeus vannamei*, the barracuda *Sphyraena ensis*, the bluntnose jacks *Hemicaranx* spp., the thread herring *Opisthonema libertate*, the weakfish *Isopisthus altipinnis*, the anchovies *Anchoa* spp., the catfish *Bagre panamensis* and the butterfish *Peprilus snyderi*. However, these groups are typified by other species and occupy distinct geographical areas (Fig. 8).

Group 2: Shallow-water stations from near San Marcos (Mexico) to northern Guatemala. This group includes 14 stations, at an average depth of 20 m, with 73 species. A very high bottom temperature (29.2 °C) and high oxygen content (always above 4 ml l^{-1}) characterize this area. Typical species are the grunt

Pomadasys axillaris, Penaeus vannamei and the drums *Stellifer* spp. The Peruvian mojarra *Diapterus peruvianus* and *Chloroscombrus orqueta* are most abundant here and in Group 3 (Table 4). Table 5 shows that the small clupeoids, *Anchoa* spp. and the yellowfin herring *Pliosteostoma lutipinnis*, account numerically for about 85 % of the catches in that area. Also, because of their high frequency, they appear as important elements in the food chain, certainly representing an important food item for predators such as *Sphyraena ensis* and *Selene peruvianus*. The coastal zone where this group is located is characterized by a series of lagoons which probably serve as nursery grounds for the shrimp (*Penaeus vannamei*). An important fishery for this species already exists in this area (Holthuis 1980). A more complete list of the species in this group is given in Appendix 1.

Group 3: Shallow waters off Nicaragua and Guatemala. This group is very similar to Group 2, and their separation possibly artificial. Group 3 consists of 11 stations with 77 species. This group is characterized by high concentrations of *Sphyraena ensis* and the Spanish mackerel *Scomberomorus sierra*, voracious predators, and *Selene peruvianus* and *Chloroscombrus orqueta*, possibly among the prey, with catches often above 1000 kg h^{-1}. The mojarras *Diapterus aureolus* and *D. peruvianus, Peprilus snyderi, Polydactylus approximans* and *Bagre panamensis* were also almost constantly present in the catches (see Tables 4 & 5 and Appendix 1).

Group 4: Gulf of Fonseca and adjacent shallow waters of El Salvador and Nicaragua. This group is well defined and extends from the border between El Salvador and Guatemala to about 12° 20′ N (Nicaragua), including the Gulf of Tehuantepec. It includes 29 stations and 123 species and exhibited a mean depth of 23 m and high temperature and oxygen levels. *Sphyraena ensis, Opisthonema libertate, Selene peruvianus* and *Diapterus peruvianus* are the dominant species, as they are in almost all the other shallow-water Groups 2 to 4. A number of species are, however, more typical of Group 4: the sabretooth anchovy *Lycengraulis poeyi*, the croakers *Bairdiella* spp., *Anchoa spinifer* and other *Anchoa* species and the Pacific seabob *Xiphopenaeus riveti* (Tables 4 & 5). The soft and muddy bottom as well as the connection to a major river in the southern part of the Gulf explains the presence of the above species. *Lycengraulis poeyi* is a large anchovy (to 23 cm total length) and is known to prey on the smaller (to about 7 cm) anchovies of the genus *Anchoa* (Whitehead et al. 1988). The smaller anchovies are the only plankton feeders among the most widespread shallow-water species. These small fishes, because numerous and ubiquitous, must play a significant role in the food chain, and they certainly represent an important food item for the larger predatory species.

Group 5: Deeper shallow waters off Nicaragua and El Salvador. This group, with 9 stations (average depth 39 m) and 83 species, can be considered as corresponding to Group 1 (sandy/shell bottoms off Guatemala and Mexico), but is located in the southern part of the area. Most of the widespread shallow-water species missing in Group 1 are present here, particularly *Peprilus snyderi, Sphyraena ensis* and *Selene peruvianus* (Appendix 1). Also, the environmental conditions are slightly different, with lower oxygen and temperature levels and a bottom with a much lower sand component. Species most characteristic are *Anchoa argentivittata, Pomadasys panamensis* and the toothed flounder *Cyclopsetta querna* (Table 4). This latter species is known to prefer soft bottoms (Chirichigno et al. 1982).

Group 6: Upper intermediate shelf-dwellers. With an average depth of 66 m, much lower oxygen content (1.8 ml l^{-1}) and lower temperatures (21.7 °C), this group appears to be within the range of the thermocline (35 to 100 m). It includes 31 stations with 127 species. The apparently high number of species is due to the fact that some of the shallow-water species which typify the groups above are also found in the shallower stations of this group, and at the same time, species with a deeper depth range appear in the deepest stations. However, all the above species are present in very small quantities as compared to their respective primary areas of distribution (Table 4). Only 2 species show a clear preference for this area: the small toadfish *Porichthys nautopaedium* and the crystal shrimp *Penaeus brevirostris*, with higher biomass than in the other areas. Other species found here were the dart squid *Loliolopsis diomedeae, Peprilus snyderi*, the searobin *Prionotus quiescens*, the lizardfishes *Synodus scituliceps* and *S. evermanni* and the scorpionfishes *Scorpaena* spp. (Table 5).

Group 7: Lower intermediate shelf-dwellers. This group is found only on the wide shelf off Nicaragua. The 13 stations exhibit average depth, temperature and oxygen values of 114 m, 15 °C and 0.7 ml l^{-1} respectively. Group 7 contains a total of 54 species; the dominant ones are also found in Group 6 (*Peprilus snyderi, Porichthys nautopaedium, Prionotus quiescens, Synodus evermanni*, the batfish *Zalieutes elater* and the sanddab *Citharichthys platophrys*) or in the deeper shelf and upper slope, such as the scorpionfish *Pontinus sierra* and the squat lobster *Pleuroncodes monodon*. This latter species constitutes 66 % by weight and 90 % by number of individuals of the total catch for the stations in this group (Table 5). However, its value in Table 4 is not the highest, because logarithmic transformation reduces the dominant effect of the 2 very large catches which account for the high value of the total catch.

Group 8: Deeper shelf and upper slope. This group includes 55 stations and 55 species and is characterized by extremely low oxygen levels, ranging from 0.3 to 0.8 ml l^{-1} (average 0.4 ml l^{-1}). Most stations in this group are from the deeper shelf and upper slope of Nicaragua and El Salvador. *Pleuroncodes monodon*, known in Central and South America as 'langostino', dominates this part of the surveyed area and was caught at extremely high rates (up to 20 t h^{-1}) off Nicaragua, while it seemed to be less abundant in the northern part. Biomass of this species, as well as numbers and frequency, was far higher than that of any other species (Table 5). Other species in this group are *Pontinus sierra*, the deepwater Pacific flounder *Monolene maculipinna*, the hake *Merluccius angustimanus*, the argentine *Argentina aliceae*, the cagua seabass *Diplectrum macropoma*, the mantis shrimp *Squilla biformis* and the nylon shrimp *Heterocarpus vicarius*. Most of these species were not consistently caught at all stations. *Argentina aliceae* and the cutlassfish *Trichiurus nitens* were only caught in the daytime hauls.

DISCUSSION

Species assemblages

The sharpest changes in species composition occur along the depth gradient, and 3 major zones of the continental shelf can be identified. The upper zone (to about 50 m depth), with oxygen values usually well above 2 ml l^{-1}, is rich in number of species (well over 200) and exhibits relatively high biomass densities. The intermediate zone (to about 100 m), widely influenced by the thermocline and thus displaying rapid changes and short-term fluctuations in physical characteristics of the water masses, still contains a high number of species (about 160), but most of them have their optima in the water layers above and below this level, and biomass densities are in fact very low here. The deeper zone has an extremely low oxygen content (usually < 1 ml l^{-1}), which is probably the main factor, together with bottom type, explaining the type of fauna found. A single species, *Pleuroncodes monodon*, dominates the environment, together with *Squilla biformis* and *Heterocarpus vicarius*, present in much smaller quantities. It seems that the above crustaceans, particularly *P. monodon*, are well suited to live in hypoxic conditions. Of the few fish species found here in considerable quantities – *Trichiurus nitens*, *Argentina aliceae* and *Diplectrum macropoma* – the first 2 are known to perform daily vertical migrations.

Analysis of the November–December survey broadly confirms the results obtained from the August–September survey. However, faunal discontinuities along the depth gradient are less clear. The largest gap on DCA Axis 1 separates the stations deeper than 150 m from the others. This seems to be due mainly to the migration of *Pleuroncodes monodon* to slightly greater depths.

Further separation of groups, within each depth stratum, is less marked. Of the shallow-water stations, Groups 1 to 5, only Group 1 (found on sandy/shell bottoms of southern Mexico) is quite distinct. The remaining groups display a very similar species composition, although with significant differences in those species' relative abundances (Table 4). Group 4 (Gulf of Fonseca and adjacent coastal areas) is also distinguished by a number of species (*Lycengraulis poeyi*, *Anchoa spinifer*, *Xiphopenaeus riveti* and *Cynoscion phoxocephalus*) highly characteristic for this area.

Most of the studies on demersal fish assemblages on continental shelves have indicated that the main faunal changes occur along the depth gradient (Fager & Longhurst 1968, Lleonart & Roel 1984, McManus 1985, Roel 1987). Physical characteristics of water masses, as well as bottom type, light intensity, pressure, etc., are mostly depth-dependent, and depth obviously reflects the combined effects of these factors. Fager & Longhurst (1968) found that separation between different assemblages in the Gulf of Guinea was related to the thermal discontinuity layer as well as to sediment type (which also changed with depth). McManus (1985) studied fish assemblages of the Samar Sea (Philippines) from 20 to 90 m depth and found a depth-dependent faunal distinction between 30 and 40 m, independent of season and substrate type. Lleonart & Roel (1984) identified structures in species composition associated with depth and latitude when analysing demersal communities of fishes and crustaceans of the Namibian coast. Roel (1987) also concluded that composition of the demersal fauna in the upwelling region off South West Africa was related mainly to depth. In this respect, he found a main boundary between the slope fauna and the shelf fauna at about 380 m depth. The area corresponding to the shelf community could be further subdivided into 5 subareas. Two of these extended over the whole shelf and did not seem to be subject to seasonal variations. The remaining 3 corresponded to the inner shelf; their extent varied between summer and winter and appeared to be independent of depth.

The above studies, as well as the present one, indicate that when the depth range is wide enough to include areas where different water layers impinge on the shelf slope, the greatest changes in species composition are depth-related. However, within each water layer, other factors – such as presence of river mouths, type of substratum, etc. – become more relevant.

Biomass

The highest biomass densities are found along the continental shelf-slope boundary. Longhurst & Pauly (1987) indicate that the distribution of benthic biomass on tropical continental shelves reflects the importance of inshore primary production and/or enrichment from rivers, and that highest benthic biomass values correspond to the inshore mixed layer. Here, regeneration of nutrients from the bottom can be directly utilized for phytoplankton production. This is the case, for example, in the tropical Atlantic (Guinea–Sierra Leone), where Longhurst (1959) found highest benthic biomass in shallow inshore waters and a minimum at the bottom of the thermocline (50 to 100 m). Rowe (1971) found an inverse relationship between biomass and depth in temperate regions, such as the north temperate Atlantic, in tropical regions such as the Gulf of Mexico, and in the upwelling area of the Pacific off Peru. However, the conclusions apply to a wide depth range (shelf to over 5000 m depth), and a high variance was found in waters shallower than 1000 m in the upwelling area off Pisco (Peru). Here the influx of organic material is so high as to cause oxygen depletion, and stressful conditions for life and maximum biomass densities are found offshore of the oxygen-poor depths. The conditions found in the area under study seem to represent another case of deviation from the general trend of biomass decreasing with depth. As shown in Fig. 9, highest biomass densities are found below 100 m depth, consisting mainly (80 %) of *Pleuroncodes monodon*. The survey report (Strømme & Sætersdal 1988) gives identical catch rates for both daytime and nighttime hauls, which suggests a strictly demersal behaviour for this species.

The reason for this apparent deviation can be deduced from the fact that the region under study, although geographically tropical, is characterized by singular hydrographic conditions. High productivity results from the processes described above (seasonal upwelling and shallow thermocline; see 'Study area') and, possibly under-utilized by pelagic herbivores, is deposited by sedimentation on the bottom. Haedrich et al. (1976) as cited by Rowe (1981) also reported highest densities of large benthic organisms (megafauna) along the continental shelf/slope boundary off northern West Africa, and they related this finding to a prominent shelf-break upwelling. It seems evident that the inverse relationship between depth and benthic biomass is to be considered a general trend but that local hydrographic conditions may introduce deviations from this pattern.

Mass occurrences of anomouran crustaceans have been reported from other regions, usually highly eutrophic, like the California Current and the Humboldt Current. The dominance of this group seems to be due mainly to their wide range of feeding mechanisms and their ability to live in oxygen-deficient waters. Benthic mass aggregations tend to occur in areas below diatom blooms and at depths corresponding to those where the oxygen-minimum layer meets the continental shelf/slope (Longhurst 1968). Low oxygen content may be responsible for a lower number of taxa and, because of reduced competition, for high densities. *Pleuroncodes monodon*, in particular, is also very abundant off central Chile, where it occurs on the deeper shelf together with another galatheid (*Cervimunida johni*) and the shrimp *Heterocarpus reedi* (Longhurst 1968). Here the environmental conditions are similar to those found in the area of the present study – i.e., oxygen-deficient waters and high productivity. However, these are not so pronounced as to produce practically anoxic conditions with a rich fauna of sulphur bacteria, such as those further north off northern Chile and Peru, where 'semiabiotic' regions can be found between the deeper shelf and upper slope areas (about 100 and 500 m depth) (Rowe 1971).

Taxonomic note

The *Pleuroncodes* species found in this area has usually been identified as *P. planipes* Stimpson (Vidal 1971, Orellana & Escoto 1981 and others). This species typifies the Baja California upwelling region, while *P. monodon* (H. Milne Edwards) has been considered to be the southern-hemisphere congener. Highest concentrations of this species are found off central Chile, at depths between 125 and 200 m (Longhurst 1968). However, Boyd (1963), as cited by Longhurst (1968), had already reported the occurrence of *P. monodon* off the west coast of Mexico and hypothesized that this species possibly occurs off Central America. This was later confirmed by Longhurst & Seibert (1971), who found young stages of *P. monodon* in micronekton nets during eastern tropical Pacific expeditions.

Pleuroncodes planipes are known to occasionally form large pelagic swarms as adults, while most species belonging to the same family (Galatheidae) are exclusively benthic. In the course of the RV 'Dr. F. Nansen' surveys *Pleuroncodes* sp. was caught only in the bottom trawl. Also, none of the pelagic acoustic recordings was attributed to this species. No significant differences were found in the catches between night and day, confirming the strictly demersal nature of the population found off Central America.

Specimens collected off Nicaragua in the course of the RV 'Dr. F. Nansen' survey programme were recently analysed by M. Türkay (Senckenberg Museum, Frankfurt, Germany), who found (pers. comm.)

that the species in fact fits the description of *Pleuroncodes monodon*, i.e. displays slightly flattened and bare pereiopods, compared to the extremely flattened and ciliated pereiopods of *P. planipes*.

I believe that the population off central America is in fact *Pleuroncodes monodon* and that the appellation *'planipes'* has been erroneously used in this area.

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Appendix 1. Two-way station-by-species table produced by the program TWINSPAN (Hill 1979). Values denote categories of abundance (in weight, W): (1) W < 10 kg; (2) 10 < W ≤ 100 kg; (3) 100 < W ≤ 1000 kg; (4) 1000 < W ≤ 10 000 kg; (5) W > 10 000 kg. Vertical lines separate station groups; station numbers along top margin (arranged vertically under group numbers). Hierarchy shown in binary notation along the bottom and right margins of the table for stations and species respectively

	1	2	3	4
	11111111111111	11111111111111	11 1111	1111111111
	42257347882678	33334455666679	38455571223	4555577888800000111347777788
	78254059191652	67843749027910	28515739393	63689283467123456346964567901
Cynoscion phoxocephalus	--------------	--------------	--2--------	-2---1--1-------1-2---2-21211
Opisthopterus spp.	--------------	--------------	---2-------	22--22----------------2-----2
Lycengraulis poeyi	--------------	--------------	------2----	1111-1111111-11111111-11-1111
Bairdiella spp.	--------------	---1----1-----	----1-1----	2--2-11-1111-2-1211--21222212
Anchoa spinifer	--------------	--------------	-----------	---1--11-111-11111---11-22111
Xiphopenaeus riveti	--------------	-11----1-2--1-	-----------	---1---11-11-2112121112222211
Parapsettus panamensis	-----1--------	-1--1---------	--11-2-1---	--1--1------111-----1-2122---
Polydactylus opercularis	--------------	21-12-111-12--	2-2--22-1-2	21-21-111111--111----2-1-12-2
Penaeus vannamei	----1-----1---	11111111121111	-1-1--11---	2111-1-1--12-111112-111-----1
Sphyraena ensis	--1-2-----2-1-	11-22321321312	23222333212	222222322112223222221111-121-
Hemicaranx spp.	------1-------	---111112--11-	-2-132--1--	1--121-11111--122-21-11---111
Opisthonema libertate	--2-2---------	111331--111111	23-1222121-	2112311221221231211-2211-121-
Opisthopterus dovii	--------------	1---11-1-1-1-1	-----1-2---	------111111-1111-------2--1-
Pliosteostoma lutipinnis	--------------	1121311222---1	---111-----	211221111-111211122122112-11-
Polydactylus approximans	------------1-	1221121112-112	222121221-2	-122-22-111112121-11222121111
Isopisthus altipinnis	--------------	-1-12--1121-11	--1-1-111--	11-2-1-1-111-11111-111111---1
Opisthopterus equitorialis	--------------	---1--1111--1-	--1-1-----1	--12---11---111-1---11---22--
Anchoa spp.	------------1-	1112311221--1-	--22--2221-	22-232221121-11211212222-2211
Oligoplites refulgens	--------------	---1111-1-2111	---1-------	-11221-1111-12111---11-1--1--
Pomadasys leuciscus	--------------	------1-------	1--1---2-1-	--2--21--1---1------1--1-----
Neoopisthopterus tropicus	--------------	----1------1-1	-------11--	-------------121211---------
Anchoa argentivittata	----------2---	------11---1-2	--1-32-2-11	-11------1---2-11-----------
Larimus acclivis	------------1-	112---1-2-1--1	-12121121-2	1111-11--111-1--11--1-21----3
Scomberomorus sierra	------1---1---	1--1-2121-1211	2322222221-	-21121-1111-211--11111-------
Larimus gulosus	--------------	-2-------2----	--2-1------	--1-----1------11-----------
Diapterus peruvianus	---------1--2-	21221211232213	222-2231222	223223211222-1-1--11-12------
Xenichthys xanti	------------1-	--------------	2-11-1----2	--1--11---1--1---1----------
Conodon macrops	---1----------	-1---11-11-1-1	1-1-1------	---------11-----------1------
Stellifer spp.	--------------	111-12-1-21--1	-----------	----------------1---111------
Larimus effulgens	--------------	---212-1---2-2	2----------	----------------------1------
Lutjanus guttatus	31----1-1--12-	--------------	--21122---1	222----1-1-1-1---1----1-----2
Albula vulpes	21------1-2-22	--------------	-1-----1122	---------1------------------
Selar crumenophthalmus	--212---111-11	--------------	22----1---2	-11------11-----------------
Caranx caballus	-1-----1211-12	----11-----1--	12------1--	----1---------------211------
Selene peruvianus	-1--11111-2-22	213312111111-1	23322222213	1222113111111111111213112112
Pomadasys panamensis	-111--1---11-1	--------1-----	--122-22---	--12---12--1---1-12---------2
Caranx caninus	22------------	----------1-1-	22---------	--1----2-------1-------------
Chloroscombrus orqueta	--214212-11212	22322221221322	33222332234	1112111111212211--1112112-1-
Chaetodipterus zonatus	------1-----11	---1----11-1--	-1----2----	--1--11-------------1-1------
Sphyrna lewini	---2--1---2---	11-----------1	-------2---	---2-2-1111--122------------
Pomadasys axillaris	---1---3-1----	22322211221212	-2------2--	---------------------1-------
Diapterus aureolus	----------1--1	111--11-1-----	-2111-121-2	-----------1-----------------2
Cynoscion reticulatus	----------1---	11--2-1-1--1-1	-21111-31-2	-1----2------11-11111-1--1---
Micropogonias altipinnis	--------------	---1-1--1---11	--2----1--2	--1---1----2---12----1-------
Bagre panamensis	---23-----2111	22-12121221-12	12-12222112	2112--2--11111-1111-11-221111
Arius spp.	---1----1-----	11-----1--1-1-	2----------	2---------------------------
Carcharhinus porosus	-1---2----1---	--------------	---122-----	---1--2-2-------------------
Lolliguncula panamensis	----------1---	----11--1----1	----11-1-11	-111--1-1-1--1111----111-111-
Carangoides ortrynter	-1---11-1112-1	--------------	-----------	----------------1--1--------
Eucinostomus gracilis	-1211113-21111	111---------1-	---1--11111	1-----2---11-1------1-1------
Galeichthys peruvianus	-21---1-11----	---1-2---1---1	---1-----1-	---1-12-------1--1--112-12--1
Pseudupeneus grandisquamis	-1222111111---	-12-----------	-1-1---111-	------1--1111--1------------
Orthopristis chalceus	22231222122222	-231221-------	2211----2-3	---------------------------1
Cyclopsetta querna	------1-------	--------------	----2-21---	1-1-----1--1----1-----------
Lutjanus peru	331-2--1------	--------------	-----------	----------------------------
Nasolamia velox	22----2-------	--------------	-----------	-------------1--------------
Sphoeroides annulatus	--------------	-1---1-----1-1	-----------	------2----1-1-1---------1---
Portunus acuminatus	----1---------	---1----1-1-1-	----------1	---------------------1---------
Pseudobalistes polylepis	-1-21-1-112222	--------------	-----------	----------------------------
Scorpaena spp.	--------------	--------------	-----------	----------------------------
Prionotus horrens	--1-----------	--------------	-----------	---1-------1---------------1
Penaeus californiensis	1-------------	--------------	-----------	-----------1---------------1
Sphoeroides lobatus	--1-11--1-----	--------------	-----------	--------------------1------
Synodus scituliceps	----1---------	-1------11--1-	---1-------	--1------11--1--------------
Peprilus snyderi	--1-1--1--2--1	21-1-2312-----	331-2-321-2	-2-2-223111212222221112--2212
Portunus asper	--------------	112-----------	---1---1---	---1------1----11-----------
Muraenidae	-----1--------	--------------	-----------	-----------1----------------
Diplectrum labarum	--------------	--------------	-----------	----------------------------
Loliolopsis diomedeae	--------------	-------1-1----	--1--------	-------1--1------1111--------
Porichthys nautopaedium	--------------	111-----------	-----------	-----1-----1---------------11
Penaeus brevirostris	--------------	--------------	-----------	----------------------------
Ophichthidae	--------------	-11-----------	-----------	--------------------1--------
Squilla panamensis	--------------	--------------	---1-------	----------------------------
Symphurus atramentatus	--------------	-----1--------	-----------	----------------------------
Lepophidium pardale	--------------	--------------	-----------	----------------------------
Gobiidae	--------------	--------------	-----------	--------1------------------1
Citharichthys platophrys	--------------	1-------------	-----------	1----------1----------------
Prionotus quiescens	--------------	--------------	-----------	---------------------------1
Synodus evermanni	--11------1---	-----1--------	-----------	-----------1------1---------
Symphurus spp.	--------------	1------1--1-1-	-----------	----------------1---11-----1-
Symphurus elongatus	--------------	-1---1---1----	-----------	----------------------------
Diplectrum euryplectrum	--------------	--------------	-----------	----------------------------
Zalieutes elater	--------------	--------------	-----------	----------------------------
Lophiodes caulinaris	--------------	--------------	-----------	----------------------------
Solenocera agassizii	--------------	--------------	-----------	----------------------------
Pronotogrammus eos	--------------	--------------	-----------	----------------------------
Cynoscion stolzmanni	--------------	--------------	-----------	----------------------------
Mursia gaudichaudii	--------------	--------------	-----------	----------------------------
Moridae	--------------	--------------	-----------	----------------------------
Pontinus sierra	--------------	--------------	-----------	----------------------------
Diplectrum macropoma	--------------	--------------	-----------	----------------------------
Hemanthias signifer	--------------	--------------	-----------	----------------------------
Monolene maculipinna	--------------	--------------	-----------	----------------------------
Pleuroncodes monodon	--------------	--------------	-----------	----------------------------
Merluccius angustimanus	--------------	--------------	-----------	----------------------------
Myctophidae	--------------	--------------	-----------	----------------------------
Heterocarpus vicarius	--------------	--------------	-----------	----------------------------
Argentina aliceae	--------------	--------------	-----------	----------------------------
Squilla biformis	--------------	--------------	-----------	-----------1-----1--1--------1
Trichiurus nitens	--------------	--------------	----1--1---	---1-11----1-11-1--1--2111111
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21212221-	211---------1---111-1- 11--1---	-------------	---	010100
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---------	-111---11211111121---- 1------1	-------------	-----------1---	010110
1----1---	--22--------2--------- 1-1--2--	-------------	---	010110
--1---1--	11112----1--1-1-1----- --------	-------------	---	010110
--------1	-111--1-----1-11------ --------	-------------	---	010110
--1-11--1	1-1221------1-121111-- 11-111--	11-1-------2-	---	010111
3222321-1	--111-----------221122 1121--21	2211113211-2-	------------------------------------2-22---------------	011
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PAPER 2

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Study of the demersal assemblages of the continental shelf and upper Angolan slope

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ABSTRACT: Structure of demersal assemblages (fish, crustaceans and cephalopods) of the continental shelf and upper Angolan slope (ca 5° S to 17° S) was studied based on the trawl survey of the RV 'Dr. Fridtjof Nansen' in February and March 1989, by means of an ordination technique, Detrended Correspondence Analysis (DCA), implemented by the computer program DECORANA and a classification technique, Two-Way Indicator species Analysis (TWIA), implemented by the computer program TWINSPAN. Correlation of DCA axis with the environmental variables showed that the thermal, depth-dependent stratification explains the main groupings, while bottom type and latitudinal gradients are the main factors within each depth stratum. A major latitudinal faunal shift takes place in the area Tombua-Cunene (Angola) and is related to the southern limit of Equatorial Water for the shallow-water assemblages and to the frontal area between the warm, southward-flowing Angola Current and the northward flowing cold Benguela Current for the subthermocline shelf assemblages. Highest biomass densities (from bottom trawl catches) were found in correspondence with the upper slope, consisting mainly of the bony fish *Synagrops microlepis* (Norman).

INTRODUCTION

Within the framework of projects sponsored by UNDP/FAO and NORAD, the Norwegian RV 'Dr. F. Nansen' carried out acoustic and bottom trawl surveys on the Angolan shelf and upper slope in 1989. The present study, based on data collected through 1 bottom-trawl survey, has as a main objective to describe the different species assemblages in relation to the environmental variables and describe the general trends in the distribution of the bottom megafauna. Groups included in the analysis are bony fishes, elasmobranchs, stomatopods, decapod crustaceans and cephalopods.

The study of Angolan marine fish fauna is also of special interest because of the major changes in species composition taking place along its shelf. The latter extends from about 5 to 17° S and encompasses a typical tropical regime in its northern part as well as a temperate one, in the south, separated by the Benguela-Angola frontal system. It has indeed been recognized by several authors that a major zoogeographic boundary is present along the Angolan coast, separating the tropical fauna of Guinean origin from the temperate fauna associated with the Benguela system (Longhurst 1962). Da Franca (1962), however, points out that there is no really sharp boundary between 2 different faunal complexes. Faunas originating outside the Angolan coast meet and partially overlap along the Angolan shelf which should thus be considered as an area of biogeographic transition between the Guineo-equatorial province and the South African province. The present study, besides describing the main species assemblages found on the Angolan shelf, will also try to define more accurately the faunal transition area referred to above by more closely correlating the environmental parameters with the faunal patterns.

Several studies of the demersal communities on the continental shelf and upper slope off West Africa are available based on multivariate analysis techniques but none has covered Angola. Domain (1972) analyzed the assemblages of the Senegal-Gambia continental shelf using Principal Component Analysis (PCA) and later extended the study to Mauritania (Domain 1980) by cluster analysis and Correspondence Analysis;

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Fager & Longhurst (1968) analyzed the demersal fish assemblages in the Gulf of Guinea based on the data from the Guinean Trawling Survey (GTS) with the multivariate analytical method described in Fager (1957); Lleonart & Roel (1983) investigated the epibenthic fish and crustacean assemblages off Namibia, from 100 to 500 m depth, by means of hierarchical classification method, based on data collected through the Benguela II cruise in 1980; Mas-Riera et al. (1990) analysed the influence of the Benguela upwelling on the structure of the demersal fish populations of southern Namibia; Roel (1987) described the demersal communities off the west coast of South Africa by Correspondence Analysis.

STUDY AREA

Bottom topography and structure. The study area (Fig. 1) includes a coastline of ca 800 nautical miles (excluding Zaire), from about 5 to 17°S and covers trawlable grounds of the shelf and upper slope to ca 750 m depth.

Fig. 2 shows a map of the Angola shelf bottom based on analysis of the echograms, while Fig. 3 shows the position of bottom samples and type of sediment. The northern part of the area, to Pta. das Palmeirinhas, is characterized by large areas of fine to coarse sand. Silt is found outside the Congo River estuary, south of Cabinda, and north of Luanda. These areas are interrupted by beds of stones, rocks and corals (Fig. 2). The central part of the Angolan shelf, from south of Pta. das Palmeirinhas to Benguela, is also characterized by alternating fields of mud, fine to coarse sand, but silt and clay dominate large areas and rocky bottoms are found mainly north of Cabo Ledo and off Cabeça da Baleia. The shelf between Tombua and the Cunene River estuary has a level bottom, with clay and silt in Baia dos Tigres and fine to coarse sand to Tombua. The bottom is rough and untrawlable south of Baia dos Tigres, deeper than 100 to 200 m.

Hydrology and biological oceanography. The general climatology of the Gulf of Guinea has been described by Wauthy (1983), including the Canary Current and Benguela Current frontal systems delimiting the tropical region north and south of the Equator respectively. The physical oceanography off Southern Angola has been described by Dias (1983) and features of the frontal system by Shannon et al. (1987). The survey report by Strømme & Sætersdal (1991) gives a description of the oceanographic conditions off Angola. The productive systems of the eastern tropical Atlantic between 20°N and 15°S were described and compared by Voituriez & Herbland (1982).

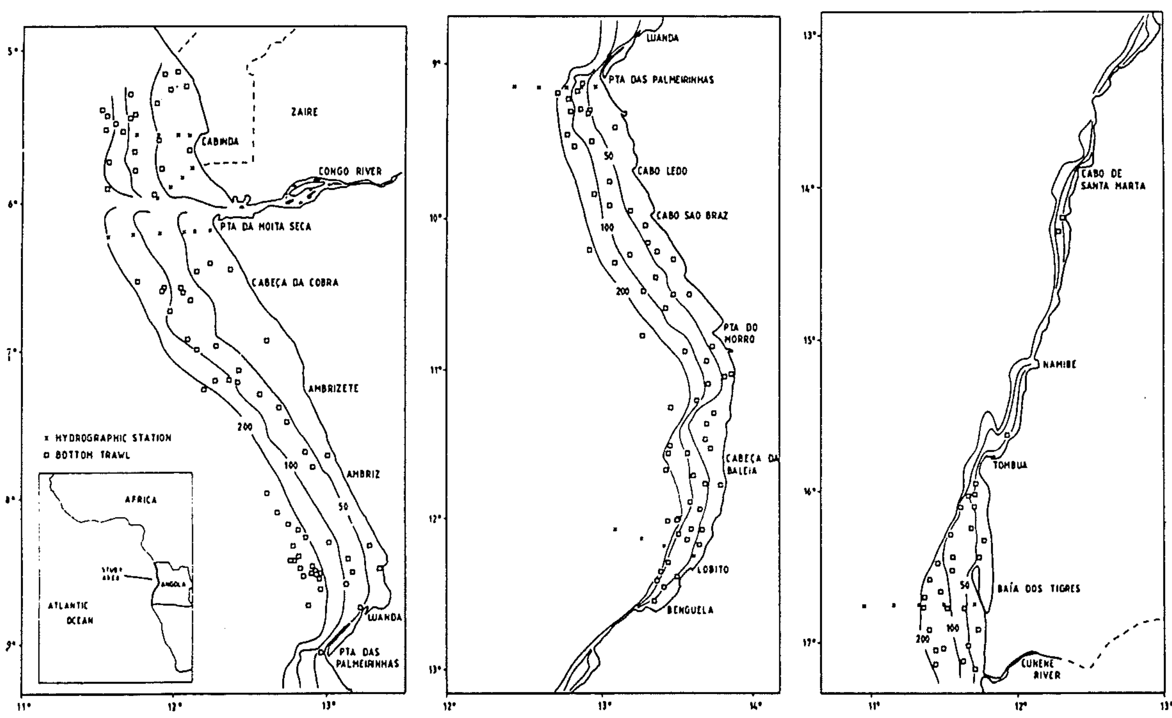

Fig. 1. Position of trawl hauls and hydrographic stations. February and March 1989

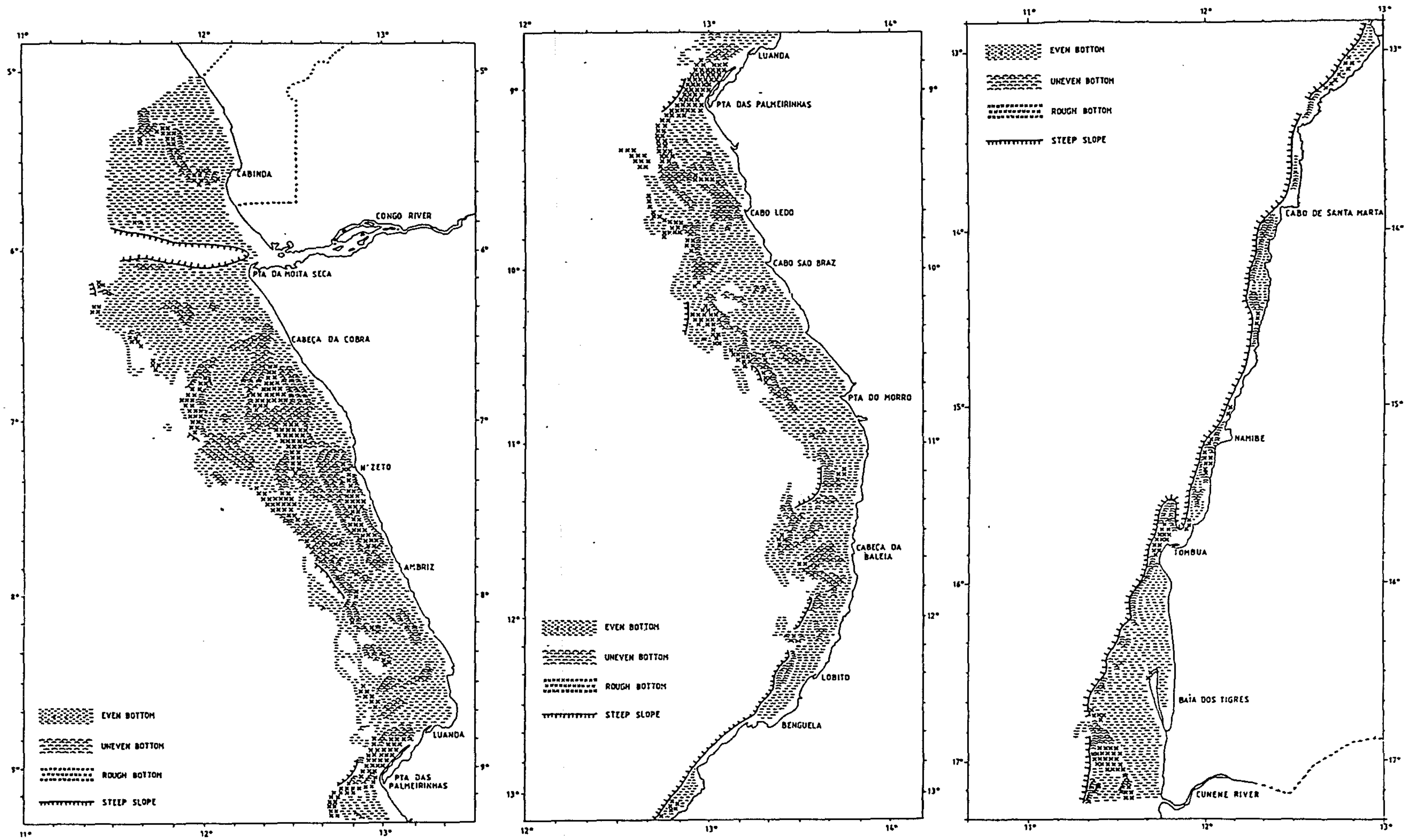

Fig. 2. Shelf bottom type inferred from echograms (redrawn from Strømme & Sætersdal 1991)

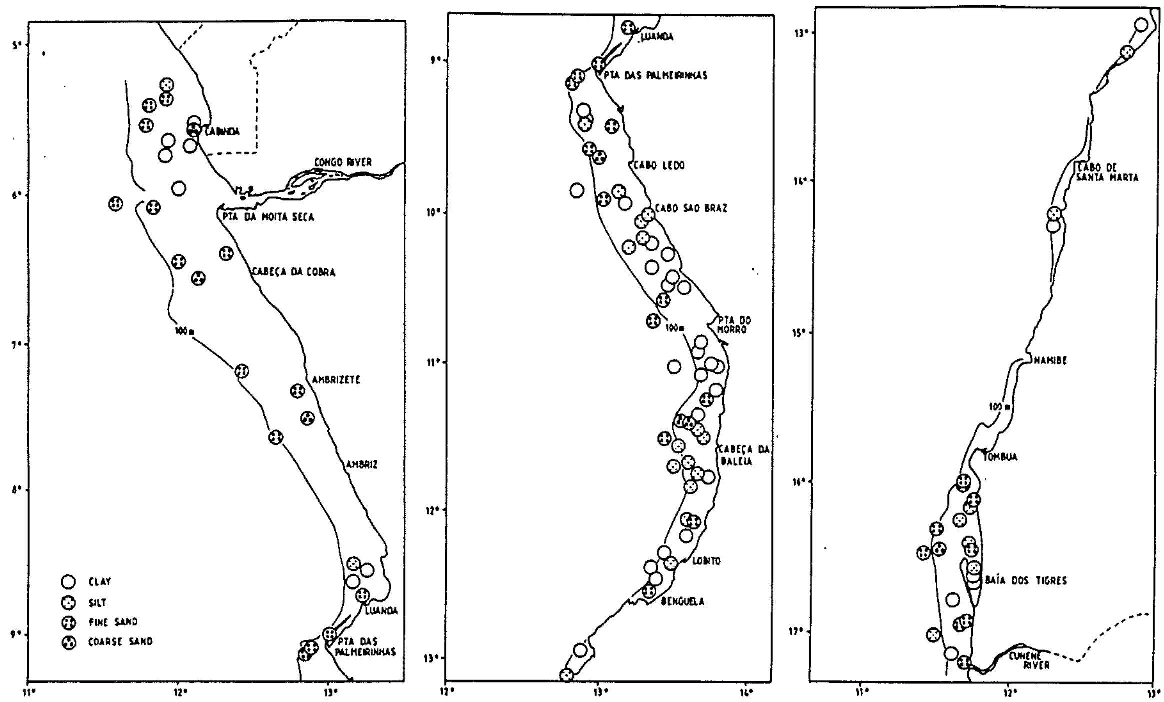

Fig. 3. Position of bottom samples and type of sediment. February and March 1989

During the austral summer (January to April, Fig. 4) the northern region (Cabinda to Pta. das Palmeirinhas) is characterized by a very shallow and marked thermocline, its upper boundary found at about 10 m depth in the north and becoming deeper (between 25 and 50 m depth) southward. In the northern part of the area the halocline is also very sharp, mainly because of the increased rainfall and the increased runoff from the Congo River. The upper water layer consists of Equatorial Water, observed to 13 to 14° S, characterized by low salinity, high temperature and reaching 30 to 40 m in thickness (Wauthy 1977). Oxygen levels usually above 2 ml l^{-1} are found to about 100 m depth, decreasing to slightly over 1 ml l^{-1} to the shelf edge. Between Pta. das Palmeirinhas and Benguela there is also a sharp thermocline between about 25 and 50 m depth and surface temperatures gradually decreasing toward the south. Surface temperatures of the northern part (to Benguela), are usually 27 to 28 °C. Bottom temperatures of 20 °C or more are found to about 50 m depth from Cabinda to Lobito. The southernmost part of the shelf, between Tombua and Cunene and particularly between 14 and 16° S is characterized by the presence of the permanent frontal system (convergence zone) between the southward flowing Angola Current and the north-moving surface waters of the Benguela Current. The front shifts seasonally through ca 2° latitude. The mechanisms responsible for maintaining the front within a relatively narrow range of latitudes seem to be, among others, the coastline orientation, bathymetry and wind stress (Shannon et al. 1987). During the austral summer the front is usually located further south, between about 16 and 18° S. The front represents the southern limit of the waters of tropical/equatorial origin, with a sharp, almost permanent thermocline and the cold waters of the Benguela Current, with coastal, permanent upwelling, which is however moderate or weak in this season. South of Tombua temperatures near the bottom are always lower than 20 °C.

During the winter, with the strengthening of the southeast trade winds, a northward flowing coastal current develops, with upwelling occurring all along the coast. This phenomenon appears to be well-developed especially off Pta. das Palmeirinhas and Lobito, and in correspondence with the capes (i.e. Cabo Ledo, Cabeça da Baleia and Pta do Morro). Surface temperatures of the northern region (from Cabinda to Lobito) are much lower, 20 to 22 °C, than in the summer. The thermocline is lifted and often broken down by the occurrence of upwelling. In the southern part (Tombua to Cunene) upwelling is at its peak, with surface temperatures near the coast down to 15 °C. Oxygen values < 2 ml l^{-1} are found from about 50 m depth and values below 1 ml l^{-1} are found at 100 m depth.

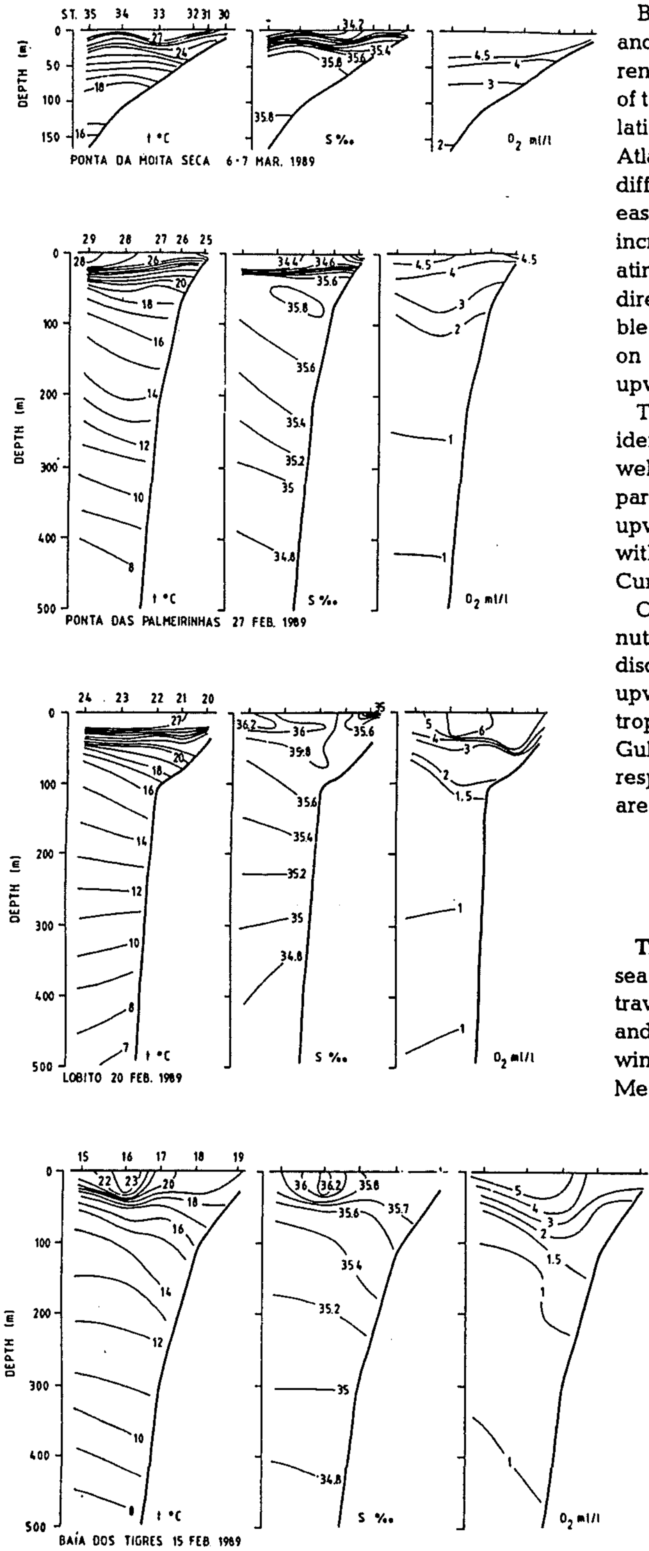

Fig. 4. Hydrographic profiles of temperature, salinity and oxygen at selected places along the Angolan coast (see also Fig. 1). February and March 1989 (redrawn from Strømme & Sætersdal 1991)

Berrit (1976) suggests that the upwelling off Gabon and Angola is not of Ekman-type because its occurrence corresponds with the time of minimum strength of the winds favourable to upwelling. Also, good correlation was found with wind strength in the western Atlantic. Voituriez & Herbland (1982) discuss the different mechanisms that might be responsible for the eastern tropical Atlantic upwelling, including the increase in wind stress in the western Atlantic generating a Kelvin wave along the Equator in the west-east direction. They however conclude that it is not possible, based on present knowledge, to draw conclusions on which mechanism is really responsible for these upwellings.

Two different highly-productive systems can be identified in Angolan waters: seasonal coastal upwelling, typifying mostly the northern and central parts southward to Tombua, and the almost permanent upwelling in the southern part of the area coinciding with the northernmost extension of the Benguela Current.

Other factors contributing to the enrichment in nutrients of the marine waters of Angola include the discharge from the Congo River and shelf-break upwelling. This phenomenon is common both in the tropics and elsewhere and reported as striking in the Gulf of Guinea (Longhurst & Pauly 1987) and possibly responsible for enhanced production at the shelf-break area.

MATERIAL AND METHODS

Trawl data. Material was collected in the summer season (13 February to 16 March). A shrimp and fish trawl was used, with headline of 31 m, footrope of 47 m and estimated headline height and distance between wings during towing of 6 and 18 to 20 m respectively. Mesh size was 2 cm, with double lining in the cod end.

Each tow had a standard duration of 30 min (other details in Strømme & Sætersdal 1991). The bottom trawl stations were randomly set along the cruise track. A total of 167 stations were sampled in the course of the above survey (Fig. 1). Of these, 4 stations considered as 'non-valid' (because of gear damage) were not included in the analysis.

Each specimen caught was identified, counted and weighed separately. The FAO species identification sheets for fishery purposes, Fishing Areas 34/47 (in part) (Fisher et al. 1981) and the Guide to the commercial marine and brackish waters of Angola (Bianchi 1986) were used for identifying the species. Congeneric species which were difficult to separate were pooled together. All station and species data were stored using the B-trieve file system (data available in ASCII format upon request to the author and with the authorization of Angolan authorities).

Hydrographic data. Samples for temperature, salinity and oxygen were taken using Nansen bottles at standard depths and along fixed transects (Fig. 1). In the present analysis, the values of these variables at each station were inferred from the nearest hydrographic station.

Data analysis. Analysis was performed with the help of multivariate analytical techniques i.e. a classification method Two-Way Indicator species Analysis (TWIA, Hill 1979), implemented by the program TWINSPAN, and an ordination method, Detrended Correspondence Analysis (DCA, Hill & Gauch 1980), implemented by the program DECORANA. The former is a divisive method that classifies sites and species and produces a sorted species by station table.. Detrended Correspondence Analysis produces an ordination of the stations based on the abundance values of the species. The ordination summarizes multivariate data in a scatter, low-dimensional diagram and it is also useful for detecting possible outliers. Furthermore, the DCA version used for this study also correlates the main gradients (axes) with given environmental variables (ter Braak 1987). As a result of the analysis, means and and standard deviations of the environmental variables are also produced for each group identified. A discussion on the validity of the above methods for this type of study is presented in Bianchi 1991.

A table of 'pseudo-*F*' values (ratios of the among-group to within-group variances) was made to evaluate the degree of conformity of a species to a site-group obtained from the above methods. A formal *F*-test cannot be performed in this case because it would be based on the same data previously used to establish the groups (Green & Vascotto 1978).

In this study biomass (wet wt) was used as a measure of abundance. Each weight (x) was converted to $\ln(x+1)$ before analysis with DCA and for calculating the 'pseudo-*F*' values. This transformation minimizes the dominant effect of anomalous catches. The addition of 1 unit is necessary to avoid problems derived by the presence of values = 0 or < 1. No transformation is necessary in the case of TWIA, where abundances are converted to numbers corresponding to different abundance classes (pseudospecies). In this study 5 'pseudospecies' were used, corresponding to classes with lower limits set at 0, 10, 100, 1000 and 10 000.

Demersal biomass densities (weight per unit area) were calculated using the 'swept-area' method by depth stratum:

$$D_j = C_j / q\, a_j$$

where D_j = density in Stratum j [tons (n mile)$^{-2}$]; C_j = catch taken in hauls in Stratum j (tons); a_j = surface of the bottom 'swept' by the trawl hauls in Stratum j (n mile^2); q = catchability coefficient (= 1, i.e. all fish in the path of the trawl were caught).

In the swept-area analysis, shallow-water pelagic species caught in the bottom trawl were not excluded. It is indeed quite difficult to differentiate between pelagic and demersal for the shallow-water species. Small pelagic fish of this depth zone are often found quite close to the bottom, some of them feed on bottom detritus and are preyed upon by both demersal and pelagic predators. Pelagic species of the deeper shelf were instead excluded from this analysis.

RESULTS

A total of 289 species comprising 3 377 403 specimens (79 964 kg) were sampled in February and March 1989. Table 1 gives the list of the most important species collected and used in the analysis.

Appendix 1 shows the results from TWIA and Fig. 5 the dendrogram representing the relationships between the various groups. The first division separates the deep water Groups (7 and 8) from the shelf Groups (1 to 6). At the second division level the shallow water assemblages (Groups 1 to 3) separate from the assemblages of the deeper shelf (Groups 4 to 6) while the 2 upper slope assemblages separate from each other also according to depth strata. At the third division level the assemblage of shallow waters (1) separates from Groups 2 and 3, found in slightly deeper waters, while the deeper shelf Groups 4 and 5 (from Cabinda to Benguela) separate from the corresponding assemblage of the Tombua-Cunene region (Group 6).

Fig. 6 shows the plot of stations on the first 2 DCA axes. The eigenvalues of the first 4 axes are 0.86, 0.46, 0.38 and 0.30 respectively, which shows that the gradient represented by the first axis is by far the most

Table 1. Main species collected in 1989 off Angola, by major taxonomic groups and families

Cephalopods

Loliginidae
- *Alloteuthis africana* Adam, 1950
- *Loligo vulgaris* Lamark, 1798
- *Lolliguncola mercatoris* Adam, 1941

Ommastrephidae
- *Illex coindetii* (Verany, 1837)
- *Todaropsis eblanae* (Ball, 1841)

Sepiidae
- *Sepia officinalis* Linnaeus, 1758

Decapod crustaceans

Solenoceridae
- *Solenocera africana* Stebbing, 1917

Aristeidae
- *Aristeus varidens* Holthuis, 1952
- *Plesiopenaeus edwardsianus* (Johnson, 1867)

Penaeidae
- *Parapenaeopsis atlantica* Balss, 1914
- *Parapenaeus longirostris* (Lucas, 1846)
- *Penaeus notialis* Pérez-Farfante, 1967

Nematocarcinidae
- *Nematocarcinus africanus* Crosnier & Forest, 1973

Palaemonidae
- *Nematopalaemon hastatus* (Aurivillius, 1898)

Geryonidae
- *Geryon maritae* Manning and Holthuis, 1981

Sharks

Squalidae
- *Centrophorus granulosus* (Bloch & Schneider, 1801)
- *Etmopterus* spp.

Squatinidae
- *Squatina oculata* Bonaparte, 1840

Triakidae
- *Mustelus mustelus* (Linnaeus, 1758)

Batoid fishes

Rajidae
- *Raja miraletus* Linnaeus, 1758

Bony fishes

Albulidae
- *Albula vulpes* (Linnaeus, 1758)
- *Pterothrissus belloci* Cadenat, 1937

Clupeidae
- *Ilisha africana* (Bloch, 1795)
- *Sardinella aurita* Valenciennes, 1847
- *Sardinella maderensis* (Lowe, 1839)
- *Sardinops ocellata* (Pappé, 1853)

Engraulididae
- *Engraulis encrasicolus* (Linnaeus, 1758)

Ariidae
- *Arius parkii* Günther, 1864

Myctophidae

Synodontidae
- *Saurida brasiliensis* Norman, 1935

Chlorophthalmidae
- *Chlorophthalmus atlanticus* Poll, 1953

Ogcocephalidae
- *Dibranchus atlanticus* Peters, 1875

Ophidiidae
- *Brotula barbata* (Bloch) in Bloch & Schneider, 1801
- *Monomitopus* spp.

Merlucciidae
- *Merluccius capensis* Castelnau, 1861
- *Merluccius paradoxus* Franca, 1960
- *Merluccius polli* Cadenat, 1950

Moridae
- *Laemonema* spp.
- *Physiculus* spp.

Macrouridae
- *Coelorinchus coelorhincus* (Risso, 1810)
- *Hymenocephalus italicus* Giglioli, 1884
- *Malacocephalus laevis* (Lowe, 1843)
- *Malacocephalus occidentalis* Goode & Bean, 1885
- *Nezumia aequalis* (Günther, 1878)

Zeidae
- *Zenopsis conchifer* (Lowe, 1852)
- *Zeus faber* Linnaeus, 1758

Fistulariidae
- *Fistularia petimba* (Lacepède, 1803)

Scorpaenidae
- *Pontinus* spp.

Triglidae
- *Chelidonichthys capensis* (Cuvier in Cuv. & Val.,1829)
- *Chelidonichthys gabonensis* (Poll & Roux, 1955)
- *Chelidonichthys lastoviza* (Bonnaterre, 1788)
- *Lepidotrigla cadmani* Regan, 1915
- *Lepidotrigla carolae* Richards, 1968
- *Trigla lyra* Linnaeus, 1758

Peristediidae
- *Peristedion cataphractum* Linnaeus, 1758

Serranidae
- *Epinephelus aeneus* (Geoffroy Saint-Hilaire, 1809)
- *Epinephelus alexandrinus* (Valenciennes, 1828)

Antiidae
- *Anthias anthias* (Linnaeus, 1758)

Acropomatidae
- *Synagrops microlepis* Norman, 1935

Branchiostegidae
- *Branchiostegus semifasciatus* (Norman, 1931)

Carangidae
- *Chloroscombrus chrysurus* (Linnaeus, 1766)
- *Decapterus punctatus* (Cuvier, 1829)
- *Decapterus rhonchus* (Geoffroy Saint-Hilaire, 1817)
- *Selar crumenophthalmus* (Bloch, 1793)
- *Selene dorsalis* (Gill, 1862)
- *Trachurus capensis* Castelnau, 1861
- *Trachurus trecae* Cadenat, 1949

Centracanthidae
- *Spicara alta* (Osorio, 1917)
- *Spicara nigricauda* (Norman, 1931)

Haemulidae
- *Brachydeuterus auritus* (Valenciennes, 1831)
- *Pomadasys incisus* (Bowdich, 1825)
- *Pomadasys jubelini* (Cuvier, 1830)
- *Pomadasys peroteti* (Cuvier, 1830)

Table 1 (continued)

Sparidae	Polynemidae
Boops boops (Linnaeus, 1758)	*Galeoides decadactylus* (Bloch, 1795)
Dentex angolensis Poll & Maul, 1953	Uranoscopidae
Dentex barnardi (Cadenat, 1970)	*Uranoscopus albesca* Regan, 1915
Dentex canariensis Steindachner, 1881	Scombridae
Dentex congoensis Poll, 1954	*Scomberomorus tritor* (Cuvier, 1831)
Dentex gibbosus (Rafinesque, 1810)	Trichiuridae
Dentex macrophthalmus (Bloch, 1791)	*Benthodesmus tenuis* (Günther, 1877)
Lithognathus mormyrus (Linnaeus, 1758)	*Lepidopus caudatus* (Euphrasen, 1788)
Pagellus bellottii Steindachner, 1882	*Trichiurus lepturus* Linnaeus, 1758
Sparus auriga (Valenciennes, 1843)	Stromateidae
Sparus caeruleostictus (Valenciennes, 1830)	*Stromateus fiatola* Linnaeus, 1758
Sparus pagrus africanus Akazaki, 1962	Ariommidae
Sciaenidae	*Ariomma bondi* Fowler, 1930
Argyrosomus hololepidotus (Lacepède, 1802)	Citharidae
Atractoscion aequidens (Cuvier, 1830)	*Citharus linguatula* (Linnaeus, 1758)
Pentheroscion mbizi (Poll, 1950)	Bothidae
Pseudotolithus senegalensis (Valenciennes, 1833)	*Arnoglossus imperialis* (Rafinesque, 1810)
Pseudotolithus typus Bleeker, 1863	Soleidae
Pteroscion peli (Bleeker, 1863)	*Dicologoglossa cuneata* (de la Pylaie Moreau, 1881)
Umbrina canariensis Valenciennes, 1843	Tetraodontidae
Mullidae	*Lagocephalus laevigatus* (Linnaeus, 1766)
Pseudupeneus prayensis (Cuvier, 1829)	Balistidae
Sphyraenidae	*Balistes capriscus* Gmelin, 1788
Sphyraena guachancho Cuvier, 1829	
Sphyraena sphyraena (Linnaeus, 1758)	

important. Table 2 shows the correlation of these with the environmental variables and with latitude. Depth, temperature and oxygen are strongly correlated with DCA Axis 1 ($r = 0.90$, -0.97 and -0.89 respectively). Axis 2 is significantly correlated only with latitude ($r = -0.75$, $p < 0.05$).

Fig. 7 shows the results from a further analysis with DCA on the deeper shelf assemblages (Groups 4 to 6). The eigenvalues are 0.53, 0.34, 0.23 and 0.18 for the first DCA axes, respectively. Table 3 shows the correlation of Axes 1 and 2 with the environmental variables and with latitude. Axis 1 is highly correlated with latitude ($r = -0.86$), but significant correlation ($p < 0.05$) is also found with temperature, salinity and oxygen. Axis 2 shows significant correlation with depth.

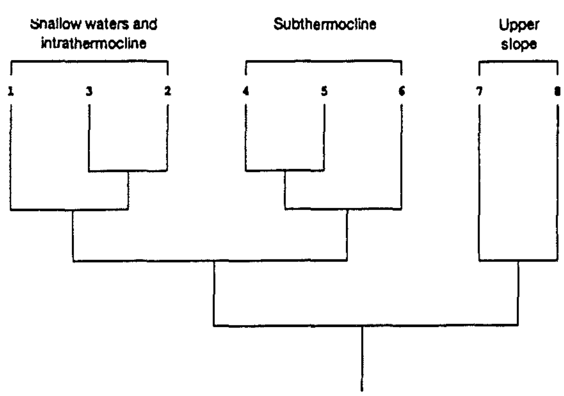

Fig. 5. Dendrogram of Station Groups 1 to 8 derived from classification with the program TWINSPAN (Hill 1979). See 'Results' for description of each station group

Table 4 presents results from the 'pseudo-*F*' analysis and Table 5 the weight, numbers and frequency of the main species in each group.

Fig. 8 shows the position of the stations after having been assigned to each group. The plot of mean biomass densities by depth stratum for northern, central and southern Angola is presented in Fig. 9 while Table 6 gives the number of stations sampled by depth stratum.

Below are descriptions of the 8 groups identified.

Group 1 – Shallow water assemblage, from northern Angola to Benguela

The 15 stations included in this group have an average depth of 24 m, temperature 23 °C and oxygen levels usually high, 3.7 ml l^{-1} on average. The species caught here are those typically found in the warm and turbid waters above the thermocline, often associated with river mouths, able to tolerate low salinities and on soft, mud bottoms. The 'pseudo-*F*' table (Table 4) shows the species characteristic of this group. Among these are the drum *Pteroscion peli*, the croaker *Pseudotolithus senegalensis*, the butterfish *Stromateus fiatola*, the African threadfin *Galeoides decadactylus* and the

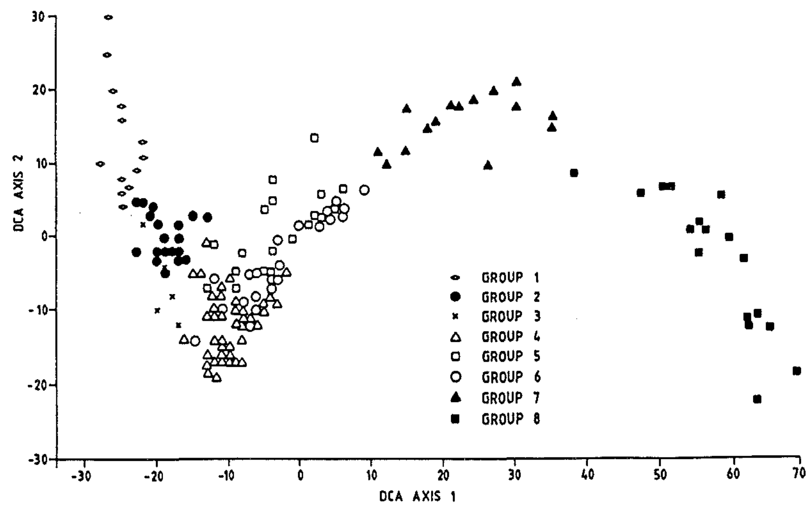

Fig. 6. Detrended correspondence analysis of bottom-trawl stations in the February-March survey 1989 (SD units × 10). Corresponding TWIA (Two-Way Indicator species analysis) Groups 1 to 8 can be recognized by the different symbols

Table 2. Pearson product-moment correlation coefficient between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations. Values with asterisk indicate significant correlation ($p < 0.05$, df 161)

Variable	Axis 1	Axis 2
Depth	0.90*	−0.04
Temperature	−0.97*	0.09
Salininity	−0.48*	−0.08
Oxygen	−0.89*	0.18
Latitude	−0.06	−0.75*

Table 3. Pearson product-moment correlation coefficient between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for the subthermocline shelf stations. Values with asterisk indicate significant correlation ($p < 0.05$, df 82)

Variable	Axis 1	Axis 2
Depth	0.14	0.55*
Temperature	−0.49*	−0.32
Salininity	−0.50*	−0.20
Oxygen	−0.65*	−0.12
Latitude	−0.86*	−0.34

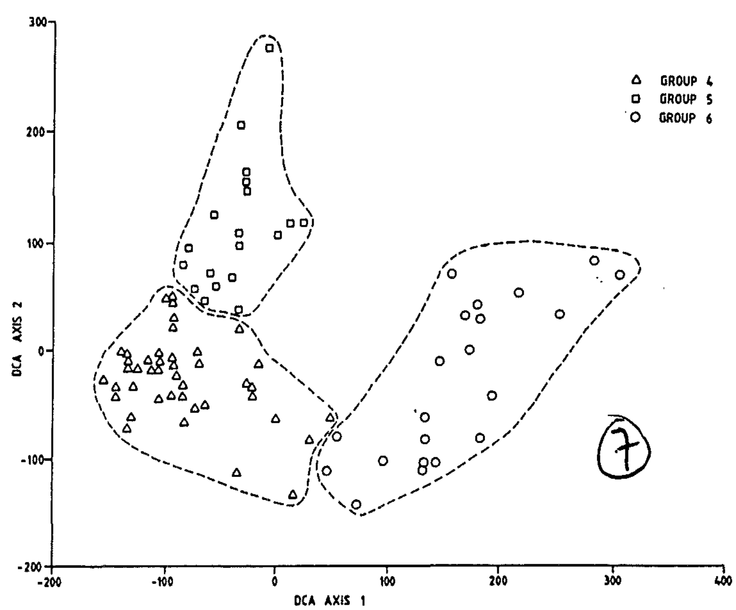

Fig. 7. Detrended correspondence analysis of intermediate-shelf bottom-trawl stations February-March survey 1989 (SD units × 10). Corresponding TWIA (Two-Way Indicator species Analysis) 4 to 6 can be recognized by the different symbols

Table 4. Two-way table based on classification and ordination analyses, showing conforming species groups within site groups. Pseudo-*F* (P-*F*) values preceded by an asterisk indicate conformity at a significance of P = 0.05 or better. The average biomass value (kg) of a species within each group, converted to ln (x+1), is preceded by an asterisk whenever the 95 % confidence interval for the mean is not overlapping. (***) indicates that a species is found only in 1 group. Mean values of environmental variables are also shown for each group, with standard deviations (in parentheses). Only the most important species are included

	Site groups								
Environmental variables	1	2	3	4	5	6	7	8	
Depth (m)	24 (14)	47 (16)	37 (12)	87 (17)	112 (41)	88 (36)	256 (56)	461 (91)	
Temperature (°C)	23 (2)	21 (2)	21 (2)	18 (1)	17 (2)	16 (1)	2 (1)	8 (1)	
Salinity (‰)	35.3 (.5)	35.7 (.0)	35.7 (.3)	35.7 (.1)	35.7 (.1)	35.3 (.1)	35.3 (.2)	34.8 (.9)	
Oxygen (ml l^{-1})	3.7 (.6)	3.0 (.6)	3.1 (.5)	2.4 (.5)	2.2 (.7)	1.8 (.4)	1.2 (.2)	1.0 (0)	
Species									P-*F*
Penaeus notialis	*0.414	0.030		0.011					*7.2
Sardinella maderensis	*0.689								***
Stromateus fiatola	*1.008	0.175		0.066					*8.1
Pseudotolithus senegalensis	*2.204	0.051							*28.0
Ilisha africana	*1.653								***
Pteroscion peli	*1.338	0.069		0.041	0.270				*9.9
Selene dorsalis	*2.836	1.617	0.323	0.109	0.220				*28.0
Galeoides decadactylus	*1.996	0.450	0.117						*20.2
Sphyraena guachancho	*2.301	1.215	0.974	0.004	0.188				*19.4
Chloroscombrus chrysurus	*2.826	0.472		0.049					*44.9
Brachydeuterus auritus	*3.452	2.671	0.932	1.116	1.302				*10.8
Trichiurus lepturus	2.174	2.851	0.204	0.911	2.619	0.124	1.341		*10.9
Sparus caeruleostictus	0.070	0.217	*1.166	0.153					*6.4
Balistes capriscus	0.593	1.734		0.066		0.030			*10.9
Pomadasys jubelini	0.978	0.976	0.525	0.047					*5.8
Lagocephalus laevigatus	0.283	0.684	0.435	0.076					*7.3
Pomadasys incisus	0.414	1.087	0.937	0.119					*3.9
Sphyraena sphyraena	0.611	0.449	0.758	0.091	0.031				*3.3
Brotula barbata		0.101		0.160	*0.643	0.084	0.178		*2.7
Alloteuthis africanus		0.507		0.554		0.078			*3.0
Lithognathus mormyrus	0.222	0.738				0.565			*3.8
Epinephelus aeneus		0.498	*1.878	0.710	0.140				*5.4
Dentex canariensis		0.433		0.104		0.066			*2.4
Fistularia petimba		0.326	0.221	0.464		0.067			*4.0
Dentex barnardi		0.268	0.614	0.701	0.274	0.158			*2.9
Pagellus bellottii		0.913	2.815	2.326	0.424	0.528			*19.7
Sparus pagrus africanus		0.052	0.213	0.374		0.079			*2.0
Saurida brasiliensis		0.514		0.269	0.972		0.199		*5.9
Dentex angolensis		0.099		1.660	1.407	0.257	0.348		*13.9
Lepidotrigla cadmani				0.243	0.414	0.169			*2.0
Dentex gibbosus		0.042		*0.638	0.073	0.182			*3.2
Penteroscion mbizi				0.060	*0.852	0.024			*5.9
Boops boops		0.017		*0.592	0.196				*4.0
Dentex congoensis				*1.383	0.189				*8.1
Lepidotrigla carolae				0.467					***
Trachurus trecae	0.206	1.015		2.862	2.362	1.829			*12.6
Umbrina canariensis		0.137	0.204	0.840	0.913	0.559			*2.9
Chelidonichthys gabonensis		0.037	0.196	0.557	0.065	0.381			*3.6
Trachurus capensis						*2.858			***
Atractoscion aequidens		0.063		0.264		*1.449			*7.6
Lepidopus caudatus						*0.550			***
Loligo vulgaris		0.056				*1.350	0.200		*15.4
Dentex macrophthalmus			0.172	1.125	0.364	*4.112	0.935		*15.6
Dicologoglossa cuneata					0.041	*0.529	0.042		*7.1
Zeus faber				0.448	0.086	*1.102	0.170		*7.9
Trigla lyra						0.412	0.164		*3.4
Merluccius capensis						0.336	0.202		*2.4
Illex coindetii				0.683	1.322	0.069	1.565	1.051	*8.0
Synagrops microlepis				0.129	2.532	0.667	*5.297	0.430	*37.1
Parapenaeus longirostris					0.650	0.014	*2.207	0.034	*35.5
Pterothrissus belloci					1.715	1.077	2.179	0.677	*12.0
Solenocera africana				0.007	0.020	0.043	0.169	0.197	*2.9
Chlorophthalmus atlanticus							*3.600	0.318	*46.1
Malacocephalus occiddentalis							0.510	0.626	*6.9
Merluccius polli					0.185	0.408	3.564	3.897	*71.3
Dibranchus atlanticus							0.101	0.762	*12.7
Aristeus varidens							0.065	*1.242	*34.2
Nematocarcinus africanus							0.143	*3.296	*46.4
Benthodesmus spp.							0.009	*1.284	*20.9
Laemonema spp.							0.752	*1.915	*23.5
Plesiopenaeus edwardsianus								*0.361	***
Centrophorus granulosus								*1.263	***
Monomitopus spp.								*0.740	***

Table 5. Total weight (W; kg), numbers (N) and frequency (F; no. of stations where found in respective group) of main species from Station Groups 1 to 8

Species	W	(%)	N	(%)	F
Group 1 (15 stations)					
Brachydeuterus auritus	2214	(21)	86498	(14)	13
Selene dorsalis	1602	(16)	12700	(2)	15
Trichiurus lepturus	1193	(12)	9138	(2)	10
Sphyraena guachancho	719	(7)	1364	(0)	11
Pseudotolithus senegalensis	682	(7)	2462	(0)	9
Chloroscombrus chrysurus	647	(6)	11254	(2)	13
Ilisha africana	587	(6)	31704	(5)	9
Galeoides decadactylus	567	(5)	13278	(2)	10
Sphyraena sphyraena	416	(4)	14596	(2)	4
Engraulis encrasicholus	270	(3)	125563	(21)	3
Pteroscion peli	149	(1)	3622	(1)	7
Balistes capriscus	108	(1)	503	(0)	3
Pomadasys jubelini	100	(1)	248	(0)	5
Nematopalaemon hastatus	82	(1)	277440	(46)	1
Stromateus fiatola	75	(1)	201	(0)	7
Sardinella maderensis	22	(0)	436	(0)	11
Penaeus notialis	15	(0)	322	(0)	5
Total	9448	(92)	591329	(97)	
Total (all species)	10317		601273		
Group 2 (21 stations)					
Brachydeuterus auritus	3779	(43)	120227	(60)	15
Trichiurus lepturus	1922	(23)	36930	(18)	17
Pomadasys jubelini	805	(9)	1568	(1)	7
Balistes capriscus	673	(8)	3161	(2)	11
Pomadasys incisus	376	(4)	2084	(1)	7
Selene dorsalis	206	(2)	684	(0)	15
Sphyraena guachancho	125	(1)	249	(0)	12
Trachurus trecae	123	(1)	16166	(8)	12
Pagellus bellottii	106	(1)	862	(0)	12
Lithognathus mormyrus	102	(1)	424	(0)	7
Epinephelus aeneus	69	(1)	14	(0)	4
Alloteuthis africana	41	(0)	9412	(5)	10
Lagocephalus laevigatus	37	(0)	62	(0)	11
Dentex canariensis	33	(0)	100	(0)	5
Galeoides decadactylus	31	(0)	65	(0)	7
Sphyraena sphyraena	31	(0)	94	(0)	7
Chloroscombrus chrysurus	21	(0)	1528	(1)	11
Fistularia petimba	21	(0)	67	(0)	4
Dentex barnardi	12	(0)	85	(0)	5
Total	8513	(96)	193782	(96)	
Total (all species)	8814		200087		
Group 3 (5 stations)					
Pagellus bellottii	207	(38)	1185	(18)	5
Pomadasys incisus	105	(19)	450	(7)	1
Epinephelus aeneus	47	(9)	20	(0)	4
Brachydeuterus auritus	26	(5)	4606	(68)	2
Dentex barnardi	21	(4)	46	(1)	1
Sphyraena guachancho	19	(4)	45	(1)	3
Sparus caeruleostictus	16	(3)	27	(0)	4
Fistularia petimba	11	(2)	14	(0)	2
Sphyraena sphyraena	9	(2)	41	(1)	3
Pomadasys jubelini	6	(1)	6	(0)	2
Lagocephalus laevigatus	4	(1)	14	(0)	2
Selene dorsalis	3	(0)	14	(0)	2
Trichiurus lepturus	2	(0)	22	(0)	1
Chelidonichthys gabonensis	1	(0)	6	(0)	2
Total	477	(88)	6496	(96)	
Total (all species)	540		6750		
Group 4 (45 stations)					
Trachurus trecae	4514	(28)	180417	(38)	37
Dentex macrophthalmus	2762	(17)	14529	(3)	12
Pagellus bellottii	1395	(9)	16979	(4)	40
Dentex congoensis	1068	(7)	29943	(6)	21
Brachydeuterus auritus	835	(5)	36432	(8)	16
Umbrina cariensis	751	(5)	2506	(0)	15
Trichiurus lepturus	529	(3)	2236	(0)	19
Dentex angolensis	442	(3)	5543	(1)	34
Epinephelus aeneus	277	(2)	66	(0)	12
Boops boops	228	(1)	12594	(3)	21
Dentex barnardi	217	(1)	563	(0)	16
Alloteuthis africana	197	(1)	99422	(21)	12
Dentex gibbosus	186	(1)	201	(0)	11
Saurida brasiliensis	163	(1)	35566	(8)	21
Lepidotrigla carolae	104	(1)	4854	(1)	14
Illex coindetii	99	(1)	4788	(1)	23
Chelidonichthys gabonensis	85	(0)	542	(0)	18
Sepia officinalis	80	(0)	258	(0)	8
Fistularia petimba	54	(0)	152	(0)	19
Zeus faber	50	(0)	220	(0)	17
Lepidotrigla cadmani	31	(0)	477	(0)	11
Sparus pagrus africanus	25	(0)	43	(0)	4
Total	14036	(89)	448331	(95)	
Total (all species)	15817		470430		
Group 5 (19 stations)					
Synagrops microlepis	4502	(52)	385464	(82)	11
Trichiurus lepturus	826	(9)	7436	(2)	17
Trachurus trecae	813	(9)	22313	(5)	16
Brachydeuterus auritus	532	(6)	7500	(2)	7
Pterothrissus belloci	323	(4)	3148	(1)	15
Penteroscion mbizi	163	(2)	2334	(0)	7
Illex coindetii	148	(2)	3169	(1)	13
Dentex angolensis	107	(1)	663	(0)	14
Umbrina canariensis	102	(1)	397	(0)	8
Brotula barbata	95	(1)	123	(0)	8
Saurida brasiliensis	73	(1)	9653	(2)	13
Parapenaeus longirostris	50	(1)	12716	(3)	14
Dentex macrophthalmus	33	(0)	288	(0)	3
Dentex barnardi	27	(0)	46	(0)	4
Lepidotrigla cadmani	21	(0)	184	(0)	6
Pagellus bellottii	18	(0)	100	(0)	7
Total	7833	(90)	455534	(97)	
Total (all species)	8671		470875		
Group 6 (24 stations)					
Dentex macrophthalmus	6853	(39)	286791	(46)	20
Trachurus capensis	5612	(32)	132867	(21)	21
Trachurus trecae	1156	(7)	116275	(19)	18
Atractoscion aequidens	468	(3)	337	(0)	12
Lepidopus caudatus	438	(2)	4902	(1)	3
Spicara alta	424	(2)	13648	(2)	3
Pterothrissus belloci	420	(2)	4809	(1)	9
Synagrops microlepis	271	(1)	23737	(4)	5
Loligo vulgaris	201	(1)	18444	(3)	15
Umbrina canariensis	156	(1)	974	(0)	6
Lithognathus mormyrus	147	(1)	502	(0)	6
Zeus faber	142	(1)	302	(0)	13
Pagellus bellottii	68	(0)	540	(0)	8
Chelidonichthys gabonensis	65	(0)	616	(0)	4
Merluccius polli	44	(0)	1084	(0)	6
Trigla lyra	39	(0)	115	(0)	5
Dicologoglossa cuneata	35	(0)	522	(0)	10
Total	16539	(94)	606465	(97)	
Total (all species)	17593		621992		
Group 7 (15 stations)					
Synagrops microlepis	6175	(52)	364356	(66)	15
Chlorophthalmus atlanticus	2646	(22)	72486	(13)	12
Merluccius polli	1212	(10)	14584	(3)	14
Dentex macrophthalmus	367	(3)	2350	(0)	5
Illex coindetii	256	(2)	3835	(1)	10
Parapenaeus longirostris	254	(2)	53205	(10)	14
Pterothrissus belloci	233	(2)	1637	(0)	12
Trichiurus lepturus	189	(2)	904	(0)	8
Laemonema spp.	84	(1)	1303	(0)	4
Malacocephalus occidentalis	37	(0)	341	(0)	3
Total	11453	(96)	515001	(93)	
Total (all species)	11904		552605		
Group 8 (17 stations)					
Merluccius polli	2459	(39)	10224	(2)	16
Nematocarcinus africanus	2009	(32)	391466	(86)	14
Laemonema spp.	207	(3)	3369	(1)	12
Centrophorus granulosus	150	(2)	38	(0)	7
Illex coindetii	116	(2)	740	(0)	8
Benthodesmus tenuis	114	(2)	3836	(1)	11
Pterothrissus belloci	107	(2)	710	(0)	4
Aristeus varidens	67	(1)	3708	(1)	13
Dibranchus atlanticus	44	(1)	3144	(1)	13
Malacocephalus occidentalis	30	(1)	416	(0)	7
Plesiopenaeus edwardsianus	20	(0)	167	(0)	10
Synagrops microlepis	19	(0)	538	(0)	7
Chlorophthalmus atlanticus	12	(0)	284	(0)	6
Solenocera africana	6	(0)	621	(0)	4
Total	5360	(85)	419261	(93)	
Total (all species)	6308		453391		

pink shrimp *Penaeus notialis*. Pelagic species usually associated with the above demersal fauna are the flat sardinella *Sardinella maderensis*, the West African ilisha *Ilisha africana* and the Atlantic bumper *Chloroscombrus chrysurus*. The highest biomass consists, however, of typically eurybathic and eurythermic species like the hairtail *Trichiurus lepturus* and the big-eye grunt *Brachydeuterus auritus* and 2 species also found in slightly deeper and cooler waters, like the guachanche barracuda *Sphyraena guachancho* and the African lookdown *Selene dorsalis*. These 4 species are the most abundant and make up 55 % of the total catches from these stations (Table 5). A very large catch (40 000 kg) of big-eye grunt between Pta. do Morro and Cabeça da Baleia was not included in the analysis because it is considered to be exceptional. The presence of this large concentration is possibly to be related to spawning activity. The shrimp *Nematopalaemon hastatus*, accounting for 46 % of the catches in this group in numerical abundance, is a typically estuarine species known to occur throughout the Angolan coast. However, it was caught only once during this survey most probably because of its very shallow depth-distribution range and estuarine habitat preferences.

This assemblage largely coincides with the 'peuplement littoral' described by Durand (1967) for Congo and by Domain (1980) for the continental shelf off Senegal and Mauritania, as well as the 'estuarine and offshore sciaenid subcommunities' of the Gulf of Guinea described by Longhurst (1965) and Fager & Longhurst (1968), of typically tropical nature. Its distribution along the Angolan coast broadly coincides with the presence of the Equatorial Water. This assemblage seems to be stable since the species composition is essentially the same as that described by those authors, despite the fishing activities of the last 20 yr.

Group 2 – Coastal species, mainly in the thermocline area, from Luanda to Benguela

This group of 21 stations was at an average depth of 47 m, with temperature and oxygen values below the values found in shallow waters (about 21 °C and 3 ml l^{-1} respectively). Several bottom samples showed that clay and silt substrate dominate this area, sometimes mixed with fine sand (Figs. 2 & 3). Coarse sand was found just north of Cabeça da Baleia, at 40 and 50 m depth. The eurybathic *Trichiurus lepturus* and *Brachydeuterus auritus* dominate most stations both in weight and numbers. Most probably, because of their ability to live at different levels of the water column, they can most easily occupy the thermocline area

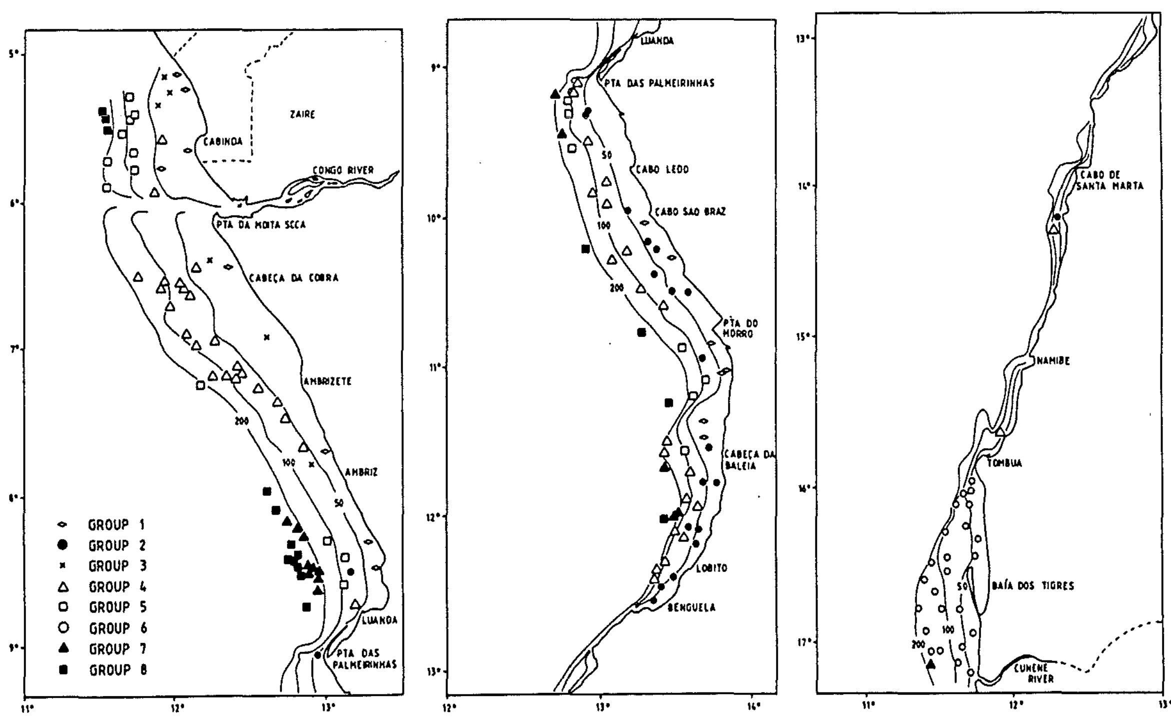

Fig. 8. Position of stations after being assigned to the different groups

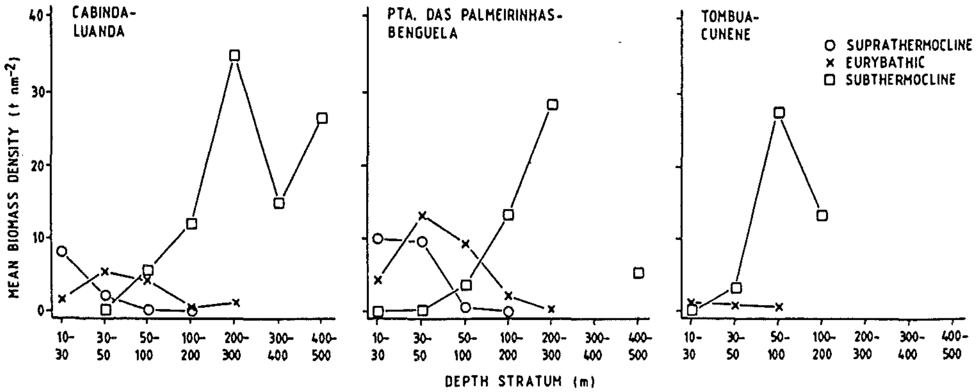

Fig. 9. Plot of mean biomass density by depth stratum from bottom trawl catches for northern, central and southern Angola (February and March 1989). The pelagic species *Ilisha africana*, *Chlorocombrus chrysurus* and *Selene dorsalis* are also included in the analysis (depth strata 10–30 and 30–50 m). For definition of species categories see 'Discussion – Biomass'

Table 6. Number of stations sampled by depth stratum for northern Angola (Cabinda-Luanda), central Angola (Pta. das Palmeirinhas-Benguela) and southern Angola (Tombua-Cunene)

Location	Depth stratum (m)						
	10–30	30–50	50–100	100–200	200–300	300–400	400–500
Cabinda-Luanda	8	7	25	8	9	4	6
Pta.Palm.-Benguela	9	10	21	12	4	0	3
Tombua-Cunene	2	6	9	9	0	0	0

characterized by a rapid change of the physical water conditions. The triggerfish *Balistes capriscus* is also a eurybathic species and an important element of this group. *Selene dorsalis* and *Sphyraena guachancho*, with a shallower depth distribution, and the red pandora *Pagellus bellottii* and the Cunene horse mackerel *Trachurus trecae*, with a deeper distribution range, were consistently caught at these stations. The grunt *Pomadasys incisus* and the striped seabream *Lithognathus mormyrus* gave relatively high catches in the Lobito-Benguela area.

Group 3 – Coastal species, in the thermocline area, in the northern part of the area, on sandy/hard bottoms

It is a group of 5 stations with an average depth of about 37 m, temperature of 21 °C, oxygen concentration of 3.1 ml l^{-1} and salinity 35.7 ‰, found off and north of Cabinda and south of the Congo River mouth to about Ambriz. This group is distinct from the other shallow water stations, because of the presence of the bluespotted seabream *Sparus caeruleostictus* and the white grouper *Epinephelus aeneus* while all the species of Group 1 are present in small quantities or absent. *Brachydeuterus auritus* and *Trichiurus lepturus* are also present in very small quantities. *Pagellus bellottii* was also consistently caught at these stations. This group also seems to belong to the tropical regime and is also found in the Gulf of Guinea and described by Longhurst (1968) as an assemblage found at the bottom of the thermocline, mainly on hard bottoms, where the species that usually dominate the thermocline area are replaced by some members of the deeper sparid assemblage, probably because of the nature of the bottom.

Four bottom samples taken in this area showed the presence of fine and coarse sand. Also, the echograms showed the presence of rough bottoms and rocky outcrops in this area. This type of assemblage is most probably an important element of the Angola fish fauna but is poorly represented in our data because of the difficulty in using bottom trawl on rocky grounds.

The following groups include species of the subthermocline assemblages of the continental shelf (50 to 150–200 m). Two major groups can be identified: an assemblage consisting, among others, of several species of Sparidae, with preference for sandy, fine sand to muddy bottoms and an assemblage found on the shelf between Tombua and Cunene, and largely coinciding with the Angola-Benguela frontal system. The first group includes a subgroup with species with a clear preference for soft bottoms. Only 1 species, the Cunene horse mackerel *Trachurus trecae* is abundant in all of the above groups. This species is described in the literature as shoaling, usually close to the bottom but sometimes pelagic and close to the surface. Because of its consistent occurrence in the demersal trawl it is included in this analysis. However, it is not clear whether, and in what way, the massive presence of the species on the bottom, especially during daytime, affects the more typically 'demersal' assemblages and whether it is trophically related.

Group 4 – Subthermocline sparid assemblage, from northern Angola to Benguela

This group includes 45 stations at an average depth of about 87 m, temperature of 18 °C, salinity 35.7 ‰, oxygen concentration 2.4 ml l^{-1}. The grab samples taken in these areas show that the bottom is mainly consisted of sand, varying from coarse to fine. Several seabream species (family Sparidae) dominate this assemblage that broadly coincides with Longhurst's 'subthermocline sparid subcommunity' (1965) of the Gulf of Guinea, also described for Congo by Durand (1967) and by Fontana (1981). The semi-pelagic *Trachurus trecae* dominates the catches both in biomass and numbers (28 and 38 %, respectively; Table 5) and was present in 80 % of the stations. *Pagellus bellottii* and the Angola dentex *Dentex angolensis* also display a high frequency of occurrence but they represent only 9 and 3 % of the catches respectively. The Congo dentex *D. congoensis*, the bogue *Boops boops*, the gurnards *Lepidotrigla carolae* and *Chelidonichthys gabonensis* are distributed mostly north of 9° S while the pink and large-eye dentex *D. gibbosus* and *D. macrophthalmus* in the south. It should be noted that *D. congoensis* is a typical tropical representative of the genus while *D. macrophthalmus* prefers temperate waters and has a typical antitropical distribution. Also, the latter is often observed in mid-waters which probably makes it more adapted to avoiding cold and low-oxygen, upwelled waters invading the shelf bottom. Although caught only in the southern stations, this species represents 17 % of the catches (Table 5). *Dentex barnardi*, another member of this assemblage, is endemic to Angola and Gabon.

Group 5 – Subthermocline assemblage of soft bottoms

Although no samples of the bottom are available for the areas where this type of assemblage is found, its species composition is indicative of the presence of soft bottoms. The group consists of 29 stations north of the Congo River as well as southward, a little deeper than stations of Group 4, depth between 70 and 140 m, average temperature of 17 °C , high salinity (35.7 ‰) and oxygen levels of 2.2 ml l^{-1} were quite distinct in species association as compared to those described under Group 4, at a similar depth range. Fifty-two per cent of the total catches within this group consists of the splitfin *Synagrops microlepis*, a species mainly of the upper slope. *Trichiurus lepturus*, indicative of soft substrate, and *Trachurus trecae* and *Dentex angolensis*, known to occur on various types of bottom, are the other dominating species. The blackmouth croaker *Pentheroscion mbizi* also characterizes the area north of the Congo River, substituted by the splitfin *Synagrops microlepis* in the more southward stations of this group. *P. mbizi* was described by Longhurst (1962) as an important species in the subthermocline sparid community in the Gulf of Guinea, is not part of the most typical sparid community described in Group 4. Other species typifying this group are: the lizardfish *Saurida brasiliensis*, the bearded brotula *Brotula barbata*, the longfin bonefish *Pterothrissus belloci*, the shortfin squid *Illex coindetii* and the deepwater rose shrimp *Parapenaeus longirostris*.

Group 6 – Subthermocline assemblage between Tombua and Cunene

This region is characterized by the lack of a sharp, inshore thermocline because of almost continuous upwelling. The term 'subthermocline' should perhaps be abandoned and used for the northern region, widely influenced by a tropical structure of the water masses. This group includes 24 stations at an average depth of 88 m, temperature of 16 °C, salinity 35.3 ‰ (possibly South Atlantic Central Water) and low oxygen levels (average 1.8 ml l^{-1}), well lower than those found at similar depths in the northern regions of the Angolan coast. Species composition greatly differs from that found in the northern regions, as could be expected from the dramatic changes in the hydrological regime. Dominating species are *Dentex macrophthalmus* (39 % in biomass; Table 5) and the Cape horse mackerel *Trachurus capensis* (32 %) , but other species like *T. trecae*, the African weakfish *Atractoscion aequidens*, the European squid *Loligo vulgaris*, the wedge sole *Dicologoglossa cuneata* and the John dory *Zeus faber* are also important elements of this assemblage. *Pterothrissus belloci* and *Synagrops microlepis* occurred in the deepest stations but considerably shallower than in northern Angola. An interesting feature of a number of species found in this area is that they either have an antitropical distribution, i.e. found on either side of the Equator but with a wide gap in their distribution usually coinciding with the tropical region, or, although found throughout the tropical region, they are most abundant north and south of it where they occur in shallower waters. *Dentex macrophthalmus* is an example of the first category. It is known to occur along the West African coast from the Strait of Gibraltar to Cape Verde and from Congo to Namibia but it is most abundant off Morocco and southern Angola, i.e. in the colder subtropical regimes. *Dicologoglossa cuneata* is very abundant on the Moroccan shelf at intermediate and shallow waters and becomes abundant again in southern Angola. It is known to occur at greater depths (400 m) off Mauritania. It was not reported from the Gulf of Guinea by the Guinean Trawling Surveys (1963/1964). This phenomenon shows the affinity of the above species for colder waters, their appearance on the intermediate shelf made possible by the occurrence of colder upwelled water.

The upper slope was not sampled throughout and stations are available from north of the Congo River, and from about Ambriz to Benguela. Two main groups are identified: from about 200 to 350 m depth and stations deeper than that. The main distinction in species composition between the 2 groups is that in the first there are still a number of shelf species not found in the deeper stations where, on the other hand, more typically slope species appear.

Group 7 – Upper edge of the continental slope

Fifteen stations are included in this group, at an average depth of 256 m, temperature of 12 °C, salinity of 35.3 ‰ and oxygen levels of 1.2 ml l^{-1}. *Synagrops microlepis* makes up 52 % in biomass, 66 % in numbers and is found at all stations of this group. The 2, more typically upper slope dwellers, the Atlantic green-eye *Chlorophthalmus atlanticus* and the Benguela hake *Merluccius polli* are the next most abundant and frequent species while *Pterothrissus belloci, Parapenaeus longirostris* and *Illex coindetii* show a high frequency of occurrence but lower abundance.

Group 8 – Deeper continental slope

Seventeen stations were sampled, with a wide range of depths (most between 350 and 550 m, one station at 750 m). A temperature of 7.9 °C, salinity of 34.8 ‰ and oxygen of 1 ml l^{-1}. Most of the stations were sampled during nighttime, when many of the benthopelagic slope species migrate toward the surface. However, a number of typically slope species appear at these stations: *Merluccius polli*, the dominant species (about 40 % of the biomass), several deep-water shrimp species like the African spider shrimp *Nematocarcinus africanus* (32 % of the catches; Table 5), the scarlet shrimp *Plesiopenaeus edwardsianus* and the striped red shrimp *Aristeus varidens*, the former being the most abundant. Codlings of the genus *Laemonena*, *Benthodesmus thenuis* and members of the family Macrouridae, also typify this slope area. *Centrophorus granulosus* is a large (to 150 cm) deep-water shark of the continental slope. It is known to feed on hake and myctophids.

DISCUSSION

Species assemblages

Depth is often the main gradient along which faunal changes occur when analysing shelf and upper slope assemblages (Fager & Longhurst 1968, McManus 1985, Lleonart & Roel 1984, Roel 1987, Bianchi 1991). The plot of all stations on DCA Axes 1 and 2 (Fig. 6) clearly shows how the station groups are arranged from left to right according to increasing depth, i.e. from the shallow water group to the deepest slope stations. Axis 1 is in fact highly correlated with depth (Table 2, Fig 10). In the present study temperature showed an even greater correlation with DCA Axis 1 (Table 2, Fig. 10) and some of the main groupings of the shelf stations are clearly related to termal stratification (Fig. 5, Table 4). For this reason the terms supra-, intra- and subthermocline are used in this study to designate the major subdivisions of the shelf stations. The importance of the presence of a sharp thermocline in the distribution of demersal fish was already shown for the Sierra Leone shelf and successively for the whole Gulf of Guinea (Longhurst 1958, 1969 respectively). The northern and central Angolan shelves seem to belong to that regime while the southern part, characterized by almost permanent upwelling, diverges from that pattern. However, while in large areas of the Gulf of Guinea this structure is permanent, off Angola the thermocline might be disrupted by the occurrence of seasonal upwelling and differences in species diversity in shallow waters should be expected. There is no clear, strong oxycline but the high correlation between oxygen and DCA Axis 1 probably accounts for the differences in oxygen concentrations found in the shelf stations (Fig 10). The 2 intra-thermocline assemblages (Groups 2 and 3) and the 3 subthermocline shelf assemblages (Groups 4 to 6) overlap strongly along Axis 1 (Fig. 6). Species composition in these groups indicates that bottom type may play an important role in the configuration of these assemblages. A further analysis of the subthermocline shelf stations, between

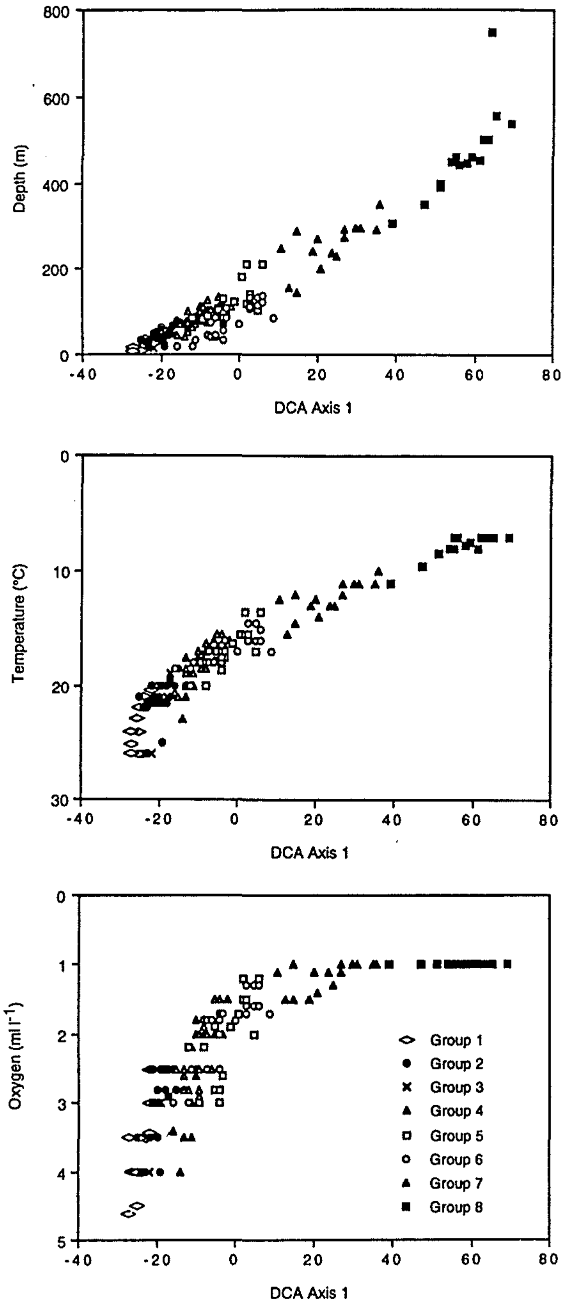

Fig. 10. Plots of DCA Axis 1 against depth, temperature and oxygen

about 70 to 150 m depth, (Fig. 7) shows that latitude is highly correlated with Axis 1 (r = 0.86). Correlation with temperature, salinity and oxygen are weaker, but still significant (Table 3). This reflects the clear separation between the assemblage found in the south, corresponding to the northern limit of the Benguela Current, and the 2 found north of Benguela which more resemble the typical assemblages originating from the Gulf of Guinea. The other 2 subthermocline shelf assemblages are well separated along Axis 2 which shows some correlation with depth only. Their separation, as can be judged from the species composition, appears to be related to bottom type. The above results agree with those of Durand (1980) for the Mauritania-Senegal shelf where in a similar way Axis 1 of Correspondence Analysis was related to depth and thermal stratification and Axis 2 to bottom type.

Biomass

Biomass densities were calculated by depth strata and for 3 major species groups, classified according to their depth-distribution range: suprathermocline species are those never below the lower limit of the thermocline (approximately 50 m depth), including mostly species of the shallow-water Group 1; eurybathic, those species found well above and below the thermocline (from shallow, inshore waters to 100 m depth), typically represented by *Brachydeuterus auritus*, *Trichiurus lepturus*, *Pagellus bellottii* and *Balistes capriscus* and finally the subthermocline species, never found in shallow waters and usually below the thermocline. This classification is obviously valid for the northern and central parts of the Angolan shelf while for the southern part, where the thermocline does not meet the shelf, the classification adopted was only shallow-water and deep water species.

The northern part of the area (from Cabinda to Luanda) shows the interesting feature, already observed in Congo by Fontana (1981) that the eurybathic species reach their highest biomass densities where the thermocline meets the shelf, while this zone clearly represents a point of separation between the suprathermocline and subthermocline groups (Fig. 9). In deeper waters densities decrease and reach a minimum between 50 and 100 m depth. At the shelf-break/upper slope region the highest bottom-trawl catches were obtained consisting mainly of *Synagrops microlepis*. This species is benthopelagic migrating to upper water layers at night. It probably feeds on small mesopelagic fishes as deduced from the mouth anatomy, superior and with conical long teeth. Domain (1980) also reports this species as very abundant at the level of the upper slope off Senegal-Gambia and suggests its potential economic value. In deeper waters, *Merluccius polli* and *Nematocarcinus africanus* are the most abundant species.

The intermediate region, between Pta. das Palmeirinhas to Benguela, shows a similar pattern to the one described above but with higher values of mean biomass densities for both the suprathermocline and eurybathic species. *Brachydeuterus auritus* is also very abundant in shallow waters and to 100 m depth. This species is probably 1 of the most plentiful fishes of shallow and intermediate waters of West Africa, from Senegal to northern and central Angola (Raitt & Sagua 1969). The success of this species might be related to its capability of adapting to different water temperatures. This feature must be important especially in the areas with seasonal upwelling as is the case for northern and Central Angola as well as several coastal areas of the Gulf of Guinea. *Balistes capriscus* has received much attention because of its tremendous increase in biomass in the Gulf of Guinea since the early 1970's, possibly a consequence of overfishing of *Sardinella aurita*, and its sudden decline in biomass in later years. Though basically demersal (a reef-fish genus) this species also moves to mid-waters to feed on plankton. In Angola it was encountered only in the central part of the country, where the ecological conditions are quite similar to those found off Ghana, i.e. strong seasonal upwelling. No such increase in biomass has, however, occurred off Angola. A second and highest peak in biomass densities is found between 200 and 300 m, consisting mainly of *Chlorophthalmus atlanticus* and, to a lesser extent, *Synagrops microlepis* and *Merluccius polli*.

There is a different situation in the area between Tombua and Cunene. The eurybathic species described above are very rare and the shelf is dominated by *Dentex macrophthalmus*. It should be noted that the shelf is very steep in its shallowest part and bottom trawl stations are available from about 70 m depth. Furthermore the shelf edge and upper slope are also very steep and, therefore, no data are available for this region. Biomass densities of the 50 to 100 m depth stratum are highest in this area as compared with the 2 areas above, where this depth stratum coincides with a minimum biomass (Fig. 9).

A comparison of northern and central Angola areas with the region between southern Mexico and Nicaragua (Bianchi 1991), also subject to seasonal upwelling, shows a similar distribution in the demersal biomass, with highest concentrations on the deeper shelf and upper slope areas and a minimum approximately between 50 and 100 m depth. The total biomass densities by depth stratum are much higher in the Eastern Central Pacific. However, little fishing occurs in the intermediate and deep waters of that region while Angolan waters have been subject to high fishing pressure for at least 20 years.

Faunal changes with latitude on the shelf area

The analysis of faunal changes with latitude has necessarily to be performed according to depth strata. A meaningful stratification seems to be: suprathermocline, shallow water assemblages and intermediate shelf assemblages. The upper slope is not included because of lack of adequate sampling especially in the southern part of the area.

As for the suprathermocline species, the tropical type of assemblage follows the inshore, warm equatorial waters which in summertime are transported by a southward flow to Lobito-Benguela and, at times, to Baia dos Tigres. Although some tropical species are found here (e.g. *Sardinella maderensis* and *Pomadasys incisus*) the more typical tropical assemblage is usually not found south of Lobito.

With respect to the intermediate-shelf, subthermocline assemblages, a major faunal change occurs in the southern part of the area. As already mentioned, the species associations found between Tombua and Cunene differ greatly from those found in northern and central Angola and the narrow shelf between Benguela and Tombua is where the major turnover of species occurs. The Angola-Benguela frontal system characterizes the area between Tombua and Cunene and south of Baia dos Tigres upwelling is constant throughout the year. It is therefore not surprising that the fauna typifying this region is different from the one found in the north. Also, the extremely narrow shelf between Benguela and Tombua might function as a physical barrier to the spreading of 'northern' species to the south and vice versa.

Several authors have discussed the position of the zoogeographic boundary separating the tropical Eastern African Region from the temperate South African Region (Briggs 1974) and suggested, on the basis of the distribution of different vertebrate and invertebrate groups, various latitudes ranging from 14° S to 18° 30' S. In particular, Longhurst (1962) discussed the distribution of the demersal fish fauna and concluded that the oceanographic frontal zone at about 14° S formed a very important boundary. The present study confirms the view that the frontal zone constitutes a major faunal boundary. However, it should be emphasized that this boundary is obviously not a stable one and a latitudinal displacement of species should be expected in connection with the seasonal and the possible inter-annual fluctuations of the front.

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Appendix 1. Two-way station by species table resulting from the program TWINSPAN. Values denote categories of abundance: 1: $W < 10$ kg; 2: $10 < W < 100$ kg; 3: $100 < W < 1000$ kg; 4: $1000 < W < 10000$ kg; 5: $W < 10000$ kg. Vertical lines separate groups of stations. Station groups along top margin

supratherm. ←—— intratherm. ——→

	1	3	2
Penaeus notialis	----11-1-11----	-----	-----1-----1---------
Sardinella maderensis	1-11111-111---1	-----	--1--------1---------
Stromateus fiatola	--21-11-111----	-----	1----------------1---
Pseudotolithus senegalensis	--1-22-222123-2	-----	-------------1-------
Ilisha africana	--1-3211332--1-	-----	---------------------
Pteroscion peli	--2-22-2221----	-----	--------------1------
Selene dorsalis	213122122112322	1--1-	-22-11122-122-1111-1-
Galeoides decadactylus	--2-22--1212312	1----	-11--1-------1---121-
Sphyraena guachancho	1-1-212--223312	-121-	1-2-21111--2-12----11
Chloroscombrus chrysurus	2233212-221-221	-----	11--1-1111-----1111--
Trichiurus lepturus	--3322-2211--11	-1---	1-2-2-1122223-2133323
Brachydeuterus auritus	223-2213222-322	---21	---1-2--1212423233321
Scomberomorus tritor	12--1-1---11--2	-11--	-----1-11----1-------
Sparus caeruleostictus	-----1--------1	111-1	1-1----------------1-
Balistes capriscus	-----------221-	-----	2133222---------2221-
Engraulis encrasicholus	------------311	-----	--1-1--11-12-1-11111-
Pomadasys jubelini	--2-2----12--2-	1--1-	-11-----1--321----1--
Decapterus rhonchus	22-------------	1--11	--1--11-1--1---------
Lagocephalus laevigatus	11-------------	--1-1	11-111111-1--1------1
Pomadasys incisus	-----1-----3---	3----	-1---------3----32221
Sphyraena sphyraena	--------1--131-	-1-11	----1---2-11-111-----
Sardinella aurita	1111----------1	---1-	--1--1----1-----1----
Brotula barbata	---------------	-----	---------1----1------
Alloteuthis africanus	---------------	-----	----1-111-1-1212---1-
Epinephelus aeneus	---------------	21-12	------------22---1-2-
Lithognathus mormyrus	------------2--	-----	--1----------1--22211
Dentex canariensis	---------------	-----	----------1-----12-21
Chaetodon hoefleri	---------------	-1---	-1-------1-----------
Fistularia petimba	---------------	-11--	2-1-------1--------1-
Dentex barnardi	---------------	2----	111---1----1---------
Pagellus bellottii	---------------	12123	--1-1-1-1112-21112---
Raja miraletus			
Sparus pagrus africanus	-------11------	---11	---------------1-----
Saurida brasiliensis	---------------	----1	-------------------1-
Citharus linguatula	----1----------	-----	----------1-11-1-----
Dentex angolensis	--------------1	-----	-------------1-------
Lepidotrigla cadmani	---------------	-----	--------------1-----1
Dentex gibbosus	---------------	-----	---------------------
Penteroscion mbizi	---------------	-----	-------------------1-
Squatina oculata	---------------	-----	---------------------
Torpedo torpedo	---------------	-----	---------------------
Boops boops	---------------	-----	1--------------------
Dentex congoensis	---------------	-----	-------------1--1----
Lepidotrigla carolae	---------------	-----	---------------------
Trachurus trecae	---------------	-----	---------------------
Spicara alta	--1----1-----1-	-----	1-111----11-2121-1-1-
Umbrina canariensis	---------------	-----	---------------------
Chelidonichthys gabonensis	---------------	-1---	--1--------1----1----
Sepia officinalis	---------------	-1-1-	--------------------1
Trachinus armatus	---------------	--1-1	---------------------
Trachurus capensis	---------------	-----	----------------1----
Mustelus mustelus	---------------	-----	---------------------
Atractoscion aequidens	---------------	-----	---------------------
Lepidopus caudatus	---------------	-----	----------------1----
Anthias anthias	---------------	-----	---------------------
Loligo vulgaris	---------------	-----	---------------------
Dentex macrophthalmus	---------------	-----	-----------------1---
Dicologoglossa cuneata	---------------	----1	---------------------
Zeus faber	---------------	-----	---------------------
Trigla lyra	---------------	-----	---------------------
Merluccius capensis	---------------	-----	---------------------
Illex coindetii	---------------	-----	---------------------
Synagrops microlepis	---------------	-----	---------------------
Parapenaeus longirostris	---------------	-----	---------------------
Todaropsis eblanae	---------------	-----	---------------------
Pterothrissus belloci	---------------	-----	---------------------
Pontinus spp.	---------------	-----	---------------------
Zenopsis conchifer	---------------	-----	---------------------
Solenocera africana	---------------	-----	---------------------
Chlorophthalmus atlanticus	---------------	-----	---------------------
Myctophidae	---------------	-----	---------------------
Galatheidae	---------------	-----	---------------------
Coelorinchus coelorhin. •	---------------	-----	---------------------
Hymenocephalus spp.	---------------	-----	---------------------
Laemonaema spp.	---------------	-----	---------------------
Peristedion cataphract. •	---------------	-----	---------------------
Malacocephalus occiddentalis	---------------	-----	---------------------
Nezumia aepualis	---------------	-----	---------------------
Merluccius polli	---------------	-----	---------------------
Etmopterus spp.	---------------	-----	---------------------
Dibranchus atlanticus	---------------	-----	---------------------
Physiculus spp.	---------------	-----	---------------------
Polychaelidae	---------------	-----	---------------------
Aristeus varidens	---------------	-----	---------------------
Plesiopenaeus edwards. •	---------------	-----	---------------------
Nematocarcinus africanus	---------------	-----	---------------------
Benthodesmus spp.	---------------	-----	---------------------
Nematocarcinus african. •	---------------	-----	---------------------
Centrophorus granulosus	---------------	-----	---------------------
Monomitopus spp.	---------------	-----	---------------------

subthermocline			slope	
4	5	6	7	8
-----------1-------------------1-------------	-------------1-----	---------------------1--	---------------	-----------------
---	-------------------	------------------------	---------------	-----------------
---------2-----------------------------------	-------------------	------------------------	---------------	-----------------
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---	-------------------	------------------------	---------------	-----------------
---------1-----------------------------------	---------21--------	------------------------	---------------	-----------------
----1------------------------2---------------	--11---------------	------------------------	---------------	-----------------
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-----------------------------------1---------	---2-------------1	------------------------	---------------	-----------------
------1--------------------------------------	-------------------	------------------------	---------------	-----------------
1-2223-221311-----------111--1----111--1-----	223211-222212-12122	----------11--1---------	12321122-------	-----------------
-----222--3-1----32-21-2-11-----2--321-------	3322--2----2-----1	------------------------	---------------	-----------------
---------1-----------------------------------	-------------------	------------------------	---------------	-----------------
------1-----1--------1--------2--------------	-------------------	------------------------	---------------	-----------------
------1-1--1-----------1---------------------	-------------------	---------------------11	---------------	-----------------
------1-1------------------------------------	-------------------	------------------------	---------------	-----------------
---------1-------------------1---------------	-------------------	------------------------	---------------	-----------------
-------------------------1-------------------	-------------------	------------------------	---------------	-----------------
-------1-1-1------------------------1--------	-------------------	------------------------	---------------	-----------------
-----2----2----------------------------------	-------------------	------------------------	---------------	-----------------
--------1-----------------1---1-------------1	--------------1----	------------------------	---------------	-----------------
---------1--------1-11--11--1-1----1-1-1-11--	-1-----------------	------------------------	---------------	-----------------
---1----1------2-------1---------------------	1--121-1---1-1-1---	----------------1---1---	--2------------	-----------------
----2-2211-1-----2---2-21----------------1---1	-1-1---------------	---11-------------------	---------------	-----------------
--------2-1-1-------2-2----1--3----1--2--121-	-------------------2	------------------------	---------------	-----------------
---	-------------------	----11-13------------2-2	---------------	-----------------
-2----1--------------------------------------	-------------------	----1-------------------	---------------	-----------------
--------1-1--1----------1-11--1--------------	-------------------	------------------------	---------------	---------------1-
----21-111-1----------11--1111-11-------11-111-	-------------------	----------------------1--	---------------	-----------------
--21-2------212--1--11-1-1121-2-----------1---	-----11----2-1-----	--2-------------------1--	---------------	-----------------
2-2-221121212-21111112-32122113212-1121222132	-1--11-----1-1--11-	---122112-------------1-1	---------------	-----------------
-----1------1111-1-1---11111-------1----2----	----1------1------1	----12-----1-------1----	---------------	----1------------
-1----2---1--11-1-----------21---------------1-	-------------------	-----1------------------	---------------	-----------------
--------111-1-111-11--11---1111---3-1-11-1--1	--11---122-11112111	------------------------	1---------1----	-----------------
---1--111-1---11-------1-------1--1-1--11----	---11-11---1-1111--	2-----------------------	-------1-------	-----------------
-2221-1------22221-111221112111112222221-1121-	--1-11111-1-1221122	2------------1-1--------	1-2------------	-----------------
---------------1--------1-1--11-1-11-1--12----	-------------1111-11	2-1---------------------	---------------	-----------------
222-----1----12-----212----2--1---------------	1------------------	--1--2------------------	---------------	-----------------
-----------------1------------------1---------	-1--1-------22-121-	---------1--------------	---------------	-----------------
2------------------1---21--11------1-1----11-1	-------------11---1-	------------------------	---------------	-----------------
-----1--1-1--1-1--11----------------------1-----	-----1-----1---1---	------------------------	---------------	-----------------
-----1---1-----11-111-1-1--1-132112-11-12-1--	1-1---1-1----------	------------------------	---------------	-----------------
--------1-----2-1--------123122-321-231212221	------1--2---------	------------------------	---------------	-----------------
---------------1-------1---111-2111-11--211--	-------------------	------------------------	---------------	-----------------
2-321333-21-12322122322321-111-432-221-13231-	322221122--1-331112	12221111311-322---11-2-1	---------------	-----------------
---1-----------1-----------211-1--1------111-	----------1--------	32---2------------------	---------------	-----------------
3322111-1-1---11------1-----2-2----2---------	----2--21--2-2-11-2	2-2--2---1----1----1----	---------------	-----------------
---1------1-1--1-------2-1111-121----1-12111-	----1-------------11-	---1122-----------------	---------------	-----------------
-----2----211----------1--1-1-----------1-----	--11--------1--1--1	----11-2---1---------23-1	---------------	-----------------
---------1----------------------1--------11----	-------------------	---11-----------------11-	---------------	-----------------
---	-------------------	1-2112-232114223343211-1	---------------	-----------------
-----------------------------------2---------	-------------1-11--	---11--12--1---------11--	---------------	-----------------
3---1-----2---------1------------------------	-------------------	323--21--1--1121-22-----	---------------	-----------------
---	-------------------	----------------23-2-----	---------------	-----------------
--11----------1------------------------------	-------------------	----------------31-------	---------------	-----------------
---	-------------------	-2-21-12221---11122--1-2	---2-----------	-----------------
3333233-------122--1--1----------------------	2---1--2-----------	43322313321-233323323---	13----------311	-----------------
---	---------------1-11	-1--111-1--1-----1-12-1-	-------1----1--	-----------------
--2--1-------11111-11--1-111-11---1-1--------	----111------------	-22-12212211-1--2-1-----	1-----------1--	-----------------
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---	-------------------	---------------12-11-----	------------2--	-----------------
--------------111111111211-1111---12-11-1-11--	--211222-22-1111-1-	----------1--1----------	3111-1212--2--1	1--2122--2-21----
---------------1---1--1----------------------	2-2323143422-------	---------2----1--13-2---	333433334333222	11--1-11------11-
---	-1-12111111121111---	--------------------1---	212121221111-11	----1------------
--------1-------1------------------------1-----	---1111-1-------1--	------1------1111111----	1----11---11-1-	------------11---
---	-1-12-1-1221312111	------------1-22212223---	112-11222--2212	----2212---------
-----------------------1---------------------	----2--------------	--------------2-1---1----	------------2-2	-----------------
---------------------------------1-----------	-----11--11-1------	--------------1---2------	11---------111-	-------1---------
----------------1----------------------------	-------1----11-----	-----------------------1----	----111----1-1-	----1111---------
---	-------------------	------------------------	-3-321-23322233	1-1-11------1--1-
---	-------------------	------------------------	----121--1-1-1-	-11-11-----------
---	-------------------	------------------------	----111------11	11---1-------1---
---	-------------------	------------------------	-21-----------1-	---------111-----1
---	-------------------	------------------------	-----------2-11	---1112-2--------
---	-------------------	------------------------	---------2-2-12	-22212222111----1
---------------1-----------------------------	-------------------	------------------------	------11-1---1-	--1-1111---------
---	-------------------	------------------------	-1---------2--2	1--11-11--1-----1
---	-------------------	------------------------	-------11--1---	-1--111-1-----1--
---	---11---1--1-------	-------------11--1112---	212-22232122233	-2222233132322232
---	-------------------	------------------------	----1--------11	--11---2-1---1--1
---	-------------------	------------------------	--------1-11---	111111121--2-111-
--------1------1-----------------------------	-------------1-----	------------------------	---------------	11-111-----------
---	-------------------	------------------------	-------1-------	---1-1--1---11111
---	-------------------	------------------------	---------------1	1121--1-111-11111
---	-------------------	------------------------	---------------	1111----1112--1-1
---	-------------------	------------------------	------------1---	--111211-2-21-1-2
---	-------------------	------------------------	------------1---	13--222221342-223
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PAPER 3

Study of the demersal assemblages of the continental shelf and upper slope of Congo and Gabon, based on the trawl surveys of the R V 'Dr. Fridtjof Nansen'

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ABSTRACT: The structure of the demersal assemblages (fish, crustaceans and cephalopods) of the continental shelf and upper slope of Congo and Gabon (from about 1 to 5°S) was studied based on the trawl survey of the R/V 'Dr. Fridtjof Nansen' in January-February 1989, by means of an ordination technique, Detrended Correspondence Analysis (DCA), implemented by the computer program DECORANA and a classification technique, Two-Way Indicator species Analysis (TWIA), implemented by the computer program TWINSPAN. Major faunal discontinuities were between the shelf and the slope assemblages and, on the shelf, between the suprathermocline and the subthermocline assemblages. Correlation of DCA axes 1 and 2 with the environ mental variables showed in fact that temperature was most highly correlated with DCA Axis 1. The lack of any correlation with Axis 2 indicates that other factors (e.g. bottom type) also play an important role in explaining the various groups. Highest biomass densities (from bottom trawl catches) were found on the deeper shelf off Gabon and in the intermediate shelf off Congo.

INTRODUCTION

This study is one of a series aimed at describing the demersal assemblages of the areas surveyed by the R V 'Dr. Fridtjof Nansen'. The main objective is to detect the general trends in the distribution of the bottom megafauna in relation to the environmental variables. The groups included in the analysis are bony fishes, elasmobranchs, stomatopods, decapod crustaceans and cephalopods.

Several studies of the demersal communities on the continental shelf and upper slope off West Africa are available based on multivariate analysis techniques: Senegal-Gambia (Domain 1972); Mauritania (Domain 1980); Gulf of Guinea (Fager & Longhurst 1968); Namibia (Lleonart & Roel 1983 and Mas-Riera et al. 1990); west coast of South Africa (Roel 1987); Angola (Bianchi in press). Durand (1967) studied the biology of the benthic fishes of the continental shelf of Congo, Fontana (1981) and Cayré & Fontana (1981) described the coastal and the deep-sea demersal stocks of Congo, respectively.

THE STUDY AREA

Bottom topography and structure. The study area (Fig. 1) includes the shelf and upper slope off Gabon and Congo, from about 1 to 5 °S. The shelf slopes gently to about 100 m depth, but it becomes steeper to 200 m depth so that 80% of the shelf area is shallower than 100 m. The upper slope is very steep throughout, except for off southern Congo. Information on bottom type was taken from navigation charts (Anon. 1976). The shelf off Gabon is dominated by sandy, sand-shell and gravel bottoms, but becomes muddy toward the shelf edge and the upper slope. Off Congo, while rocky areas and outcrops are found in the inshore part of the shelf, its intermediate and deeper parts are dominated by muddy, mud-sand bottoms. This might be due to the transport by currents of sediments from the Congo River Estuary.

Hydrography and biological oceanography. Wauthy (1983) has described the general oceanography of the Gulf of Guinea while the survey report by Sætersdal (1989) gives a description of the oceanographic conditions in the area at the time of the survey. The productive systems of the eastern tropical Atlantic between 20 °N and 15 °S were described and compared by Voituriez & Herbland (1982).

The circulation pattern in this area varies seasonally and can be related to the general circulation pattern of the Equatorial Atlantic Ocean, i.e. the westward flowing South Equatorial Current (SEC), forming the northern part of the south Atlantic gyre, and the eastward flowing subsurface South Equatorial Counter Current (SECC). The former originates between about Cape Lopez (Gabon) and 15 °S (Angola). During the austral summer (January-February) there is a general movement in north-west direction (Wauthy, 1983) and low-salinity waters originating from the Congo River can be traced as far north as Cape Lopez. In this period, because of the intensive solar radiation, surface waters reach high temperatures (28 to 30 °C) and a shallow and sharp thermocline is found at about 20-30 m depth in the north, becoming deeper (between 25 and 50 m depth) southward (Sætersdal, 1989). Temperatures of 20 to 18 °C are found at about 50 m depth and at the shelf edge, respectively. The halocline is also very sharp, mainly because of the increased rainfall and the increased runoff from the Congo River (Fig. 2). During the austral winter, the main water movement is westward, because of the reinforcement of the South East Trade winds. Surface temperatures are 3 to 5 °C lower and the thermocline not as sharp. Low-salinity surface waters are now only found in the south (from the Congo River) and in the north (off northern Gabon) originating from the Gulf of Biafra. The raising of the thermocline, cooling of the surface waters and increase of primary production have been interpreted as signs of upwelling.

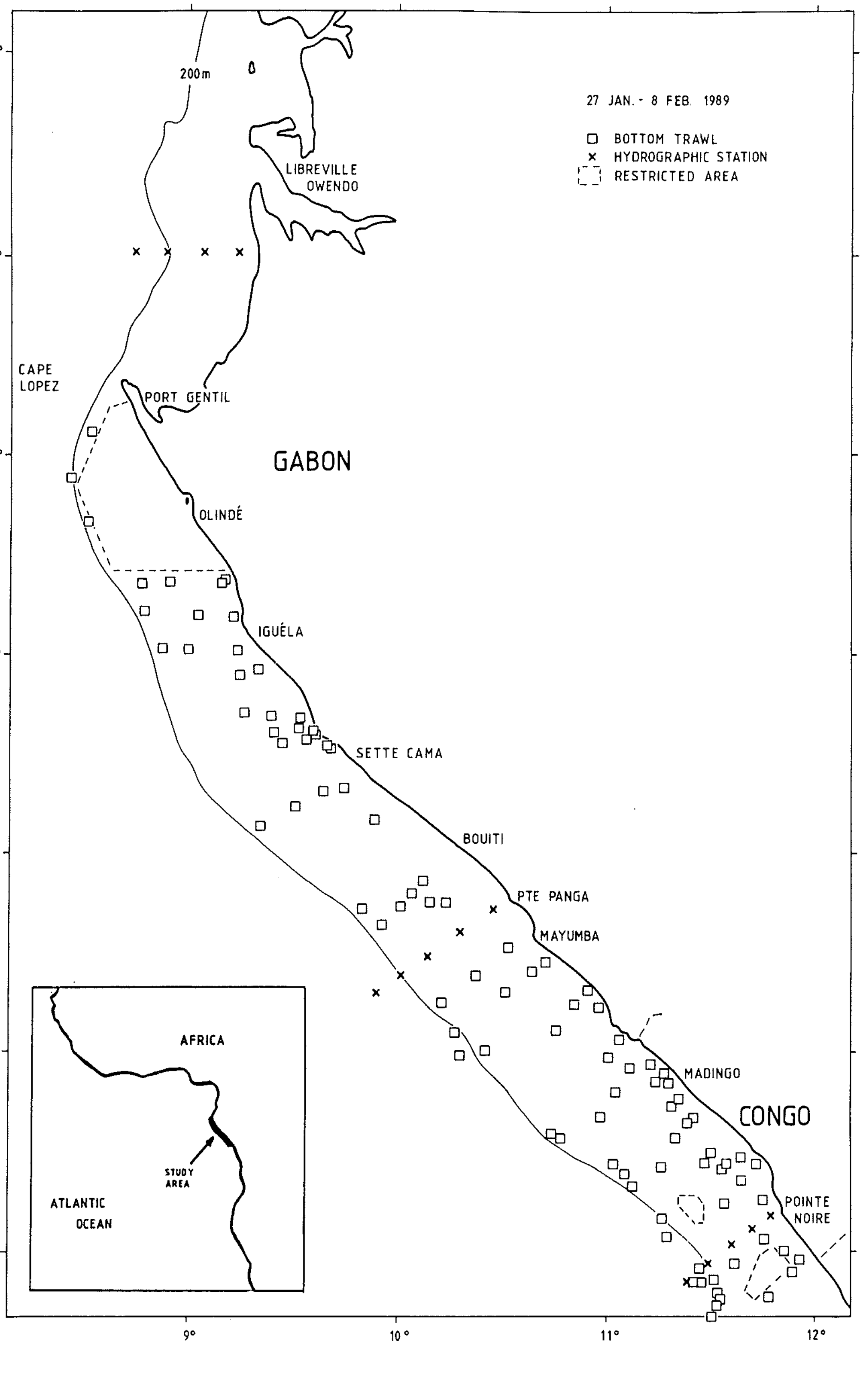


Figure 1. Position of trawl hauls and hydrographic stations. January-February 1989

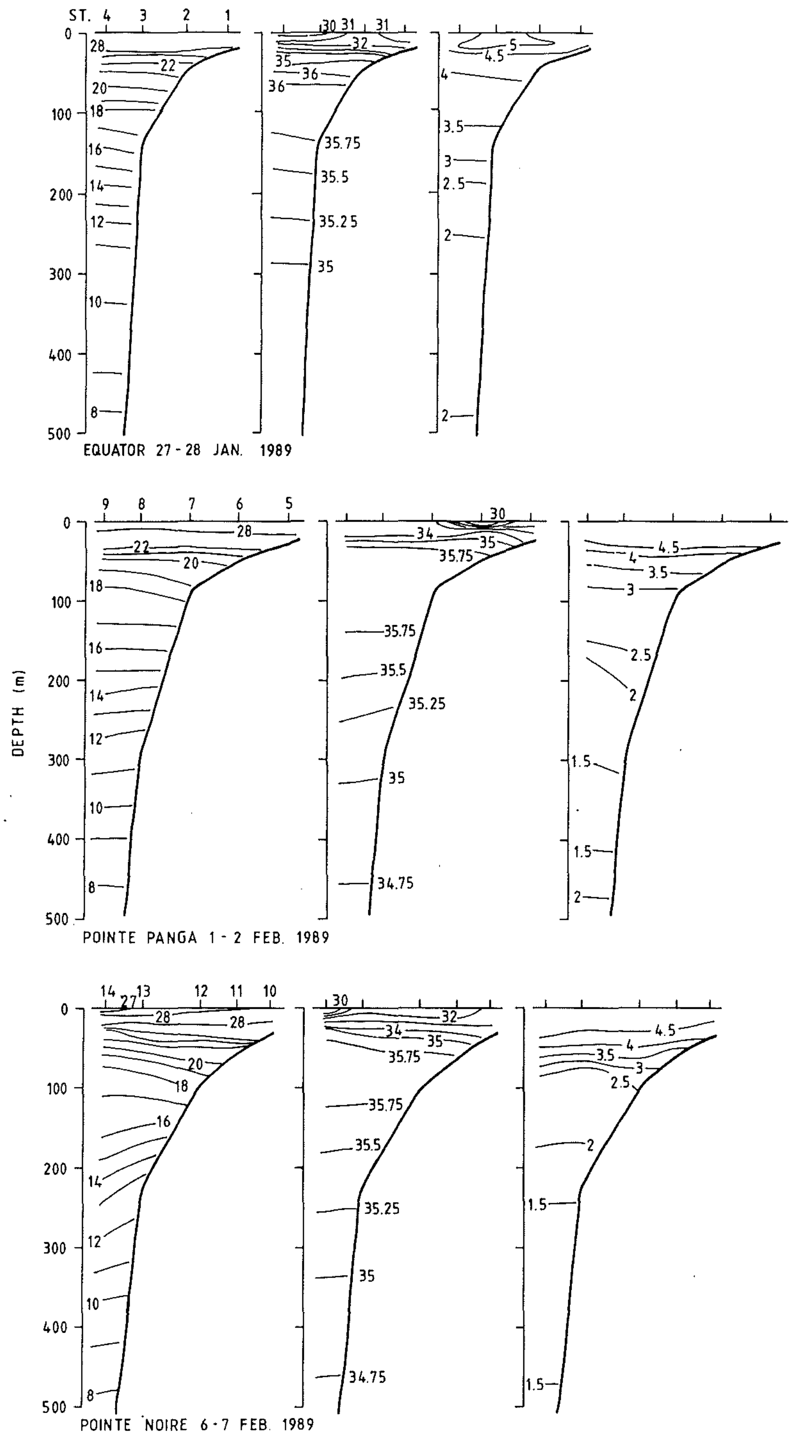


Figure 2. Hydrographic profiles for temperature, salinity and oxygen at selected places along the Congo and Gabon coasts (see also Fig 1). January-February 1989

Relatively high oxygen levels (O_2 > 2.5 ml l^{-1}) are found throughout the shelf, all year round (Anon. 1986).

Factors contributing to the enrichment in nutrients are related to seasonal upwelling, the discharge from the Congo River and shelf-break upwelling (Longhurst & Pauly 1987). Voituriez & Herbland (1982) argue that the seasonal upwelling of this region does not seem to be wind-induced and that there is no real strong vertical transport. This upwelling might be due to increasing strength of the winds in the western Atlantic originating a Kelvin wave along the Equator in a west-east direction. It should be emphasized that the seasonal upwelling in this area, although responsible for higher primary production, does not entail the dramatic changes typical of stable upwelling systems as for example oxygen depletion on the shelf bottom and clear uptilting of the thermocline. According to Voituriez & Herbland (1982), the word upwelling should not be used for these systems unless its meaning is expanded to all situations where the upper nitrate-depleted layer does not exist, independently from the mechanism of enrichment.

MATERIAL AND METHODS

Trawl data. Material was collected in 1989, during the summer season (28 January to 8 February). A shrimp and fish trawl was used, with headline of 31 m, footrope of 47 m and estimated headline height and distance between wings during towing of 6 and 18-20 m respectively. Mesh size was 2 cm, with double lining in the cod end. Each tow had a standard duration of 30 min. Other details on the gear used can be found in Sætersdal (1989). The bottom trawl stations were randomly set along the cruise track. A total of 96 stations were sampled in the course of the above survey (Fig. 1). Of these, 2 stations considered as 'non-valid' (because of gear damage) were not included in the analysis.

Each specimen caught was identified, counted and weighed separately. The FAO species identification sheets for fishery purposes, Fishing Areas 34/47 (in part) (Fisher et al. 1981) and the Guide to the commercial marine and brackish waters of Angola (Bianchi 1986) were used for identifying the species in the catches. Congeneric species which were difficult to separate were pooled together. All station and species data were stored using the B-trieve file system (data available in ASCII format upon request).

Hydrographic data. Samples for temperature, salinity and oxygen were taken using Nansen bottles at standard depths and along fixed transects (Fig. 1). In the present analysis, the values of these variables at each station were inferred from the nearest hydrographic station.

Data analysis. The analysis was performed with the help of multivariate analytical techniques i.e. a classification method Two-Way Indicator species Analysis (TWIA, Hill 1979), implemented by the program TWINSPAN, and an ordination method, Detrended Correspondence Analysis (DCA, Hill & Gauch 1980), implemented by the program DECORANA. The former is a divisive method that classifies sites and species and produces a sorted species by station table, showing the hierarchical classification in binary notation. Indicator species are also part of the output from this method. These are species showing clear ecological preferences and are used to identify particular environmental conditions. Detrended Correspondence Analysis produces an ordination of the stations based on the abundance values of the species. The ordination summarizes multivariate data in a scatter, low-dimensional diagram and it is also useful for detecting possible outliers. The use of methods based on Correspondence Analysis has proven particularly useful in ecological studies, mainly because the underlying ecological model is unimodal (Jongman et al. 1987). The use of DCA has been criticized (Jackson & Somers, 1991) because of the instability of the results when varying the number of segments. However, this seems to be true when the number of samples is small as compared to the chosen number of segments and for short gradients. In the case of long gradients this effect is smaller and, conversely, the arch effect and compression of the extremes becomes stronger when using CA without detrending. Therefore, it was still found more appropriate to use DCA in this study. Also, the DCA version used also correlates the main gradients (axes) with given environmental variables (ter Braak 1987). As a result of the analysis, average values and SD of the environmental variables are also produced for each group identified.

In this study biomass (wet weight) was used as a measure of abundance. Biomass seems to be ecologically appropriate and can be more relevant for practical applications as for example in fishery management.

Each weight ($\underline{x}$) was converted to $\ln(\underline{x}+1)$ before analysis with DCA This transformation minimizes the dominant effect of anomalous catches. The addition of 1 unit is necessary to avoid problems derived by the presence of values = 0 or values < 1. No transformation is necessary in the case of TWIA, where abundances are converted to numbers corresponding to different abundance classes (pseudospecies). In this study 5 'pseudospecies' were used, corresponding to classes with lower limits set at 0, 0.5, 5, 50 and 500 kg.

Demersal biomass densities (weight per unit area) were calculated using the 'swept-area' method by depth stratum:

$$\underline{D}_j = \underline{C}_j / \underline{q}\, \underline{a}_j$$

where $\underline{D}_j$ = density in Stratum $\underline{j}$ (tons per naut. mile square), $\underline{C}_j$ = catch taken in hauls in Stratum $\underline{j}$ (tons), $\underline{a}_j$ = surface of the bottom 'swept' by the trawl hauls in Stratum $\underline{j}$ (naut. mile square), $\underline{q}$ = catchability coefficient (= 1, i.e. all fish in the path of the trawl were caught).

In the swept-area analysis, shallow-water pelagic species caught in the bottom trawl were not excluded. It is indeed quite difficult to differentiate between pelagic and demersal for the shallow-water species. Small pelagic fish of this depth zone are often found quite close to the bottom, some of them feed on bottom detritus and are preyed upon by both demersal and pelagic predators.

RESULTS

A total of 354 species comprising 1 050 018 specimens (31 161 kg) were sampled in January-February 1989. Table 1 gives the list of the most important species collected and used in the analysis.

Appendix 1 shows the results from TWIA. The first division separates the deep water, slope Groups (7, 8 and 9) from the shelf Groups (1 to 6). At the second division level the shallow water assemblages (Groups 1 and 2) separate from the assemblages of the deeper shelf (Groups 3 to 6) while Group 7 separates from the two deeper slope assemblages. At the third division level further separation into groups does not reflect any longer depth stratification. Fig. 3 shows the plot of stations on the two first DCA axes. The eigenvalues of the first four axes were 0.91, 0.47, 0.38 and 0.28 respectively, which shows that the gradient represented by the first axis is by far the most important. Table 2 shows the correlation of these with the environmental variables and with latitude. Depth, temperature and oxygen are strongly correlated with DCA Axis 1 ($r = 0.92, -0.98$ and -0.93 respectively) and significantly correlated with salinity. Axis 2 is not significantly correlated with any of the above variables.

Table 1. Main species collected in 1989 off Congo-Gabon, by major taxonomic groups and families

Cephalopods

Loliginidae
Loligo vulgaris Lamark, 1798

Ommastrephidae
Illex coindetii (Verany, 1837)
Todaropsis eblanae (Ball, 1841)

Sepiidae
Sepia bertheloti Orbigny, 1838
Sepia officinalis Linnaeus, 1758

Octopodidae
Octopus vulgaris Cuvier, 1797

Decapod crustaceans

Solenoceridae
Solenocera africana Stebbing, 1917

Aristeidae
Aristeus varidens Holthuis, 1952
Aristeus antennatus Risso

Penaeidae
Parapenaeopsis atlantica Balss, 1914
Parapenaeus longirostris (Lucas, 1846)
Penaeus notialis Pérez-Farfante, 1967
Penaeus kerathurus (Forsskål, 1814)

Nematocarcinidae
Nematocarcinus africanus Crosnier & Forest, 1973

Portunidae
Portunus validus (Herklots, 1851)

Polychaelidae

Palinuridae
Panulirus regius De Brito Capello, 1864

Sharks

Squalidae
Centrophorus uyato (Rafinesque, 1809)
Etmopterus spp.

Squatinidae
Squatina oculata Bonaparte, 1840

Triakidae
Mustelus mustelus (Linnaeus, 1758)

Carcharhinidae
Rhizoprionodon acutus (Rüppel, 1937)

Sphyrnidae
Sphyrna lewini (Cuvier, Griffith & Smith, 1834)

Batoid fishes

Rhinobatidae
Rhinobatos albomaculatus Norman, 1930

Rajidae
Raja miraletus Linnaeus, 1758

Torpedinidae
Torpedo marmorata Risso, 1810

Dasyatidae
Dasyatis margarita (Günther, 1870)

Bony fishes

Albulidae
Pterothrissus belloci Cadenat, 1937

Clupeidae
Ilisha africana (Bloch, 1795)
Sardinella aurita Valenciennes, 1847
Sardinella maderensis (Lowe, 1839)

Gonostomatidae
Yarrella blackfordi Goode & Bean, 1896

Ariidae
Arius heudeloti Valenciennes, 1840
Arius latiscutatus (Günther, 1894)
Arius parkii Günther, 1864

Myctophidae

Synodontidae
Saurida brasiliensis Norman, 1935
Trachinocephalus myops (Forster, 1801)

Ogcocephalidae
Dibranchus atlanticus Peters, 1875

Ophidiidae
Brotula barbata (Bloch) in Bloch & Schneider, 1801

Merlucciidae
Merluccius polli Cadenat, 1950

Moridae
Physiculus spp.

Macrouridae
Coelorinchus coelorhincus (Risso, 1810)
Malacocephalus laevis (Lowe, 1843)
Malacocephalus occidentalis Goode & Bean, 1885

Trachichthyidae
Hoplostethus cadenati Quero, 1974

Zeidae
Zenopsis conchifer (Lowe, 1852)

Fistulariidae
Fistularia petimba (Lacepède, 1803)

Percophidae
Bembrops heterurus (Miranda Ribeiro, 1915)

Platycephalidae
Grammoplites gruveli (Pellegrin, 1905)

Scorpaenidae
Neomerinthe folgori (Postel & Roux, 1964)
Pontinus spp.

Triglidae
Chelidonichthys gabonensis (Poll & Roux, 1955)
Lepidotrigla cadmani Regan, 1915
Lepidotrigla carolae Richards, 1968

Dactylopteridae
Dactylopterus volitans (Linnaeus, 1758)

Peristediidae
Peristedion cataphractum Linnaeus, 1758

Serranidae
Epinephelus aeneus (Geoffroy Saint-Hilaire, 1809)

Priacanthidae
Priacanthus arenatus Cuvier, in Cuv. & Val., 1829)

Acropomatidae
Synagrops microlepis Norman, 1935

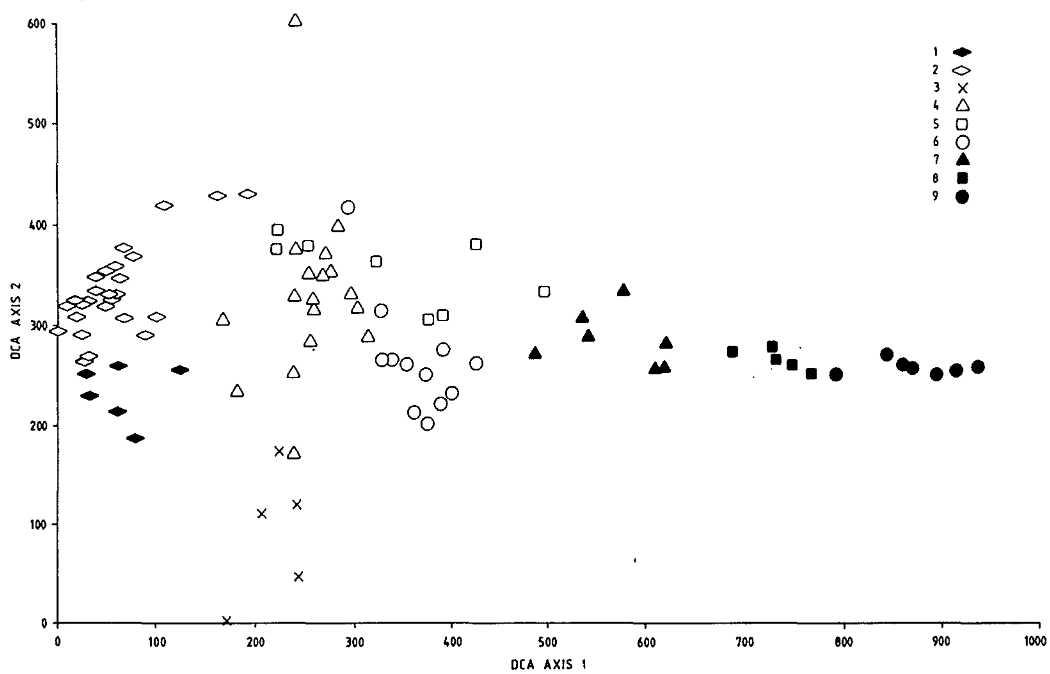


Figure 3. Detrended correspondence analysis of bottom-trawl stations in the January-February survey 1989 (SD units x 100). Corresponding TWIA (Two-Way Indicator species analysis) Groups 1 to 9 can be recognized by the different symbols

Table 2. Pearson product-moment correlation coefficient between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations. Values with asterisk indicate significant correlation ($p < 0.05$, df 91).

Variable	Axis 1	Axis 2
Depth	0.92 *	-0.12
Temperature	-0.98 *	0.11
Salininity	0.55 *	-0.00
Oxygen	-0.93 *	0.05

Fig. 4 shows the position of the stations after having been assigned to each group. The average values of the measured environmental variables are presented in Table 3 while Table 4 provides, by station groups and for the most important species, total weight and numbers.

Table 3 . Average values and standard deviations (in parenthesis) of the environmental variables for station groups 1 to 9, January-February 1989

Stat. Groups	1	2	3	4	5	6	7	8	9
Number of st.	6	26	5	18	8	12	7	5	7
Env.variables									
Depth(m)	11 (1)	21(10)	39(9)	40(14)	79(18)	93(22)	219(22)	353(41)	554(104)
Temper.(°C)	28.1(0.1)	27.1(2.1)	22.2(2.9)	21.3(2.2)	19.2(1.0)	18.7(1.5)	13.3(0.6)	10.3(0.9)	7.6(0.9)
Salin.(‰)	32.0(0.0)	33.3(1.1)	35.2(0.8)	35.3(0.6)	35.8(0.1)	35.8(0.3)	35.3(0.0)	35.0(0.1)	34.7(0.0)
Oxyg.(ml 1-1)	4.8(0.0)	4.6(0.3)	4.0(0.4)	4.1(0.4)	2.9(0.3)	3.2(0.4)	1.8(0.2)	1.5(0.0)	1.9(0.3)

Below is the description of the different groups identified.

Group 1 - Shallow water assemblage (off Gabon). The 6 stations included in this group have an average depth of 11 m, temperature 28 °C, high oxygen concentrations (4.8 ml l^{-1}, on average) and low salinity (32 ‰). They were sampled off Gabon, north of Sette Cama (Fig. 4). The indicator species is the spiny turbot Psettodes belcheri that was caught at all stations of this group (Appendix 1). This species is known to occur on sandy and rocky bottoms. Other common species were the bluespotted seabream Sparus caeruleostictus, African threadfin Galeoides decadactylus, the tonguesole Cynoglossus browni, the spiny lobster Panulirus regius, the stingray Dasyatis margarita, the bumper Brachydeuterus auritus. A number of pelagic species usually associated with the above demersal fauna were the West African ilisha Ilisha africana and the Atlantic bumper Chloroscombrus chrysurus, the guachanche barracuda Sphyraena guachancho. No species was really dominating in biomass and a number of species are known to occur in deeper waters. The juveniles of several species were found here (Sætersdal, 1989), i.e. the bumper, threadfin, barracuda and other non identified species and this indicates that the area where the stations of this group were sampled is a nursery area.

Group 2 - Shallow water assemblage (mainly off Congo) . Twenty-six stations, mainly off Congo and southern Gabon are included in this group, at an average depth of 21 m, high temperature and oxygen concentrations (27.1 °C and 4.6 ml l^{-1}, respectively). Brachydeuterus auritus dominated both in biomass and numbers (Table 4) while typical demersal species of this group were the croakers Pseudotolithus senegalensis and P. typus, the threadfins Galeoides decadactylus and Pentanemus quinquarius. A number of

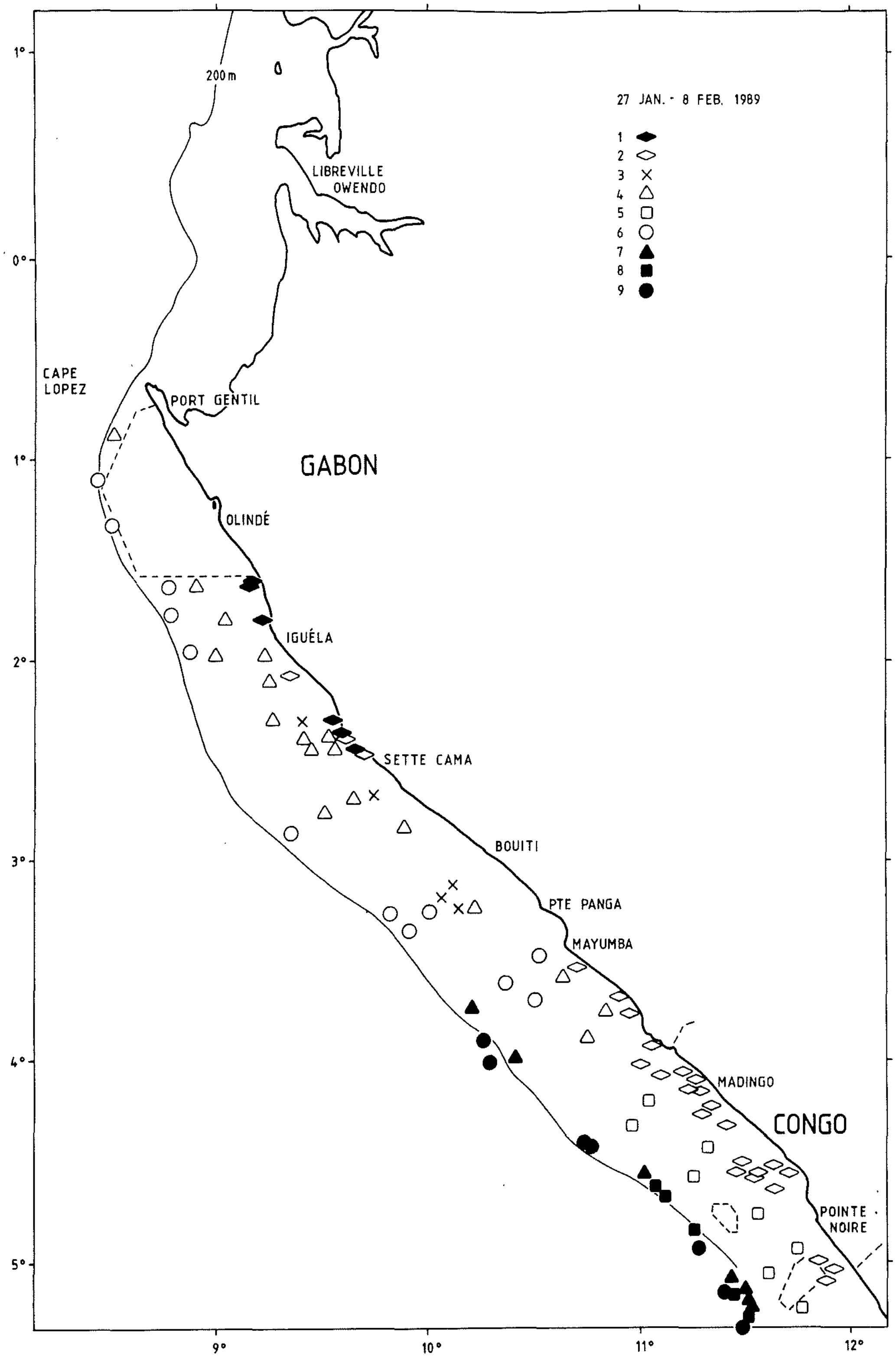


Figure 4. Map showing the position of the stations after having being assigned to the different groups

Table 4. Total weight (W in kg), numbers (N) and frequency (F: no. of stations where found in the respective groups) of main species from station Groups 1 to 9. Catch rate = total W/F

Species	W	(%)	N	(%)	F
Group 1 (6 stations)					
Sparus caeruleostictus	66	(8)	126	(1)	4
Dasyatis margarita	62	(8)	100	(1)	5
Panulirus regius	46	(6)	68	(0)	5
Galeoides decadactylus	35	(4)	340	(2)	5
Psettodes belcheri	34	(4)	87	(0)	6
Brachydeuterus auritus	33	(4)	9 922	(60)	5
Pseudotolithus typus	31	(4)	63	(0)	3
Sphyraena guachancho	30	(4)	146	(1)	5
Chloroscombrus chrysurus	24	(3)	613	(4)	4
Cynoglossus browni	22	(3)	100	(1)	5
Balistes punctatus	17	(2)	42	(0)	4
Pomadasys rogeri	12	(2)	46	(0)	4
Sepia officinalis	11	(2)	20	(0)	4
Ilisha africana	9	(1)	732	(4)	3
Scomberomorus tritor	8	(1)	12	(0)	5
Pseudotolithus senegalensis	8	(1)	10	(0)	3
Rhinobatos albomaculatus	8	(1)	14	(0)	4
Pseudupeneus prayensis	5	(1)	126	(1)	4
Fistularia petimba	2	(0)	10	(0)	4
Total	463	(57)	12 577	(77)	
Total (all species)	806		16 407		
Catch rate	134				
Group 2 (26 stations)					
Brachydeuterus auritus	1 460	(17)	77 002	(26)	26
Pseudotolithus senegalensis	761	(9)	2 145	(1)	24
Chloroscombrus chrysurus	592	(7)	21 107	(7)	23
Sphyraena guachancho	570	(7)	1 440	(0)	20
Ilisha africana	556	(7)	38 290	(13)	23
Galeoides decadactylus	424	(6)	7 289	(2)	25
Pteroscion peli	418	(6)	16 222	(5)	22
Pentanemus quinquarius	337	(4)	29 255	(10)	15
Pseudotolithus typus	280	(3)	1 149	(0)	14
Selene dorsalis	151	(2)	4 139	(1)	24
Trichiurus lepturus	142	(2)	3 588	(1)	18
Parapenaeopsis atlantica	139	(2)	50 135	(17)	19
Portunus validus	115	(1)	302	(0)	15
Cynoglossus canariensis	100	(1)	690	(0)	15
Arius latiscutatus	96	(1)	88	(0)	10
Cynoglossus browni	95	(1)	534	(0)	11
Panulirus regius	72	(1)	117	(0)	15
Arius heudeloti	46	(0)	142	(0)	11
Penaeus notialis	38	(0)	781	(0)	16
Sardinella maderensis	18	(0)	1 127	(0)	18
Total	6 410	(76)	258 612	(86)	
Total (all species)	8 487		299 881		
Catch rate	326				
Group 3 (5 stations)					
Lutjanus fulgens	1 406	(27)	2 096	(16)	5
Plectorhynchus mediterraneus	1 044	(20)	888	(7)	3
Sparus caeruleostictus	701	(13)	1 466	(12)	5
Dentex canariensis	530	(10)	895	(7)	5
Epinephelus aeneus	159	(3)	36	(0)	3
Sparus auriga	96	(2)	50	(0)	3
Lutjanus dentatus	59	(1)	8	(0)	2
Sepia officinalis	55	(1)	80	(1)	3
Fistularia petimba	33	(1)	193	(2)	3
Pseudupeneus prayensis	29	(1)	477	(4)	5
Boops boops	19	(0)	1 568	(12)	3
Trachinus armatus	6	(0)	166	(1)	3
Total	4 137	(79)	7 923	(62)	
Total (all species)	5 256		12 731		
Catch rate	1 051				
Group 4 (18 stations)					
Pagellus bellottii	465	(23)	11 785	(17)	16
Sparus caeruleostictus	218	(11)	445	(1)	7
Sepia officinalis	197	(10)	427	(1)	17
Chelidonichthys gabonensis	160	(8)	2 116	(3)	12
Syacium micrurum	94	(5)	5 603	(8)	17
Saurida brasiliensis	56	(3)	12 686	(19)	12
Trachynocephalus myops	41	(2)	994	(1)	11
Raja miraletus	35	(2)	93	(0)	11
Sepia bertheloti	32	(2)	617	(1)	8
Pseudupeneus prayensis	24	(1)	543	(1)	15
Octopus vulgaris	22	(1)	47	(0)	8
Alloteuthis africana	17	(1)	5 395	(8)	7
Fistularia petimba	16	(1)	157	(0)	12
Grammoplites gruveli	11	(0)	785	(1)	15
Uranoscopus polli	6	(0)	57	(0)	9
Total	1 394	(70)	41 750	(62)	
Total (all species)	1 996		67 756		
Catch rate	111				
Group 5 (8 stations)					
Brachydeuterus auritus	2 032	(55)	154 056	(69)	8
Saurida brasiliensis	244	(7)	41 190	(18)	8
Trachurus trecae	228	(7)	8 520	(4)	7
Pagellus bellottii	180	(5)	3 340	(1)	7
Pentheroscion mbizi	120	(3)	2 792	(1)	8
Trichiurus lepturus	69	(2)	1 654	(1)	7
Sepia officinalis	56	(2)	468	(0)	7
Dentex angolensis	46	(2)	372	(0)	5
Illex coindetii	25	(1)	576	(0)	5
Citharus linguatula	22	(1)	686	(0)	8
Lepidotrigla cadmani	21	(1)	226	(0)	5
Brotula barbata	12	(0)	38	(0)	6
Parapenaeus longirostris	7	(0)	868	(0)	7
Total	3 062	(83)	214 786	(96)	
Total (all species)	3 694		222 760		
Catch rate	462				
Group 6 (12 stations)					
Dentex congoensis	1 930	(32)	68 261	(30)	11
Trachurus trecae	1 651	(27)	74 948	(33)	10
Boops boops	585	(10)	24 352	(11)	11
Pagellus bellottii	517	(9)	18 628	(8)	12
Epinephelus aeneus	115	(2)	30	(0)	6
Lepidotrigla carolae	110	(2)	3 882	(2)	9
Spicara alta	102	(2)	9 699	(4)	8
Chelidonichthys gabonensis	83	(1)	1 505	(1)	12
Lepidotrigla cadmani	70	(1)	2 374	(1)	7
Priacanthus arenatus	54	(1)	638	(0)	5
Dentex angolensis	46	(1)	527	(0)	6
Saurida brasiliensis	35	(1)	3 550	(2)	7
Sepia bertheloti	28	(0)	613	(0)	10
Dentex canariensis	21	(0)	34	(0)	4
Citharus linguatula	19	(0)	958	(0)	7
Total	5 364	(89)	209 997	(91)	
Total (all species)	6 045		228 928		
Catch rate	504				

Table 4. Continued

Species	W	(%)	N	(%)	F
Group 7 (7 stations)					
Centrophorus uyato	406	(20)	54	(0)	2
Squatina oculata	122	(6)	20	(0)	6
Pterothrissus belloci	120	(6)	921	(2)	6
Illex coindeti	119	(6)	1 447	(4)	7
Synagrops microlepis	103	(5)	8 726	(24)	4
Pentheroscion mbizi	94	(5)	770	(2)	2
Ariomma bondi	92	(5)	2 296	(6)	1
Brotula barbata	83	(4)	145	(0)	4
Etmopterus polli	55	(3)	10	(0)	1
Merluccius polli	38	(2)	730	(2)	7
Bembrops heterurus	36	(2)	1 162	(3)	5
Parapenaeus longirostris	30	(2)	3 609	(10)	7
Myctophidae	21	(1)	6 531	(18)	4
Zenopsis conchifer	20	(1)	54	(0)	5
Physiculus spp.	4	(0)	170	(0)	4
Total	1 343	(67)	26 643	(73)	
Total (all species)	2 005		36 543		
Catch rate	286				
Group 8 (5 stations)					
Nematocarcinus africanus	551	(32)	116 976	(80)	4
Merluccius polli	414	(24)	2 168	(1)	5
Centrophorus uyato	164	(9)	67	(0)	4
Pterothrissus belloci	156	(9)	1 038	(1)	5
Benthodesmus tenuis	101	(6)	6 038	(4)	5
Illex coindetii	73	(4)	638	(0)	5
Physiculus spp.	60	(3)	1 206	(1)	5
Neomerinthe folgori	16	(1)	351	(0)	3
Coelorinchus coelorhincus	5	(0)	189	(0)	4
Total	1 545	(89)	129 334	(89)	
Total (all species)	1 745		145 582		
Catch rate	349				
Group 9 (7 stations)					
Physiculus spp.	145	(13)	1 754	(9)	6
Malacocephalus occidentalis	121	(11)	1 560	(8)	7
Merluccius polli	107	(10)	305	(2)	4
Coelorinchus coelorhincus	97	(9)	1 886	(10)	7
Polychaelidae	59	(5)	3 908	(20)	7
Illex coindeti	59	(5)	444	(2)	6
Etmopterus spp.	58	(5)	368	(2)	6
Yarella blackfordi	44	(4)	4 242	(22)	6
Aristeus antennatus	14	(1)	349	(2)	6
Aristeus varidens	9	(1)	481	(2)	5
Benthodesmus spp.	9	(1)	468	(2)	4
Total	722	(64)	15 765	(81)	
Total (all species)	1 126		19 430		
Catch rate	162				

benthopelagic and pelagic species were caught in association with these: Chloroscombrus chrysurus, Ilisha africana, the drum Pteroscion peli, the African lookdown Selene dorsalis and typical fish predators as the hairtail Trichiurus lepturus and Sphyraena guachancho. This corresponds to the shallow water assemblage described also by Durand (1967) for Congo and by Domain (1980) for the continental shelf off Senegal and Mauritania, as well as with the 'estuarine and offshore sciaenid subcommunities' of the Gulf of Guinea described by Longhurst (1965) and Fager & Longhurst (1968). This assemblage also typifies the shallow waters of northern and central Angola (Bianchi, in press).

Groups 3 - Coastal assemblages, just below the thermocline, on sandy/hard bottoms. This is a group of 5 stations with an average depth of about 39 m, temperature of 22°C, oxygen concentration of 4 ml l^{-1} and salinity 35.2 ‰, between Pointe Panga and Sette Cama. The golden African snapper Lutjanus fulgens, the grunt Plectorhynchus mediterraneus, Sparus caeruleostictus, the white grouper Epinephelus aeneus, the Canary dentex Dentex canariensis and the seabream Sparus auriga made up 75 % of the catches of Group 3 while all species of Groups 1 and 2 were either present in small quantities or absent, probably because of the markedly lower temperature. The Navigation Charts (1976) report mainly sand, shingle and gravel in this area and this fits with the substratum preferences of the above species as reported in the literature (Fischer et al. 1981). Also, Brachydeuterus auritus and Trichiurus lepturus, species with preference for soft bottoms, were completely absent.

Group 4 - Coastal assemblage, just below the thermocline, on sandy bottoms. This group is almost identical to group 3 in its values for environmental variables (Table 3) and largely overlaps in geographical location (Fig. 4). A number of species were common to both groups: the goatfish Pseudupeneus prayensis, the cornetfish Fistularia petimba, the weever Trachinus armatus, the cuttlefish Sepia officinalis, the red pandora Pagellus bellottii and Sparus caeruleostictus. Others were found in group 4 but not in group 3: the Guinea flathead Grammoplites gruveli, ray Raja miraletus, the bluntnose lizardfish Trachinocephalus myops, the octopus Octopus vulgaris, the Gabon gurnard Chelidonichthys gabonensis and the Brazilian lizardfish Saurida brasiliensis.

Both Group 3 and 4 seem to correspond to the one described for the Gulf of Guinea by Longhurst (1968) as an assemblage 'found at the bottom of the thermocline, mainly on hard bottoms, where the species that usually dominate the thermocline area are replaced by some members of the deeper sparid assemblage, probably because of the nature of the bottom'. The differences between the two groups appearing in Appendix 1 and Table 4 might be due to the presence, in some locations, of spawning aggregations were only a few species dominate.

The following groups (5 and 6) include species of the subthermocline assemblages of the continental shelf (50 to 150-200 m). Two major groups where identified: an assemblage consisting, among others, of several species of Sparidae, with preference for sandy, fine sand to muddy bottoms and an assemblage including species with a clear preference for soft bottoms. The Cunene horse mackerel Trachurus trecae, Pagellus bellottii and Citharus linguatula were abundant in both groups.

Group 5. Subthermocline assemblage of soft bottoms, off Congo. Navigation charts (Anon. 1976) show the presence of mud, mud-sand bottom for the area where this type of assemblage is found. Its species composition confirms the presence of soft bottoms. A group of 8 stations, at an average depth of 79 m, temperature of 19 °C, high salinity (35.8 ‰) and oxygen levels of 2.9 ml l^{-1} were quite distinct in species association. Fifty-five percent of the catches consisted of Brachydeuterus auritus. An additional 30% consisted of Saurida brasiliensis, Trachurus trecae, Pagellus bellottii , Pentheroscion mbizi, Trichiurus lepturus, Sepia officinalis and Dentex angolensis. Brotula barbata and Parapenaeus longirostris were less abundant but quite common. This assemblage is almost identical in species composition to the one described for the muddy bottoms of northern Angola (Bianchi, in press). However, there the dominating species is the splitfin Synagrops microlepis (52%), a species mainly of the upper slope. In fact that assemblage was described from a group of stations with a deeper depth range.

Group 6. Subthermocline sparid assemblage, off Gabon. This group includes 12 stations at an average depth of about 93 m, temperature of 18.7 °C, salinity 35.8 ‰, oxygen concentration 3.2 ml l^{-1}. The bottom is mainly sandy (Anon. 1976). Several seabream species (family Sparidae) dominate this assemblage that broadly coincides with Longhurst's 'subthermocline sparid subcommunity' (1965) of the Gulf of Guinea, also described for Congo by Durand (1967). Dentex congoensis and the bentho-pelagic Trachurus trecae dominated the catches both in biomass and numbers (59% and 63%, respectively, Table 4) and were present in almost all stations. Two additional species, Boops boops and Pagellus bellottii accounted for an additional 20%.

The slope stations range between 200 and 696 m depth. They have been divided into three groups following the TWINSPAN divisions. However, they seem to represent an almost perfect gradient, where species from shallower depths are gradually replaced by deeper water representatives (see Appendix 1).

Group 7. Upper edge of the continental slope. Seven stations are included in this group, at an average depth of 219 m, temperature of 13.3 °C, salinity of 35.3 ‰ and oxygen levels of 1.8 ml l^{-1}. There is no really dominating species. Squatina oculata is the indicator species while Centrophorus uyato accounts for 20% of the catches in biomass but has a low frequency (30%). Pterothrissus belloci and Illex coindeti were the other two most abundant species. Synagrops microlepis, that made up 52 % in biomass in the corresponding assemblage found off Angola, is definitely less abundant here (5%).

Group 8. Deeper continental slope (300-400 m). Five stations were sampled , with the average depth of 353 m, temperature of 10.3 °C , salinity of 35.0 ‰ and oxygen of 1.5 ml l^{-1}. Two species dominated the catches: the African spider shrimp Nematocarcinus africanus, the indicator species (32% of the catches) and Merluccius polli (about 24%). In common with the shallower slope Group 7 are Pterothrissus belloci, Illex coindetii, Parapenaeus longirostris, Physiculus spp. and Benthodesmus thenuis. Species with a deeper range appearing in this group are the grenadiers Coelorinchus coelorhinchus.

Group 9 - Deeper continental slope (400 to 700 m). Eight stations, average depth 554 m, temperature of 7.6 °C , salinity of 34.7 ‰ and oxygen of 1.9 ml l^{-1}. Bony fishes typical of this group are the grenadiers Coelorinchus coelorhinchus, Malacocephalus occidentalis, the bristlemouth Yarella blackfordi. Species of Physiculus and Merluccius polli, also found in the two other slope groups, contributed to 23 % of the catches in biomass. the lantern shark Etmopterus spp. represented the sharks in this depth range. A number of crustaceans also appeared as important elements of the fauna: lobsters of the family Polychaelidae, the shrimps Aristeus antennatus and A. varidens.

The plot of mean biomass densities by depth stratum for Gabon and Congo is presented in Fig. 5 while Table 5 gives the number of stations sampled by depth stratum. In Congo the maximum biomass on the shelf is given by the eurybathic species (mainly Brachydeuterus auritus) while the slope maximum occurs between 300 and 400 m and is mainly due to Nematocarcinus africanus and Merluccius polli. Off Gabon, an additional group was defined, consisting of eurythermic species with preference for hard substratum (corresponding to Group 3 of the assemblage analysis). Its maximum is at 30-50 metres while the eurybathic species found off Congo are very poorly represented. A maximum is found in the deeper part of the shelf, consisting of species of the 'sparid community' (Dentex congoensis, Trachurus trecae and Boops boops).

DISCUSSION

Species assemblages. The first TWIA division separates the shelf stations from the slope ones and thus constitutes the sharpest discontinuity. The faunal discontinuity is probably accentuated by the steepness of the shelf between about 120 and 200 m and no station could be sampled in that depth range. DCA Axis 1 shows high correlation with temperature, oxygen and depth. These variables co-vary and it is difficult to interpret their effects separately. Temperature seems to be important in separating the shallow water groups from the intermediate shelf ones. The thermocline seems to give rise to a distinct boundary and groups 1 and 2, from shallow waters, have average temperatures 5 to 6 °C higher than groups 3 and 4, just below the thermocline, while oxygen values are above 4 ml l^{-1} in the four groups (Table 3). From Appendix 1 is also clear that most of the shallow water species are confined to groups 1 and 2, i.e. where waters have high temperature and oxygen values. The slope groups are also characterized by temperature values well below the values found on the shelf. Oxygen may play some role for the species in the deeper part of the shelf and on the slope. Depth, as already discussed in Bianchi, 1991, is a spurious variable as it entails all possible other factors varying along the water column (temperature, oxygen, salinity, pressure, light intensity etc.).

The importance of the presence of a sharp thermocline in the eastern Atlantic at shallow depths was already recognized by Longhurst (1966). Apart from clearly segregating shelf assemblages, the occurrence of cool subthermocline water at relatively shallow depths enables a number of cool sub-tropical fish to penetrate in the tropical region and explains how species of the family Sparidae, one of the most important demersal fishery resource, mostly represented in the Mediterranean, South Africa and the more temperate coasts of West Africa, can be so very abundant in the tropical area as well.

DCA axis 2 did not show any significant correlation with the environmental variables used in this study. Groups 1 and 2 are separated along this axis, as well as group 3 from group 4 and group 5 from groups 4 and 6 (Fig. 3). This axis might reflect factors like differences in bottom type (i.e. group 5 against 6), spawning aggregations (Group 3) or presence of nursery areas (Group 1).

Longhurst's description of the assemblages of the Gulf of Guinea derived from the data of the Guinean Trawling Survey largely coincides with the above groups. The 'sciaenid community' of estuarine areas and shallow waters corresponds to Group 2. Pseudotolithus senegalensis

and P. typus, Pteroscion peli are the dominating sciaenids and were chosen to represent this group because of their importance in fisheries. However, the eurybathic Brachydeuterus auritus dominate this group. The 'sparid community', characterized by a number of seabreams (family Sparidae) together with other families of sandy deposits (Triglidae, Mullidae, Synodontidae and Platycephalidae) is also represented in the area under study, by its shallow component (Group 4, off Gabon) and deeper-shelf component (Group 6, also off Gabon). The latter represents the typical 'sparid community' where about 80 % of the catches consist of Dentex congoensis (32%), Trachurus trecae (27%), Boops boops (10%) and Pagellus bellottii (9%).The intermediate shelf assemblage found off Congo seems to be rather different and this is possibly due to the muddy substratum found here. Although some elements of the 'sparid community' are found here (e.g. Dentex angolensis, Saurida brasiliensis, Trachurus trecae) other species with more affinity for muddy bottoms appear (Pentheroscion mbizi, Brotula barbata). Brachydeuterus auritus accounts for 55% of the catches here. However, its presence in this assemblage is only seasonal (Durand, 1967). The values of the environmental variables are rather similar for the two Groups (Table 3) and it seems evident that bottom type plays an important role in the faunal composition of these assemblages. Longhurst has not described this difference and included Pentheroscion mbizi in the typical 'sparid assemblage'.

Durand (1967) described the distribution, abundance and seasonal variations of the benthic fishes of the Congo continental shelf. It is interesting to compare the results from that study with the present one in order to find possible differences in the dominating species. He describes the shallow water assemblage as 'peuplement littoral' and this corresponds to Group 2 (this group includes mostly shallow waters off Congo). Pseudotolithus senegalensis, P. typus and Pteroscion peli made up 60% of the catches (possibly excluding the eurybathic species). In the shallow water group off Congo, the above species represent 18% in biomass of the catches (about 30 % without the eurybathic species). Also, Ilisha africana, described as coming after the above species in Congo, seems now to be relatively more abundant and accounts for 7% of the catches from the assemblage.

As for the deeper shelf assemblage, Dentex angolensis was reported as the dominant species while it definitely did not appear as dominant in 1989. The shelf assemblage off Congo (Group 5, Table 4) shows that, at least in the warm season, Brachydeuterus auritus dominates (55%) while D. angolensis accounts only for 2% of the catches.

The observed decline in the relative abundances of Pseudotolithus and Dentex angolensis might be due to high fishing pressure directed at these valuable groups.

As for the slope assemblages, no indication of zonation is given by Durand while we could identify at least 2 major groups (7 and 8-9). The one described by Durand seems to correspond with Group 7 and some dominating species (Squatina oculata and Pterothrissus belloci)
are also dominating the catches of the upper slope assemblage represented by Group 7. Two large catches of Centrophorus uyato accounted for 20% of the catches in Group 7 while this species is not mentioned by Durand.

Biomass distribution. Because of the differences found in the assemblage structure of Congo and Gabon (South of Cape Lopez), these two sections were analyzed independently. The analysis was performed by grouping the species according to their ecological preferences. For Congo, the analysis was performed by dividing the species in 4 groups: shallow water, suprathermocline species, eurybathic (Brachydeuterus auritus, Trichiurus lepturus, Sphyraena guachancho, Raja miraletus, Cynoglossus canariensis, Selene dorsalis and Cynoponticus ferox), deeper shelf species and slope species.

It is interesting to note that while in correspondence with the thermocline area the shallow water and deeper shelf groups have a minimum, the eurybathic species reach here their maximum. Brachydeuterus auritus belongs to a typical demersal family (Haemulidae = Pomadasyidae) but it is often observed off the bottom suggesting a semi-demersal type of behaviour. Its evolutionary success might be related to the instability of the thermocline area which would make this area inhabitable for most species. As already observed by Durand (1967) the thermocline is subject to important seasonal fluctuations causing a minimum of demersal biomass. Brachydeuterus auritus seems to have developed as a eurythermic/eurybathic species capable of adjusting to environmental fluctuations. Also, its feeding habits suggest the capability of feeding both in intermediate waters as well as on the bottom. Although Brachydeuterus is also found together with shallow water species as well as deeper ones, its maximum of occurrence is in areas where the other species, that form the target of various fisheries, do not occur so that this species is possibly not subject to the same fishing pressure.

An additional category was defined for Gabon i.e. 'eurybathic B' of Fig.5, consisting of species found at similar depth ranges as the species of the eurybathic group mentioned above but with preference for hard bottoms (species of Lutjanus, Dentex, Sparus, Pagellus and Epinephelus, but with a shallower depth distribution as compared with the respective congeneric species).

Fig. 5 shows how the above species groups are distributed according to depth. The maximum observed on the deeper shelf off Gabon (Fig 5, lower) is quite remarkable. However, about 30% of this value is represented by a few high catches of Trachurus trecae. The remaining species are all typical demersal and alone they would still amount to a maximum value in this depth zone. The high fish densities observed off Congo between 300 m and 400 m depth are largely due (about 70%) to the spider shrimp Nematocarcinus africanus and the hake Merluccius polli.

Table 5. Number of stations used for swept area estimates, by depth stratum

Depth stratum	10-30	30-50	50-100	100-200*	200-300	300-400	400-500	500-700
Congo	14	4	7	2	5	4	1	3
Gabon	19	14	8	5	2	0	1	2

* all stations of this depth stratum were between 100 and 115 m (the continental shelf is very steep to 200 m)

The higher catches and fish densities observed in the deeper part of the shelf seem to deviate from the general conception that in tropical areas highest biomass densities are found in shallow, suprathermocline waters (Longhurst & Pauly 1987). On the one hand, the definition 'tropical' should not be related to the latitudinal position of a given area but rather to the type of oceanographic regime there found. Thus Gabon and Congo, although definitely tropical in position, are subject to processes of enrichment (seasonal upwelling) that are probably responsible for the deviations in the distribution of demersal biomass described above. On the other hand, there is also a problem with the definition of 'demersal'. If 'demersal' is meant to cover only truly benthos-feeding animals, about 70 % of the species of Table 1 should not be included in the analysis, the results might be different and may be consistent with the general view of decreasing demersal biomass with increasing depth. However, I have preferred to include all species consistently caught in the bottom trawl as their presence near the bottom might reflect some type interaction with the benthic ecosystem. Studies on stomach contents are obviously needed to establish the possibility of trophic relationships.

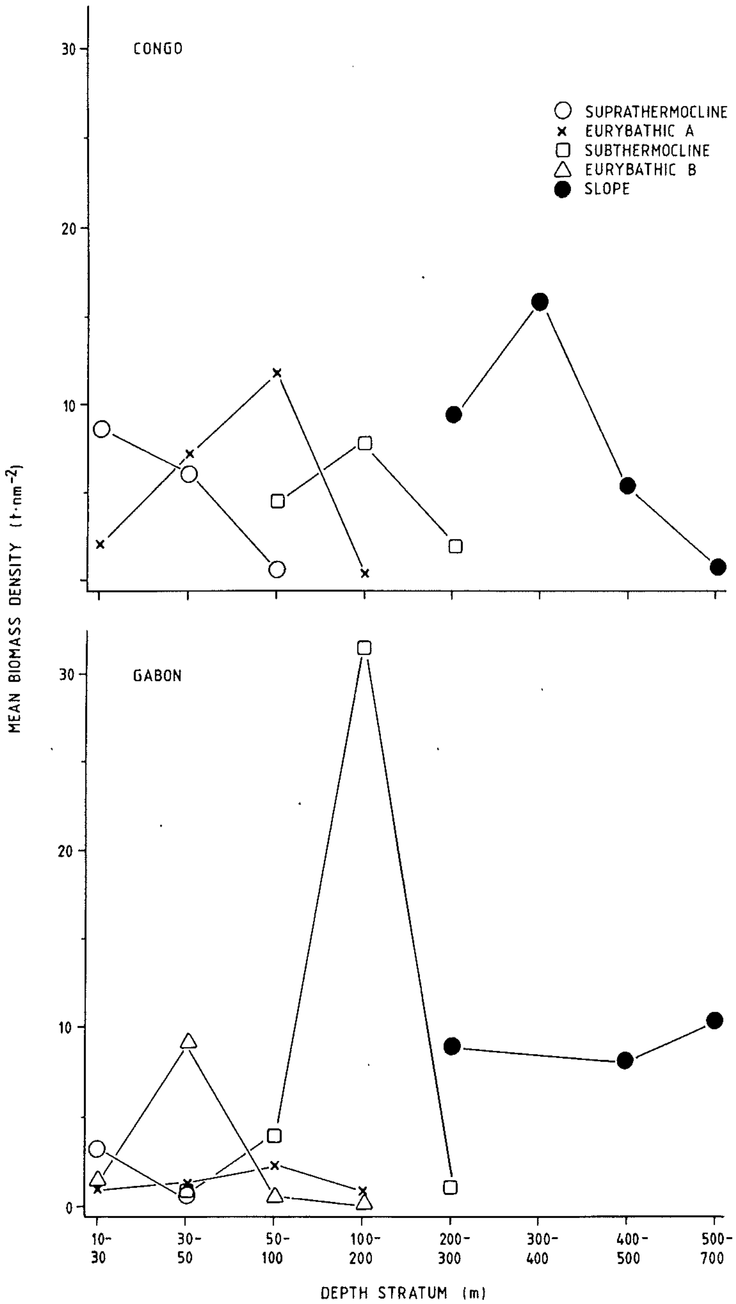
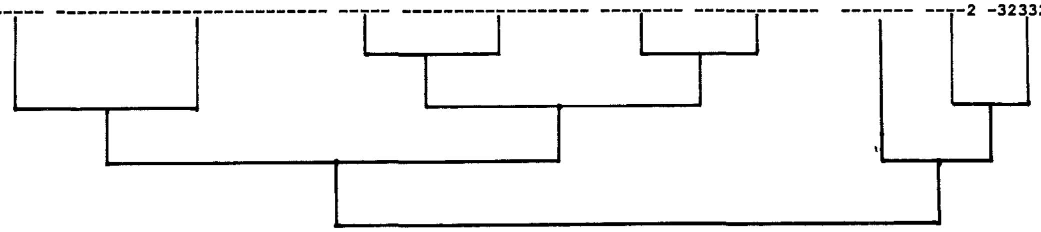


Figure 5. Plot of mean biomass density by depth stratum, January-February 1989, from bottom trawl catches for Congo (upper) and Gabon (lower). For definition of species categories see the 'Biomass' section of the discussion.

Appendix 1. Two-way station by species table resulting from the program TWINSPAN. Values denote categories of abundance: 1: w < 0.5 kg; 2: 0.5 < w ≤ 5 kg; 3: 5 < w ≤ 50 kg; 4: 50 < w ≤ 500 kg; 5: w > 500 kg. The dendrogram showing the hierarchical relationship between the various groups, substitutes the binary notation produced by the program

	← shelf →						← slope →		
	1	2	3	4	5	6	7	8	9
Mustelus mustelus	----32	------3---3223--3------2--	-3--3	-----------2-2-22-	--------	------2-----	------3	-----	-------
Trichiurus lepturus	------	-32----223232333232--3223-	-----	------------------	3232232-	------------	-3233--	-----	-------
Cynoglossus canar.	------	-3----31-2--3223--2-122333	-----	---------2--------	-----2--	---3--------	-------	-----	-------
Sardinella maderen.	1-1-1-	212222-12-2--12-12221-12--	-----	1----1------------	--------	------------	-------	-----	-------
Galeoides decadact.	322-33	3333434432233233333413323-	-----	-----31-----------	2-2-----	------------	-------	-----	-------
Pseudotolithus typ.	22---3	-333--33-24433--33------22	-----	------------------	--------	------------	-------	-----	-------
Dicologoglossa cun.	1-----	--3------1-----221---233-3	-----	-------------1----	--------	------------	--1----	-----	-------
Chloroscombrus chr.	-22-33	-3-33332333334443332233-23	-----	------------------	--------	------------	-------	-----	-------
Arius latiscutatus	----22	-2--33----23----33-3-22---	-----	-----------2------	--------	------------	-------	-----	-------
Sardinella aurita	--1-2-	2221223333-232333232133-12	-----	------------------	42--2---	------------	-------	-----	-------
Ilisha africana	--2-23	-32233-4333334343323-32222	-----	-----1------------	--------	------------	-------	-----	-------
Pseudotolithus sen.	--2-33	243433332344333333-3-33334	----4	-----2------------	2-------	------------	-------	-----	-------
Parapenaeopsis atl.	------	233323---333121223-3123---	-----	-----13-----------	--2-----	------------	-------	-----	-------
Arius heudeloti	----33	----2223-23--22-222-------	-----	------------------	--------	------------	-------	-----	-------
Pomadasys jubelini	----3-	-3-3--2322-22-------------	-----	------------------	--------	------------	-------	-----	-------
Portunus validus	-----2	333---2233--23--22--2332--	-----	------------------	--------	------------	-------	-----	-------
Pteroscion peli	--2--2	233-32-223433333221--33343	-----	------------------	--------	------------	-------	-----	-------
Pentanemus quinqua.	------	-333---3-344322433---33---	-----	------------------	--------	------------	-------	-----	-------
Cynoglossus browni	322-22	-3-331-3--332----222------	-----	------------------	--------	------------	-------	-----	-------
Sphyraena guachanc.	323-32	33-24323433333333332-----2	-----	------------------	3333--3-	------------	-------	-----	-------
Eucinostomus melan.	22--2-	1-----322-----1----3122---	-----	-----3------------	--------	------------	-------	-----	-------
Panulirus regius	332-22	--32-1-321233223-----22-2-	-----	------------------	--------	------------	-------	-----	-------
Dasyatis margarita	123-33	-24332-3-2---------3------	-----	------------------	--------	------------	-------	-----	-------
Scomberomorus trit.	2222-2	-2--22222----2------2-----	2----	------------2-----	--------	------------	-------	-----	-------
Brachydeuterus aur.	222-33	43433243442344333342333444	-----	--2--2---4--1212--	54533242	--22--3-----	-------	-----	-------
Penaeus notialis	1-----	232----1-2--2222--22-22232	-----	212---11-2-1--1---	2-3---1-	------------	-------	-----	-------
Pomadasys rogeri	222--2	-2-23----2-222----23------	-1---	--2--32-----------	--------	------------	-------	-----	-------
Rhinobatos albomac.	-2223-	--3-1-2---2---------------	-----	23---2-------2----	--------	------------	-------	-----	-------
Psettodes belcheri	223333	-----1--------------------	23---	2-----------2-----	--------	------------	-------	-----	-------
Balistes punctatus	222-3-	-------3------------------	3----	--------2---1--22-	--------	------------	-------	-----	-------
Grammoplites gruv.	------	--1-----------2------22323	----2	222122212211-1-2-1	---1-1--	-113--2-----	1------	-----	-------
Uranoscopus polli	21---2	---------------------12---	----2	-2-12-111-1--12---	--2-----	----2-------	-----3-	-----	-------
Raja miraletus	------	2-2------2----2----3222231	-----	332---3--222-2222-	-3-22--3	--221-2--2--	2------	-----	-------
Pseudupeneus pray.	21--22	----2-21-----------2-11---	12322	222-1311211122-13-	1-------	---3--3-----	-------	-----	-------
Syacium micrurum	21--2-	1-11----1----------22221--	---13	33322232222222-122	------1-	--1--1-2----	-------	-----	-------
Fistularia petimba	11--22	--------------------------	23-2-	---222-1211222-22-	--------	3-1---------	-------	-----	-------
Trachynocephalus m.	31---1	--------------------------	----2	2323-3333--1--1-1-	--------	------------	-------	-----	-------
Trachinus armatus	------	--------------------------	-2-12	22133--13-----2---	--------	------------	-------	-----	-------
Sparus caeruleosti.	323-3-	-------------------2------	33444	4----3--34--2--24-	--------	------------	-------	-----	-------
Acanthurus monrov.	----3-	--------1-----------------	4-43-	------------------	--------	------------	-------	-----	-------
Lutjanus fulgens	----2-	--------------------------	32544	------------------	--------	------------	-------	-----	-------
Sparus auriga	------	--------------------------	1-4-3	------------------	--------	-------1----	-------	-----	-------
Plectorhynchus med.	------	--------------------------	--533	------------------	--------	----------3-	-------	-----	-------
Octopus vulgaris	------	--------------------------	-----	---12--1-322-2-2--	----2---	-1-23-------	-2-----	-----	-------
Sepia officinalis	22-2-2	----22-3--------------2---	-333-	34233333233323232-	23322-23	-2-3--------	-------	-----	-------
Alloteuthis afric.	------	--------------------------	-----	--1-2-----2-2-23-2	1-----21	222-------11	-------	-----	-------
Pagellus bellottii	------	-------------------------3	-2-33	333334233-2313343-	32333-33	443433424333	-------	-----	-------
Chelidonichthys ga.	------	--------------------------	----3	33334-333--122---1	-2--2-32	232323323222	-------	-----	-------
Epinephelus aeneus	------	--3-----------------21----	--434	2-------------323-	2-----34	33--3---33-3	-------	-----	-------
Saurida brasilien.	------	2--------------1----------	-----	123---2--322-21211	22343244	322---3-22-2	-------	-----	-------
Trachurus trecae	------	--------------------------	-----	2--------1--------	3-334234	-313424452-1	-------	-----	-------
Spicara alta	------	--------------------------	-----	---------------1--	---1----	---133-41222	-------	-----	-------
Priacanthus arenat.	------	--------------------------	-----	------2------2-22-	----2--2	----33323---	-------	-----	-------
Boops boops	------	--------------------------	--323	------2-2---------	---1-1--	2312423443-1	-------	-----	-------
Citharus linguatula	------	--------------2----2-----2	-----	-------2-----2----	22232312	22-3--1-32-1	--1----	-----	-------
Dentex congoensis	------	--------------------------	-----	---------3---3-1--	---1--2-	43-344445333	2----3-	-----	-------
Lepidotrigla car.	------	--------------------------	-----	----1--1---1-2-1--	---2----	-2-3233232-2	2------	-----	-------
Sepia bertheloti	22--2-	---------------1----------	---23	-----233222--2---1	--3-----	2213-2323-22	3------	-----	-------
Dentex canariensis	-2----	--------------------------	33434	---------3--1-----	---22--3	------32-2-2	-3-----	-----	-------
Torpedo torpedo	-----2	-------------------3---233	----3	2---2-2------1---2	-----322	----22---1--	22-----	-----	-------
Ariomma bondi	------	--------------------------	-----	-------------1-1--	---33--4	----44-3-1--	4------	-----	-------
Lepidotrigla cadm.	------	--------------------------	-----	---------1---2----	---32322	----333332-1	3-----2	-----	-------
Dentex angolensis	------	--------------------------	-----	---------------2--	---33333	-----322-233	2--3--3	-----	-------
Pentheroscion mbi.	------	-----------------------2--	-----	------------------	32333322	------------	-3-4---	-----	-------
Brotula barbata	------	--------------------------	-----	------------------	2--22222	-----2------	-323--3	-----	-------
Squatina oculata	------	--------------------------	-----	---------------2--	--------	----233-----	-333333	-----	-------
Parapenaeus longir.	------	-----------------------3-2	-----	------------------	21-22211	------------	1323322	-2-22	---1---
Pterothrissus bel.	------	--------------------------	-----	------------------	----23--	------------	23333-3	23334	-------
Zenopsis conchifer	------	--------------------------	-----	------------------	--------	------------	22123--	-2-1-	-------
Illex coindetii	------	--------------------------	-----	-------------1-11-	---32123	-----2---2-2	3233333	33233	323333-
Centrophorus uyato	------	--------------------------	-----	------------------	--------	------------	--4---4	3433-	-------
Merluccius polli	------	--------------------------	-----	------------------	---1----	------------	2222223	43444	3333---
Physiculus spp.	------	--------------------------	-----	------------------	-----1--	------------	--2112-	23333	3433-23
Neomerinthe folgori	------	--------------------------	-----	------------------	--------	------------	-----22	-2-23	3-1-2--
Benthodesmus spp.	------	--------------------------	-----	------------------	--------	------------	--3--21	22333	3222---
Polychaelidae	------	--------------------------	-----	------------------	--------	------------	--1----	3---2	2323333
Coelorinchus coel.	------	--------------------------	-----	------------------	--------	------------	----12-	-2222	3332333
Malacocephalus occ.	------	--------------------------	-----	------------------	--------	------------	-----1-	-2---	3333333
Etmopterus spp.	------	--------------------------	-----	------------------	--------	------------	------2	---3-	332222-
Aristeus varidens	------	--------------------------	-----	------------------	--------	------------	------1	3-1--	12112--
Nematocarcinus afr.	------	--------------------------	-----	------------------	--------	------------	-------	3-444	1------
Aristeus antennatus	------	--------------------------	-----	------------------	--------	------------	-------	-----	-222222
Yarella blackfordi	------	--------------------------	-----	------------------	--------	------------	-------	----2	-323322



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PAPER 4

The relative merits of using numbers and biomass in fish community studies

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ABSTRACT: In descriptions of fish communities, the question of which measure of abundance should be used, whether numbers or biomass, has never been addressed. While both measures are often available, the common practice is to use numerical abundance for such descriptions, without any explicit justification for this choice. In order to contribute to the clarification of this issue, we have compared correspondence analyses/TWIA-classifications performed on both the numerical density and the biomass of the same trawl catches from a region outside the western coast of Africa. The situation in which the quantitative aspect of the samples is disregarded, represented by presence/absence analyses, is illustrated for comparison. As it appeared likely that the length of the ecological or biogeographical 'gradient' would be of importance in how different the results of the two abundance measures would emerge, a series of subsamples of the total material, representing shorter ecological gradients was also analysed. The analyses show that in most situations the choice between numbers and biomass matters little. However, in the case of short ecological 'gradients', when all or the large majority of species are common to all samples studied, and the individual fish sizes are different, there may be a marked difference in the patterns shown by the alternative measures of abundance.

INTRODUCTION

In the quantitative description of animal communities, numerical abundance is most commonly used as abundance measure. This trend is also reflected in the study of fish communities (Day & Pearcy 1968; Markle & Musick 1974; Haedrich et al. 1975; Chavez 1979; Yañéz-Arancibia et al. 1980; Haedrich et al. 1980; Colvocoresses & Musick 1984; Mahon & Smith 1989; Bennet 1989; Costa 1986; Mas-Riera et al. 1991; Bergstad 1991), with the exception of a few, fishery-related studies, where it seemed more natural to use biomass values (Gabriel & Tyler 1980; Overholtz & Tyler 1984, McManus 1985 and 1989; Bianchi 1991). Presence/absence has also been used by some authors (Fager & Longhurst 1968; Warburton 1978; Vargas Maldonado et al. 1981; Lleonart & Roel 1984; Yañéz-Arancibia et al. 1985; Rainer 1984; Roel 1987).

While a number of authors have discussed which importance value to use in the description of community structures by, for example diversity measures, (e.g. Wilhm 1968 and Bechtel & Copeland 1970), in the case of the multivariate analytical techniques, used to identify species associations in a given sampling area, the question of which of these values should be used does not appear to have been seriously addressed.

In the present study we confine ourselves to considerations of the use of numerical abundance versus biomass in the case of multivariate analysis techniques to detect patterns of species associations by, in particular, (Detrended) Correspondence Analysis (DCA, Hill & Gauch 1980) and Two-Way Indicator species Analysis (TWIA, Hill 1979).

MATERIALS AND METHODS

Materials. The data used in the present study are taken from the investigation on the demersal assemblages outside Congo and Gabon (Bianchi 1992b). The data were collected in January-February 1989, and comprise a total of 94 stations and 314 species. The geographical area included, and the equipment used, are described in Bianchi (1992b). Both numbers and biomass were recorded for each species caught in this survey, but only the biomass values were used in the analysis of the demersal assemblages. In the present article, analyses based on the numerical abundances are compared with equivalent analyses based on biomass values. Presence/absence values are included as well, whenever it was felt appropriate.

As there is reason to believe that the lengths of the environmental gradients covered are of importance for the inter-pretation of the results, several data sets representing ecological gradients of different lengths, are included in the study. Thus, in addition to the complete material (as presented in Bianchi 1992b) representing the longest gradient (approx. 9.4 S.D.-units), successive subsets of the total are used to represent shorter gradients. Thus a medium gradient (5.4 S.D.-units) is represented by a subset of 75 stations and 3 short gradients (2.6, 2.3, and 1.7 S.D-units) consist of 24, 21, and 16 stations respectively.

Methods. In line with the policy adopted in a series of papers by the first author, on the benthic assemblages outside the coast of several tropical areas, viz the Pacific coast of Central America (Bianchi 1991), Angola (Bianchi 1992a) and Congo-Gabon (Bianchi 1992b), DCA and TWIA have been singled out for detailed analysis. These techniques have been in common use among community ecologists for several years (e.g. Jongman et al. 1987), and should need no further introduction. The computer programs for the implementation of DCA and other ordination techniques are all included in the program package CANOCO (ter

Braak 1990). While a certain element of arbitrariness is introduced in DCA via the detrending procedure (see Jackson & Somers 1991), this is probably of no concern as long as the same method is used throughout. In the present case, the default value (26) of number of segments in the detrending procedure is used.

TWIA (implemented by the program TWINSPAN, Hill 1979) produces a hierarchical classification in which the number of groups is doubled at each division level. Thus at division level one, two groups are generated, four groups at level two, and so on. TWIA is related to (D)CA in the sense that the ranking of the stations is based on the first (D)CA-axis. However, the way the abundances are used in these two programs are different. While abundance values are used as input to DCA, in TWIA, the abundance values are replaced by so-called pseudospecies. The pseudospecies cut levels for numerical abundance were set to reflect the range of abundances in the data set (0, 10, 100, 1000 and 10 000). The cut levels for biomass were chosen so that a rough correspondence to the categories used for numerical abundance was established, thus facilitating comparison between the results. The mean weight for all fishes caught was calculated, and cut levels roughly corresponding to 10, 100, 1000, and 10 000 such 'average' fishes were selected. The resulting cut levels were then rounded to 0, 0.5, 5, 50, and 500 kgs.

Presence/absence was used as an 'abundance measure' in two ways: To serve as a comparison with numerical abundance and biomass for the data sets representing the three longest gradients in the DCA, and, with the help of TWINSPAN, to define 'independent' groups of reference stations for all the data sets. For the two longest gradients, the number of groups thus defined was eight, while the number of groups varied between four and seven for the three shortest gradients. The TWINSPAN groups defined in this way were used to identify and circumscribe faunally-related stations in the various DCA plots, with the four groups generated at level two of TWINSPAN as main groups, and the extra groups generated at level three as subgroups.

Both numerical and biomass values were $\ln(x+1)$-transformed before analysis with DCA. This is common practice in community studies to reduce the influence of aberrant high values, give less weight to dominant species, and thus to increase the weight given to the qualitative aspect of the data.

The results from the DCA analyses based on numerical abundance and biomass (DCAn and DCAb) were compared by RDA (Redundancy Analysis), the canonical form of PCA (Principal Component Analysis). The Pearson product-moment-, and Spearman rank correlation coefficients between the station scores on each of the four axes obtained from DCAn and DCAb are also presented.

The station scores from DCAn and DCAb were used as analogues of species abundances and environmental variables respectively, in the input to RDA. To test the hypothesis that the results from the two ordinations are completely independent, a Monte Carlo permutation test was performed, using the residuals after fitting 'environmental' (i.e. DCAb) variables (ter Braak 1990). As this hypothesis was rejected for all our data sets, and the F-type test criterion was considered unsuitable for comparing the results across different gradient lengths, the sum of all canonical eigenvalues (trace) was used as a measure of how well the two sets agreed. As the sum of all unconstrained eigenvalues in PCA/RDA is always equal to 1 (because of the scaling of the species data, ter Braak 1990), in this case the sum of the canonical eigenvalues is equal to the ratio between the two sets.

The results from TWINSPAN were compared by calculating the proportions of stations common to corresponding clusters at each level of classification. This was done with a variant of the Jaccard index of similarity:

$$S_j = \frac{\sum_{i=1}^{m_j} c_i}{\sum_{i=1}^{m_j} (a_i+b_i+c_i)}$$

where Sj expresses the similarity between the classifications derived from numerical and biomass abundances, for division level j; mj is the number of clusters at division level j; ci is the number of shared elements of the ith cluster; ai and bi are the elements unique to the ith cluster of each classification. Sj varies between 0 (no element in common in any of the clusters) and 1 (all elements in corresponding clusters are shared).

RESULTS

Long gradient. Fig. 1 shows all 94 Congo-Gabon stations in a plane defined by the first two DCA-axes, based on numerical abundance (upper) and biomass (lower). Table 1 shows the eigenvalues and the gradient lengths for both of these abundance measures, as well as for presence/absence data. The first axis of this data set covers a gradient of about 9 standard deviations and the stations are arranged from left to right according to increasing depth (from about 10 to 750 m depth). The similarity between the two plots is striking and the various station groups lie in similar positions and with approximately the same degree

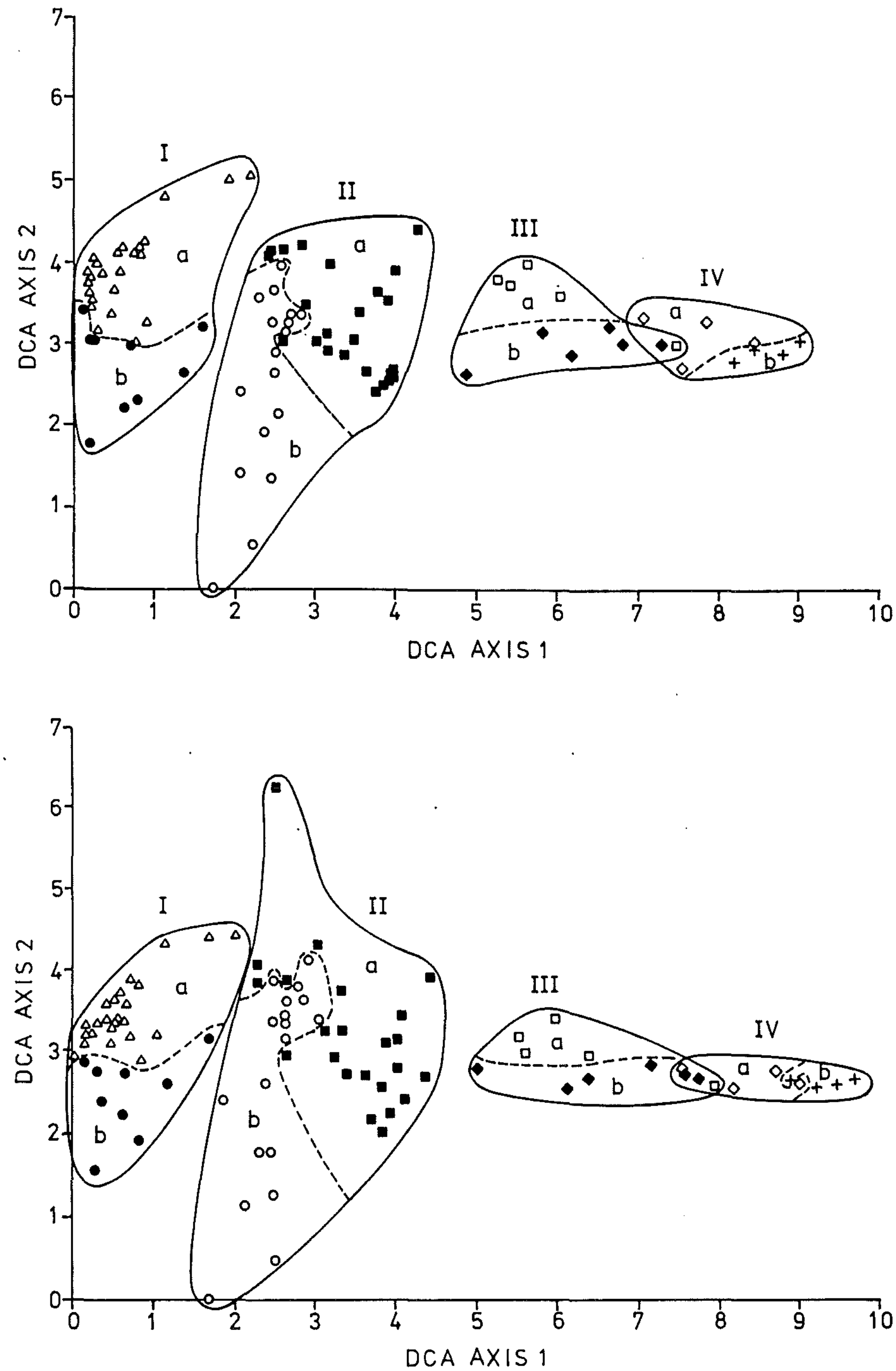


Figure 1. Detrended correspondence analysis of the 94 stations of the Congo-Gabon material, long gradient (SD units). Upper: plot based on numerical abundance; lower: based on biomass. The eight groups from TWINSPAN based on presence/absence data.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue				
DCAn	0.883	0.415	0.335	0.256
DCAb	0.907	0.467	0.381	0.285
DCAp/a	0.868	0.424	0.326	0.247
Length of gradient				
DCAn	8.7	4.9	3.3	3.3
DCAb	9.4	6.0	3.2	5.0
DCAp/a	8.6	5.0	3.2	4.0

Table 1. Eigenvalues and lengths of environmental gradient (SD units) for the first four Axes of DCAn, DCAb and DCAp/a,long gradient

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue				
DCAn	0.746	0.455	0.266	0.183
DCAb	0.773	0.482	0.411	0.254
DCAp/a	0.697	0.430	0.246	0.191
Length of gradient				
DCAn	5.1	5.2	3.4	2.8
DCAb	5.4	5.0	5.3	5.0
DCAp/a	5.0	4.7	3.7	2.3

Table 2. Eigenvalues and lengths of environmental gradient (SD units) for the first four Axes of DCAn, DCAb and DCAp/a, medium long gradient

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue				
DCAn	0.401	0.226	0.147	0.062
DCAb	0.365	0.257	0.143	0.095
DCAp/a	0.389	0.221	0.148	0.100
Length of gradient				
DCAn	2.5	2.3	1.7	1.3
DCAb	2.6	2.2	2.1	1.8
DCAp/a	2.5	2.2	1.7	1.7

Table 3. Eigenvalues and lengths of environmental gradient (SD units) for the first four Axes of DCAn, DCAb and DCAp/a, short gradient (24 stations)

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue				
DCAn	0.281	0.168	0.102	0.038
DCAb	0.311	0.181	0.117	0.086
Length of gradient				
DCAn	2.3	1.7	1.4	1.3
DCAb	2.4	2.0	1.7	1.5

Table 4. Eigenvalues and lengths of environmental gradient (SD units) for the first four Axes of DCAn and DCAb, short gradient (21 stations)

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue				
DCAn	0.230	0.172	0.109	0.039
DCAb	0.245	0.170	0.067	0.031
Length of grad.				
DCAn	1.7	1.7	1.5	1.2
DCAb	1.8	1.8	1.5	1.2

Table 5. Eigenvalues and lengths of environmental gradient (SD units) for the first four Axes of DCAn and DCAb, short gradient (16 stations)

of overlap between groups. However, some minor differences in the position of a few stations are apparent, especially along the second axis. In particular, the uppermost station (in subgroup IIa) in the biomass plot appears as an outlier. This is due to the presence of some rare species, combined with relatively low biomass for the common species. These common species still dominate in terms of numerical abundance, however, so that this particular station does not deviate from the majority of the stations in this subgroup in the DCAn plot. The apparent similarity between the two ordinations is confirmed by the high value of the trace (0.927, Table 6), as well as a very high F-ratio. The correlation (Table 6) between axis 1 in the DCAn and DCAb is very high, and still rather high for axes 2. For the lower axes the correlation is low or negative, and probably not significantly different from zero. The general impression is that the groups appear somewhat better defined and perhaps with less overlap in the DCAn than in the DCAb plot.

	Pearson	Spearman	RDA	
			overall F-ratio	trace
Long gradient (8.7, 9.4 SD)				
Axis 1	0.997	0.992	281.14	0.927
Axis 2	0.889	0.885		
Axis 3	0.657	0.054		
Axis 4	-0.124	-0.105		
Medium gradient (5.1, 5.4 SD)				
Axis 1	0.993	0.988	183.62	0.913
Axis 2	0.943	0.927		
Axis 3	0.499	0.328		
Axis 4	0.648	0.601		
Short gradient (2.5, 2.6 SD)				
Axis 1	0.975	0.951	19.98	0.882
Axis 2	0.838	0.843		
Axis 3	0.347	0.414		
Axis 4	0.568	0.278		
Short gradient (2.3, 2.4 SD)				
Axis 1	0.883	0.861	7.94	0.665
Axis 2	-0.016	0.014		
Axis 3	-0.511	-0.635		
Axis 4	0.257	0.300		
Short gradient (1.7, 1.8 SD)			4.03	0.594
Axis 1	0.866	0.900		
Axis 2	-0.088	-0.156		
Axis 3	0.020	-0.038		
Axis 4	-0.011	-0.021		

Table 6. Summary of the various correlations between scores from the DCA based on numerical abundance and biomass

As seen in Table 7, the correspondence is absolute between the two TWINSPAN classifications for level 1, and still very high for level 2. For levels 3 and 4 the correspondence is still acceptable, while there is a sharp decline for level 5.

TWINSPAN Division	Gradient				
	Long (9.4)	Medium (5.4)	Short (2.6)	Short (2.4)	Short (1.8)
1	1	1	1	0.83	0.60
2	0.94	0.90	0.85	0.52	0.45
3	0.81	0.83	0.55		
4	0.81	0.63			
5	0.62				

Table 7. Modified Jaccard similarity indexes (Sj) for TWINSPAN classifications based on numerical versus biomass abundance, for gradients of five different lengths

Medium gradient. To illustrate a medium long gradient (approx. 5 S.D.-units), the 75 samples constituting groups I and II from the first analysis were selected. This data set consists of the shelf stations down to about 200 m depth. Fig 2 shows the ordinations based on numerical abundances and biomass values respectively. Compared to the first analyses, the direction of the major gradient (axis 1) is now reversed. The similarity between the two ordinations is still high, reflected in a trace value only slightly lower than the one for the longer gradient, and is also apparent from the Pearson and Spearman correlation coefficients for the first two axes. There is actually a higher correlation between axes 2 than in the case of the long gradient (Table 6). The impression is still that DCAn results in somewhat more well-defined groups with higher resolution than DCAb, especially as regards the clear distinction between the two subgroups of group I. It is also obviuous that the eigenvalues and lengths of gradients for axis 2 are actually much higher relative to the values for axis 1, for the medium than for the long gradient (Tables 1 and 2).

The similarity between the TWINSPAN classifications for this gradient is perfect at the first division level, becomes slightly lower at the second and third, and drops abruptly at the fourth division level (Table 7). Thus only about 60% of the stations at this level are shared between the eight clusters of the classification based on numbers and the one based on biomass values.

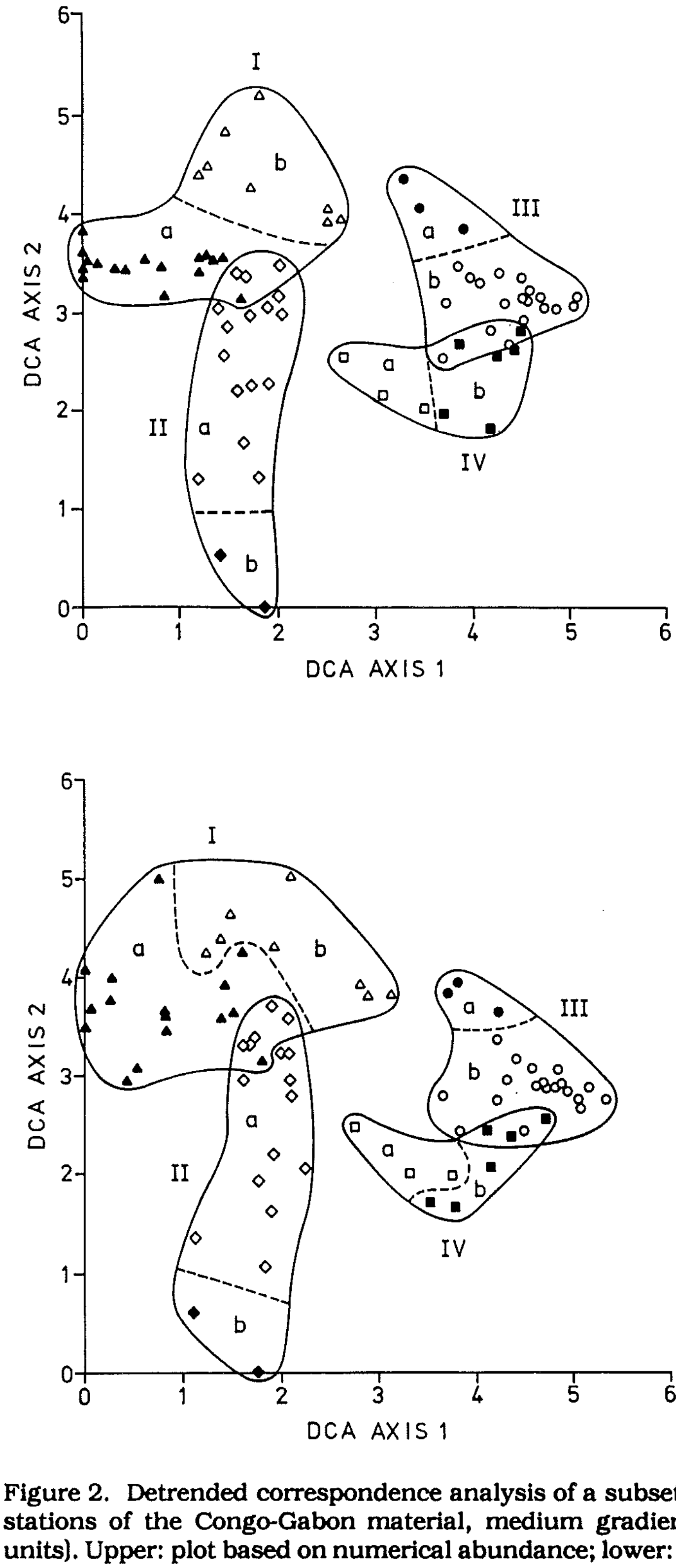


Figure 2. Detrended correspondence analysis of a subset of 75 stations of the Congo-Gabon material, medium gradient (SD units). Upper: plot based on numerical abundance; lower: based on biomass. The eight groups from TWINSPAN based on presence/absence data.

Short gradients. To illustrate a number of 'short' environmental gradients, the 24 stations belonging to group III in the plots used for medium gradient were selected. This data set was then further reduced in two steps, first by removing a group of three stations clearly separated from the remaining groups in Fig. 3, and finally a further five, somewhat scattered, stations, to show what happens with data sets representing really short environmental gradients below values of, say, two. Figs 3, 4 and 5 show the plots resulting from DCAn and DCAb for these data sets, representing about 2.5, 2.3 and 1.7 S.D.-units respectively. Visual inspection of the plots shows that the similarity is still very high in the case of the longest (24 station 'gradient') of the three 'short' gradients, while the correspondence falls off steeply between this and the next (21 station 'gradient') plots. This impression is confirmed by the values of the correlation coefficients in Table 6, where the trace for the RDA analysis is still high for the 24 station plots while it falls off to a significantly lower level for the remaining plots. The same result is shown by the correlation between individual axes, for which an apparent discontinuity in the gradual decline of these values is seen between the 24 station values and the ones for the 21 station analysis. This is mainly due to a change in ranking of the axes, as the former axis 1 becomes axis 2 after removal of the three stations in groups III and IV in Fig. 3. Thus the correlation between axes 1 falls from 0.98 to 0.88, while that for axes 2 falls from 0.84 to zero, for this small drop in length of environmental gradient (from 2.5 and 2.6 in the former case to 2.3 and 2.4 in the latter). While it is still fairly easy to identify corresponding groups in the two DCA plots for the 24 station 'gradient', such an identification is only possible with some difficulty for two or three of the subgroups in the plots for the 21 station 'gradient', and none of the groups in the 16 station 'gradient' plots can be so identified. The dramatic drop in the F-ratios from the medium to the short gradients as shown in Table 6, is less easily interpreted. The comparisons between the TWINSPAN classifications (Table 7) show that while, for the 24 station classification, the correspondence is still excellent to good for the first two levels (down to 0.55 at the third level, however), only for the first level an acceptable correspondence remains for the 21 station classification, and very little, if any, similarity is evident for the two levels shown for the 16 station classification.

DISCUSSION

When discussing the relative merits of various measures of abundance (or 'importance value') for multivariate analyses of animal communities, it is important to take into account the purpose of the investigation, as well as the nature of the data. Thus, in a purely exploratory survey, when the sole purpose is to establish coarse 'associations' of organisms living in a particular geographical region, it is probably unnecessary to proceed beyond presence-absence. The only condition is that the samples (or catches) are large

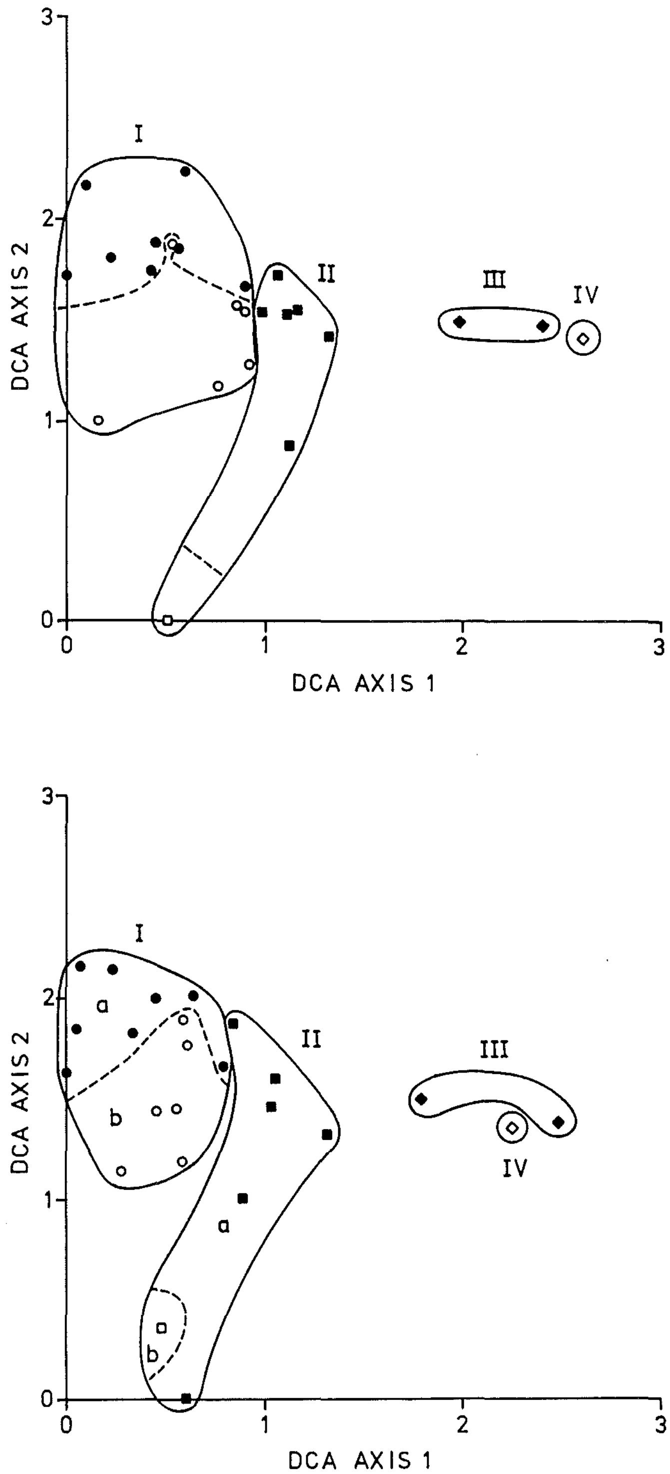
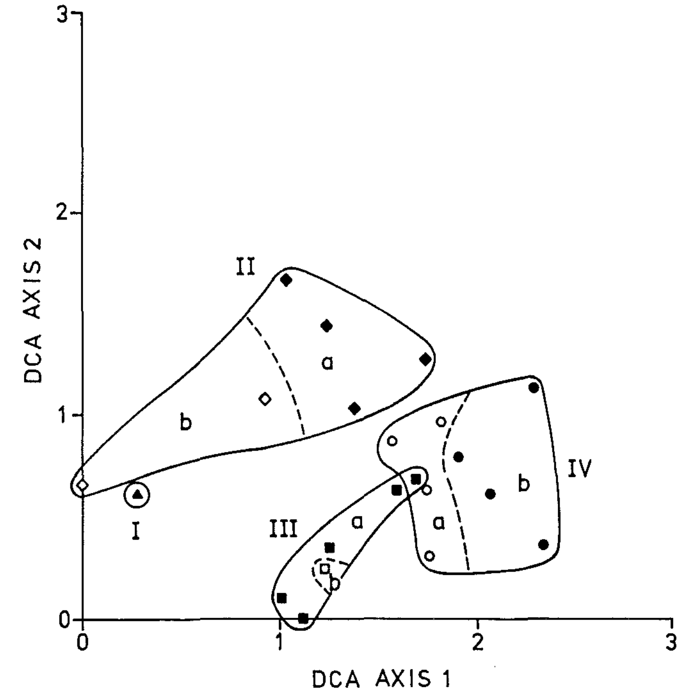


Figure 3. Detrended correspondence analysis of a subset of 24 stations of the Congo-Gabon material, short gradient (SD units). Upper: plot basedon numerical abundance; lower: based on biomass. The four groups from TWINSPAN based on presence/absence data.



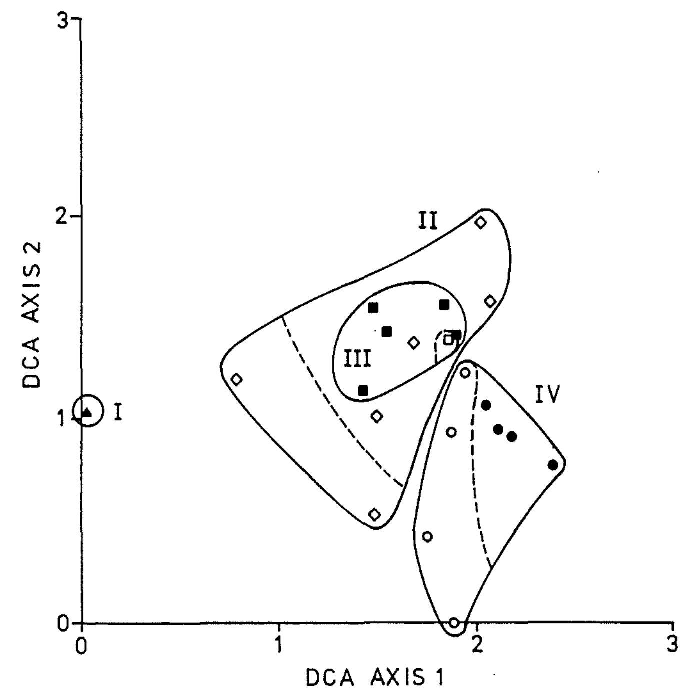


Figure 4. Detrended correspondence analysis of a subset of 21 stations of the Congo-Gabon material, 'shorter' gradient (SD units). Upper: plot based on numerical abundance; lower: based on biomass. The four groups from TWINSPAN based on presence/absence data.

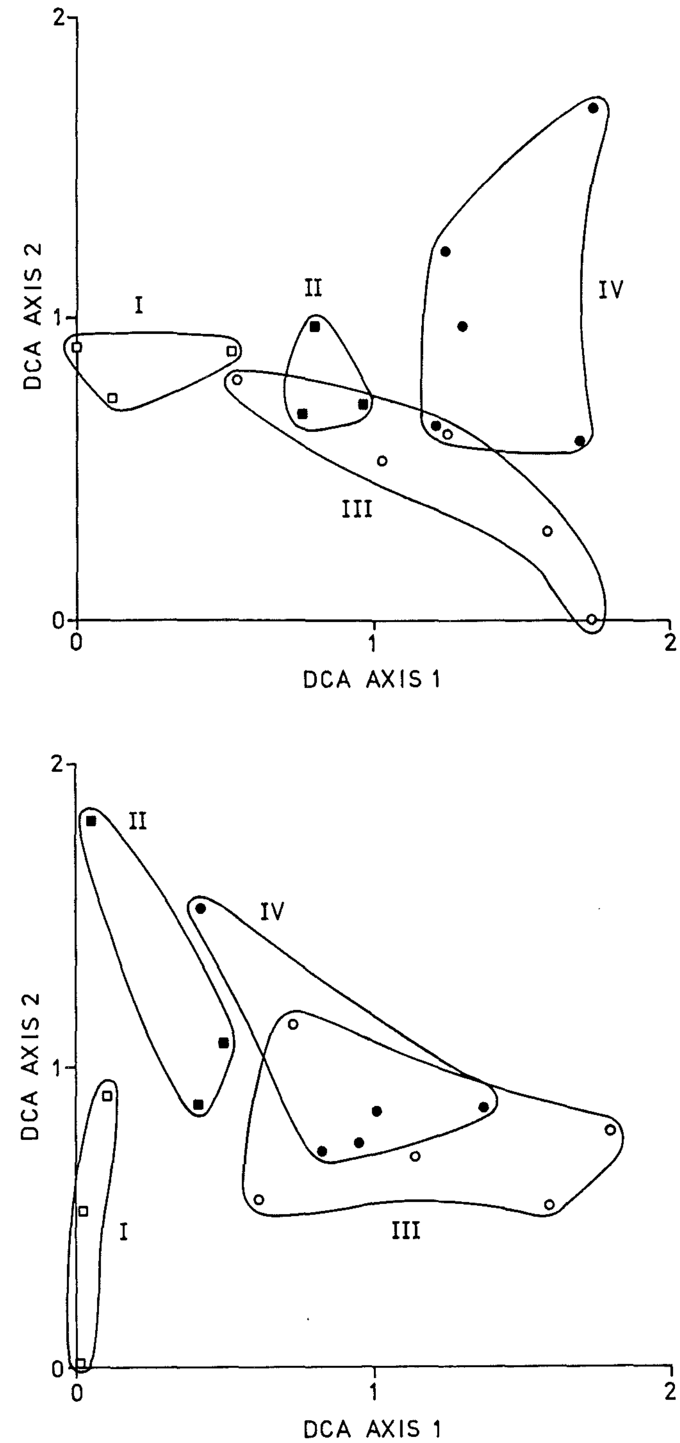


Figure 5. Detrended correspondence analysis of a subset of 16 stations of the Congo-Gabon material, shortest gradient (SD units). Upper: plot based on numerical abundance; lower: based on biomass. The four groups from TWINSPAN based on presence/absence data.

enough for the stray singletons to be unimportant. In cases when finer detail is wanted, and especially when correlations with environmental or biotic data are to be established, the choice between numbers (or numerical density) and biomass could be critical. Of course, if all the organisms of interest are more or less of the same size, the distinction will become academic, and can safely be ignored. In comparing fish communities, especially if based on trawl catches in which a wide spectrum of size categories is represented, the choice could be critical, however. The problem of which value (either numbers or biomass) should be representative of species abundance in community studies rises just because there is usually a wide variation in individual weight among species and within the same species at different ages.

It appears from our study that the choice between these two abundance values is not critical in the case of community analyses based on methods related to Correspondence Analysis, including TWINSPAN. This is true for data sets covering long gradients, while a clear decreasing correspondence is shown when analysing short gradients.

There is a high degree of correspondence between the plots based on numbers and biomass for the three longest environmental gradients, while the correspondence deteriorates rapidly somewhere between a gradient of 2.6 and 2.3 S.D.-units (Table 6 and 7). Thus, while much valuable information is to be gleaned from a juxtaposition of the two categories of plots, for most investigations covering long environmental gradients (more than about 2.5 S.D.-units), biomass and numbers seem to be about equally suitable as abundance measures for exploratory studies of fish communities. The increase in correlation between axes 2 from the long to the medium DCA's (Table 6), may be because the influence of the outlier station in the long gradient biomass plot, is much reduced in the corresponding medium gradient plot.

The reason for the similarity in the results of ordinations/classifications using different types of abundance data can be explained by the nature of CA and related methods. The double standardization implied in the algorithm (to species total for a species and to site total for a site) reduces the quantitative aspect of the data. For this reason, and particularly if the data have been log-transformed, the differences between the use of numbers or biomass will be minimal. This is obviously true only when the data analysed cover long gradients, i.e. where there is a clear succession of species along a gradient, in the area covered. In the case of short gradients as for example in the extreme case where all species are common to all sites, the quantitative aspects will become more important and the differences in the results based on numerical abundance and biomass will become more conspicuous.

The two different aspects implied in abundance data viz the **qualitative** aspect (presence or absence of the species) and a the **quantitative** aspect i.e. regarding differences in abundance when the species is present are thus differently stressed depending on the multivariate analysis techniques used and/or the length of the ecological gradient covered by the data set.

The generality of these conclusions may of course be challenged on the grounds that this particular data set is incapable of illustrating the many facets of natural fish communities representing various environmental/biogeographical gradients. A more ideal approach would probably be to analyse a series of simulated fish communities, in which the environmental gradient is varied over a broad spectrum, and various levels of noise are introduced. With the fragmentary knowledge of the assemblage rules for fish communities, this possibility is not very realistic at the moment, and we could not see any realistic alternative to the present investigation for our purpose. Another possible objection to the generality of the results is that other multivariate methodologies might be more sensitive to the choice of abundance measures than DCA and TWINSPAN, and we do not of course claim that our conclusions could be extrapolated to other such methods.

An investigation of this type is incapable of settling the question of which abundance measure is 'best', whenever the correspondence between two alternatives is small or nonexistent. When, as in this case, the correspondence falls from excellent or good to dismal with a shrinking environmental gradient, it may be suspected to be due to the fact that there is really no natural pattern in the data, and that any attempt at grouping would be equally meaningless. A possible explanation for lack of meaningful patterns in material of this kind, is the presence of sampling 'noise', which would be more serious the shorter the gradient sampled. The potential effects of such sampling noise cannot be disregarded in our chosen example. A trawl of the kind used in this investigation is not at all immune to such criticism, and both the way it works, as well as seasonal and diurnal variations in the swimming behaviour of the animals sampled, will influence the reproducibility of the catches. Thus it is perhaps best to restrict this kind of investigation to environmental gradients longer than approx. 2.5 S.D.-units. In the spirit of Gordon (1982, p. 134), it might be wise only to accept as 'good' groups, those clearly identifiable from analyses of both numerical abundance and biomass.

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PAPER 5

Demersal assemblages of the Northern coast of South America (Orinoco River to Maroni River)

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Abstract - Exploratory data analyses were performed on two sets of data from the trawl surveys of the R/V 'Dr. Fridtjof Nansen' off the northern coast of South America, from the mouth of the Orinoco River (Venezuela) to the Maroni River (border between French Guyana and Suriname). Detrended Correspondence Analysis (DCA) and Two-Way Indicator Analysis (TWIA) showed that the main faunal discontinuity is found in the transition from the shallow-water assemblages to the intermediate and deeper shelf assemblages. Comparison with results from previous surveys indicate some important changes in the abundance of some commercially important fish species, especially the whitemouth croaker Micropogonias furnieri (Desmarest).

INTRODUCTION

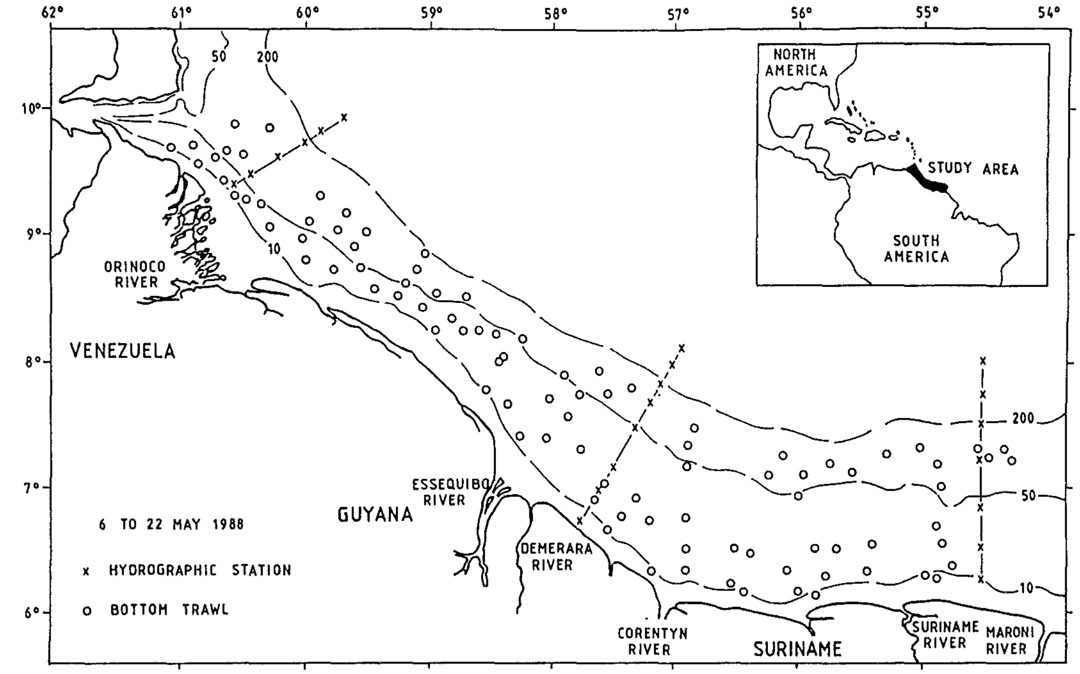
The area under study has been covered by several resources surveys since the mid forties, the main aim of which has been to assess the fishery resources of the continental shelf. Species groups and communities have been described by several authors in the light of the ecological conditions found in the area. In the period 1957-59, the RV 'Cape St. Mary' investigated the demersal trawl potential off Guyana (Mitchell & McConnell 1959). This survey also produced important information on the marine fish fauna of that area, its distribution and biology and a description of the recurrent species groups (Lowe-McConnell 1962, 1966). The R/V La Salle surveyed the area under study (from Trinidad to Suriname) in 1967, covering mainly the shallow coastal areas (Gines & Cervigon 1968). In the period 1980-1981 a trawl survey was conducted by the R/V Bonito (Losse 1982) but the results consisted mainly in catch rates of major resources groups.

In 1988 the Norwegian R.V. 'Dr. Fridtjof Nansen' carried out four acoustic and trawl surveys of the continental shelf off Suriname, Guyana and Eastern Venezuela, i.e. between the Maroni and the Orinoco Rivers. A report including standing stock biomasses for the main resource groups, catch rates as well as a description of the physical environment has already been issued (Strømme & Sætersdal 1989). This study is based on two of the above surveys, chosen to represent the most extreme climatic conditions of this area, and is aimed at investigating species associations occurring in the bottom trawl, correlate them with the ecological conditions found in the area by using multivariate analysis techniques and compare these with the previous descriptions based on a more subjective base. The approach is similar to other studies covering the Eastern Central Pacific (Bianchi 1991), Angola and Congo-Gabon (Bianchi 1992 a & b).

STUDY AREA

The study area (Fig. 1) comprises the shelf off Suriname, Guyana and eastern Venezuela, from the Maroni River estuary to the Orinoco Delta. The continental shelf is widest off the Maroni River estuary (about 100 nautical miles) and narrows toward Trinidad to about 35 nautical miles. The shelf break lies at depths of 90 to 100 metres. The continental slope is very steep and falls to depths of several thousand metres within a few miles from the coast (Strømme & Sætersdal 1989). The topography is rather smooth, with soft mud deposits inshore, to 40 to 60 m depth, originating from the many rivers among which the Orinoco, the Essequibo, the Suriname, the Maroni are the largest. Some of the deposits also originate from outside the area, particularly from the Amazon River. Large migrating mudbanks (slingmud) are found near the coast with the result that depths near the coastline are always changing. These banks were observed in the course of the 'Dr. Fridtjof Nansen' surveys and made bottom trawling impossible in those locations. The coastal zone is easily recognizable because of the green-brown colour of the water. The mud deposits are the substratum for a rich invertebrate fauna forming the main food item of many bony fishes and several species of sharks and rays. At greater depths, to the shelf edge, sandy or rocky bottoms become predominant. The depth extent of the above zones may be different along the shelf, especially in front of major rivers where the muddy substratum is wider (Gines & Cervigon 1968) or where the shelf slopes more abruptly and mud sediments are found in deeper waters as well as in the north-west section of the British Guyana shelf (Lowe-McConnell 1962). The overlying waters are first greenish and become definitely blue at the edge of the shelf. As off West Africa, the rocky bottoms consist of relics of coral reefs, growing there when the sea level was lower during glacial epochs (Lowe-McConnell 1987). The extent of 'brown' water occurring inshore is variable and depends on tidal movements and seasons.

The climate in this region is tropical with high mean annual temperatures (above 25 °C). There is one main rainy season, from about July to September, associated with the Intertropical Convergence (ITCZ). This period is also characterized by the weakening of the North East trade winds, otherwise blowing throughout the year.



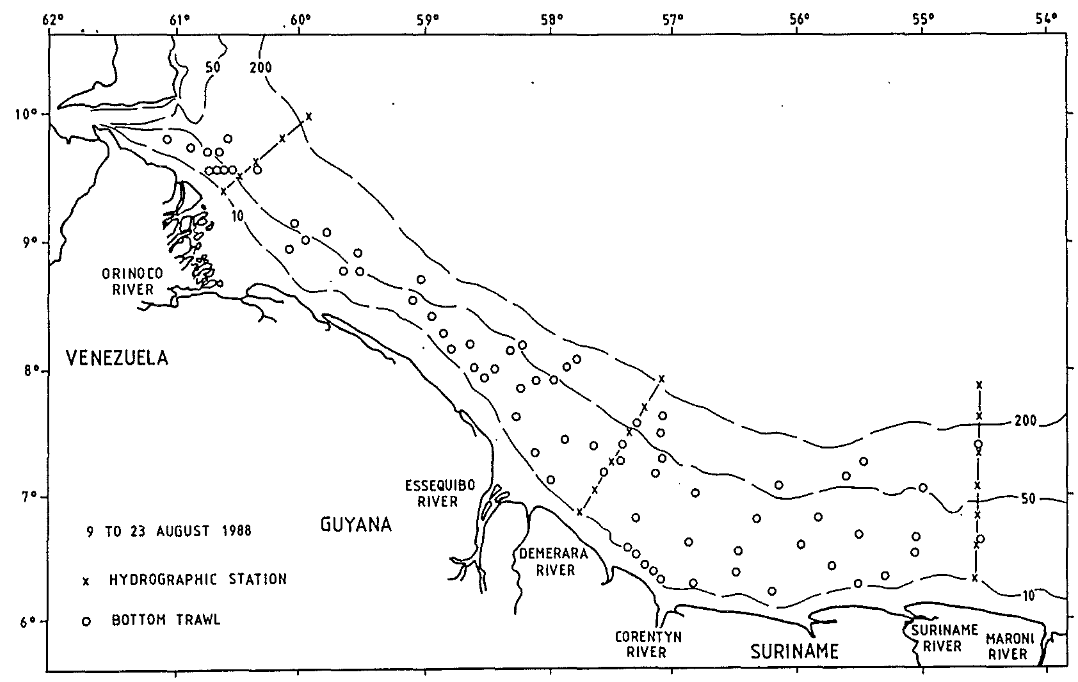


Figure 1. Position of trawl hauls and hydrographic stations. Upper: May 1988; lower August 1988

Circulation in the upper layers of the area is largely derived from the North and South Equatorial Current systems, their strength varying seasonally with the intensity of the North East and South East Trade winds. When the westward flowing South Equatorial Current reaches the eastern Brazilian coast, it splits into a northwest and southern branch. The northwest branch flows on the Guyana's and Suriname shelves (known as Guyana Current), after joining the southern branch of the North Equatorial Current. One of the main effects of the flowing of the Guyana Current in the area under study, is the transport of freshwater and sediments originating from the Amazon and the many other rivers along the north east coast of South America.

The survey report (Strømme & Sætersdal 1989) provides a description of the hydrographic conditions at the time of the surveys. No sharp thermocline develops at any time of the year and high temperatures (above 22 °C) and oxygen levels (above 3 ml/l) are found throughout the shelf. A limited region with low oxygen content close to the bottom was observed in August west of the Orinoco River, possibly cruised by the high production, due to the increase in the water runoff in this period, and limited exchange. Temperature, salinity and oxygen profiles from data collected in the course of the 'Dr. Fridtjof Nansen' surveys are presented in Figs. 2, 3 and 4.

Salinity is much lower in nearshore areas and in surface waters in the summertime. The upper layer of low density water must affect negatively the supply of nutrients which otherwise occurs, although in a limited form, the rest of the year. In fact, the sloping of the isotherms observed outside the summer season could represent a weak upwelling in subsurface waters which, although not very strong, might represent a major process affecting primary production on the shelf region (Gade in Strømme & Sætersdal 1989). This upwelling can be ascribed to the presence of a surface ocean current, viz the Guyana Current.

Wind-driven upwelling does not occur (the main winds blow toward the coast) and the main source of nutrients probably comes from the river discharges.

MATERIALS AND METHODS

Trawl data. Material was collected on two cruises in 1988 (5 to 22 May and 12 to 22 August), chosen to represent the most extreme climatic conditions (dry/windy and rainy/calm respectively). The gear used, the same as in all the 'Dr. F. Nansen' surveys was a shrimp and fish trawl, with mesh size of 2 cm and double lining in the cod end. Each tow

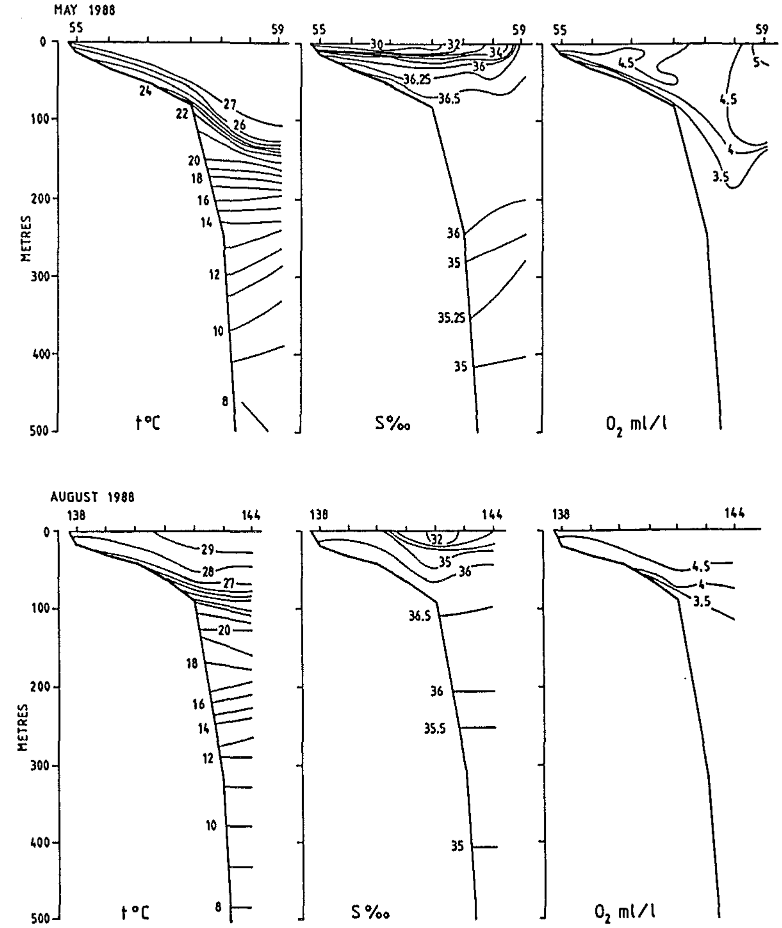


Figure 2. Hydrographic profiles for temperature, salinity and oxygen, west of Maroni River (see Fig 1 for position). Redrawn from Strømme & Sætersdal 1989

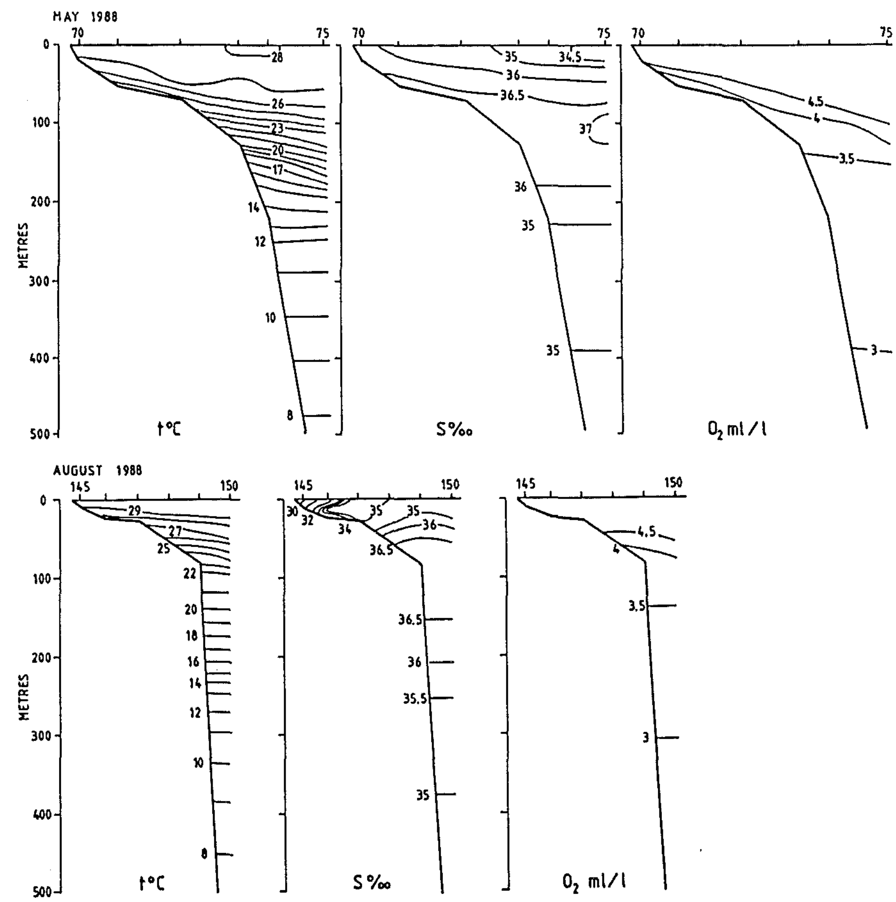


Figure 3. Hydrographic profiles for temperature, salinity and oxygen, east of Demerara River (see Fig 1 for position). Redrawn from Strømme & Sætersdal 1989

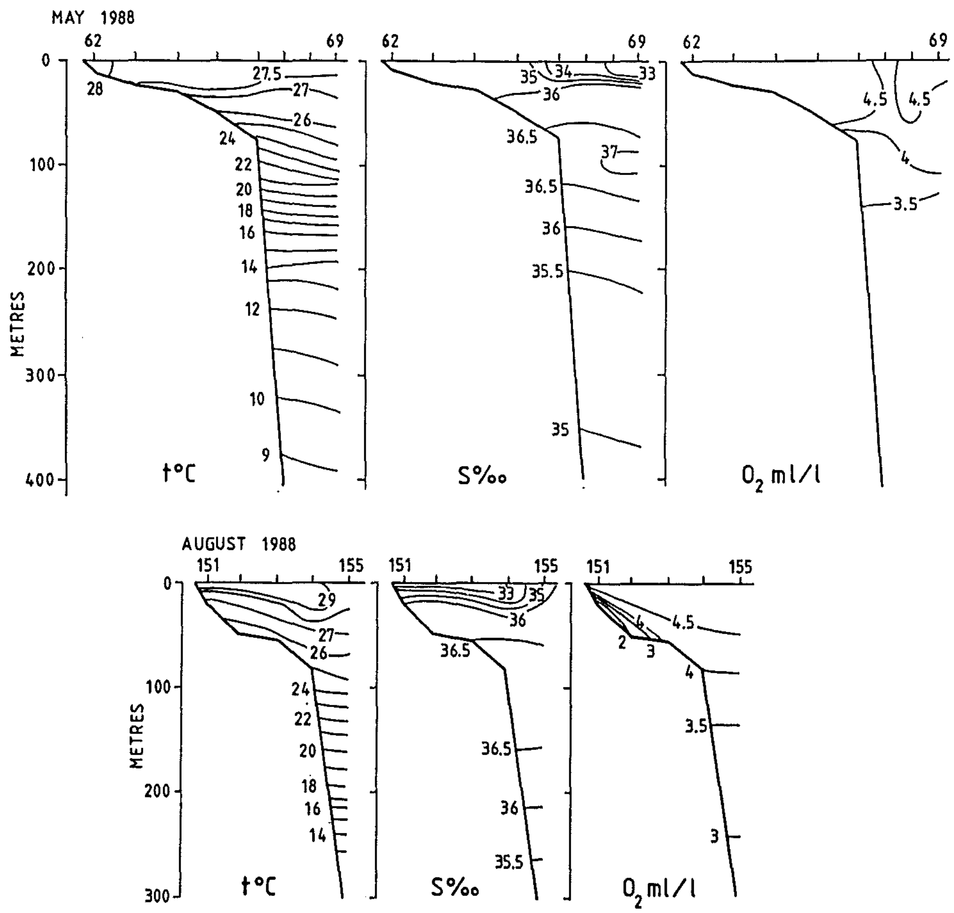


Figure 4. Hydrographic profiles for temperature, salinity and oxygen, Orinoco (see Fig 1 for position). Redrawn from Strømme & Sætersdal 1989

had a standard duration of 30 minutes. Other details on the gear used may be found in Strømme and Sætersdal (1989). The bottom trawl stations used in this analysis were randomly set along the cruise track. A total of 94 and 72 stations were included in the analyses for the above surveys, respectively (Figure 1). About 30% of the stations were sampled during nighttime in both surveys. These are indicated and differences in day-night compositions are discussed whenever relevant.

A total of 247 species, 34 354 kg and 1 388 386 individuals where sampled in the course of the May survey while the corresponding figures for the August survey were 221, 19 924 and 1 246 684. Table 1 gives the main species identified in the course of the surveys. Each specimen caught was counted and weighed separately. For the present analysis congeneric species which were difficult to separate were pooled together. All station and species data were stored using NAN-SIS (Strømme, in press) and data available in ASCII format upon request to the author.

Table 1. List of main species collected in the study area, by major taxonomic groups and families. The asterisk indicates species belonging the endemic genera found on either side of tropical America

CEPHALOPODS

LOLIGINIDAE
Loligo plei Blainville
Loligo pealei LeSueur
Lolliguncula brevis (Blainville)

DECAPOD CRUSTACEANS

PALAEMONIDAE
Nematopalaemon schmitti (Holthuis)

PENAEIDAE
Penaeus brasiliensis Latreille
Penaeus notialis Perez-Farfante
Penaeus subtilis Perez-Farfante
* *Xiphopenaeus kroyeri* (Heller)

PORTUNIDAE
Portunus spp.

SHARKS

CARCHARHINIDAE
Carcharhinus limbatus (Valenciennes)
Rhizoprionodon porosus (Poey)

TRIAKIDAE
Mustelus canis (Mitchell)
Mustelus higmani Springer & Lowe

BATOID FISHES

RHINOBATIDAE
Rhinobatos percellens (Walbaum)

DASYATIDAE
Dasyatis geijskesi Boeseman

GYMNURIDAE
Gymnura micrura (Bloch)

BONY FISHES

ALBULIDAE
Albula vulpes (Linnaeus)

CLUPEIDAE
Chirocentrodon bleekerianus (Poey)
* *Harengula jaguana* (Poey)
* *Opisthonema oglinum* (LeSueur)
Pellona harroweri (Fowler)
* *Odontognathus mucronatus* (Lacepède)
Sardinella aurita Valenciennes

ENGRAULIDIDAE

* *Anchoa* spp.
* *Anchoa hepsetus* (Linnaeus)
* *Anchoa lyolepis* (Evermann & Marsh)
* *Anchoa spinifer* (Valenciennes)
* *Anchoviella lepidentostole* Fowler
* *Lycengraulis* spp.

ARIIDAE
Arius grandicassis Valenciennes
Arius quadriscutis Valenciennes
Bagre bagre (Linnaeus)
Bagre marinus (Mitchill)

SYNODONTIDAE
Saurida normani Longley
Synodus foetens Linnaeus
Synodus poeyi Jordan
Trachinocephalus myops (Forster)

OPHIDIIDAE
* *Lepophidium* spp.
* *Lepophidium profundorum* (Gill)
Ophidion spp.

BATRACHOIDIDAE
* *Porichthys* spp.
* *Porichthys pauciradiatus* Caldwell & Caldwell

SCORPAENIDAE
Scorpaena brasiliensis Cuvier

TRIGLIDAE
Prionotus punctatus (Bloch)
Prionotus stearnsi Jordan & Swain

DACTYLOPTERIDAE
Dactylopterus volitans (Linnaeus)

SERRANIDAE
* *Diplectrum bivittatum* (Valenciennes)
* *Diplectrum formosum* Linnaeus
* *Diplectrum radiale* (Quoy & Gaimard)
Serranus phoebe Poey

PRIACANTHIDAE
Priacanthus arenatus Cuvier in Cuv. & Val.

CARANGIDAE

Caranx crysos (Mitchill)
Caranx hippos (Linnaeus)
Chloroscombrus chrysurus (Linnaeus)
Carangoides ortrynter (Jordan & Gilbert)
Decapterus punctatus (Cuvier)
Hemicaranx amblyrhynchus (Cuvier)
* *Oligoplites* spp.
Selar crumenophthalmus (Bloch)
Selene setapinnis (Mitchill)
Selene vomer (Linnaeus)
Trachurus lathami Nichols

LUTJANIDAE
Lutjanus griseus (Linnaeus)
Lutjanus purpureus Poey
Lutjanus synagris (Linnaeus)
Pristipomoides macrophthalmus (Müller & Troschel)
Rhomboplites aurorubens (Cuvier)

GERREIDAE
* *Diapterus rhombeus* (Cuvier)
Eucinostomus spp.

HAEMULIDAE
* *Anisotremus virginicus* (Linnaeus)
* *Conodon nobilis* Linnaeus
* *Orthopristis ruber* (Cuvier)
* *Haemulon aureolineatum* Cuvier
* *Haemulon boschmae* (Metzelaar)
* *Haemulon plumieri* (Lacepède)
* *Haemulon steindachneri* (Jordan & Gilbert)

SPARIDAE
* *Calamus penna* Valenciennes
* *Calamus pennatula* Guichenot

SCIAENIDAE
* *Bairdiella* spp.
* *Ctenosciaena gracilicirrhus* (Metzelaar)
* *Cynoscion acoupa* (Lacepède)
* *Cynoscion jamaicensis* (Vaillant & Bocourt)
* *Cynoscion similis* Randall & Cervigon
* *Cynoscion virescens* (Cuvier & Valenciennes)
* *Isopisthus parvipinnis* (Cuvier)
* *Larimus breviceps* Cuvier & Valenciennes
* *Macrodon ancylodon* (Bloch & Schneider)
* *Menticirrhus americanus* (Linnaeus)
* *Micropogonias furnieri* (Desmarest)
* *Nebris microps* Cuvier
* *Paralonchurus brasiliensis* (Steindachner)
* *Stellifer* spp.
Umbrina coroides (Cuvier)

MULLIDAE
Upeneus parvus (Poey)

EPHIPPIDIDAE
Chaetodipterus faber (Broussonet)

POMACANTHIDAE
Pomacanthus arcuatus (Linnaeus)

SPHYRAENIDAE
Sphyraena guachancho Cuvier
Sphyraena picudilla (Poey)

TRICHIURIDAE
Trichiurus lepturus Linnaeus

SCOMBRIDAE
Scomberomorus brasiliensis Collette, Russo & Zavalla-Camin
Scomberomorus cavalla (Cuvier)

STROMATEIDAE
* *Peprilus paru* (Linnaeus)

ARIOMMIDAE
Ariomma bondi Fowler

BOTHIDAE
Cyclopsetta cittendeni Bean
Syacium spp.

BALISTIDAE
Balistes vetula Linnaeus

OSTRACIIDAE
Acanthostrascion quadricornis (Linnaeus)

Hydrographic data. Temperature, salinity and oxygen data were used in the present analysis to examine the relationships of the different species assemblages with the physical environment. For the above variables, values were assigned to each trawl station from the nearest hydrographic station at a similar depth. Details on sampling methods and on oceanographic data can be found in Strømme & Sætersdal (1989).

Data analysis. The primary objective was to identify major patterns of species associations from the trawl data and relate them to the more significant environmental factors. The methods used in the present study are the same as those used in Bianchi 1991 & 1992 a, b, i.e. Two-Way Indicator species Analysis (TWIA), implemented by the computer program TWINSPAN (Hill, 1979) and Detrended Correspondence Analysis (DCA) implemented by the computer program DECORANA (Hill & Gauch 1980). The suitability of these methods to this type of study is discussed in Bianchi (1991).

The relationship between station groups and environmental variables was analyzed using the DECORANA program in the package CANOCO (version 3.10, ter Braak 1990) which also has the option of correlating the first ordination axes with environmental variables (in this case depth, salinity, oxygen and temperature). This option also produces the mean and SD of the environmental variables for each group.

N2-diversity (Hill 1973) for each trawl station is presented graphically i.e. a DCA plot where each station is pictured by a symbol the size of which is directly proportional to its diversity index (Smilauer 1990). N2 diversity is the inverse of Simpson's index:

$$S_I = \sum_{i}^{s} \frac{n_i (n_i - 1)}{N (N-1)}$$

where n_i is the number of individuals of species i and N is the total number of individuals of all species.

In this study biomass (wet weight) was used as a measure of abundance. As shown in Bianchi & Høisæter (in press), results based on biomass or numerical abundance are almost identical when using the above methods over long ecological gradients. Logarithmic transformation (ln(x + 1)) was applied to the data before analysis with DECORANA. The 'cut levels' used to define the TWINSPAN pseudospecies were (in kg): 0, 0.5, 5, 50 and 500.

RESULTS

Appendix 1 (a and b) shows the two-way ordination of species and stations obtained with TWINSPAN for the May and August surveys respectively, and includes a dendrogram summarizing the hierarchical relationships between the various groups. In Appendix 1a (May survey) the first dichotomy separates the intermediate and deep shelf stations (Groups 1 to 3) from intermediate/shallow water stations (Groups 4 to 6). The values of the measured environmental parameters do not show any great variation, with high temperature and oxygen values and minor variations in salinity. The only clear trend is the decreasing values of depth from Group 1 to Group 6 (Table 2). At the second division level Group 1 (mostly night stations of intermediate shelf) separates from groups 2 and 3 while Group 4 devides from the shallowest stations (Groups 5 and 6). At the third division level, the deepest shelf stations (Group 2), typified by species of hard bottoms, separates from Group 3 (intermediate shelf stations and stations in the northern part of the area, outside the Orinoco Delta) and the two shallo-water groups further separate, also according to a depth gradient.

Table 2 . Average values and standard deviations (in parenthesis) of the environmental variables for station groups 1 to 6, May 1988

Stat. Groups	1	2	3	4	5	6
Number of st.	18	17	24	8	15	12
Env.variables						
Depth(m)	54 (21)	72(16)	38(16)	43(24)	26(8)	15(3)
Temper.(°C)	25.4(1.2)	23.7(1.3)	25.9(1.4)	25.4(1.7)	26.4(1.0)	26.9(0.8)
Salin.(‰)	36.2(0.2)	36.3(0.1)	36.3(0.2)	36.2(0.3)	36.2(0.3)	35.9(0.4)
Oxyg.(ml l^{-1})	4.0(0.4)	3.7(0.3)	4.2(0.4)	3.9(0.5)	4.3(0.3)	4.5(0.3)

In the August survey (Appendix 1b), the first division is located approximately in the same position as in the May survey (Fig. 5) while the subsequent divisions are different. At the second division level the stations of the intermediate and deeper shelf show a boundary perpendicular to the coast located approximately where the shelf narrows in an east-west direction. Groups 4 and 5, including the stations with shallower depth ranges, are this time characterized by higher temperature and lower salinity, which is related to the summer/rainy season (Table 3). Further subgroups seem to be due to day-night variations in the catches (Group 1 versus 2) or special conditions like the low oxygen levels found northwest of the Orinoco Delta (Group 6).

Figure 6 (upper and lower) shows the ordinations of the stations for the May and the August surveys, as obtained with the program DECORANA. The station groups show a

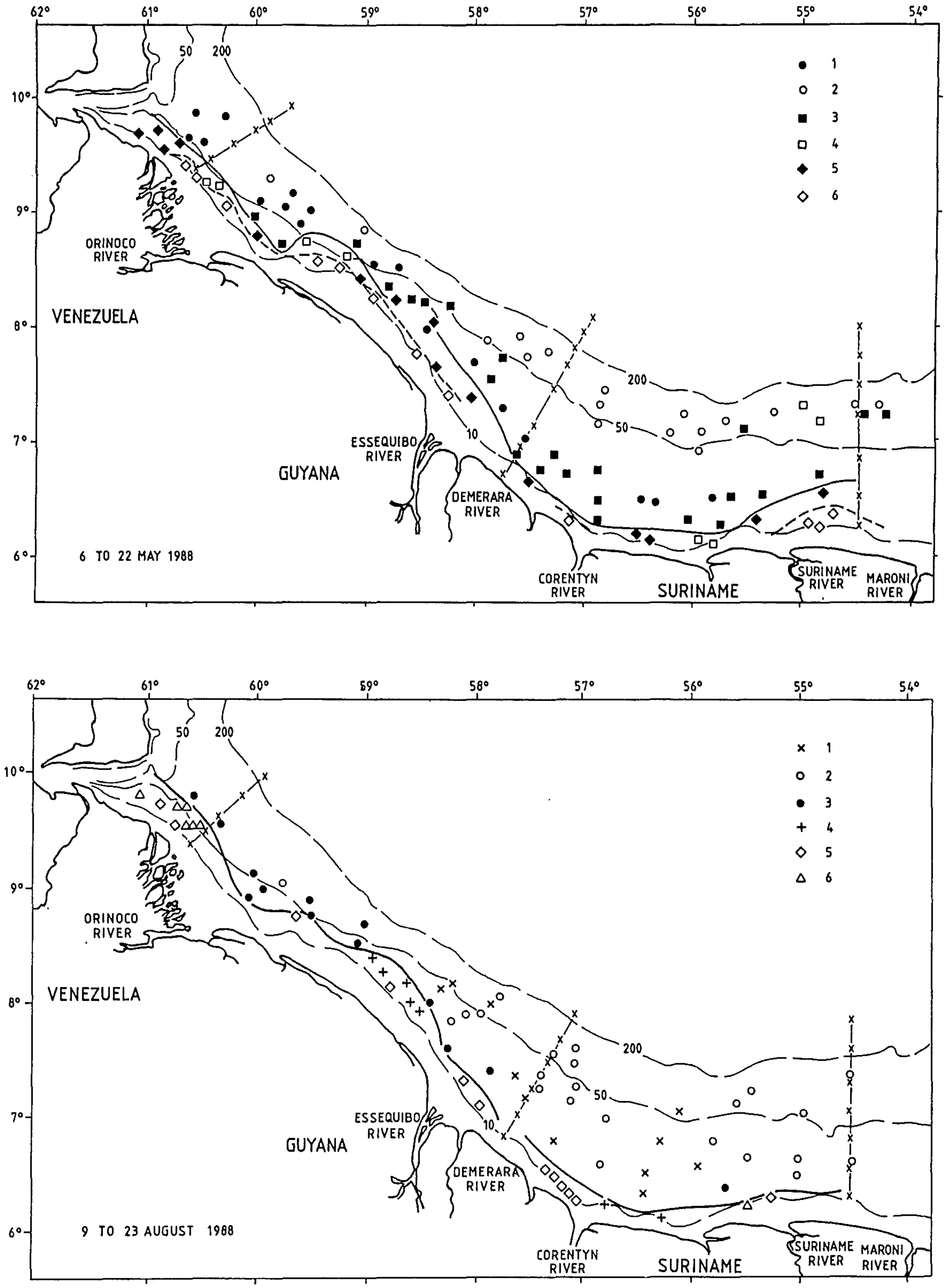


Figure 5. Maps showing the position of the stations after having being assigned to the different groups. Divisions based on TWIA divisive clustering. Upper: May survey; Lower: August survey

similar relationship as the one derived from TWINSPAN, but the DCA plot allows us to see the relationship along a second dimension (Axis 2). As for the May survey, this axis separates the night stations of soft bottoms (Group 1) from the intermediate stations sampled at daytime (Group 3) and the deeper shelf group (Group 2). Correlation of DCA Axis 1 with the environmental variables shows significant correlation in all cases, with depth having the highest correlation. Axis 2 is not significantly correlated with any variable and appears to represent mainly the day/night variations (Table 4).

Table 3. Average values and standard deviations (in parenthesis) of the environmental variables for station groups 1 to 6, August 1988

Stat. Groups Number of st.	1 11	2 24	3 11	4 7	5 12	6 7
Env.variables						
Depth(m)	37 (12)	49(19)	47(18)	25(5)	20(7)	35(13)
Temper.(°C)	26.9(0.8)	25.9(1.4)	25.9(1.2)	27.7(0.5)	28.1(0.9)	25.9(1.3)
Salin.(‰)	35.1(1.0)	35.8(1.0)	36.1(0.8)	33.9(0.7)	33.2(1.9)	36.3(0.2)
Oxyg.($ml\ l^{-1}$)	4.4(0.4)	4.1(0.4)	4.2(0.3)	4.8(0.1)	4.5(0.8)	2.8(0.9)

Table 4. Inter-set correlations between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations of the May survey, 1988. Values with asterisk indicate significant correlation ($p < 0.05$).

Variable	Axis 1	Axis 2
Depth	-0.77 *	-0.17
Temperature	0.59 *	0.21
Salininity	-0.47 *	-0.06
Oxygen	0.56 *	0.10

The length of the gradient represented by Axis 1 is 6.3 standard deviations for the May survey, which means that the stations at the extreme of the axis have no species in common and belong to completely different ecosystems (Jongman et al. 1987).

In the August survey the gradient represented by Axis 1 is shorter (Table 5), although the coverage was similar to the previous survey. Groups 1 and 2 are strongly overlapping, while Group 3 appears as well separated (Fig 6, lower). Thus the difference between the deeper hard bottom group and the intermediate shelf one seems less distinct in August than in May. Group 6, while in the TWINSPAN classification is placed at the extreme of the

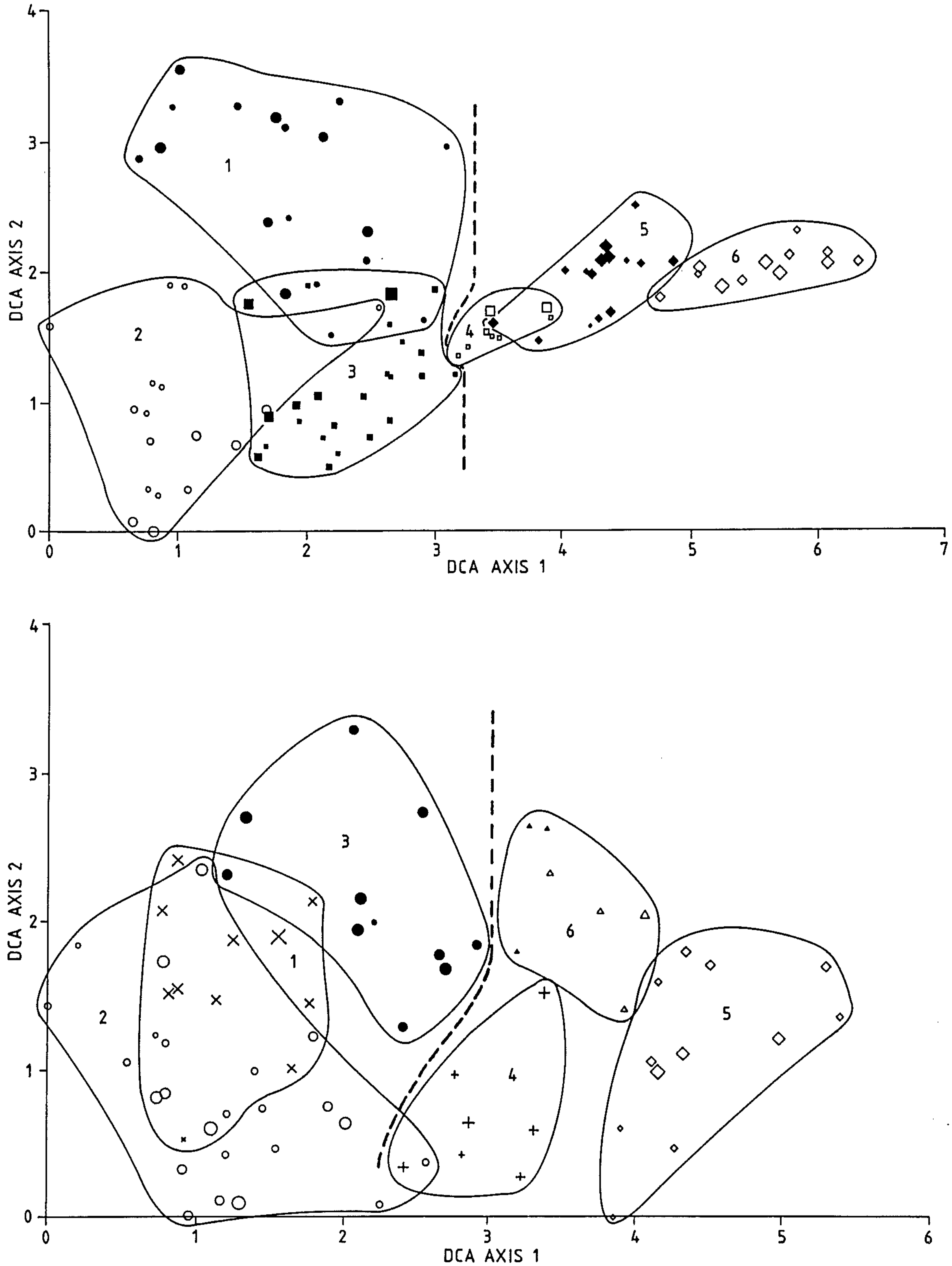


Figure 6. Detrended correspondence analysis of bottom-trawl stations for the May survey (1988) (SD units). Corresponding TWIA (Two-Way Indicator species analysis) Groups 1 to 6 as well as demarcation from first TWIA division are also indicated. N2 diversity of trawl stations shown by symbol sizes (directly proportional to the diversity value). Upper: May survey; lower: August survey

gradient, is instead intermediate between Groups 4 and 5 along DCA Axis 1 (Fig. 6). The separation of the groups appears less clear, with a general trend of 'shrinking of the gradient', reflecting the movements to and from the coast of some of the deeper shelf species and some of the shallow water ones, respectively. Lowe McConnell (1962) describes a general tendency for fish in 'sciaenid Zone II' to move inshore in the summer, when the trade winds cease to blow and the waters are clearer. This is confirmed by our investigations (compare for example Groups 5 and 6 of Appendix 1 a with Group 5 of Appendix 1 b). Furthermore there seems to be a shoreward movement of the deeper shelf lutjanids (Rhomboplites and L. purpureus) that now overlap more with the shallower L. synagris.

Table 5. Length of main gradient of DCA Axis 1 and eigenvalues for DCA Axes 1 to 4 for the May and the August surveys, 1988

	May	August
Length of main gradient (SD units)	6.3	5.4
Axis 1	0.77	0.70
Axis 2	0.45	0.38
Axis 3	0.34	0.30
Axis 4	0.24	0.22

The correlation with the environmental variables and Axis 1 is significant in all cases except oxygen while Axis 2 although with low values, shows significant correlation with all variables (Table 6).

Table 6. Inter-set correlations between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations of the August survey, 1988. Values with asterisk indicate significant correlation ($p < 0.05$).

Variable	Axis 1	Axis 2
Depth	-0.66 *	0.35 *
Temperature	0.58 *	-0.38 *
Salininity	-0.59 *	0.29 *
Oxygen	0.22	-0.29 *

The following description refers to the groups identified during the May survey, which should reflect the situation of most of the year, i.e. with the north-east trade winds and dry climate. Comparison is made with the groups identified during the rainy season (August survey).

Tables 7 and 8 show the catches in weight and numbers for the main species in each group for the May and the August surveys respectively.

Group 1. Intermediate-shelf stations (mostly night hauls). This group includes a number of stations of the intermediate shelf outside the Orinoco Delta and along the Guyana and Suriname shelves, at an average depth of 54 m. About 80% of these stations were sampled during nighttime. Dominating species in terms of frequency of occurrence and numerical abundance are the goatfish Upeneus parvus, the gerreids Eucinostomus spp., the lizardfish Saurida spp., the penaeid shrimps Penaeus notialis and P. brasiliensis and the toadfish Porichthys spp. In terms of weight, the lutjanid Pristipomoides macrophthalmus represented 17% of the catches. The sciaenid Cynoscion jamaicensis was also important in terms of weight and frequency. This group, which appears as very well defined in Appendix 1 a, seems to correspond to Groups 1 and 3 of the August survey for the positions of the trawl hauls and species composition. It is however quite remarkable that these groups are separated along the coast into a group outside the Orinoco delta (G. 3, Appendix 1 b) and a group mainly off Suriname (G. 1, Appendix 1 b) in the August survey. Penaeus notialis now does not co-occur with the congeneric P. brasiliensis, the former mainly found in the Orinoco stations and the latter in the Suriname stations. This Orinoco group is characterized by a higher number of species common both to groups of the left and right side of Appendix 1 b and a few taxa appearing as peculiar of this area (Serranus phoebe, Ciclopsetta cittendeni and Syacium spp.).

Group 2. Deeper-shelf, hard bottom assemblage. This comprises seventeen stations at an average depth of 72 m, characterized by low temperature (23.7 °C) as compared to the other groups all with values over 25 °C. Dominating species (in weight and frequency of occurrence) is the lutjanid Rhomboplites aurorubens. Other 'red fish' are important components of this assemblage viz Lutjanus purpureus, Pristipomoides macrophthalmus and Priacanthus arenatus. Other dominating species in the trawl catches were pelagic/semi-pelagic species (the horse mackerel Trachurus lathami, the scads Selar crumenophthalmus and Decapterus punctatus and the clupeid Sardinella aurita). During the August survey we can recognize this group as Group 2 (Appendix 1 b). This however includes also stations of the intermediate shelf mainly off Suriname. This might be due to two different factors: during the August survey the deeper shelf has fewer stations while in the August survey a higher number of stations was sampled in the intermediate shelf (30-50 m). Furthermore, there seems to be more overlap between the intermediate shelf species and those of the deeper part of the shelf. This might be due to perpendicular movements to and from the coast of some species. In particular, Upeneus parvus and Pristipomoides macrophthalmus have a shallower depth range in the summer season (Strømme & Sætersdal 1989). About half of the demersal trawl catches consist of pelagic/semipelagic species that

Table 7. Total weight (W in kg), numbers (N) and frequency (F: no. of stations where found in the respective groups) of main species from station Groups 1 to 6, May 1988

Species	W (%)	N (%)	F	Food preferences
Group 1 (18 stations)				
Pristipomoides macrophthalmus	385 (17)	9 218 (10)	10	small fishes, larger plankton
Upeneus parvus	324 (14)	19 560 (22)	17	small bottom invertebrates
Cynoscion jamaicensis	159 (7)	1 716 (2)	11	crustaceans and fishes
Saurida spp.	138 (6)	7 192 (8)	14	small fishes
Eucinostomus spp.	118 (5)	14 120 (16)	16	bottom-dwelling invertebrates
Hemicaranx amblyrhynchus	104 (5)	896 (1)	6	
Loligo plei	50 (2)	3 058 (3)	14	
Chloroscombrus chrysurus	43 (2)	2 740 (3)	9	
Penaeus notialis	36 (2)	1 020 (1)	15	
Penaeus brasiliensis	26 (1)	818 (1)	15	
Priacanthus arenatus	26 (1)	334 (0)	10	
Porichthys spp.	25 (1)	2 570 (3)	15	
Rhomboplites aurorubens	21 (1)	310 (0)	8	
Lutjanus purpureus	11 (0)	102 (0)	8	
Penaeus subtilis	5 (0)	242 (0)	11	
Total	1 471 (65)	63 896 (72)		
Total (all species)	2 252	88 580		
Catch rate	125	4 921		
Group 2 (17 stations)				
Rhomboplites aurorubens	993 (23)	16 998 (18)	17	bottom invert., small fishes
Trachurus lathami	861 (20)	24 426 (26)	10	small invertebrates
Selar crumenophthalmus	335 (8)	5 370 (6)	12	pel. & bot. invert., fish
Lutjanus purpureus	299 (7)	159 (0)	11	fish
Sardinella aurita	277 (6)	7 352 (8)	6	planktonic organisms
Decapterus punctatus	235 (5)	8 938 (9)	6	planktonic invertebrates
Pristipomoides macrophthalmus	164 (4)	2 633 (3)	16	
Priacanthus arenatus	127 (3)	3 144 (3)	13	small fishes, crust., polychaetes
(larvae)				
Loligo plei	20 (0)	907 (1)	7	
Total	3 311 (75)	69 927 (75)		
Total (all species)	4 408	93 709		
Catch rate	259	5 512		
Group 3 (24 stations)				
Lutjanus synagris	1 990 (23)	2 577 (2)	13	fishes, bottom invertebrates
Chloroscombrus chrysurus	1 741 (20)	26 422 (23)	20	
Lutjanus purpureus	874 (10)	809 (1)	8	fishes, plankt. & bent. inv.
Scomberomorus brasiliensis	479 (6)	1 345 (1)	12	fishes (clupeoids, carangids)
Loligo plei	334 (4)	15 966 (14)	15	
Scomberomorus cavalla	251 (3)	78 (0)	6	
Selar crumenophthalmus	151 (2)	2 797 (2)	17	
Eucinostomus spp.	146 (2)	2 836 (2)	8	
Opisthonema oglinum	117 (1)	2 311 (2)	15	
Sardinella aurita	103 (1)	13 556 (12)	8	
Priacanthus arenatus	31 (0)	226 (0)	14	
Total	6 217 (72)	68 923 (60)		
Total (all species)	8 609	114 468		
Catch rate	359	4 769		

Table 7. Continued

Species	W (%)	N (%)	F	Food preferences
Group 4 (8 stations)				
Peprilus paru	148 (15)	1 138 (3)	7	jellyfish, small fishes, inv.
Selene setapinnis	116 (12)	1 112 (3)	5	small fishes and crustaceans
Rhizoprionodon porosus	89 (9)	102 (0)	6	small fishes, squid, shrimp
Engraulis eurystole	79 (8)	31 622 (80)	2	variuos zoopl., fish larvae
Hemicaranx amblyrhynchus	77 (8)	342 (1)	4	
Scomberomorus cavalla	63 (6)	30 (0)	6	
Scomberomorus brasiliensis	58 (6)	80 (0)	6	
Total	630 (64)	34 426 (87)		
Total (all species)	988	39 700		
Catch rate	123	4 962		
Group 5 (15 stations)				
Trichiurus lepturus	2 022 (22)	42 838 (7)	14	Fish, crustaceans
Pellona harroweri	1 518 (17)	108 858 (17)	14	Zooplankton ?
Chirocentrodon bleekerianus	1 210 (13)	186 699 (30)	12	" ?
Harengula jaguana	922 (10)	33 159 (5)	14	" ?
Anchoviella lepidentostole	848 (9)	167 272 (27)	8	" ?
Selene setapinnis	535 (6)	1 653 (0)	10	
Cynoscion jamaicensis	386 (4)	4 788 (1)	9	Crustaceans, fishes
Chaetodipterus faber	293 (3)	354 (0)	4	Benthic & planktonic invert.
Macrodon ancylodon	257 (3)	9 259 (1)	7	Shrimp, fishes
Scomberomorus brasiliensis	248 (3)	302 (0)	10	
Peprilus paru	187 (2)	2 676 (0)	13	
Hemicaranx amblyrhynchus	163 (2)	1 628 (0)	10	
Rhizoprionodon porosus	144 (2)	502 (0)	6	
Micropogonias furnieri	134 (1)	506 (0)	6	
Sphyraena guachancho	102 (1)	208 (0)	7	
Opisthonema oglinum	29 (0)	684 (0)	10	
Anchoa spinifer	15 (0)	3 234 (0)	9	
Total	9 013 (85)	564 620 (90)		
Total (all species)	10 637	627 526		
Catch rate	709	41 835		
Group 6 (12 stations)				
Macrodon ancylodon	1 249 (17)	36 277 (8)	12	shrimp, fishes
Xiphopenaeus kroyeri	952 (13)	95 403 (22)	11	detritus
Trichiurus lepturus	423 (6)	14 304 (3)	11	fish, crustaceans
Cynoscion virescens	423 (6)	339 (0)	10	shrimp, fish
Dasyatis geijskesi	380 (5)	68 (0)	5	
Anchoa spinifer	310 (4)	26 809 (6)	9	small fishes, crustaceans
Peprilus paru	301 (4)	6 489 (1)	12	jellyfish, small fish, inv.
Penaeus subtilis	262 (3)	8 018 (2)	10	
Stellifer spp.	259 (3)	13 385 (3)	9	
Arius grandicassis	227 (3)	272 (0)	7	
Bagre bagre	220 (3)	3 313 (1)	12	
Chaetodipterus faber	181 (2)	68 (0)	5	
Micropogonias furnieri	151 (2)	205 (0)	6	
Arius quadriscutis	143 (2)	378 (0)	5	
Nematopalaemon schmitti	122 (2)	90 404 (21)	3	
Harengula jaguana	116 (2)	3 058 (0)	9	
Nebris microps	103 (1)	702 (0)	8	
Anchoviella lepidentostole	99 (1)	11 054 (3)	5	
Hemicaranx amblyrhynchus	93 (1)	2 566 (1)	5	
Isopisthus parvipinnis	66 (1)	2 152 (0)	7	
Total	6 080 (81)	316 264 (74)		
Total (all species)	7 464	424 403		
Catch rate	622	35 366		

Table 8. Total weight (W in kg), numbers (N) and frequency (F: no. of stations where found in the respective groups) of main species from station Groups 1 to 6, August 1988

Species	W (%)	N (%)	F
Group 1 (11 stations)			
Eucinostomus spp.	438 (28)	25 236 (26)	9
Upeneus parvus	138 (9)	13 380 (14)	9
Lutjanus synagris	92 (6)	302 (0)	6
Chloroscombrus chrysurus	71 (4)	5 232 (5)	7
Loligo plei	67 (4)	9 998 (10)	5
Pristipomoides macrophthalmus	61 (4)	6 094 (6)	6
Dactylopterus volitans	28 (2)	740 (1)	10
Penaeus brasiliensis	28 (2)	774 (1)	8
Rhomboplites aureorubens	27 (2)	374 (0)	7
Porichthys spp.	24 (1)	2 362 (2)	7
Acanthostrascion quadricornis	24 (1)	286 (0)	8
Priacanthus arenatus	23 (1)	284 (0)	8
Prionotus punctatus	19 (1)	548 (1)	9
Haemulon steindachneri	19 (1)	296 (0)	7
Lepophidium profundorum	19 (1)	1 020 (1)	7
Total	1 078 (68)	66 926 (70)	
Total (all species)	1 582	96 328	
Catch rate	144	8 757	
Group 2 (24 stations)			
Sardinella aurita	1 002 (14)	25 164 (21)	10
Chloroscombrus chrysurus	624 (9)	21 152 (17)	18
Lutjanus synagris	468 (7)	940 (1)	12
Lutjanus purpureus	459 (6)	444 (0)	13
Rhomboplites aurorubens	357 (5)	7 179 (6)	18
Pristipomoides macrophthalmus	293 (4)	5 272 (4)	11
Priacanthus arenatus	280 (4)	3 790 (3)	21
Selar crumenophthalmus	238 (3)	4 466 (4)	15
Eucinostomus spp.	230 (3)	6 330 (5)	18
Scomberomorus cavalla	201 (3)	295 (0)	13
Upeneus parvus	169 (2)	8 402 (7)	17
Opisthonema oglinum	132 (2)	4 798 (4)	8
Decapterus punctatus	131 (2)	4 162 (3)	5
Synodus poeyi	108 (1)	793 (1)	11
Loligo plei	62 (1)	9 874 (8)	11
Total	4 754 (67)	103 061 (84)	
Total (all species)	7 104	122 051	
Catch rate	296	5 082	
Group 3 (11 stations)			
Orthopristis ruber	1 440 (39)	10 868 (23)	1
Ctenosciaena gracilicirrhus	281 (8)	8 850 (19)	5
Cynoscion jamaicensis	223 (6)	2 044 (4)	10
Peprilus paru	62 (2)	448 (1)	6
Upeneus parvus	48 (1)	1 697 (4)	11
Synodus poeyi	42 (1)	762 (2)	5
Eucinostomus spp.	40 (1)	2 391 (5)	9
Prionotus punctatus	34 (1)	566 (1)	8
Haemulon steindachneri	29 (1)	490 (1)	8
Trichiurus lepturus	23 (1)	252 (0)	6
Serranus phoebe	23 (1)	2 042 (4)	7
Selene setapinnis	20 (0)	491 (1)	6
Porichthys pauciradiatus	19 (0)	816 (2)	6
Penaeus notialis	15 (0)	423 (1)	10
Lepophidium profundorum	15 (0)	604 (1)	6
Penaeus subtilis	15 (0)	545 (1)	8
Total	2 329 (64)	33 289 (71)	
Total (all species)	3 652	47 043	
Catch rate	332	4 276	

Table 8. Continued

Species	W	(%)	N	(%)	F
Group 4 (7 stations)					
Chirocentrodon bleekerianus	405	(17)	219 320	(48)	4
Anchoa hepsetus	363	(15)	160 014	(35)	3
Cynoscion jamaicensis	132	(5)	1 580	(0)	5
Rhizoprionodon porosus	122	(5)	228	(0)	6
Lutjanus synagris	117	(5)	342	(0)	5
Diapterus rombeus	92	(4)	534	(0)	5
Scomberomorus cavalla	86	(4)	226	(0)	7
Sphyraena guachancho	85	(4)	270	(0)	5
Opisthonema oglinum	70	(3)	9 610	(2)	7
Selene setapinnis	68	(3)	784	(0)	6
Chloroscombrus chrysurus	56	(2)	984	(0)	6
Sphyraena picudilla	54	(2)	474	(0)	4
Scomberomorus brasiliensis	38	(2)	52	(0)	2
Micropogonias furnieri	25	(1)	72	(0)	4
Hemicaranx amblyrhynchus	20	(1)	110	(0)	5
Trichiurus lepturus	11	(0)	130	(0)	4
Total	1 744	(73)	340 730	(86)	
Total (all species)	2 393		461 092		
Catch rate	342		65 870		
Group 5 (12 stations)					
Trichiurus lepturus	479	(11)	8 900	(2)	11
Anchoa spp.	397	(9)	189 222	(39)	8
Harengula jaguana	342	(8)	12 210	(2)	9
Cynoscion jamaicensis	290	(7)	5 378	(1)	6
Macrodon ancylodon	282	(6)	3 566	(1)	8
Pellona harroweri	223	(5)	46 742	(9)	11
Chirocentrodon bleekerianus	222	(5)	42 584	(9)	6
Stellifer spp.	154	(4)	9 284	(2)	4
Anchoa spinifer	150	(3)	17 208	(3)	8
Selene setapinnis	107	(2)	2 526	(0)	6
Xiphopenaeus kroyeri	104	(2)	54 826	(11)	3
Hemicaranx amblyrhynchus	89	(2)	1 022	(0)	5
Micropogonias furnieri	75	(2)	1 734	(0)	6
Peprilus paru	65	(1)	1 644	(0)	9
Bagre bagre	57	(1)	832	(0)	8
Isopisthus altipinnis	56	(1)	1 872	(0)	7
Penaeus subtilis	29	(1)	1 542	(0)	4
Total	3 121	(72)	401 092	(82)	
Total (all species)	4 309		490 624		
Catch rate	359		40 885		
Group 6 (7 stations)					
Ctenosciaena gracilicirrhus	271	(31)	7 002	(24)	7
Cynoscion virescens	163	(18)	2 612	(9)	7
Trichiurus lepturus	84	(9)	962	(3)	5
Chirocentrodon bleekerianus	47	(5)	10 698	(36)	3
Selene setapinnis	52	(6)	3 136	(11)	4
Lepophidium profundorum	18	(2)	330	(1)	4
Eucinostomus gracilis	6	(0)	224	(1)	4
Harengula jaguana	1	(0)	108	(0)	4
Total	642	(73)	25 072	(85)	
Total (all species)	884		29 546		
Catch rate	126		4 221		

occur on the bottom during daytime. It is possible that when close to the bottom they become part of the benthic trophic web.

This assemblage is referred in the literature as 'the red fish assemblage' (Lowe-McConnell 1962) but no good description really exists in terms of relative species abundances. Lowe-McConnell (1962) reports the presence of smaller lutjanids (Rhomboplites, Ocyurus and Lutjanus synagris). Also in our case the species entering the trawl were mostly smaller lutjanids but the composition of the dominating species differs somewhat: Ocyurus was not caught in this area at all while L. synagris has a definitely shallower range, occupying mainly waters of the intermediate shelf. Interesting is the appearance of the bigeye Priacanthus arenatus. During both surveys this species appeared as a common component of this assemblage and formed 3% of the catches. In the taxonomic literature (Randall 1978), it is usually reported as occurring close to reef areas, in small aggregations. In the Eastern Atlantic, off Gabon in 1985 (Anon. 1987), this species was caught as part of the sparid subthermocline community, with catches up to 1 t/h. However, during the 1989 survey (Bianchi 1992 c) it was never caught in such large amounts and constituted 1% of the catches in that community. This indicates that this species may be subject to population booms. Its diet appears as quite variable, based on both fish and invertebrate larvae and polychaete worms.

Group 3. Intermediate shelf assemblage. The 24 stations of this group were sampled at depths between about 25 and 70 m (av. 38 m) and should largely correspond to what is described in the literature as 'silver fish, Zone III' (Lowe-McConnell 1962). However, according to our observations this assemblage also includes a number of fishes of the 'red zone'. About 30 % of the catches were represented by the snappers Lutjanus synagris (23 %) and L. purpureus (10 %). Of more silvery type is Chloroscombrus chrysurus (20 %) and the Spanish mackerel Scomberomorus brasiliensis (6 %). The squid Loligo plei, representing 4 % of the catches in weight, was numerically important (14 %) and rather frequent.

In the course of the August survey, this area is occupied by stations of groups 1, 3 and (partly) 2. These are discussed above under Group 1.

The above groups represent the assemblages found in the intermediate and deeper shelf, where most species are not interacting with the coastal environment. Spawning of the dominating taxa occurs offshore. The following station groups represent the coastal environment. This separation is reflected in the output of TWINSPAN and coincides with the first division (Appendix 1a, b).

Group 4. This group includes 8 stations appearing as intermediate between the deeper and shallower parts of the shelf. Two deep stations off Suriname are also included. They are characterized by the presence of pelagic/semipelagic species as dominating taxa. A group included species feeding on smaller fishes and crustaceans (i.e. the pomfret Peprilus paru, the carangids Selene setapinnis and Hemicaranx amblyrhynchus and the anchovy Engraulis eurystole) and a group representing the accompanying larger predators (Rhizoprionodon porosus and the Spanish mackerels Scomberomorus cavalla and brasiliensis). On the other hand, all the species typical of the shallow waters are missing. It is difficult to say whether this association has a clear ecological meaning. However, group 4 of the August survey bears strong similarities with this group both in species composition and location i.e. separating the shallow water assemblages from the open, deeper shelf ones. Most of the species are of pelagic/semipelagic type but in the August survey a few demersal species were also caught, i.e. Lutjanus synagris and Cynoscion jamaicensis. Also there is more overlap between some of the species of the intermediate shelf with those of the shallowest part of the shelf and this is probably due to the extension, during the rainy season, of the estuarine environment.

Group 5. The 15 stations of this group have an average depth of 26 m. The dominating species are again pelagic/semipelagic, including smaller, zooplankton feeders (the clupeoids Pellona harroweri, Chirocentrodon bleekerianus, Harengula jaguana and Anchoviella lepidentostole) and fish predators (Trichiurus lepturus). The above species accounted for about 70 % of the catches in weight and about 80 % in numbers). More typical demersal fishes also occurred, including Cynoscion jamaicensis, Macrodon ancylodon and Micropogonias furnieri.

Lowe-McConnell (1962) describes a Golden Fish Zone II (from 20 to 60 m) off Guyana based on the trawl catches of the R.V. 'Cape St. Mary' in 1957-59, indicating this zone as the most important for the commercial catches, with Micropogonias furnieri representing 43 % of all the catches (Lowe-McConnell 1966). During our investigations this species never appeared as dominating and made up 2% at most of the groups where it was found. This species feeds typically on various benthic invertebrates and has an obligatory demersal habitat (Isaak 1988). It has been subject to intensive fishing because of its high economic value and it is also taken as bycatch for the intensive shrimp fisheries occurring all along the coast under study, which, combined with its relatively slow growth (reaches the commercial size of 50 cm at the age of 7 years, Isaak 1988) may explain this important reduction in biomass.

Group 6. The stations of this group represent the deeper range of the shallowest assemblage found in this area (Lowe-McConnell's 'Brown fish' Zone I). This assemblage is mostly found in very shallow waters and was not properly sampled because of the operational depth range of the R.V. 'Dr. F. Nansen'. The sciaenid Macrodon ancylodon is dominating together with its main prey viz the penaeid shrimp Xyphopenaeus kroyeri. Other large predators include Trichiurus lepturus, Cynoscion virescens, Isopisthus parvipinnis, mainly ichthyophagous, and sea catfishes Arius spp. and Bagre spp., stingrays Dasyatis mainly feeding on bottom invertebrates. Macrodon ancylodon was reported as one of the most abundant fishes off Guyana by Lowe-McConnell as representing 18 % of the total catch off Guyana. This species represents 17 % in weight of the catches in this group.

Figure 6 (upper and lower) also displays the N2 diversity for the trawl stations on the ordination diagrams. The shallowest group (Group 6) of the May survey appears as the one with consistently higher diversity while the deep shelf, hard bottom Group 2 has mostly low diversity levels. In the August survey the highest diversity values are found in the intermediate shelf which might represent the high degree of overlap during this season. Furthermore, Group 6 (August survey) appears as having mostly low diversity values and this well fits with its position in the low oxygen waters found north west of the Orinoco Delta (Fig 4 and 6).

DISCUSSION

A main feature of the environmental conditions encountered in the study area is the water discharge from the Amazon, Essequibo and Orinoco rivers, carrying silt and soft mud together with nutrients into coastal waters. Another important factor is the absence of a sharp and shallow thermocline (typical of, for example, the Eastern Central Pacific and West Africa). Strongest zonation was found between the coastal environment and the intermediate and deeper shelf environments. In fact, the first division of TWINSPAN, corresponding to the midpoint of Axis 1 of the DCA plots for both surveys, separates the above major environments which seems to be indicative of the presence, along this shelf, of two principal ecosystems: the coastal one, largely depending on the river runoff and the open shelf one, where the food web based on phyto- and zooplankton production becomes relatively more important. Oxygen, temperature and salinity never appear as key factors in explaining the observed patterns.

In shallow waters, heavily influenced by discharges of major rivers, and with muddy bottoms, detritus feeders and their predators are the main components of the megafauna. The stirring up of shallow waters by the winds must be at the base of the phyto- and zooplankton production and the associated populations of numerous species of clupeoid fishes. Furthermore, spawning activities and larval development of many of the species of this zone is strictly related to the presence of river outlets and brackish-water environments.

Waters are particularly turbid in the shallowest zones, allowing only the species adapted to stand those conditions. It is interesting for example that Chloroscombrus chrysurus, also found off tropical west Africa, does not seem to be able to stand the extreme estuarine environment off the northern coast of south America. Off west Africa this is one of the main components of the catches in the shallow-waters (Bianchi 1992 a, b). In the area under study this species clearly belongs to the intermediate shelf. This is made possible by the high temperature and oxygen near the bottom throughout the shelf.

Moving out from the shore, pelagic/semipelagic species become more dominant in the catches. Group 4 (May survey, Appendix 1 a), appearing as intermediate between the shallow- and deep water groups, consists only of pelagic species. A similar type of association was found off Mozambique, parallel to the shallow waters associated to the mangrove systems. Also here, the catches consisted only of pelagic species (including Scomberomorus).

In the intermediate and deeper shelf, factors that determine the further subdivision into sub-communities, seem to be related to type of substratum and day/night associations. The intermediate shelf is still heavily influenced by the muddy deposits originating from the rivers and there is still a rich bottom fauna including commercially exploited shrimps species and their predators. Here, however, waters are much clearer (Losse, 1982, McConnell 1962). Shrimp and vertebrate species' diel rhythms give rise to different associations, one with species active at night and one with species caught mainly by daytime. In the intermediate shelf, the energy flow originating from the bottom deposits is probably less important while the production taking place in the upper water column must be proportionally more significant, judging from the dominating species. Gade (in Strømme & Sætersdal 1989) mentions for this area, the elevation of water from 100 m to abuot 50 m depth from the surface (due to the hydrostatic effect caused by the Guyana Current) as a major process liable to affect primary production.

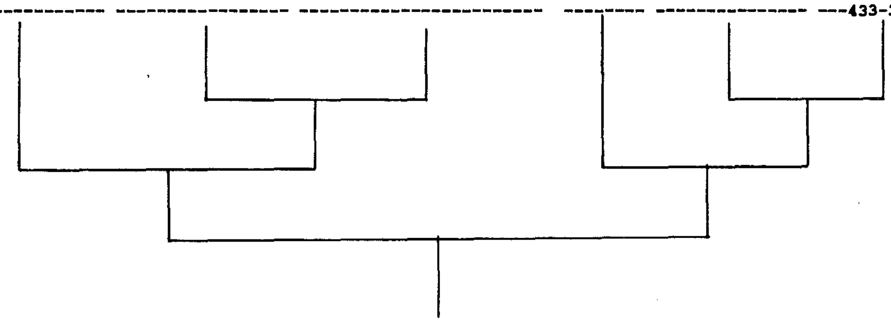
Another subcommunity consists of several lutjanid species, with the largest biomass and numbers represented by the small Rhomboplites and Pristipomoides. This assemblage is at the opposite extreme of both DCA plots as the shallow and muddy waters. This was designated by Lowe-McConnell as the 'red-fish' assemblage with lutjanid snappers. However, there is a high percentage of pelagic species (Trachurus, Sardinella etc.) in the catches, due to the presence of these species near the bottom during daytime. The larger lutjanids are poorly represented. This might be due, however, to the fact that our sampling is limited to trawlable areas. The deeper part of the shelf is characterized by the presence of areas with rough bottoms which are the preferred substratum of the above species. The trophic significance of smaller pelagic fishes near the bottom for considerable long periods (daytime) might be important but cannot be evaluated unless stomach content studies are available for the larger predators.

A high percentage of the catches in the intermediate and deeper parts of the shelf consisted of carangids represented by many genera and species. Berry & Smith-Vaniz (in Fisher ed. 1978) report for all carangid species of the western Central Atlantic that spawning occurs offshore, sometimes far away from the coast. Also, most species feed on small fishes, crustaceans, fish larvae and smaller zooplankton. It is possible that cannibalism in the species of this family is an important way of accessing phytoplankton and small zooplankton food sources through their own larvae.

The descriptions obtained above, largely confirm the more 'subjective' descriptions of the assemblages by Lowe-McConnell in terms of the species associations. Differences in the relative abundance of various species in each assemblage cannot be quantitatively assessed, but some important differences appeared: the evident decrease of Micropogonias furnieri, economically one of the most important fish species and, possibly, changes in the lutjanid community with a clear dominance of the small genera Pristipomoides and Rhomboplites instead of the larger Lutjanus.

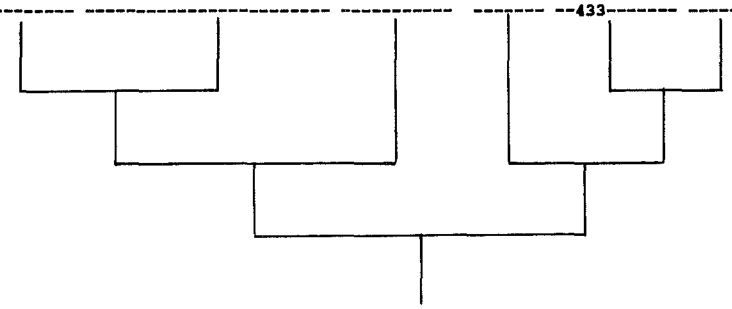
Zoogeographic footnote: Rosenblatt (1967) compared the marine tropical shelf fishes of the eastern Pacific with those of the western Atlantic and found that 25% of the total number of genera on either side consists of New World endemics. Rosen (1975) explained this phenomenon, also based on evidence from other faunistic groups, by Tethyan distribution followed by allopatric speciation (vicariance) due to tectonic events, i.e. the emergence of the Panamian Isthmus. Many of the genera (and even one species, Anchoa spinifer !) identified in the course of the survey off the northern coast of south America belong to the New World endemics (Table 1). Most of the common genera of fish belong to the shallow water assemblages (families Clupeidae, Engraulididae, Haemulidae and Sciaenidae) while only Diplectrum and Porichthys (family Serranidae and Batrachoididae respectively) are from intermediate depths. The extreme ecological conditions found in the intermediate and deep part of the shelf in the Eastern Central Pacific (Bianchi 1991) is certainly responsible for the great differences in the faunas on either sideat these depths. While Diplectrum and Porychthys are poorly represented in the Atlantic in terms of biomass and number of species, they appear more successful in the Pacific. Here, some of the species of these genera occupy areas with low oxygen concentrations and their relatively greater abundance might be explained by their ability to stand those conditions combined with reduced competition.

	1	2	3	4	5	6
	deeper and intermediate shelf			shallower part of the shelf		
	********** ******	*	**		* *	* ** **
Penaeus notialis	-22-22233222112-22	-----------------	-------2----------------	--------	-----------212-	----------1-
Mustelus higmani	-----2222-------2-	-----------------	---3--------------------	--------	----------4----	------------
Porichthys spp.	122222122122-222--	-----------------	--1-1--3----------------	--------	-----------211-	------------
Penaeus brasiliensis	222211121-222112--	--------1--------	-------1---------------2	--------	---------------	------------
Saurida spp.	--33333322231221--	----------1------	------------------------	--------	------------1--	------------
Lepophidium spp.	--3-3--32--1-2-2--	-----------------	-------2----1-----------	--------	---------------	------------
Diplectrum formosum	---1322---1-11-2--	---------1-------	---------------2-------2	--------	---------------	------------
Upeneus parvus	33333222113432321-	-1-----2-2------1	----2-2---1222-1---41--3	--------	---------------	------------
Eucinostomus spp.	3221212322242--112	223------------2-	-----133-2-1------1---44	--------	-1-------2---1-	------------
Lutjanus purpureus	-3221222-2--------	33-343----23-1232	222--453--1---1---------	---2----	---------------	------------
Pristipomoides macro.	444432131-1-------	22-22333323212324	-----1------------------	-1------	---------------	------------
Rhomboplites aureor.	332-2-11--1----2--	44333424333222433	32--3342-2-------------2	-1------	---------------	------------
Trachurus lathami	1--1-222----------	-3-34434132---3--	1-----2-----------------	21------	---------------	------------
Selar crumenophthalmus	---1--------313-2-	---34343332--1321	3-1-3-32321131131--3-22-	22-2--3-	---------1-----	------------
Priacanthus arenatus	22212-----231--3-1	233-33-313--12222	12--22-32-21221----21--3	--------	-2-------------	------------
Loligo plei	222-132212--33222-	--------22-222-22	-2--12-1233333344--3-3--	--2-----	-3-----------1-	------------
Sardinella aurita	--2---------1-2212	4-422-4--2-------	------2--2-43-3--2---32-	--------	1-------1------	------------
Decapterus punctatus	1--1------2-2-----	324----2-2-----1-	----------13-1---3-3---2	--------	---------------	------------
Chloroscombrus chrys.	--------1323-33211	342------------2-	--223142421-414-22542324	---1-132	-2122------1-21	-223----2---
Lutjanus synagris	-------1-12--1-3--	-3------------23-	-----233-22----2-2435333	-----2--	44----3--------	------------
Sphyraena guachancho	--------2-23222---	-----2--------4--	---331333--------------2	-----223	4323---222-----	------------
Opisthonema oglinum	------------32332-	----------------1	2-----3222--3-3-32323233	-----32-	13-322-31--11-1	---2------12
Cynoscion jamaicensis	-2-223333--322---3	-----------------	----2--3----------------	-----132	42----333433-1-	1--------2--
Hemicaranx amblyrhyn.	---------223433---	-----3----1------	33-2--3-----32---2--313-	-33--2-2	-33322332---3-2	-3-2---24--3
Scomberomorus brasil.	-----22-------2---	-4---3-----------	3-32-2-2--------3143334-	--223233	4333333322-----	33-3-3-3---2
Scomberomorus cavalla	------------------	-----------------	-----3-3--33--------42--	3333--32	------3-2-3----	-32---------
Chaetodipterus faber	-------------2-2--	-----------------	----------------2---32--	----3--3	-3-4-43--------	--34--23---3
Peprilus paru	-----3-222------3-	-------2---------	23122-------------------	2422-243	1-332233333-113	423214233223
Rhizoprionodon porosus	-3----------------	-----3------3----	2--3---2----------------	3--33232	--2-2-4-2-3---2	---3-3-----3
Trichiurus lepturus	----------------12	-----3-----------	2--12--3-----1-3-2----2-	23---3--	43432253-443424	-33444323234
Selene setapinnis	--------12------2-	-----------------	-212---2-----------3----	3-33--33	1--23--3-442311	33---3------
Harengula jaguana	-------------21---	-----------------	------------3-----------	--------	41213244341-334	-21322132--4
Anchoviella lepidant.	------------------	-----------------	-------3----------------	--------	-2--2--353--334	-33-13--2---
Chirocentrodon bleeker.	------------------	-----------------	-------3----------------	-------3	44--1143-534232	-2----------
Pellona harroweri	------------------	-----------------	------------------------	--------	43222154343233-	-----3----2-
Penaeus subtilis	----211121-1-11-12	-----------------	--1----1----------------	------1-	--------11-22-2	4132--221222
Micropogonias furnieri	------------------	-----------------	------------------------	-------2	3-----33-34-2--	---2--322-34
Isopisthus parvipinnis	-------2----------	-----------------	------------------------	--------	----1-----233-2	---242-111-2
Macrodon ancylodon	------------------	-----------------	----------1------------1	------2-	3---2-4----4322	434443434344
Bagre bagre	------------------	-----------------	-----------------------1	--------	--2---4----32-2	413322323223
Cynoscion virescens	------------------	-----------------	------------------------	--------	-----343-3-----	43-3433333-3
Stellifer spp.	------------------	-----------------	------------------------	------3-	-------113313--	1--243333-33
Anchoa spinifer	------------------	-----------------	------------------------	--------	--2-211-13--221	-342-233423-
Nebris microps	------------------	-----------------	------------------------	--------	---------------	32--3-32-323
Xiphopenaeus kroyeri	------------------	-----------------	------------------------	--------	------------1--	5333333334-3
Arius grandicassis	------------------	-----------------	------------------------	--------	---------2-----	---44-23-323
Dasyatis geijskesis	------------------	-----------------	------------------------	--------	---------------	---3---4-444
Penaeus schmitti	------------------	-----------------	------------------------	--------	--------1-----1	-----112-113
Arius quadriscutis	------------------	-----------------	------------------------	--------	---------------	---433-3-3--



Appendix 1a. Two-way station by species table resulting from the program TWINSPAN. Values denote categories of abundance: 1: w < 0.5 kg; 2: 0.5 < w ≤ 5 kg; 3: 5 < w ≤ 50 kg; 4: 50 < w ≤ 500 kg; 5: w > 500 kg. The dendrogram showing the hierarchical relationship between the various groups, substitutes the binary notation produced by the program; the asterisk indicates night stations. a: May survey; b: August survey

	1	2	3	4	5	6
	deeper and intermediate shelf			shallower part of the shelf		
	******* * *	* * * **	* ******		* *	*** *
Serranus poebe	-----------	------------22----------	--1112333--	-------	------------	-------
Cyclopsetta cittendeni	2----------	------------------------	-22--2222--	-------	------------	-------
Penaeus notialis	----1-----2	-----------1------------	212212222-2	----1--	-------1----	-------
Syacium spp.	2--12-2----	-------------2--------22	-----221232	-------	------------	--1-1--
Porichthys paucirad.	-----2--1-3	-------------1--------12	--1--22223-	-------	-----------1	-12--1-
Prionotus punctatus	22-2112-222	1----2-------2--------22	112--23-232	------3	-----3------	-111--2
Lepophidium spp.	2----2-----	------------------------	2------3---	-------	-----------2	-------
Haemulon steindachneri	132-2-2-3-1	--------------------3244	--12122123-	------3	-----------2	-------
Priacanthus arenatus	-22-223-322	2--2222224123-4223334332	--2--2--23-	-------	------------	-------
Trachurus lathami	-----------	---3---3--112-----------	-----------	-------	------------	-------
Rhomboplites aureorub.	22-1222-3--	---1322233-3443--2334333	-----2--3--	-------	------------	-------
Decapterus punctatus	1222212----	----1--42-----3----3----	-----------	-------	------------	-------
Penaeus brasiliensis	322232--2-2	----2---1-1-221-------12	-----1--233	-------	------------	-------
Dactylopterus volitans	1221233123-	--------1-1--2--1-----22	2--------31	-------	------------	-------
Porichthys spp.	32222-2--1-	------------------------	----------2	-------	-----1------	-------
Upeneus parvus	334122--333	22313-13333333233---2---	22322321323	-------	------1-----	-------
Diplectrum formosum	122-1-2-2--	2--1-21--2-----1-1----2-	---------32	-------	------------	-------
Lutjanus purpureus	----1---331	---4-----2-1434-2-333332	----233-3--	-----3-	------------	-------
Pristipomoides macroph.	332--21-3--	---331-3221-442-------2-	-----3223--	-------	------------	-------
Chloroscombrus chrys.	2-22313--3-	144-312-21----3223433232	21-2--2--22	-223232	-----23-----	-------
Selar crumenophthalmus	----21-----	2--22--4121-3--11-332-22	--2111-----	--2222-	------2-----	-------
Eucinostomus spp.	234-324-344	31--12--22-2-32343232333	322-22213-3	---233-	------------	22-22--
Lutjanus synagris	-22---2-242	3-----1-2------322344333	--2-1----3-	33--333	------------	-------
Loligo plei	--2-2--2-42	23--232---22---332--3---	--2-2------	31-1---	---------1--	-------
Synodus poeyi	-----2----3	----21131-1-34----2---22	2--1-333---	2---22-	------------	-------
Sardinella aurita	3-3-22--2--	2-1121-42-----51------2-	-----------	31-----	------------	-------
Diplectrum radiale	11222-2-22-	--------1------2--------	-----------	------2	-----1------	--1----
Synodus phoetens	--333-21---	-2----------------------	----2-----2	---2---	------------	-------
Lepophidium profundor.	-2222-2-2-2	-------------3----------	--11-2--232	-------	------------	--2223-
Opistonema oglinum	-2-22---222	134---------223---23----	322--------	3332212	-2-4-13-2---	-------
Scomberomorus cavalla	--------33-	333-32--32-33--2--4--2-3	-22-23----2	3233332	33-----2----	22-----
Chaetodipterus faber	-----------	2---------------2---3-22	-----------	----223	---------3--	-------
Sphiraena picudilla	----2------	22---------3------------	22322------	--2323-	--------3---	2------
Hemicaranx amblyrhyn.	----2----32	--4-2------2----1-------	2-2-2-----2	--22132	-2-32-4-3---	-----3-
Sphyraena guachancho	-2--------2	-24-3---3-----------3---	2---3-----3	234-32-	------3-2---	--2----
Rhizoprionodon porosus	-----------	----4-------2----3-4----	23---------	243223-	-2---3---22-	-------
Selene setapinnis	-----------	2---3--------3---12-2---	223-2-2--2-	-332333	---2-2342-3-	-31--23
Peprilus paru	-----------	------------------------	233-1-3--1-	-3122--	23222-3-212-	--1--1-
Ctenosciaena gracilic.	-----------	------------------------	3-22--2--4-	-1----3	-----3----3-	2233434
Penaeus subtilis	-----------	------------------------	222---22122	-------	--3322------	-12-233
Cynoscion jamaicensis	-2-122-----	2-3--------222----------	322-2233342	3232--4	-----2342-34	3333333
Anchoa epsetus	----------3	------------------------	-----------	443----	-------42---	-------
Scomberomorus brasil.	-----------	-2--3-----------2-------	-----------	-23----	-------333--	-------
Chirocentrodon bleek.	-----------	------------------------	-----------	444---2	------443123	--3--33
Micropogonias furnieri	---22------	-2----------------------	----------2	--222-3	---333-331--	---33-3
Harengula jaguana	-----------	21-1--------------------	1-3-2-2----	-------	-2332-44433-	21---11
Trichiurus lepturus	-----------	-----------2------------	--3-2-2123-	-2-1223	-34443443333	-232-33
Pellona harroweri	-----------	------------------------	-----------	-1-----	-23232443133	-2---21
Anchoa spp.	-----------	------------------------	-----------	-------	3444-43---23	-3-----
Anchoa spinifer	-----------	------------------------	-----------	--1---2	--33314132--	------2
Macrodon ancylodon	-----------	------------------------	-----------	------3	--34334432--	------3
Arius grandicassis	-----------	------------------------	-----------	------3	-1--3--3----	-------
Bagre bagre	-----------	------------------------	-----------	------2	-23333-22--2	-------
Odontognathus mucron.	-----------	------------------------	-----------	-------	-3332-------	-------
Isopisthus parvipinnis	-----------	------------------------	-----------	----2--	--3333-32--3	-------
Xiphopenaeus kroyeri	-----------	------------------------	-----------	-------	--433-------	-------



Appendix 1b.

Acknowledgements: I wish to thank Gunnar Sætersdal and Tore Høisæter for reading the manuscript and providing helpful comments; S. Myklevoll for drawing the figures.

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PAPER 6

Study of the demersal assemblages of the continental shelves of the North-Western Indian Ocean based on the trawl surveys of the R/V 'DR.FRIDTJOF NANSEN' (1982-1984)

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Abstract- The structure of the demersal assemblages (fish, crustaceans and cephalopods) of the continental shelves of Pakistan, Oman, Yemen, Ethiopia and Somalia was studied from the data obtained in the course of the surveys carried out by the R.V."Dr. F. Nansen" in 1982 to 1984, by means of ordination techniques, Detrended Correspondence Analysis (DCA) and a classification technique, Two-way Indicator Species Analysis (TWIA). Where possible, correlation between DCA Axes 1 and 2 with depth, temperature, oxygen and salinity was estimated in order to explain the patterns observed. The intermediate and deeper parts of the shelf throughout the area appear deeply influenced by the presence of the oxygen-minimum layer of the Arabian Sea which is seasonally enhanced off Pakistan, Oman, Yemen (southern coast) and Somalia by the occurrence of upwelling. An exception was the northern coast of Oman, that appeared under the influence of Gulf waters and the coast of Ethiopia (Red Sea).

INTRODUCTION

In the period 1982-1984 the Norwegian R/V 'Dr. Fridtjof Nansen' carried out a number of trawl surveys in the Western Indian Ocean, covering the continental shelves of Pakistan, Oman, Ethiopia (in part), Yemen (southern coast) and Somalia (Fig. 1). The aim of this study, which utilises some of those surveys (Table 1), is to describe the general patterns of demersal assemblages, based on the above data and relate them to the hydrographic conditions and depth. Of particular interest is the influence of the oxygen-minimum layer of the Arabian Sea on the bottom megafauna as well as the occurrence of upwelling in some of the areas.

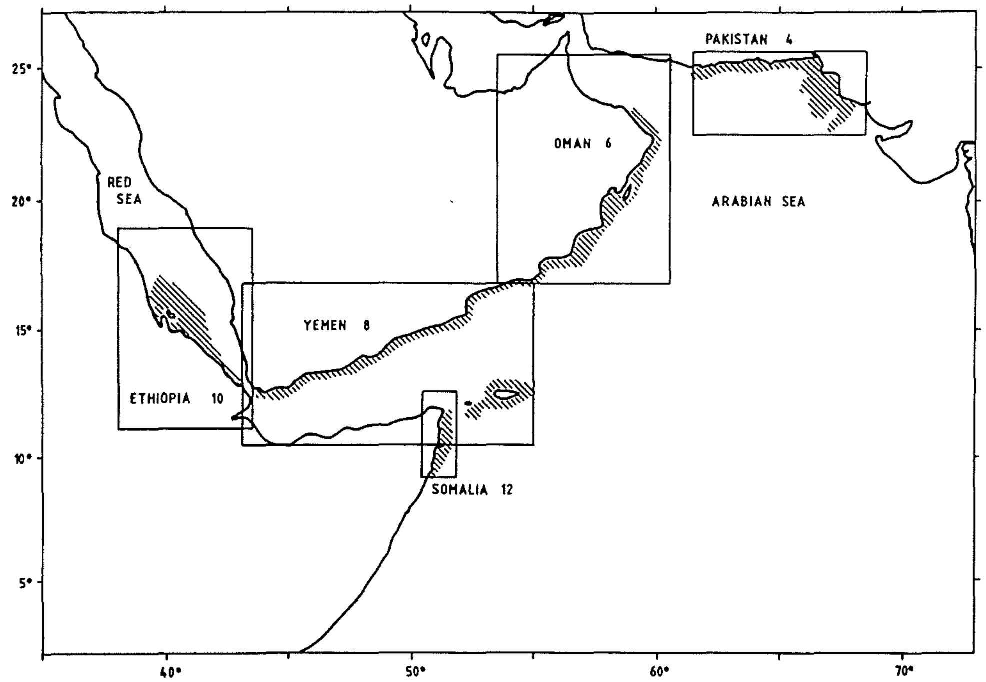

Fig. 1. Areas of the North-West Indian Ocean surveyed by the R.V. 'Dr. Fridtjof Nansen', 1982-1984

Table 1. List of the surveys of the R/V 'Dr. Fridjof Nansen' in the northern part of the Western Indian Ocean (1982-1984) used in this study. BT: number of bottom trawl stations

Country	Date	BT	Depth range (m)
Pakistan	5/ 9 to 16/ 9 1983	43	15-300
	20/ 1 to 2/ 2 1984	84	10-146
Oman	1/ 3 to 19/ 3 1983	37	15-140
	7/11 to 11/12 1983	52	15-104
Yemen	14/ 2 to 28/ 2 1984	47	17-196
	12/ 8 to 4/ 9 1984	35	10-172
Ethiopia	11/ 3 to 19/ 3 1984	25	25-229
Somalia	28/ 2 to 4/ 3 1984	18	17-208
	24/ 8 to 30/ 8 1984	21	23- 87

Longhurst and Pauly (1987) have provided a general description of the demersal assemblages of the Indo-Pacific area based on a number of scattered works from the early 1950's to the 1970's. Although very valuable, this description possibly suffers from being based on outdated reports and literature.

The taxa included in the analysis are bony and cartilaginous fishes, stomatopods, decapod crustaceans and cephalopods.

STUDY AREA

The study area includes the continental shelves of the north and west Arabian Sea, including Pakistan, Oman and Yemen (southern coast), and part of Ethiopia and northern Somalia. The general oceanographic characteristics of this area are well described through numerous documents produced as a result of the International Indian Ocean Expedition (1959-1965), i.e. the Oceanographic Atlas of the International Indian Ocean Expedition (Wyrtki 1971) and the volume 'The Biology of the Indian Ocean' (Zeitzschel & Gerlach eds. 1973). The northern part of the Indian Ocean is characterized by a seasonally changing monsoon gyre, not found anywhere else in the oceans (Wyrtki, 1973). From about November to April the North East monsoon dominates north of the Equator inducing an east-west flow carrying low-salinity waters from the Bay of Bengal to the eastern Arabian Sea (Fig 2 upper). This drift, nowhere very strong, appears to be rather shallow and exerts little influence on the waters below the thermocline. No upwelling develops though some shoaling of the thermocline seems to occur in the northern part of the Arabian Sea, off Karachi. This circulation pattern changes drastically when the South West monsoon starts blowing in April and water starts to flow along the Somali coast. In July the Somali Current has attained its greatest strength and causes strong upwelling, particularly along the northern part of the coast, between 5 and 10 °N. The major flow is now toward the east which also causes strong upwelling off Oman, though here no coastal current develops (Fig. 2 lower). Another remarkable feature of the Arabian Sea is the presence of a low-oxygen layer between about 200 and 1000 m where oxygen concentrations can be as low as 0.2 ml l^{-1} (Fig. 3). The reason for the presence of this oxygen-minimum layer seems to be the large organic input from the highly productive upwelling regions, combined with inhibition of downward mixing by the strong tropical thermocline and inflow of oxygen depleted waters from the Banda Sea. Below is a description, by country, of the hydrographic conditions found in the course of the survey activities.

Pakistan. During the first survey (Table 1 & Fig. 4), the thermocline appeared to be strong and limited to the upper 50 m in the western part of the coast, with temperatures dropping from 28 °C to 20 °C (Fig. 5 a) (Nakken 1983). Here oxygen levels below 1 ml l^{-1} are found already at about 40 m depth. Eastward, the thermocline appeared to be deeper.

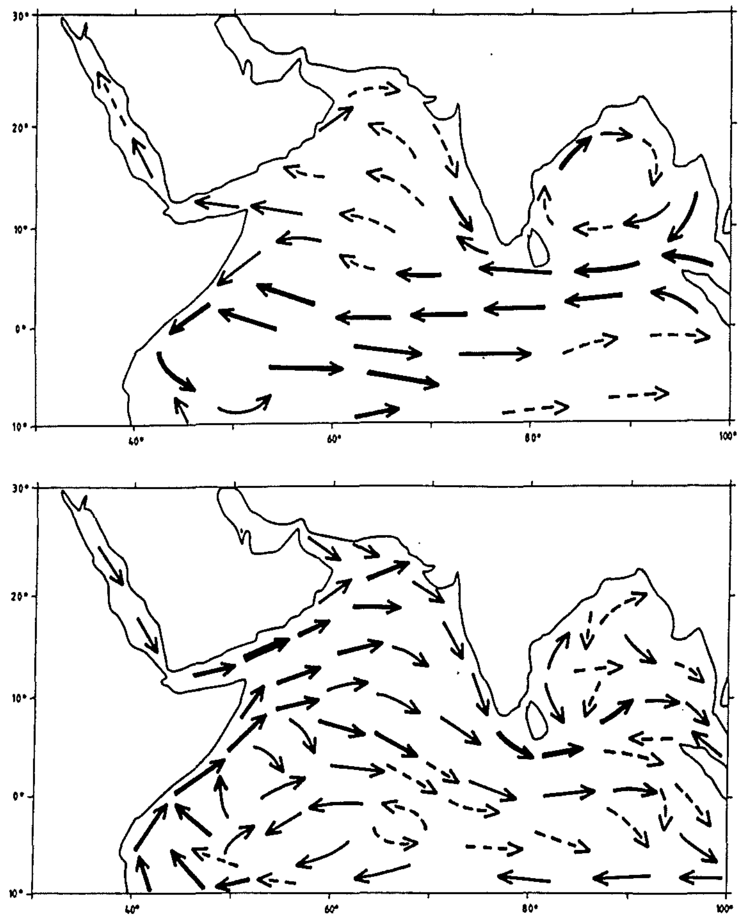

Fig. 2. Major patterns of surface currents in the northern Indian Ocean. Upper: North-East monsoon period; lower: South-West monsoon period. Redrawn from Zeitzschel & Gerlach, 1973

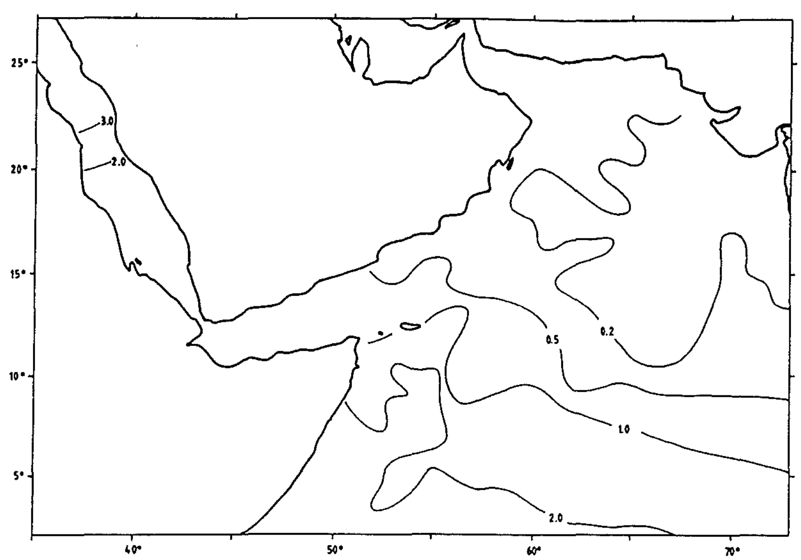

Fig. 3. Extension of the oxygen minimum layer in the Arabian Sea, at 200 m depth Redrawn from Wyrtki, 1971

Furthermore, the 1 ml $^{-1}$ isoline was between about 60 and 90 m depth. Large parts of the shelf bottom were thus dominated by hypoxic conditions. The effect of the outflow from the Indus river, usually strongest at this time of the year, was observed close to its delta as an upper layer of low-salinity water (29-30 ‰). The second survey included in this study took place in January-February 1984 (Fig. 4) (Sætre 1984). This period coincides with the minimum outflow of the Indus River and North-East trade winds. The mixed upper layer which in the previous survey reached only about 30 m depth, extends now to about 150 m.

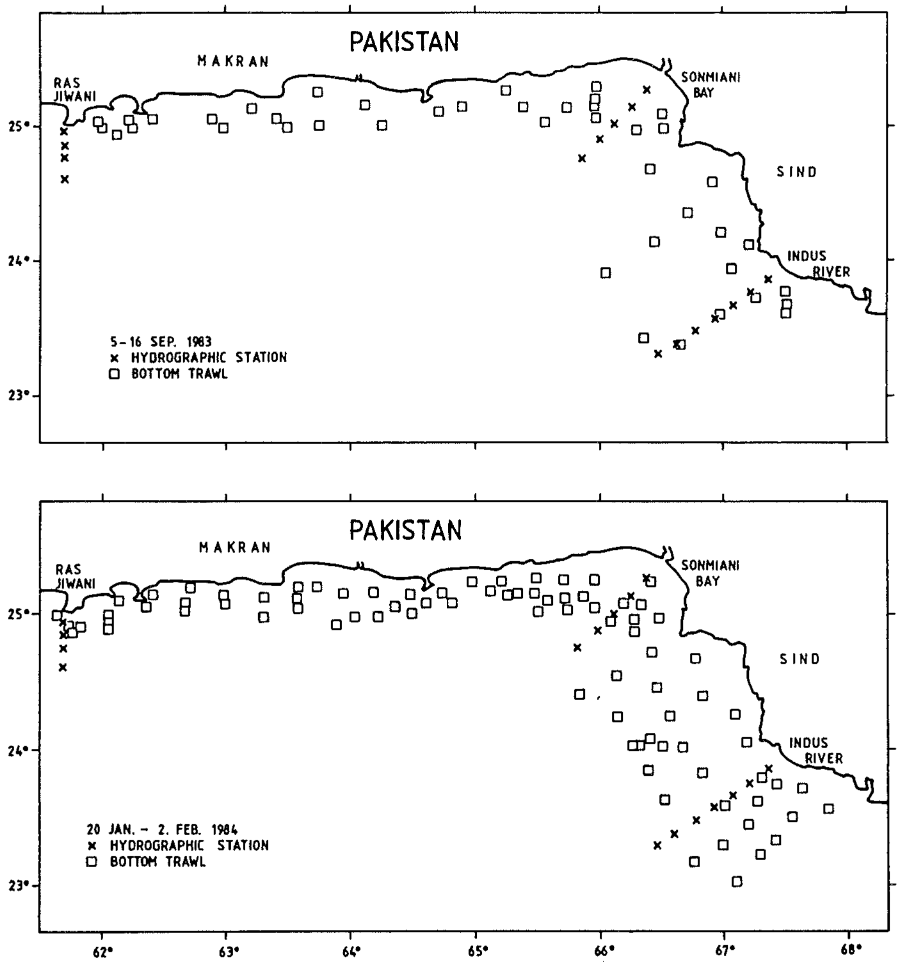

Fig. 4. Position of trawl hauls and hydrographic stations, Pakistan. Upper: September 1983 survey; lower: January 1984 survey

As a result, the oxygen-rich waters reach much deeper and no part of the shelf bottom has hypoxic conditions. Water temperatures are quite uniform throughout the shelf, ranging from about 21 °C to 23 °C (Fig. 5 b). This is not in agreement with Wyrtki's description given above (lifting of the isolines outside Karachi).

Fig. 5a Fig. 5b

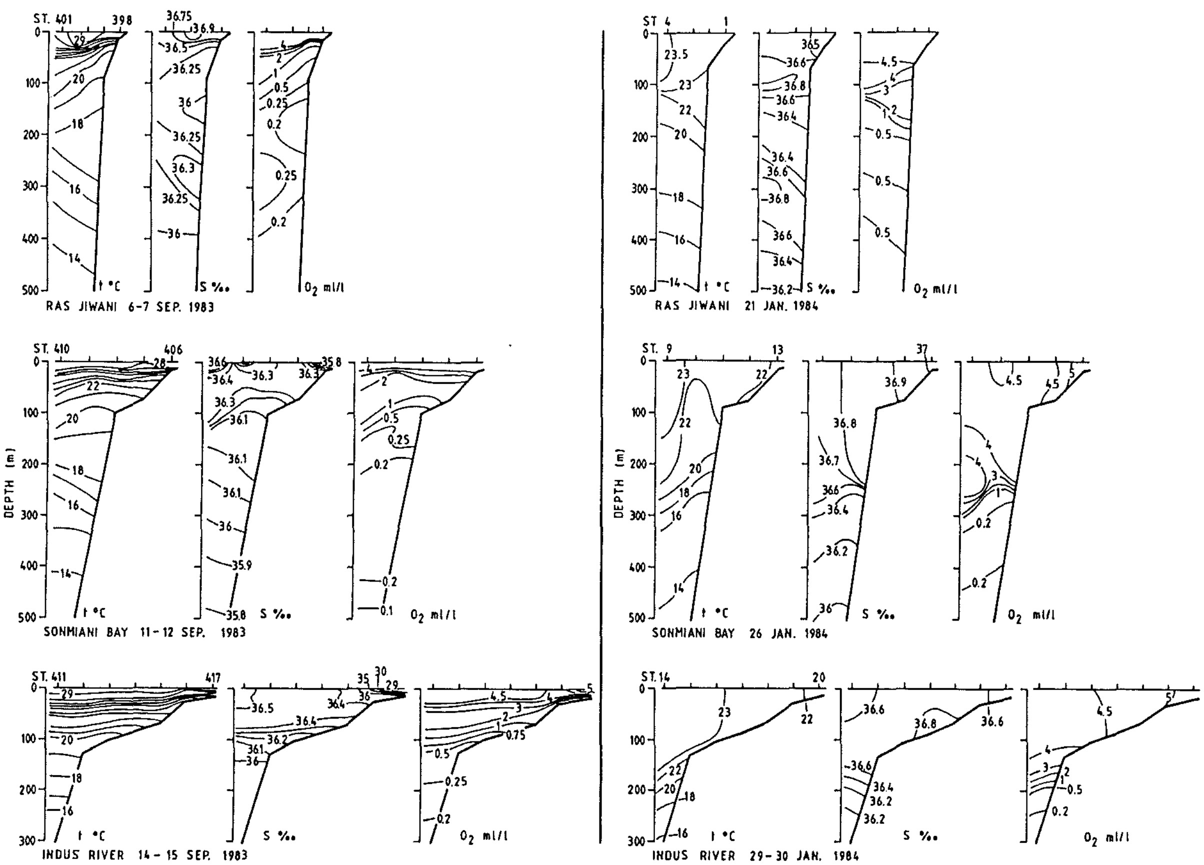

Fig. 5. Hydrographic sections off Pakistan. a: September 1983 survey; b: January 1984 survey. Position of the sampled stations is shown in Fig. 4

Some information on bottom type was found in Qureshi, 1961. The eastern part of the Pakistan shelf is very wide and influenced by the mud and detritus discharge of the Indus River. The bottom is mainly muddy, with a few stretches of sand. The western coast (Makran) consists of large bays. The sea bed is mostly mud, with patches of corals and rocks. The shelf is narrow, mostly shallow (< 50 m depth).

Oman. The two surveys (Table 1) took place in the pre-monsoon and post-monsoon period respectively (Figs. 6 and 7). The common, and probably most relevant feature, is the low oxygen content encountered at relatively shallow depths. The 1 ml l^{-1} isoline meets the shelf

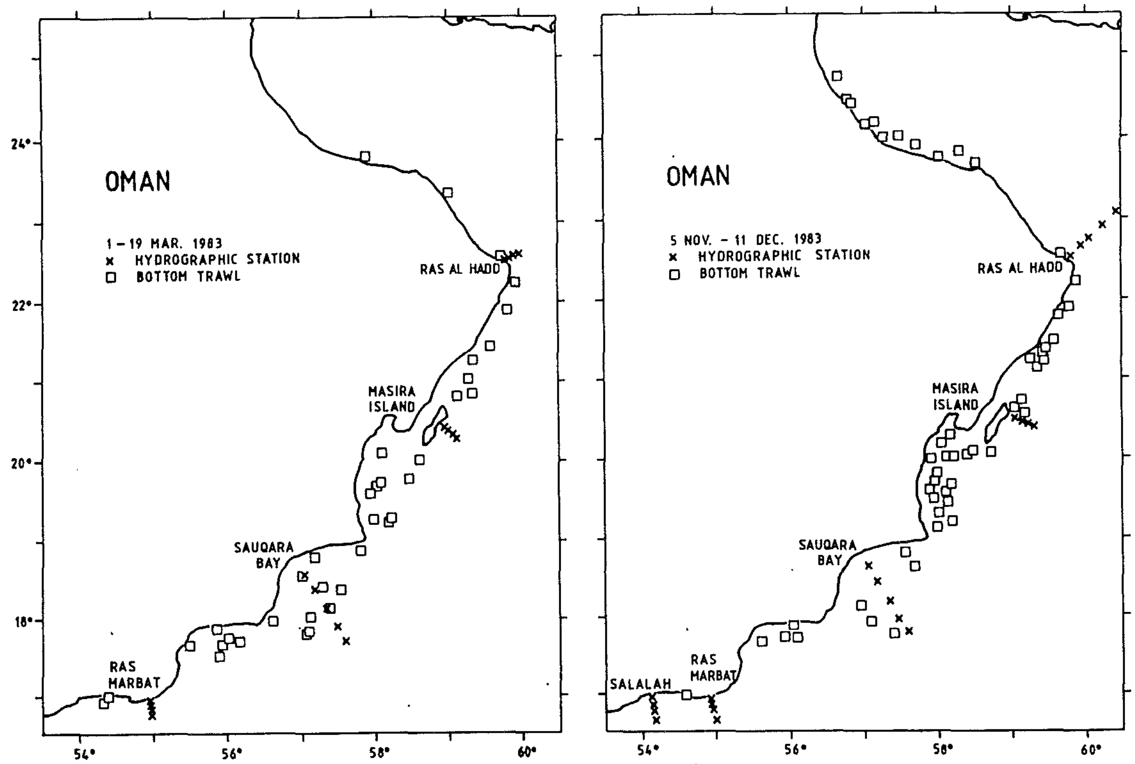

Fig. 6. Position of trawl hauls and hydrographic stations, Oman. Left: March 1983 survey; right: November-December 1983 survey

just below 100 m in the March survey while it appears shallower in the November/December survey when this isoline is found at 50 m depth off Masira Island and Sauqara Bay. These low oxygen levels are the indication of a post South-West-monsoon phase. Also the thermic structure of the water is different from that of the March survey. The lower thermocline reached a depth of 100-150 m in the March survey, while in the November/December survey was located between about 20 and 50 m depth almost throughout the coast. Water temperatures in November/December were higher on the surface by 2 to 3 degrees throughout and lower at about 100 m depth (Strømme 1983 and Strømme & Tilseth 1984).

Fig. a

Fig. b

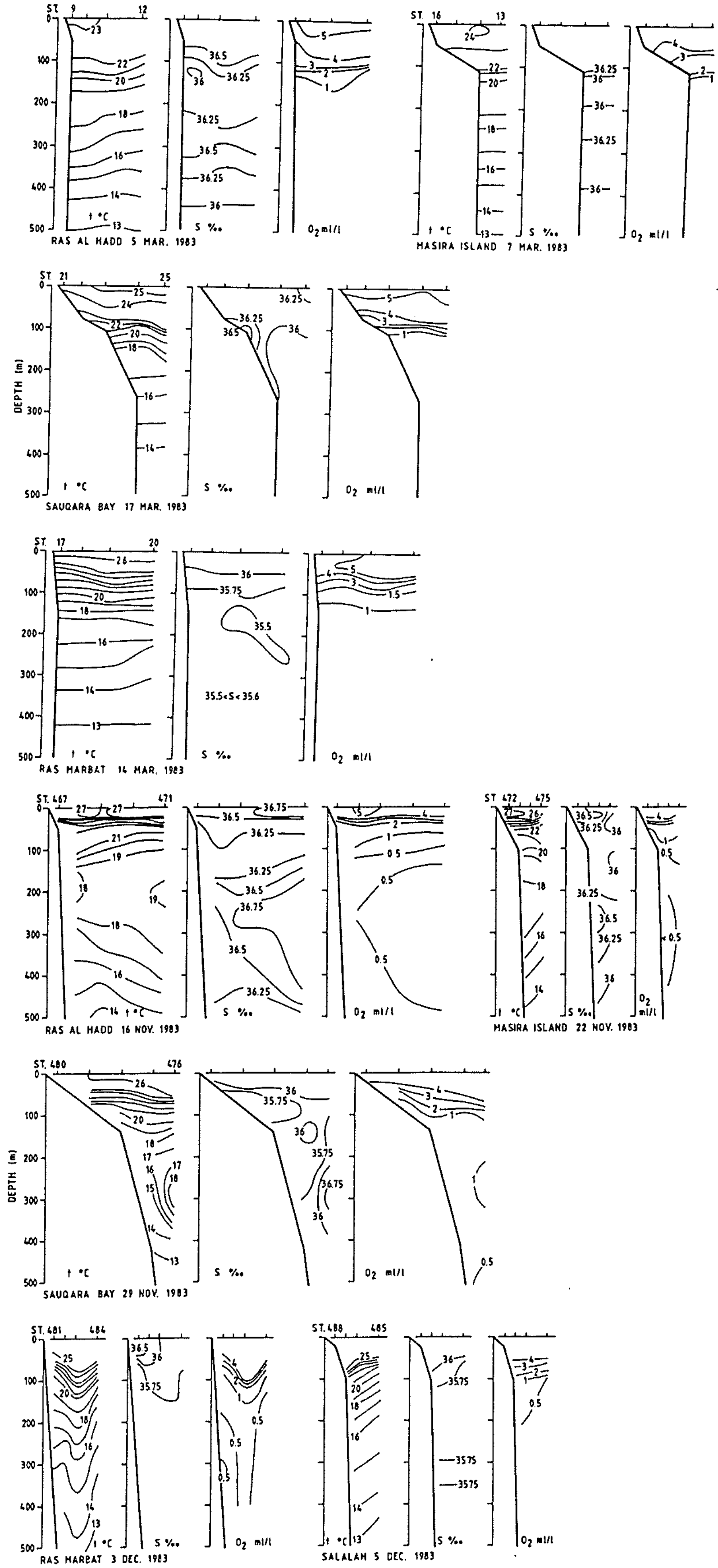

Fig. 7. Hydrographic sections off Oman. a: March 1983 survey; b: November-December 1983 survey. Position of the sampled stations is shown in Fig. 6

Yemen (southern coast). The two surveys available for Yemen (Table 1 and Fig. 8) show the two extreme hydrographic conditions of this area (Fig. 9). During the first survey the mixed waters of the upper layer reached a depth of 100 m, being warm (24-25 °C) and well oxygenated. The bottom of the thermocline (with temperatures of 16-17 °C) was found around 200 m. A sharp oxycline coincided with the thermocline and oxygen levels of 0.5 to 1 ml l^{-1} were also found around 200 m depth (Blindheim, 1984). In August, there were clear signs of upwelling, especially off Mukalla and Ras Fartak. The thermocline appeared uplifted, with temperatures falling to 16 °C between 50 and 100 m. Off Mukalla temperatures of 17 °C were found at the surface, close inshore and hypoxic waters (0.5 ml l^{-1}) were found from 50 m depth (Strømme 1984). The occurrence of upwelling was not detected off Yemen by the International Indian Ocean Expedition.

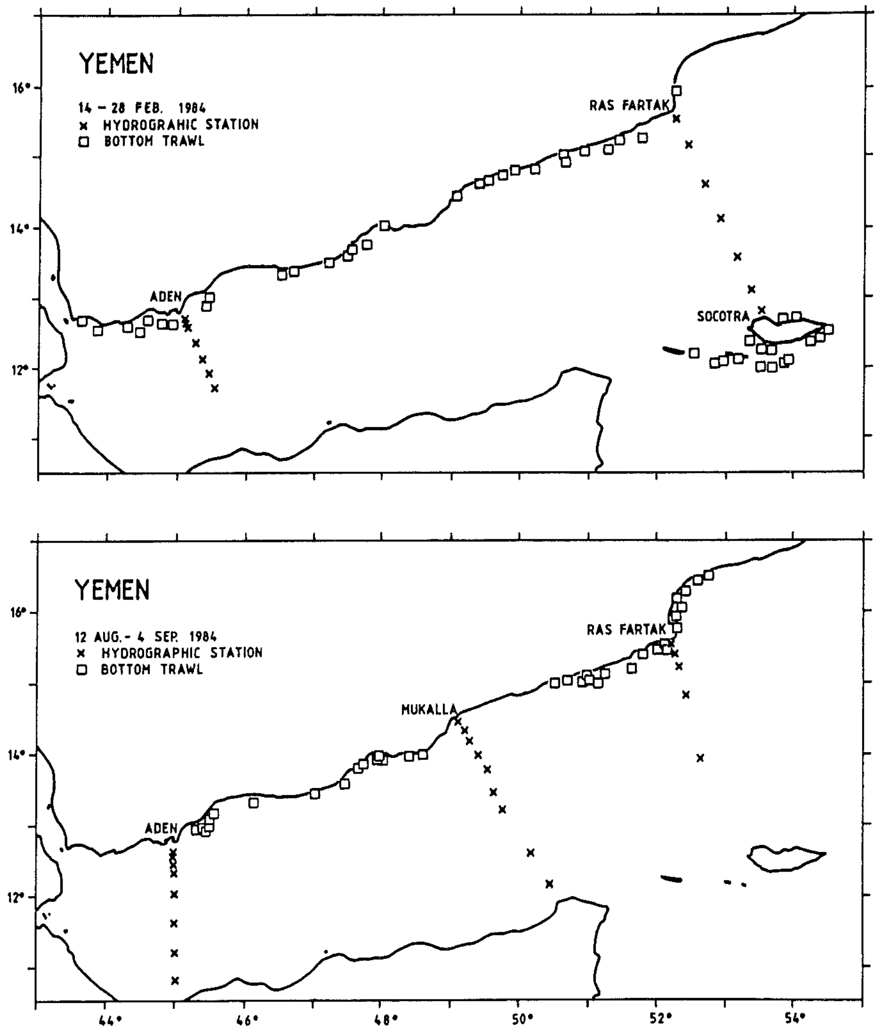

Fig. 8. Position of trawl hauls and hydrographic stations, South Yemen. Upper: February 1984 survey; lower: August 1984 survey

Fig. a

Fig. b

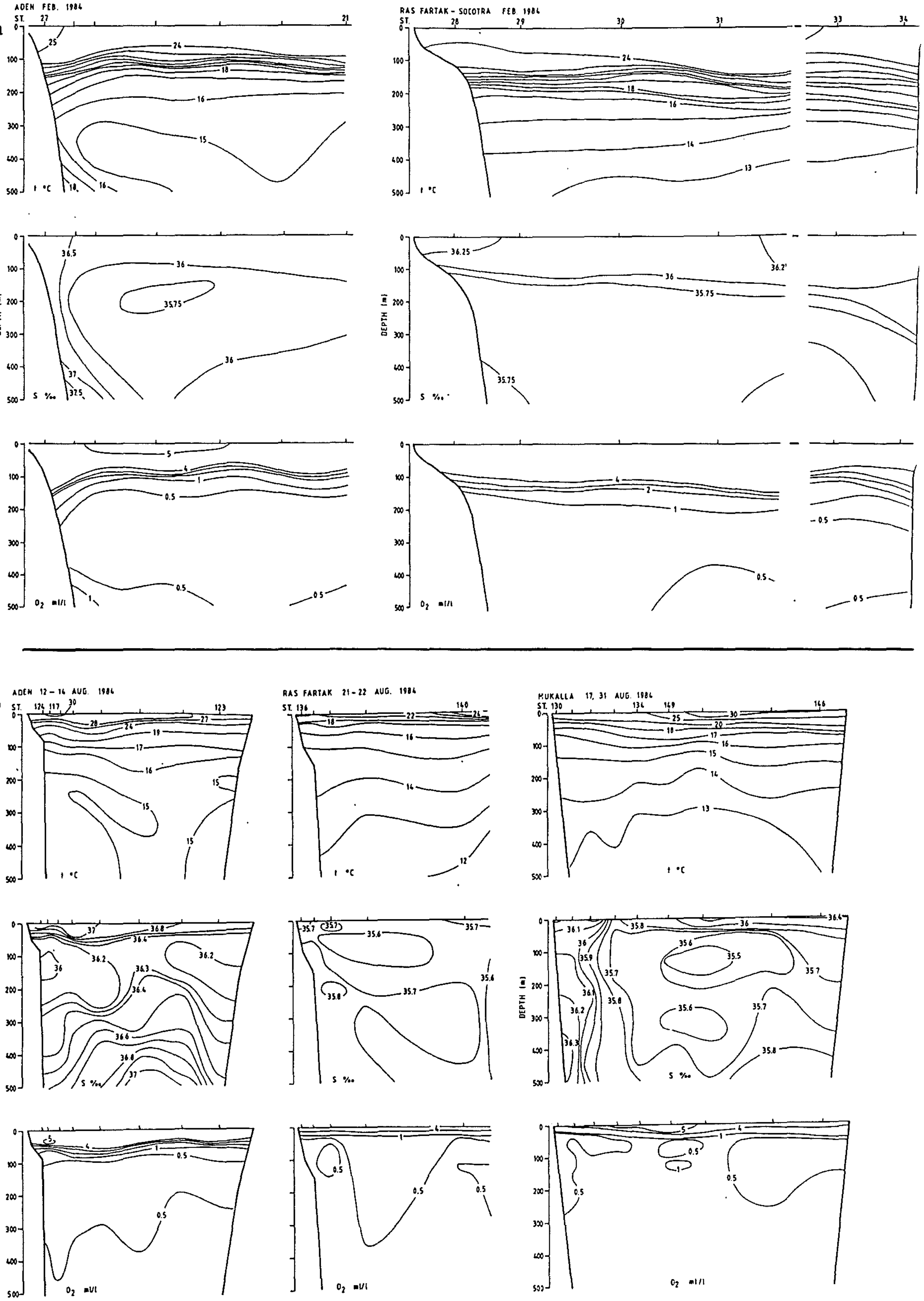

Fig. 9. Hydrographic sections off South Yemen. a: February 1984 survey; b: August 1984 survey. Position of the sampled stations is shown in Fig. 8

Ethiopia. Only one survey is available for Ethiopia and this took place in March 1984 (Fig. 10). The shelf edge is at about 100 m depth and the slope is very steep. Shelf waters had temperatures of 23 to 24 °C throughout and oxygen levels between 3 and 5 ml l^{-1}. Levels of 1 ml l^{-1} were found from about 200 m depth (Fig. 11) (Blindheim, 1984). Salinity was between about 38 and 40 ‰, increasing with depth. The lower salinity at the surface might indicate a influx of water from the Gulf of Aden.

Somalia. Only the northern part of the east coast of Somalia was covered (Table 1 and Fig 1), from Ras Asir to Ras Mabber (Fig. 12). The two series of hydrographic stations sampled in the first survey, off Ras Asir and Ras Hafun respectively, showed an upper mixed layer with high temperatures and oxygen levels to about 75 to 100 m depth (Fig. 13 a). Oxycline and thermocline almost coincided and oxygen levels lower than 1 ml l^{-1} were found in waters deeper than 100 to 125 m. The second survey took place during the South West monsoon period and only one hydrographic section is available for this period (Fig. 13 b). The surface 16 and 17 °C isotherms (Strømme 1985) show clear signs of upwelling, strongest south of Ras Hafun and gradually decreasing northwards. A small area directly south-east of Ras Hafun seemed to be less affected by upwelling (surface temperatures of 20 °C).

MATERIALS AND METHODS

Trawl data. A shrimp and fish trawl was used with a headline of 31 m, footrope 47 m, estimated headline height and distance between wings during towing of 6 and 18-20 m respectively. The mesh size was 2 cm, with double lining in the cod end. Each tow had a standard duration of 30 minutes. The bottom trawl stations used in this analysis were randomly set along the cruise track.

Species identifications and weighing and counting was performed on a subsample and the values then raised by a factor equal to the ratio between the weight of total catch and the weight of the sample. Congeneric species or species belonging to the same family were pooled together when difficult to separate. All station and species data were stored using NAN-SIS (Strømme, in press) and all data are available in ASCII format upon request to the author.

Hydrographic data. Temperature, salinity and oxygen data were used to examine the relationships of the different species assemblages with the physical environment. For the above variables, values were assigned to each trawl station from the nearest hydrographic station at a similar depth. Details on the equipment used may be found in the 'Dr. Fridtjof Nansen' reports.

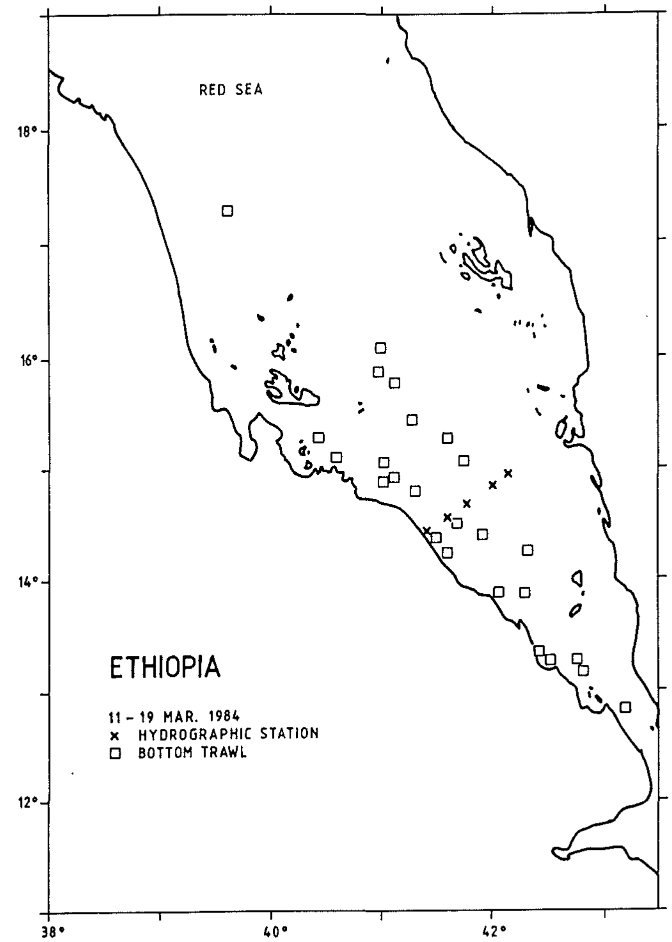

Fig. 10. Position of trawl hauls and hydrographic stations, Ethiopia March 1984 survey

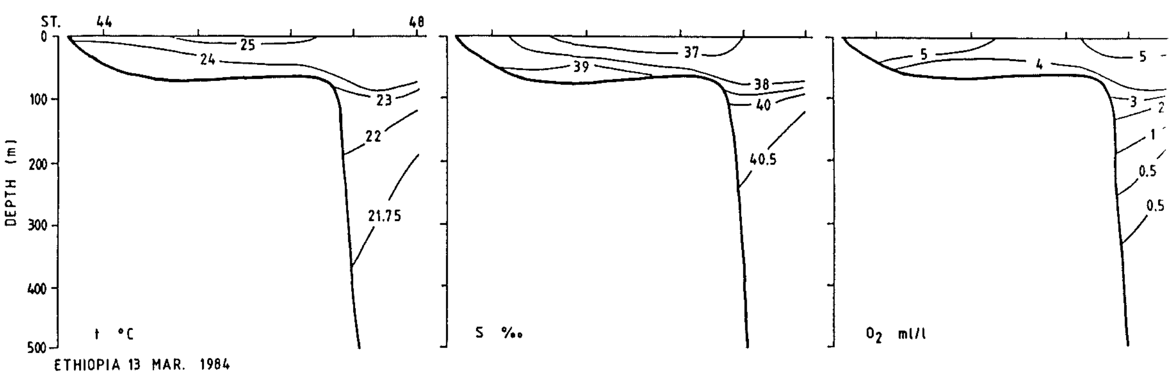

Fig. 11. Hydrographic sections off Ethiopia, March 1984 survey. Position of the sampled stations is shown in Fig. 10

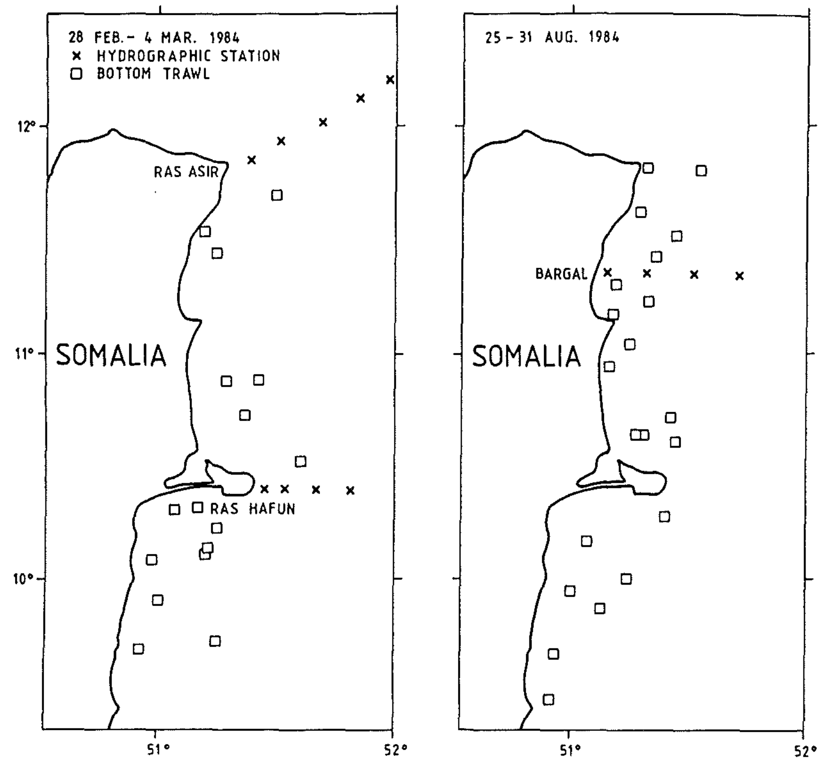

Fig. 12. Position of trawl hauls and hydrographic stations, Somalia. Left: March 1984 survey; right: August 1984 survey

Fig. a

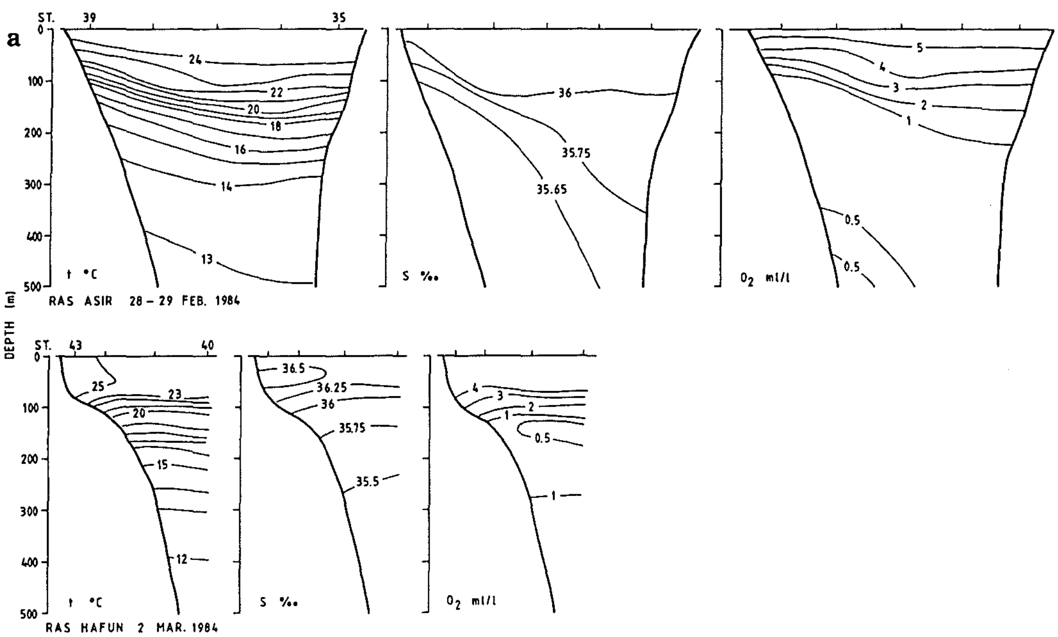

Fig. b

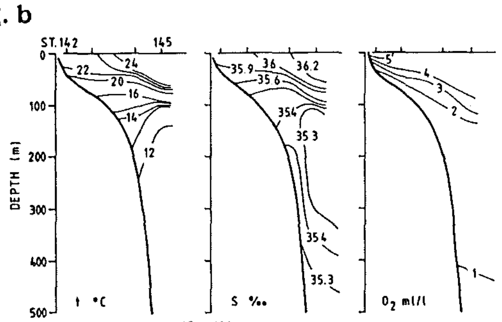

Fig. 13. Hydrographic sections off Somalia; a: March 1984 survey; b: August 1984 survey. Position of the sampled stations is shown in Fig. 12

Data analysis. The primary objective was to identify major patterns of species associations from the trawl data and relate them to available values for environmental factors to explain the patterns observed. The methods used in the present study are the same used in Bianchi (1991 and 1992 a,b), i.e. the classification method Two-Way Indicator species Analysis (TWIA), implemented by the computer program TWINSPAN (Hill 1979) and the ordination method Detrended Correspondence Analysis (DCA) implemented by the computer program DECORANA (Hill & Gauch 1980). The suitability of these methods to this type of study is discussed in Bianchi (1991).

The relationship between station groups and environmental variables was analyzed using the DECORANA program package CANOCO (version 3.10, ter Braak 1990), which also has the option of correlating the first ordination axes with environmental variables (in this case depth, salinity, oxygen and temperature). In some cases the slope stations were not included in the DCA analysis. These stations were obviously different and behaved as 'outliers'.

Each weight (x) was converted to ln(x+1) before analysis with DECORANA. This transformation minimizes the dominant effect of anomalous catches. Pseudospecies cut levels for TWINSPAN were set at (in kg): 0, 10, 100, 1000 and 10 000.

RESULTS

Pakistan. Appendix 1 a shows the two-way ordination of species and stations obtained with TWINSPAN for the September survey. The first dichotomy separates the four slope stations (Group D, average depth 223 m) from the shelf stations (Groups A-C). At the second division level Group C (deeper part of the shelf, range 36 to 100 m, average 66 m) separates from Groups A and B, i.e. the more coastal stations (average depth 23 and 34 m respectively). The third division level divides Group A from B, representing the shallower stations west of Karachi and off the Makran coast and the latter the shallow stations near the Indus River estuary. Analysis of the shelf stations with DCA confirmed the presence of the above groups (Fig. 14). The eigenvalues of the first four axes are 0.53, 0.44, 0.26 and 0.19 respectively. Plots of DCA Axis 1 against depth, temperature and oxygen are shown in Fig. 15. The correlation coefficients between DCA Axis 1 and 2 and the above environmental variables are shown in Table 2. DCA axis 1 is highly correlated with depth, and also significantly correlated with temperature and oxygen while there is no significant correlation with Axis 2. In fact, as it appears from the station ordination with DCA, Groups A and B (the shallower waters groups) are not separated along axis 1 but they appear separated from Group C (the deeper shelf group). Axis 2, not being correlated with any of the environmental variables

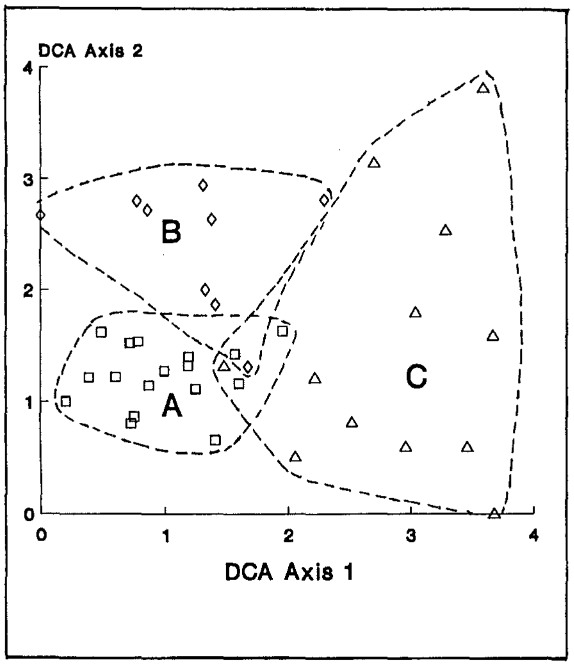

Fig. 14. Detrended correspondence analysis for Pakistan, September 1983 survey (SD units). TWIA Groups A to C encircled by broken lines

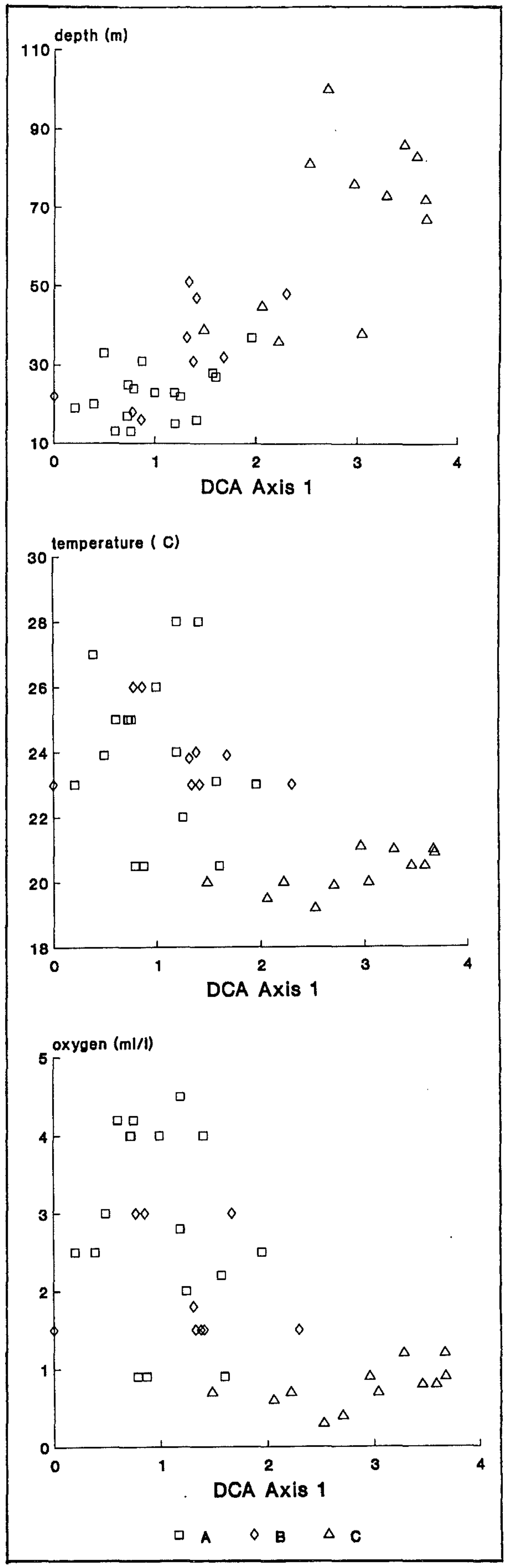

Fig. 15. Plot of station scores on DCA (Detrended Correspondence Analysis) Axis 1 against depth, temperature and oxygen for Pakistan, September 1983 survey

used in this study, must be explained by another variable. The proximity of stations of Group B to the Indus River Delta and/or bottom type might explain the difference.

Table 2. Pearson product-moment correlation coefficient between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations, Pakistan, September 1983 survey. Values with asterisk indicate significant correlation ($p < 0.05$, df 35).

Variable	Axis 1	Axis 2
Depth	0.76 *	0.29
Temperature	-0.57 *	0.06
Salinity	-0.24	-0.05
Oxygen	-0.56 *	-0.21

Group A contains stations with oxygen concentrations mostly above 2 ml l^{-1} (Fig. 15). Various species of catfishes, genus Arius, the tigertooth croaker, Otolithes ruber, the javelin grunter, Pomadasys kaakan and the hairtail Trichiurus lepturus were the most frequent and constituted most of the biomass of this group. Group B consists of a number of stations off the Sindi coast and the Delta of the Indus River. This group is the richest in species and very large catches (up to several tons/hour) were often obtained. Species of the genus Johnius and species of tonguesoles, family Cynoglossidae were the indicator species of Group B. Group C includes stations of the deeper part of the shelf, with the lowest oxygen concentrations ($O_2 < 2$ ml l^{-1}, Fig. 15). The Japanese threadfin bream, Nemipterus japonicus, is the indicator species for this group. Only the hairtail Trichiurus lepturus was also caught consistently at these stations. The fauna seemed to be rather poor, in accordance with what could be expected from the low oxygen levels. Group D includes only the four deepest stations (not included in DCA). The gaspers (genus Champsodon), typified this group.

Appendix 1 b shows the TWINSPAN classification of stations and species from the January 1984 survey and Fig.16 the plot of stations on DCA Axes 1 and 2. The eigenvalues of the first 4 axes were 0.37, 0.31, 0.24 and 0.20 respectively. These values are quite low compared to the previous survey indicating a higher homogeneity in the station species compositions. Fig. 17 shows the plot of DCA Axis 1 with depth. Group C includes the deepest stations. No plot was made for oxygen and temperature because the values for these environmental variables were practically constant throughout the shelf in the course of this survey (23 to 25 ° and > 4 ml l^{-1} respectively). Table 3 shows the correlations of DCA Axis 1 and 2 with the environmental variables. The highest correlation with depth reflects the differences between the two main Groups B and C, while the faint correlations with the other

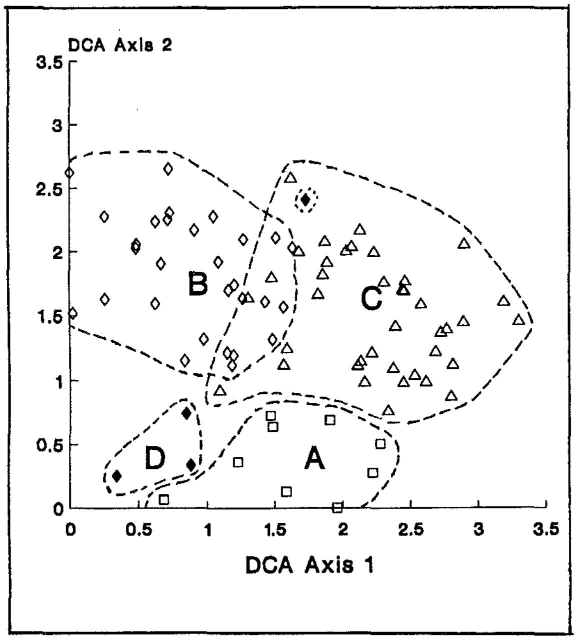

Fig. 16. Detrended correspondence analysis for Pakistan, January 1984 survey (SD units). TWIA Groups A to D encircled by broken lines

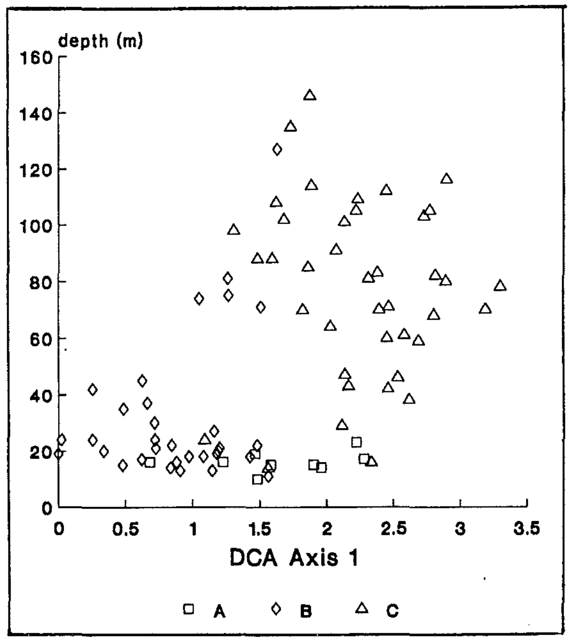

Fig. 17. Plot of stations scores on DCA (Detrended Correspondence Analysis) Axis 1 against depth for Pakistan, January 1984 survey

environmental parameters reflect the rather uniform conditions found on the shelf at this time of the year. Parallel to the remarkable environmental change, the bottom fauna identified during this survey displays a rather different distribution pattern. The wide shelf of the Sindi coast is now occupied by a larger number of species. Besides the species found in the course of the September survey, Nemipterus japonicus and Trichiurus lepturus and Saurida tumbil, still among the most abundant ones, other species, that had only been found in the shallowest stations now seem to invade the whole shelf. In particular, Pomadasys kaakan, Arius spp., Argyrops spinifer and Nemipterus metopias. The main groups (B and C), separated at the first division level, correspond approximately to the shelf off Makran and Sind respectively. However, this difference also reflects the deeper range of the stations off Sind (Group C) as compared to those off Makran (Group B). Here the catches were characterized by the consistent presence of cephalopods (Loliginidae), butterfly rays (Gymnuridae) and the shallow water sparid Acanthopagrus berda

Table 3. Pearson product-moment correlation coefficient between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations, Pakistan, January 1984 survey. Values with an asterisk indicate significant correlation ($p < 0.05$, df 78)

Variable	Axis 1	Axis 2
Depth	0.43 *	0.53 *
Temperature	-0.38 *	-0.29 *
Salinity	-0.29 *	0.10
Oxygen	-0.16	0.29 *

Oman. Appendix 2 a shows the TWINSPAN classification of species and stations for the March, pre-SW-monsoon survey. The first dichotomy of TWINSPAN separates two major groups, the first including Groups A and B, with the spangled emperor Lethrinus nebulosus, as indicator species, the seabreams Chemeirius nufar and Argyrops spinifer and the second (including Groups C and D) with the Arabian scad Trachurus indicus, the two-horn gurnard Lepidotrigla bentuviai, the Arabian pandora Pagellus affinis, the Indian scad Decapterus russelli and Nemipterus japonicus. At the second division level, Group A separates from B and Group C from D. Group A has as indicator species two groupers, Epinephelus areolatus and gabriellae, the redspot Lethrinus lentjan and species of cardinal fishes, family Apogonidae. Group B is characterized by Carangoides chrysophrys and Argyrops spinifer while Group C separates from D, the latter having , in addition, Saurida tumbil, Pomadasys stridens and Trichiurus lepturus. Analysis with DCA showed a similar pattern in the station groupings but Group D did not appear well separated from Group C. The eigenvalues were 0.67, 0.39, 0.31 and 0.24 respectively. Fig. 18 shows the plot of station scores on DCA Axis 1 and 2, Fig. 19 the plots of DCA scores on Axis 1 and the values for depth, temperature and oxygen. The plots of DCA Axis 1 with depth show that though Groups A and D have some shallower and some deeper stations respectively, DCA scores are not strongly correlated with this variable. Table 4 shows the results of the correlation between DCA Axes 1 and 2 and the environmental variables. Although some correlation appears with temperature, depth and oxygen, this is very weak and visual inspection of the graphs shows that this might be due to the fact that a few stations at the extremes of Axis 1 also have extreme values for the above variables.

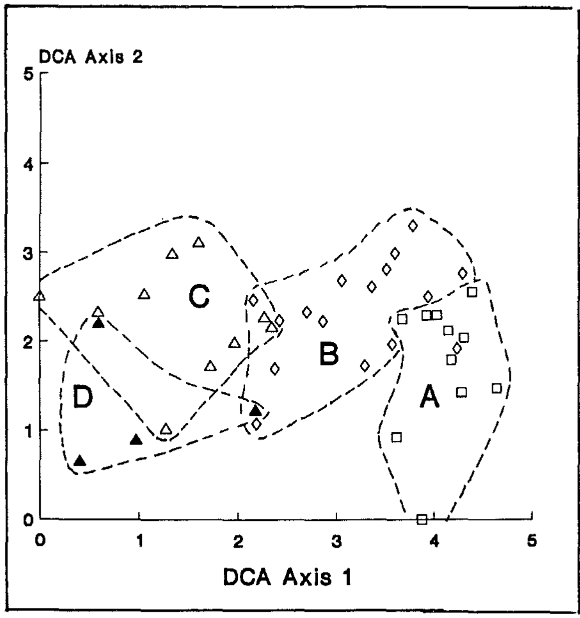

Fig. 18. Detrended correspondence analysis for Oman, March 1983 survey (SD units x 100). TWIA Groups A to D encircled by broken lines

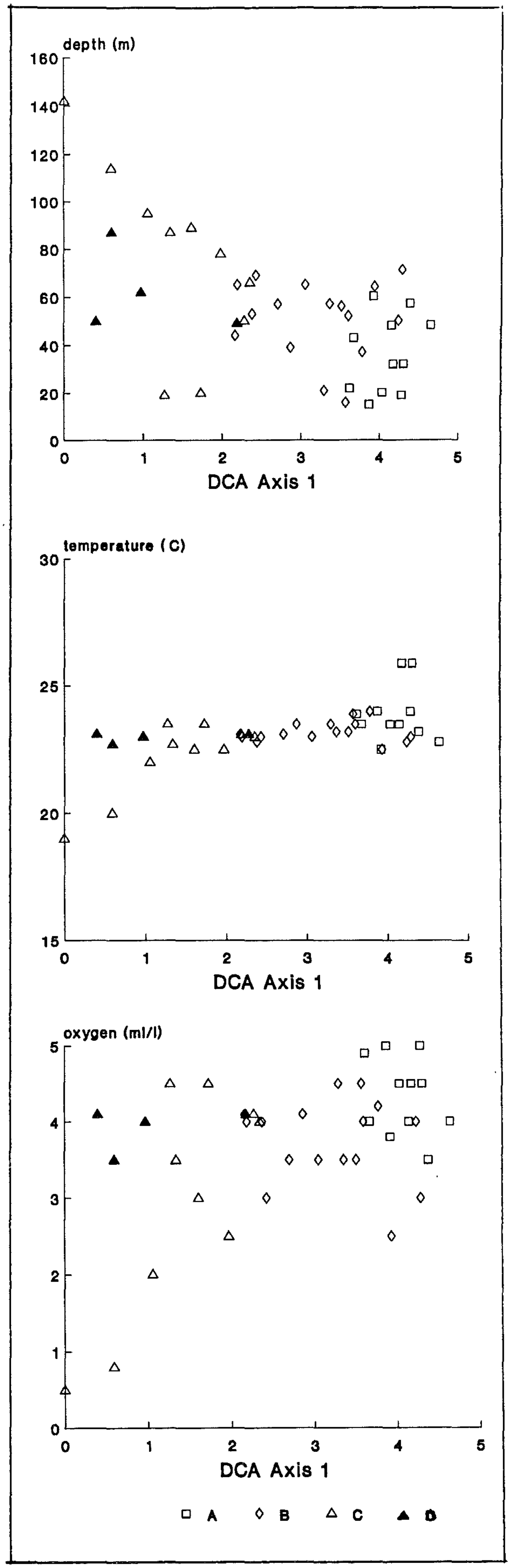

Fig. 19. Plot of station scores on DCA (Detrended Correspondence Analysis) Axis 1 against depth, temperature and oxygen for Oman, March 1983 survey

Table 4. Pearson product-moment correlation coefficient between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations, Oman, March 1983 survey. Values with asterisk indicate significant correlation ($p < 0.05$, df 38).

Variable	Axis 1	Axis 2
Depth	-0.45 *	0.54 *
Temperature	0.47 *	-0.26
Salinity	-0.35	-0.26
Oxygen	0.41 *	-0.51 *

Appendix 2 b shows the results from TWINSPAN for the November-December survey, i.e. in the post- SW-monsoon period. The letters identifying the different groups were chosen as to follow the indicator species found during the first survey. However, not all the groups are directly comparable as this survey also covered the northern coast of Oman. The first division separates Groups B and C, with Nemipterus japonicus as indicator species, from Group A with Lethrinus nebulosus, Carangoides chrysophrys, Cheimerius nufar and Loxodon macrorhinus as the indicator species, together with other taxa typical of Groups A and B of the former survey. However, the area where the above assemblages were found was sampled less intensively in the course of the second survey and the distinction between the two groups does not appear. Group C corresponds approximately to Group C and D of the previous survey and we find, among the dominant species, Nemipterus japonicus, Decapterus russelli and Trachurus indicus, Pagellus affinis etc. Group B corresponds to the stations along the northern coast, with Sphyraena putnamiae as indicator species and lacking most species of Group A and Group C. Other species exclusively found off northern Oman were Nemipterus bipunctatus (= N. delagoae), Platycephalus spp., Lutjanus bengalensis and Saurida tumbil. Fig. 20 shows the plot of DCA Axes 1 and 2 and Fig. 21 the plot of DCA Axis 1 and depth, temperature and oxygen. The correlations between DCA Axis 1 and 2 are shown in Table 5. Axis 1 is significantly correlated only with salinity. The negative sign indicates the decreasing S trend with increasing DCA values. In fact, Group B (off the northern coast) is under the influence of water from the Gulf, characterized by high salinity ($S > 37$ ‰). Differences between Groups A and C along Axis 1 may be due to bottom type. The significant correlations between DCA Axis 2 and depth, oxygen and temperature are not related to differences between the groups but within Group C. It is of interest to note that only stations of Group C are found were oxygen concentrations are below 1,5 ml l^{-1}.

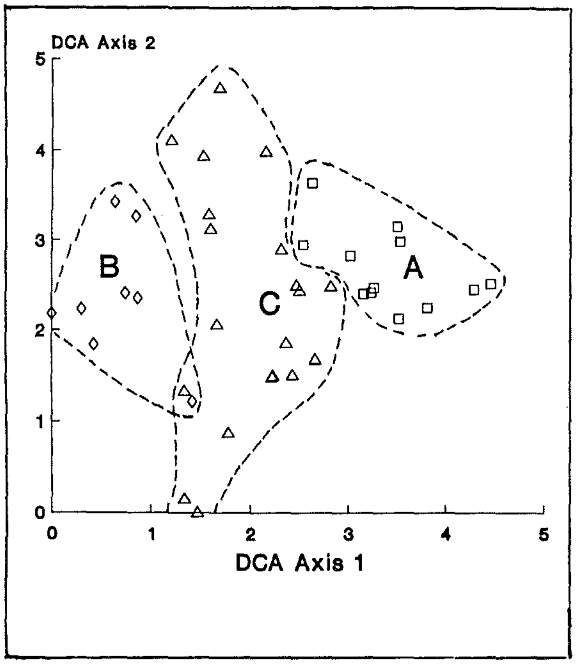

Fig. 20. Detrended correspondence analysis for Oman, Nov.-Dec. 1983 survey (SD units). TWIA Groups A to C encircled by broken lines

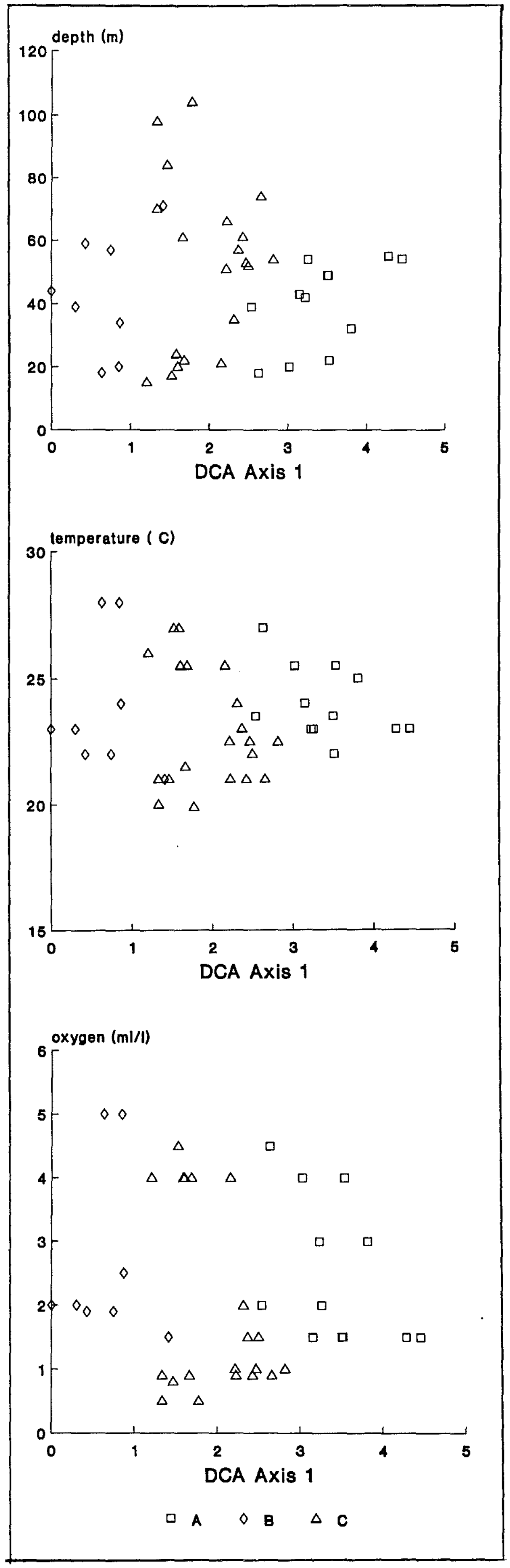

Fig. 21. Plot of station scores on DCA (Detrended Correspondence Analysis) Axis 1 against depth, temperature and oxygen for Oman, Nov.-Dec. 1983 survey

Table 5. Pearson product-moment correlation coefficient between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations, Oman November-December 1983 survey. Values with an asterisk indicate significant correlation ($p < 0.05$, df 37)

Variable	Axis 1	Axis 2
Depth	0.03	-0.88 *
Temperature	-0.10	0.83 *
Salinity	-0.50 *	0.20
Oxygen	-0.17	0.79 *

Yemen. The two surveys (March and August 1984) covered the southern shelf during the main, contrasting hydrological conditions related to the North East and South West monsoon respectively. During the first survey the shelf off Socotra was also investigated[1] . Appendix 3a shows the classification of species and stations obtained with TWINSPAN. Most of the stations of Group A, resulting from the first division, correspond to those carried out off Socotra while Groups C and B are mainly stations off Yemen mainland. Indicator species for Group A are butterflyfishes (Family Chaetodontidae) but a number of typically hard bottom species are found only here: Lutjanus sebae and L. bohar, Lethrinus nebulosus and L. elongatus to mention some of them. The depth range was 24 to 93 m (average 41 m). The hydrographic section between Ras Fartak (Yemen mainland) and Socotra indicates that these stations are located above the thermocline and the oxycline, with T > 23°C and O_2 > 4 ml l^{-1} respectively for all the stations. The plot of DCA Axes 1 and 2 (Fig. 22) shows how Group A appears as well separated from Groups B and C and Fig. 23 shows that the separation is not due to depth. The eigenvalues of DCA were 0.85, 0.71, 0.52 and 0.41 for the first 4 axes respectively. Table 6 shows the results of the correlation between DCA Axes 1 and 2 and the environmental variables. Significant correlation, though not very strong, is found only with depth. Stations of Group B, located along Yemen mainland, are mostly shallow water (depth range 16 to 36, average 26 m) are characterized by the presence of Sphyraena putnamiae, Arius thalassinus but they also share some of the common species of Group C, Nemipterus japonicus, Saurida undosquamis and Sepia faraonis. Group C includes stations, mainly from the mainland, with a wide depth range, from 17 to 194 m depth (average 63 m). Nemipterus japonicus and Saurida characterize this group.

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[1] Although this area is geographically closer to Somalia, politically is part of Yemen. The data collected off Socotra were stored under the Yemen project and for this reason they had to be analyzed together with the data from the southern coast of Yemen. Obviously, it would have been more logical to analyze them together with the data from Somalia.

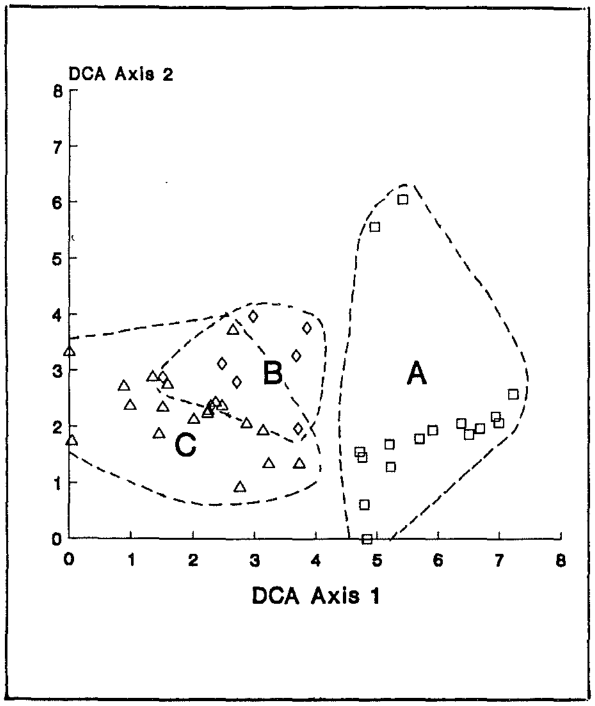


Fig. 22. Detrended correspondence analysis for South Yemen, February 1984 survey (SD units). TWIA Groups A to C encircled by broken lines

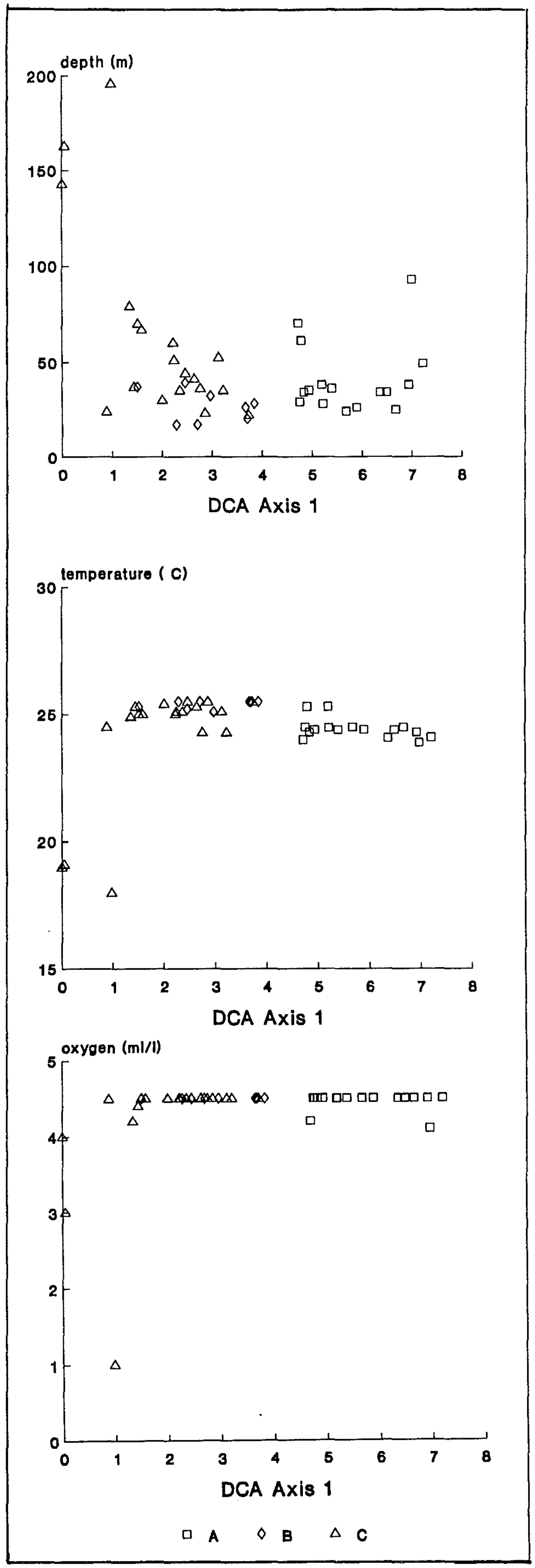


Fig. 23. Plot of station scores on DCA (Detrended Correspondence Analysis) Axis 1 against depth, temperature and

Table 6. Pearson product-moment correlation coefficient between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations, Yemen (southern coast), February 1984 survey. Values with asterisk indicate significant correlation ($p < 0.05$, df 40).

Variable	Axis 1	Axis 2
Depth	-0.41 *	0.06
Temperature	0.21	-0.01
Salinity	0.31	0.37
Oxygen	-0.37	0.01

Appendix 3 b shows the sorted TWINSPAN species by station table for the second survey which took place in August 1984 i.e. in the full upwelling season. This time Socotra Island and the area west of Aden were not surveyed. The first division separates Groups A and B from Group C. Stations of Group A are slightly deeper (average depth 60 m) but with a wide depth range (20 to 172 m) and they are located almost throughout the coast with the exception of the area between Aden and somewhere midway between Aden and Mukalla. Indicator species is Callionymus marleyi, a small (to 10 cm) dragonet reported to inhabit sand bottoms of shallow coastal areas (Fischer & Bianchi 1984) and feeding on small bottom invertebrates (however, this might be a misidentification of the closely related Bathycallionymus, also reported from the area, but known to occur in deep waters, near the edge of the shelf, Nakabo, 1982). Catches up to 2.3 tonnes were obtained at depths of 85 m outside Ras Fartak were oxygen concentrations were 0.5 ml l^{-1}. Lepidotrigla bentuviai and Saurida undosquamis were found, in combination with C. marleyi and Nemipterus japonicus, in a few stations. Group B includes only four stations, mainly around the Ras Fartak area, and with an average depth of 33 m (range 17 to 71 m). The stations of this group are characterized by the presence of Arius thalassinus and very high catches of Nemipterus japonicus, one at 15 m and another at 74 m depth. Off Ras Fartak oxygen concentrations fall to below 1 ml l^{-1} at about 30 m. Group C includes mostly shallow water stations east of Aden and two stations east of Ras Fartak. The depth range is 10 to 61 m. Indicator species are Fistularia petimba, Thenus orientalis and Loligo spp. Fig. 24 shows the plot of DCA axes 1 and 2, which confirms the relationship derived from the TWINSPAN classification. Eigenvalues resulting from DCA analysis were 0.88, 0.63, 0.53 and 0.36, reflecting a high total variance in the species data. Table 7 shows the correlation between Axes 1 and 2 and the environmental variables. Significant correlation is found between Axis 1 and temperature, salinity and oxygen. This reflects the fact that Group C, best separated on the first axis, includes mainly shallow water species, some of them close to Aden where high salinity, oxygen and temperature values where found to 50-60 m depth (see also Fig. 25).

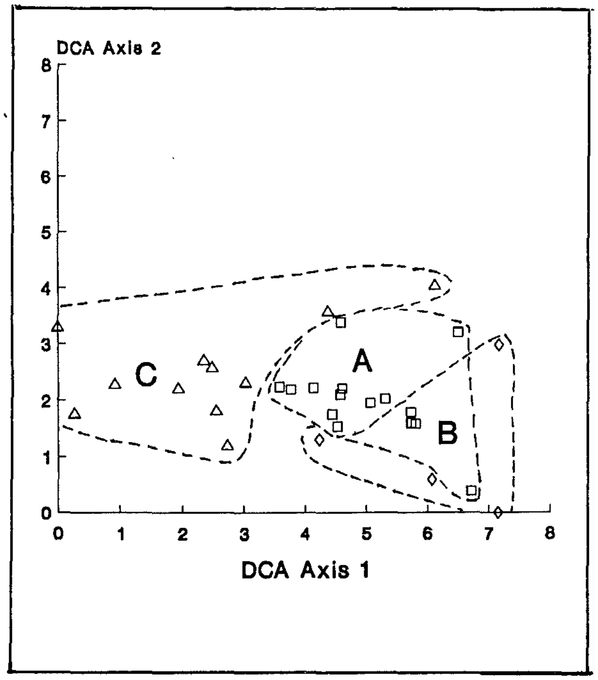


Fig. 24. Detrended correspondence analysis for South Yemen, Aug.-Sept. 1984 survey (SD units). TWIA Groups A and C encircled by broken lines

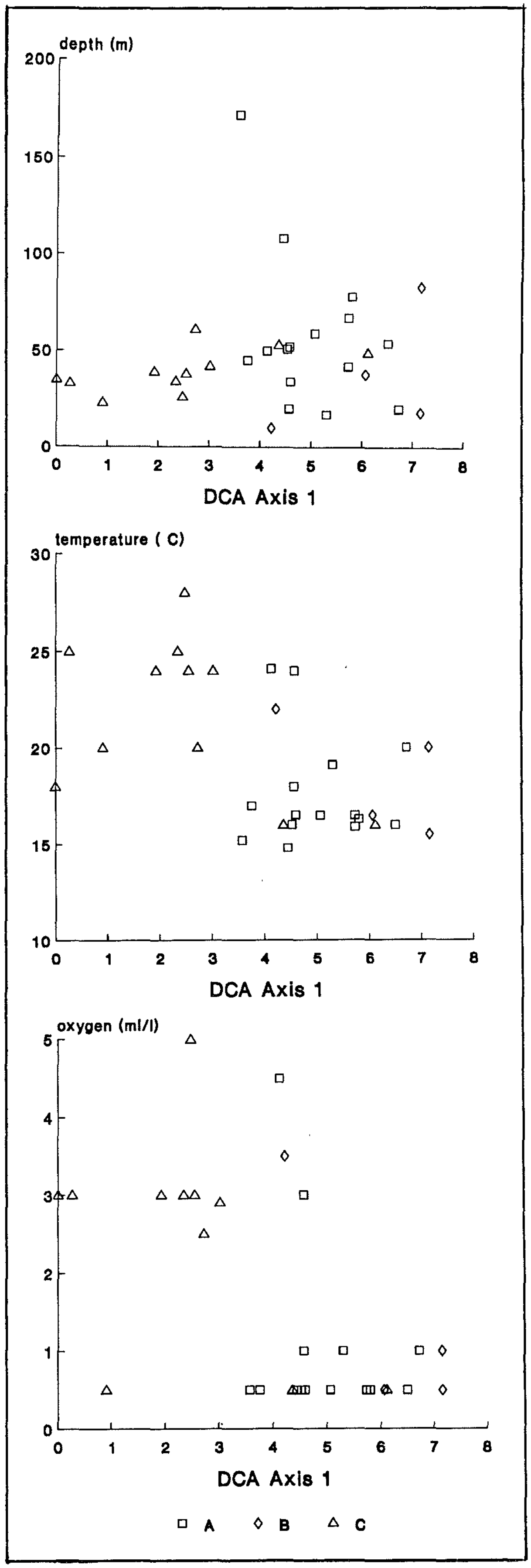


Fig. 25. Plot of station scores on DCA (Detrended Correspondence Analysis) Axis 1 against depth, temperature and oxygen for South Yemen, Aug.-Sept. 1984 survey

Table 7. Pearson product-moment correlation coefficient between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations, Yemen (southern coast) August 1984 survey. Values with an asterisk indicate significant correlation ($p < 0.05$, df 40)

Variable	Axis 1	Axis 2
Depth	0.11	0.10
Temperature	-0.75 *	-0.06
Salinity	-0.72 *	-0.02
Oxygen	-0.86 *	-0.00

Ethiopia. Only one survey is available for this area (March 1984). The shelf waters are well oxygenated and temperatures are above the thermocline values throughout the shelf. Most of the stations were shallower than 70 m, 2 stations were sampled at about 220 m depth. Two major groups appear in the output of TWINSPAN (the deep-water stations are not included) (Appendix 4). Group A includes species with a depth range between 30 and 50 m (average 41 m), mostly characteristic of intermediate waters possibly close to rocky bottoms. Typical of this group are Lutjanus sanguineus (= L. coccineus), Diagramma pictum, Lethrinus nebulosus and L. lentjan, Gymnocranius griseus and the threadfin Nemipterus bipunctatus. Squids, also common in the next group, appeared almost in all the catches. The other major group (called C to keep comparability with those groups from other areas also having Nemipterus japonicus as indicator species) include stations from 25 to 86 m depth (average 49 m) were the species above either do not appear or only sporadically. Nemipterus japonicus, Saurida tumbil and S. undosquamis, Carangoides malabaricus and Priacanthus hamrur typify this assemblage. In Fig. 26 the above two major groups are easily identifiable. Table 8 and Fig. 27 show that no correlation is present with any of the environmental variables and Axis 1. The significant correlation between Axis 2 and depth and oxygen indicates the presence of a gradient, possibly within Group C. Temperature and salinity had constant values at all shelf stations and therefore they do not appear in Table 8.

Somalia. The first survey last only a few days (end of February, beginning of March 1984), in the period of North East monsoon. High oxygen and temperature levels were found deeper than 100 m. Appendix 5 a shows the results from TWINSPAN. Two major groups seem to emerge. Group A is well defined and besides the indicator species, Diagramma pictum, Epinephelus chlorostigma and Parupeneus pleurotenia, other species of typically hard bottoms were present like Lethrinus nebulosus. The depth range of the stations from this group was 14 to 81 m (average 45). Group B is defined by the lack of the above species. Decapterus russelli, Saurida undosquamis and Saurida tumbil were among the most

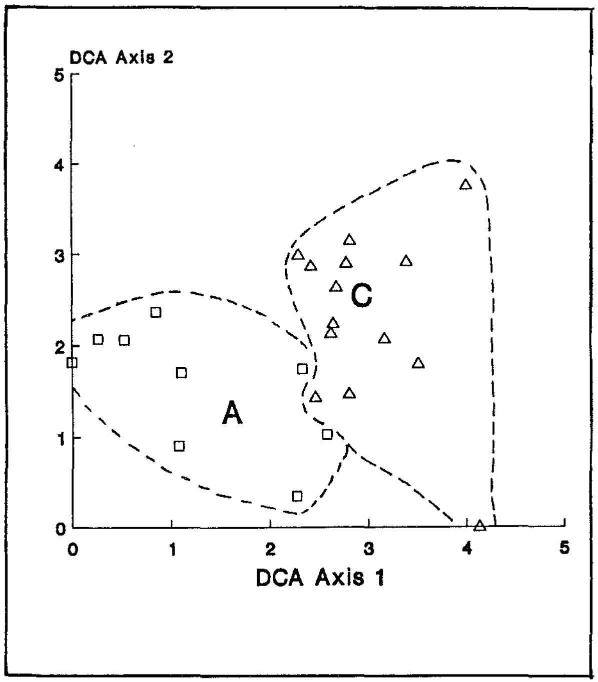


Fig. 26. Detrended correspondence analysis for Ethiopia, March 1984 survey (SD units). TWIA Groups A and C encircled by broken lines.

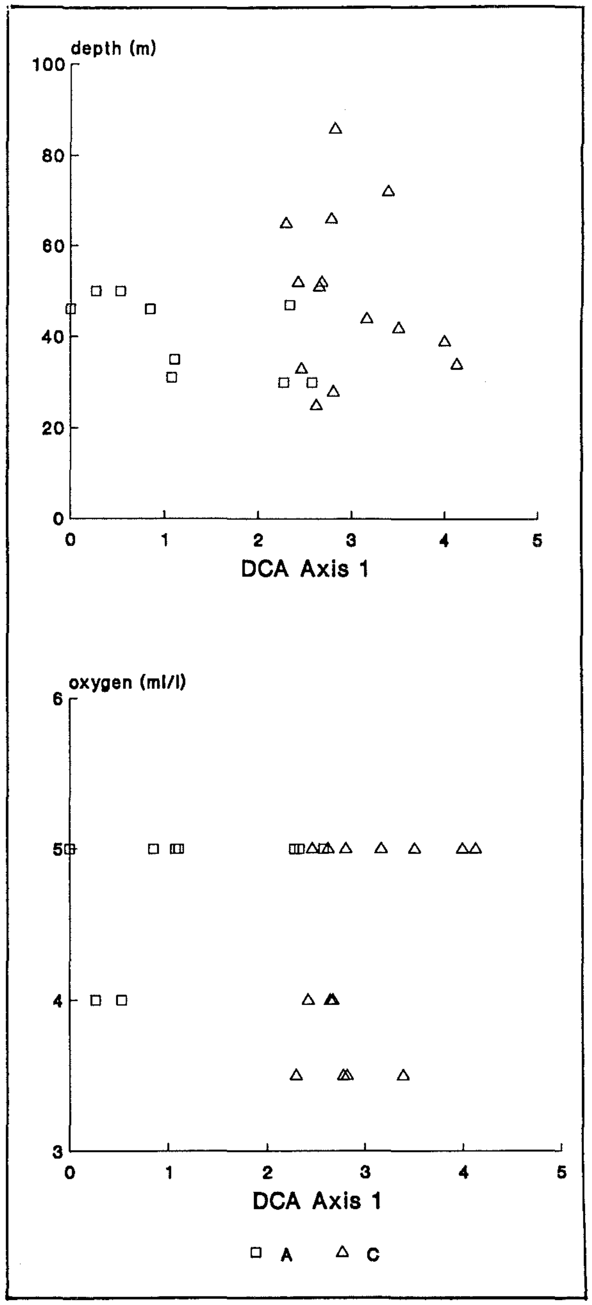


Fig. 27. Plot of station scores on DCA (Detrended Correspondence Analysis) Axis 1 against depth, temperature and oxygen for Ethiopia, March 1984 survey

common species but these were occasionally caught also in Group A. Fig. 28 shows the DCA ordination of the stations, showing some overlap between the above groups and the presence of an important gradient along Axis 2 only for Group B. There is no significant correlation with any of the measured parameters (Table 9 and Fig 29).

Table 8. Pearson product-moment correlation coefficient between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations, Ethiopia, March 1984 survey. Values with asterisk indicate significant correlation ($p < 0.05$, df 20). Temperature and salinity were automatically excluded by CANOCO because of their negligible variance.

Variable	Axis 1	Axis 2
Depth	-0.03	0.61 *
Oxygen	0.05	-0.56 *

Table 9. Pearson product-moment correlation coefficient between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations, Somalia, February 1984 survey. Values with asterisk indicate significant correlation ($p < 0.05$, df 13).

Variable	Axis 1	Axis 2
Depth	0.34	-0.20
Temperature	0.31	0.12
Salinity	0.09	-0.48
Oxygen	-0.26	0.04

The second survey took place during the upwelling season. Clear signs of upwelling were found south of Ras Hafun. Appendix 5 b shows the results of the TWINSPAN classification. The two major groups have similar depth ranges (30 to 81 and 23 to 85 respectively) and averages (54 and 56 respectively) also quite similar to those of the previous survey. However, the species composition is quite different. In particular, all the indicator species of Group A of the March survey have disappeared. These were the typically hard bottom dwellers, and possibly also not able to tolerate low oxygen levels. Indicator species of Group A of the August survey were the seabream Cheimerius nufar, species of porcupine fishes Diodon, the cardinal fishes Apogonidae and the sharks Holohalaelurus spp. Group B was characterized by Saurida undosquamis and Pagellus affinis as indicator species of this group. Fig. 30 shows the DCA plot where the above groups appear well separated along Axis 1. Fig. 31 shows that this difference is not depth-related.

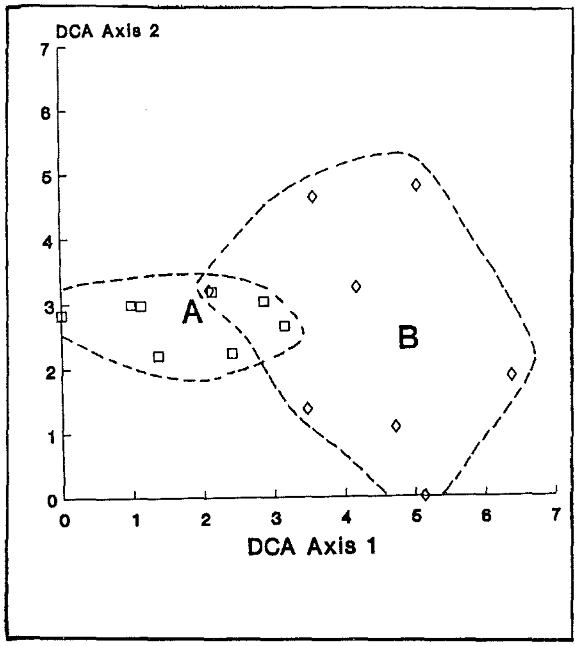


Fig. 28. Detrended correspondence analysis for Somalia, March 1984 survey (SD units). TWIA Groups A and B encircled by broken lines

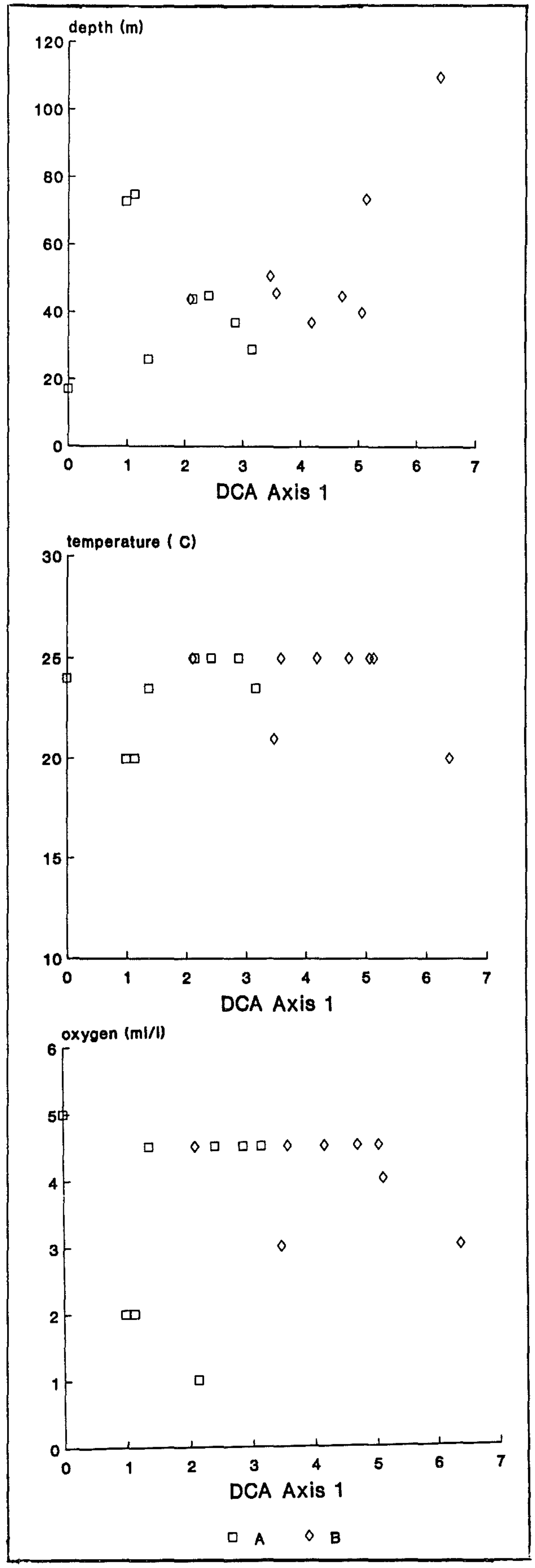
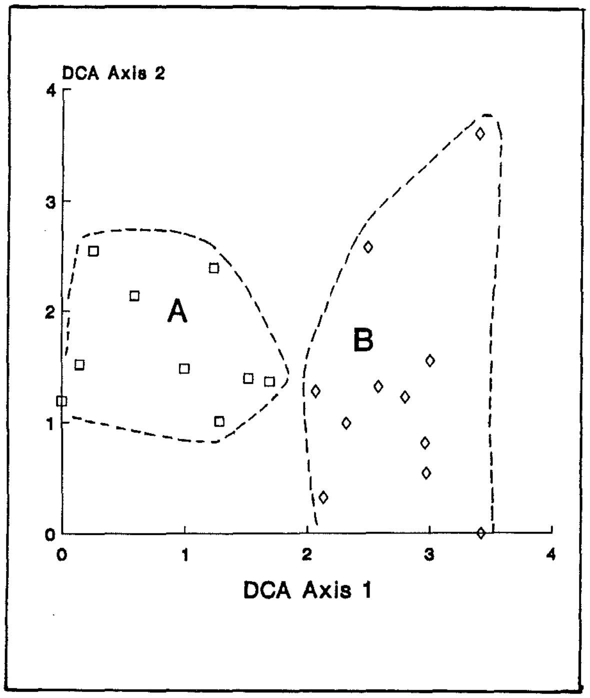


Fig. 29. Plot of station scores on DCA (Detrended Correspondence Analysis) Axis 1 against depth, temperature and oxygen for Somalia, March 1984 survey



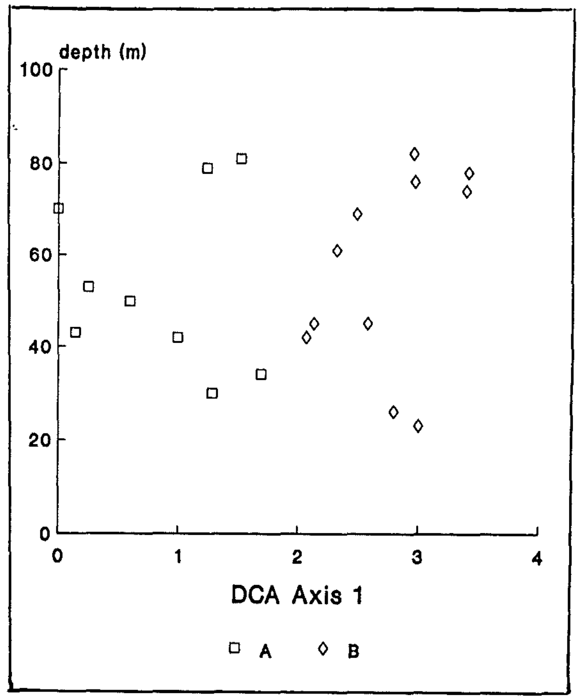


Fig. 30. Detrended correspondence analysis for Somalia, August 1984 survey (SD units). TWIA Groups A and B encircled by broken lines.

Fig. 31. Plot of station scores on DCA (Detrended Correspondence Analysis) Axis 1 against depth for Somalia, August 1984 survey

DISCUSSION

Species assemblages

Pakistan. The September survey corresponded with the South West monsoon period and, although no upwelling occurs off Pakistan, oxygen-depleted waters (concentrations < 1 ml l^{-1}) are found from about 80 m depth throughout the shelf and from about 50 m depth off the eastern coast. Also, already at 20-30 m depth oxygen concentrations are below 2 ml l^{-1}. The wide shelf off the Sindi coast displayed in fact an extremely low species diversity, with few species consistently caught at all stations. These species must be able to tolerate the low oxygen concentrations or be able to carry out vertical migrations. Hairtails are typically benthopelagic but the other abundant species, Nemipterus japonicus, is described in the literature as typically demersal (Russell, 1990). This species was also caught in the pelagic trawl in the upper water layers, over a bottom depth of about 80 m (Nakken 1983). This is also known from other survey programmes (Kesteven et al 1981). Diet of both species includes a wide variety of invertebrates as well as fishes. This might indicate the plasticity of the environmental adaptations of the above species allowing them to occupy areas with stressful (in this case hypoxic) conditions, while other species are pushed to shallow waters.

The high catches obtained in the shallow water stations can be explained as a result of migration by many species to oxygen-rich waters. This is confirmed by the results obtained from the January survey when a much higher number of species are found together with N. japonicus and T. lepturus, i.e. Pomadasys kaakan, Nemipterus metopias and Lactarius lactarius. In shallow waters (Group B) other species are dominant: cephalopods, (family Loliginidae), butterfly rays (Gymnura) Carangoides malabaricus and the Spanish mackerel Scomberomorus guttatus among the most important ones. Argyrops spinifer was found throughout the shelf. It is remarkable that the main groups include stations with very wide depth ranges, well reflecting the almost homogeneous hydrographic conditions throughout the shelf.

The Pakistan shelf (excluding shallow coastal waters) may be divided into two major zones: one shallow zone with relatively stabile temperature and oxygen values, where most of the shelf fish fauna finds shelter during the SW monsoon season, and a deeper zone (from about 50-80 m) where the environmental conditions change dramatically on a seasonal basis: during the SW monsoon period, when oxygen concentrations and temperature are low, only a few species, able to swim to upper water layers, are found here. During the NE monsoon, when values for the above variables are comparable to those found in shallow waters, this zone is 'invaded' by a rich and diverse fauna.

Oman. Both surveys were performed during 'hybrid' seasonal periods, i.e. just before and just after the SW-monsoon season and the coverage were slightly different. The patterns that seemed to emerge from the first survey indicate the presence of three main groups, with differences in average depth (average depth 36, 51 and 73 m respectively, for Groups A, B and C-D). Groups A and B are the shallowest and are also typified by species of rocky and sandy bottoms. Group C-D, mostly off the shelf south of Ras al Hadd and in the deeper part of the shelf southward is instead characterized by species with a deeper range and able to migrate to avoid oxygen-depleted waters. Trachurus indicus and Nemipterus japonicus are both able to perform vertical migrations. As off Pakistan, the latter species was caught several times in the pelagic trawl (Strømme 1986). None of the environmental variables used in this study seems to definitely explain the patterns observed.

The second survey showed how the fauna off the northern coast is quite different from the fauna south of Ras al Hadd and is probably an extension of the Gulf fauna, which is also reflected by the high salinity water typical of that region. Furthermore, no upwelling occurs along the northern coast.

The upwelling off Oman and the associated increase in phosphate, chlorophyll a and zooplankton were described by Currie et. al. (1973). The occurrence of oxygen-depleted waters on the shelf, as a consequence of upwelling, was observed in the November 1983 survey and is a well-known event. As for Pakistan, the dominating species found in these areas, subject to periodical stressful conditions, must have developed special adaptations. Besides Nemipterus japonicus, Trachurus indicus is the dominant species where the strong upwelling occurs. It is described in the literature as demersal and feeding on small crustaceans and fish fry (Fischer & Bianchi, 1984). In the Gulf, it was described as occurring close to the bottom, feeding on anchovies and preyed upon by Lutjanus malabaricus, Diagramma pictum and Saurida undosquamis (Anon. 1981). This species was definitely observed and caught both pelagic and close to the bottom (Strømme, 1986). Its occurrence in the bottom trawl has characterized Group C of both surveys. The capability of this species to live and feed both close to the bottom and in upper water layers is well adapted to the environmnetal conditions found in the region, with upwelling and increase in zooplankton on a seasonal basis. Walsh (1976) compared the ecological strategies of the more stable upwelling ecosystems off South West Africa and Peru, against the more unpredictable upwelling systems off, for example, California and Panama. There seems to be a tendency in the evolutionary strategies to form short food chains where the upwelling is stable throughout the year while more inefficient, but environmentally more adaptable zooplanktivorous fish characterize more unstable habitats. This might certainly explain the presence of Trachurus indicus in this habitat while the substitution of a species (i.e. a clupeoid) with a shorter food chain would be highly improbable. As regards the effects of upwelling on the bottom megafauna, there are two different aspects: the enrichment of the bottom by falling organic matter (both in the form of faecal pellets and ungrazed phytoplankton) and the seasonal appearance of oxygen depleted waters. The upwelling off Oman is not a coastal phenomenon only, but extends well offshore into the Arabian Sea (Wyrtki 1973). Underutilized primary production has been considered as one of the main sources of the oxygen minimum layer (Anon. 1985) which, in turn, negatively affects the bottom fauna. 'Real' demersal fishes (snappers and groupers) were found mainly in the southern part. Here, apart from possible differences in bottom type, the shallow waters associated with the numerous islands and bays might serve as a shelter for these species during the upwelling season.

Yemen. The March survey mostly emphasized the difference between the fauna off Socotra and the fauna off Yemen mainland, the former consisting of typical demersal perciformes (snappers, emperors, sweetlips and butterfly fishes), the latter with two, depth-related major groups, both with, among others, threadfins and lizardfishes. Again, this may be explained by differences in bottom type (for which however we have no data) or by the fact that the narrow shelf off Yemen is seasonally exposed to hypoxic waters. The August 1984 survey was performed in this period and showed a much depauperate fauna (probably there is a higher degree of patchiness in this period due to avoidance by most species of hypoxic waters), with Callionymus marleyi displaying a clear ability to live with very little oxygen. This species was caught at the shelf edge both in the bottom trawl and in the pelagic trawl near the surface.

Ethiopia. The clear distinction between the groups identified does not seem to be related to the water characteristics and depth and are possibly related to type of substratum. Group A contains several species of snappers, sweetlips and emperors while the largest Group C is dominated by Nemipterus japonicus and Saurida undosquamis/tumbil. The two deep-water stations (where O_2 levels are about 1 ml l^{-1}) were also dominated by nemipterids and lizard fishes (Saurida). None of the species caught were Red Sea endemics and they all have a wide distribution range in the Indo-Pacific.

Somalia. It appears difficult to understand the factors contributing to the patterns observed in this area. Apart from the possible presence of different substrates, the seasonal occurrence of strong upwelling and the configuration of the coast might cause the presence of habitats the size of which cannot be deeply analyzed with the available data.

The presence of Boops boops in some catches just south of 'the Horn' is rather surprising as this species (typically Mediterranean/eastern Atlantic) had never been reported from the Western Indian Ocean (although our record is unpublished, some specimens were deposited at the National Museum of Natural History, Paris). The most significant factor of the August survey (during the upwelling season) is probably the absence of several species of snappers, groupers and sweetlips that were widely present on the shelf in the course of the March survey, indicating their possible migration to shallower waters or to areas protected from the processes connected with the occurrence of upwelling.

Finally, the main pattern in the assemblages occurring on the shelf areas of the Arabian Sea, emerging from this study, appears to be related to the capability of the various species to adapt to the seasonal occurrence of oxygen-depleted waters. The possible escapement routes are shown in Fig. 32, well known to occur in other areas (i.e. the Gulf of California). Species of group A are usually more 'typically' demersal and possibly not able to perform vertical migrations and thus pushed into shallower waters, while species of type B are able to avoid the oxygen-depleted waters possibly through short-time vertical migrations. Trichiurus lepturus and Trachurus indicus are typical examples and these species were caught both in the bottom and pelagic trawl. More surprisingly is the presence in the latter group, of some species known to be 'typically demersal' such as the threadfin Nemipterus japonicus, present in the deeper part of the shelf throughout and the dragonet Callionymus marleyi, found in large quantities at the shelf edge off the southern coast of Yemen during the upwelling season.

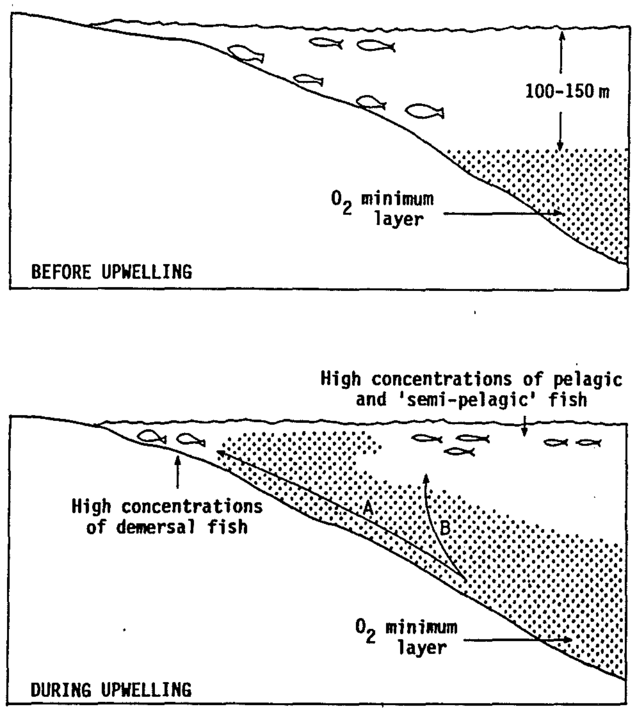


Fig. 32. Possible escapement routes to avoid oxygen-depleted waters. Modified from Moyle & Cech, 1988

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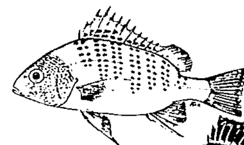
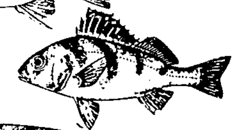
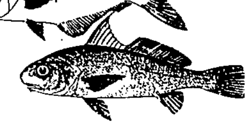
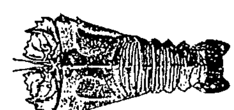
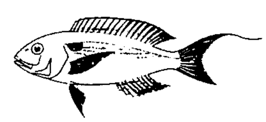
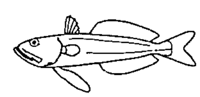
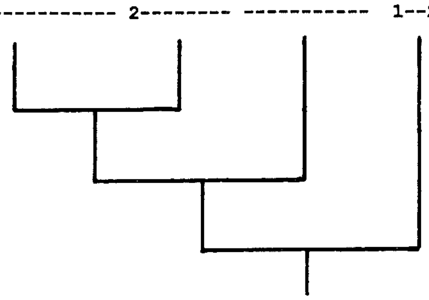
	A	B	C	D
Depth (m)	13-33 (23)	16-51(34)	32-100(66)	126-300
Arius spp.	221-21-131131-124	-31---1--	11---------	----
Lutjanus argentimacul.	-----2-----1---11	---------	-----------	----
Gymnura spp.	---1-132-2-2-2---	33-------	--2--------	----
Pteromylaeus bovinus	-2---2----------2	3--------	-----------	----
Rhinoptera spp.	----22---1---1---	---------	-----------	----
Acanthopagrus spp.	-----22-3-21----1	-3---2---	--1--------	----
Pampus argenteus	-1---11-2-------2	----21-21	-----------	----
Thryssa mystax	-1-1--2----------	-----1-2-	-----------	----
Muraenesocidae	------3--222----2	-31------	-----------	----
*Otolithes ruber	-111--31212212121	331-222--	---1-------	----
Parastromateus niger	--------1-----1-2	3--------	-----------	----
Pomadasys opercularis	-------------11-2	---------	-----------	----
*Pomadasys kaakan	2122-22-2-21211-3	441123--2	--31-------	----
Carcharhinus spp.	2----------------	33-------	-----------	----
*Pomadasys maculatum	--11--------1---2	341131-31	1----------	----
Carangoides spp.	-----2----------1	4--------	-----------	----
Drepane punctata	--1--2-----11---1	331111--2	--1--------	----
*Cynoglossidae	----1------------	32---11-1	-----------	----
*Lactarius lactarius	-1221--121------1	33-111-11	-----------	----
Shrimp	----1------------	----2121-	-----------	----
Torpedinidae	-----------------	-31------	-----------	----
Opishtopterus tardoore	-11---1----------	-----11-1	-----------	----
Polynemus sextarius	------2----------	--1-21-22	----1------	----
Carangoides talampar.	-2---------------	-3-------	-----------	----
Dasyatis spp.	-1----------2----	43-------	-----------	----
Carangoides malabar.	----------1-1----	---11--21	-----------	----
Parapenaeopsis atlant.	----------2--1---	-----2--2	-----------	----
*Johnius spp.	-----------21----	44121--32	-----------	----
Thryssa spp.	------------1----	2--1--1-1	-----------	----
Metapenaeus monoceros	---1-------------	--12----1	-----------	----
Tetraodontidae	-----------------	-21-----1	-----------	----
Apogonidae	-----------------	---211121	----------1	----
Argyrosomus spp.	-----------------	-----2--2	-----------	----
Polynemus spp.	-----------------	34-2-----	-----------	----
Ephippus orbis	-----------------	32-------	-----------	----
Otolithes cuvieri	-----------------	-4-------	-----------	----
Upeneus vittatus	------------1--1-	2-111----	---1-------	1---
Argyrops spinifer	22----2---213--12	33-------	---22-----2	----
Saurida spp.	1---1------------	23-------	----------2	----
Psettodes erumei	-----12-----1--1-	3312---3-	1-212------	----
Gerres filamentosus	-----------------	----1---1	----1------	----
Upeneus spp.	-----------------	-3-------	----1------	----
Pomadasys stridens	---------------1-	-2-----1-	----1------	----
Penaeus semisulcatus	-----------------	--12-----	----1------	----
Leiognathus spp.	1----------------	121------	---122-----	----
*Thenus orientalis	1----------------	1-111--1-	---11-----1	----
Rhizoprionodon acutus	1----11----------	---------	2-22-------	----
Sepia faraonis	21-1-------------	---------	2--12------	----
Epinephelus undulosus	-1----2----------	---------	21---------	----
Epinephelus diacanthus	-------2--2-2---1	---------	-1-11-1----	----
Sepia spp.	-----------------	-2-------	-11-------2	----
Gymnura natalensis	-1------3---1----	---------	---2-------	----
Ariomma indica	---1-------------	---------	-----1-11--	----
*Trichiurus lepturus	33332222322231312	43111-1-1	222242333--	2---
*Nemipterus japonicus	---1-------------	2212-----	-1122211123	3---
Sphyraena obtusata	-----------------	--1------	----12-----	1---
Saurida tumbil	------------1----	--1------	----22-11-1	2---
Sciaenidae	----1-2---32----2	3-12-2133	-------1-42	32--
Octopodidae	----1------------	---------	----1------	2--1
Platycephalus spp.	-----------------	---11----	---1-------	2-1-
*Champsodon spp.	-----------------	---------	----------1	1321
Solenocera spp.	-----------------	---1-----	-----------	-11-
Harpadon nehereus	-----------------	------1--	-----------	--2-
Acropoma japonicum	-----------------	2--------	-----------	1--2



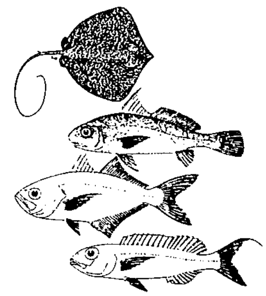




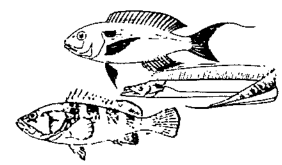



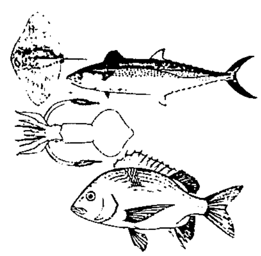


Appendix 1a. Two-way station by species table for Pakistan resulting from the program TWINSPAN. Values denote categories of abundance: 1: w < 10 kg; 2: 10 < w ≤ 100 kg; 3: 100 < w ≤ 1,000 kg; 4: 1,000 < w ≤ 10,000 kg; 5: w > 10,000 kg. The dendrogram showing the hierarchical relationship between the various groups, substitutes the binary notation produced by the program. a: September 1983 survey; b: January 1984 survey

	A	C	B	D
Depth (m)	10-23(16)	10-146 (72)	11-127(33)	16-116
***Rays**	3-432----	---22---------------------------------	------------------------------	----
Lutjanus argentim.	---------	1---2-2--------211--22-2-2-----2-------	----------------2-------------	----
**Johnius spp.*	---------	1--21-------1332-13-31-2121--------121-	------------------------------	----
Otolithes cuvieri	---------	--------1---1---223221-2121-----21-----	------------1-----------------	----
Carcharhinus spp.	---------	--------1----2-----------2-----------21	------------------------------	----
Shrimps	-1-------	-1-22111-2221-1---1--------------------	------------------------------	----
Polynemus sextarius	--------1	2--------1--1-2-2-2222-112------1--12--	11----------------------------	----
Apogonidae	---------	----------111--------1----1-----------2	-----------------1------------	----
**Lactarius lactarius*	---1----2	1------1113-113223--21133222-211-121-1-	1--1--23111-1-----1-----------	----
Pampus argenteus	11-------	--1---111-2--2------3222321-------1----	-------21-1----------------1-	----
Platycephalus spp.	---1-122-	21112221222221-111---1-2-----1-12--111-	---111----11------------------	-1-1
Polynemus spp.	---1--2--	---2-1-11-1--2-211------1--1-----1---1-	------1--------1--------------	----
Thryssa spp.	--22-1--1	1-11------1---2111-----11-1-----------1	--------1-1-------------------	----
Metapenaeus spp.	---------	2-------2-------11-1---2--1--------1---	------1---------------------1	---1
Saurida spp.	---------	212-----1--22--1-----------------------	------------------------------	---2
Ariomma indica	---------	------------------1-------1--3122--11---	1-1---------------------------	---1
**Nemipterus metopias*	-122-2232	31--32-122-3233222-31--2-2-332323333333	121--12---1--11-1----2-11--1-	12-3
Sphyraena obtusata	---------	--1-------------11------222------232--2	-----11-----------------------	-1-2
Upeneus vittatus	-----22-1	2-1----1-21-1--1----1--1---1-12------2-	1--1-1-2----------------------	-1--
Otolithes ruber	---3-13-2	--22---1--2--222-1--221--112-------122	---1--11--2-------------------	-2--
**Nemipterus japonicus*	---21---2	2--3232322222211-22232-212222121222222-	11-11221-1112---2111---1---1-	-11-
Sepia spp.	---------	111-1----2-2-----1-1-1-1-1-------------	--1--11--11-1----2---1-1-1---	1---
Psettodes erumei	---1-2---	11-2--11-11---------211---1----------1-	---1--1-----111-11-1----1----	----
Triglidae	-----1---	2-1-----12--21------------------------1	-----1---11------1-----------	-1--
Tetraodontidae	-----1---	11---1---1------------------1---1---	-----------------111--------2	----
Pomadasys maculatus	-----2---	1-1--2---1----312---2111--1-1-11-----2-	3-31-21--11-----1-1-1-------1	-1--
Argyrosomus spp.	---321---	--------2------3--3-22--------------1--	2--2--------------------------	2---
Saurida tumbil	-1-1-222-	---12221222--1--1-----12--1221212---122	1--1111-11221---11211----1-11	-11-
**Trichiurus lepturus*	22-------	--221212122-1222222131212232-1221-21223	-23-1-13232221-22--------1131	----
Pomadasys kaakan	---222332	2-2222222222-12312222--223-2-111-1221--	--1211--2221211121--1-1-----1	22-2
**Epinephelus diacan.*	-----23--	2----------1-1----2--------1211112-2--1	12-2---1---------1-----------	2212
Drepane punctata	---------	2----11------11-1----------------------	1--1------1-1---1--------1--1	-1--
Pomadasys stridens	-----3331	--1--1---------12-----1--------------1-	2-32111--2--------------------	-3--
Argyrops spinifer	-1--12232	21--1321-1211--2-1---222221221-11212-11	2-2321-11-112-2212211121-2-1-	3322
Arius spp.	1-4342332	--22-221-121-122-22-3-322-1--111-2-2---	1212-223--32211-1---1212-2-22	----
Sharks	22-----32	---------1----2---------------2--------	22----------1-----1---------1	----
Leiognathus spp.	-----1222	--1-------21---1--1-------1--1-----1---	---1-1-------------------11-	22--
Pomadasys olivaceum	-----22--	---------------------------------------	------------------------------	21--
Decapterus russelli	--2--222-	11--------------1-----------333----11--	--11-2--1------------1313----	-21-
Diagramma pictum	-----2--2	---------------------------------------	--12--------------------1---	-2--
Cheimerius nufar	-----2---	---------------1-----------------------	---1----1--------------------	22--
Rhizoprionodon acu.	---------	------------2--122------2---1-1-2-2223	---1222--1------11--222222-2-	---2
Carangoides malab.	2----122-	1--------------11------1--1--11--12--2-	1-12111211-11-1--11111-1-11--	-2--
Dasyatis spp.	-----1---	-2-----------2---2--3----31-----------	2---212-2-3-11---1------23---	22--
**Gymnura spp.*	---------	---------------2----2--1--1-1------222-	222322132321-222--121122-12--	---2
Pteromylaeus bovin.	---------	1-----------2----------2-2----------2-	2-2-1-2---2--12-21---1---22--	----
**Scomberomorus gutt.*	---------	--------------------111-11-----1--2----	11-21-11-2-311-21----2-----1-	----
*Loliginidae	1----122-	11--------------11--11--121--122-131--2	12221122-2122221221222332222	1122
Thenus orientalis	---------	------1-----1-------------------1-------	--11-----1-----11-------1---	----
Gerres filamentosus	-----1--1	----1-1--------------------------------	---1----111-1--1-1--1----1---	12--
**Acanthopagrus berda*	1--21-2-2	--1-1-11-------1-----------------------	---112-2112111---122--1------	2-2-
Sphyraena jello	-----2---	---------------1-----------------------	------------1-1----1--2-----	-2--
Alepes djeddaba	1----12--	---------------------------------------	---1----11--1--------1--2---1	----
Epinephelus malab.	-3-2-2---	---------------------------------------	---2-2----3------------2------	----
Parastromateus niger	---------	--------------------------2------------	2---1-2---------1-----------2-	----
Alectis indicus	---------	---------------------------------------	----------1-111----------12--1	-1--
Rachycentron canadus	---------	---------------------------------------	-----22-1--11--------1--13---	----
Scomberoides commer.	---------	-------------------------1-------------	2------1-----1----------1-2-22	----
Scomberomorus comm.	---------	------------------------1--------------	---2--1----1---111--111211212	-2-2

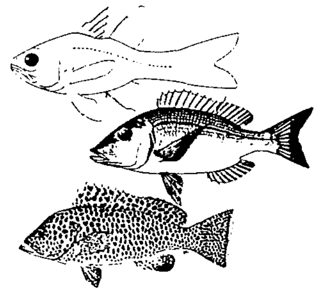


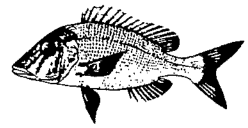


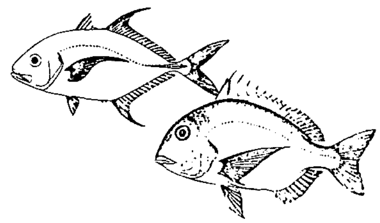


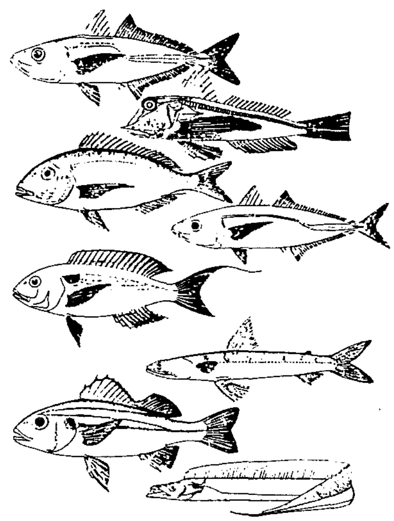
Appendix 1b.

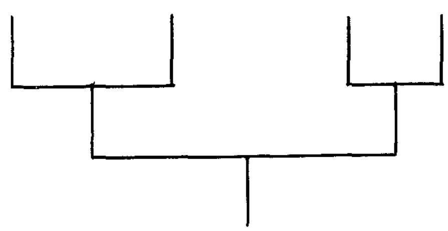
	A	B	C	D
Depth (m)	15-60 (36)	16-71 (51)	18-140 (73)	50-85 (66)
**Apogonidae*	-113-1111-1	----------------	------1---	2--1
**Lethrinus lentjan*	1213----123	---1----------1-	----------	1---
**Epinephelus gabriellae*	11--2223--2	--21---11-------	-------1--	2---
**Epinephelus areolatus*	--1-131211-	222---1-1-------	----------	----
Siganus spp.	-2-2-1---1-	---1--1----1----	----------	----
Plectorhynchus schotaf	-2-2-2-1---	---1----11-1----	----------	----
Gnathanodon speciosus	----1-----2	---2---------1-2	----------	----
Diagramma pictum	---21------	--12------------	----------	----
Plectorhynchus flavom.	-----1----2	2--1------------	----------	----
**Lethrinus nebulosus*	111233231-3	23-222213212--2-	-----1----	2---
Scolopsis taeniatus	---11--2-1-	21----1-------1-	-----11---	----
Rachycentron canadum	-----------	--------1-2-21--	----------	----
Alectis indicus	-----------	---22-----------	-----1----	----
Trachinotus blochii	-----------	---1-11----1----	----------	----
**Carangoides chrysophrys*	-------1--1	22-2222-1-2222-1	1--2-2----	2---
Cheimerius nufar	--1222-21-2	332212212--3--3-	----22-2--	2-1-
**Argyrops spinifer*	---1-1--133	21221-211--1132-	---222----	3---
Albula vulpes	-----------	2--------------2	----------	3---
Fistularia petimba	----21---2-	11--111-1-------	-12-11----	----
Lagocephalus spp.	----1-----1	2--1--1---------	-----11---	----
Mustelus spp.	-----------	--1-1-1--------1	--2-------	----
Sphyraena putnamiae	---1------2	----2-1---------	----31----	----
Carangoides spp.	-------1-13	---1------------	----121---	---1
Arius thalassinus	1--2------2	1--1---1-1-1-221	2212-21---	23--
Carangoides malabaricus	-----------	--------------21	---2---1--	----
Sardinella longiceps	-----------	--------------2-	-1--1--1--	----
Sepia spp.	---1-----1-	--------1--1--11	11---111--	----
Rhizoprionodon acutus	-----2-----	--1-2-1-----1-21	322-22----	----
Loligo spp.	-----------	--------1--21-2-	2122-2----	----
Tetrosomus gibbosus	---------1-	---1------------	---2--1---	----
Gastrophysus lunaris	-----------	----2----------1	---2---2--	----
Plotosidae	-2-1-------	----------------	---2-11---	----
**Trachurus indicus*	-----------	----------------	2432-1--1-	--2-
**Lepidotrigla bentuviai*	-----------	---------------1	-212112-22	-1-2
**Pagellus affinis*	-1-1-----2-	----1-----------	-2223--343	2-21
**Decapterus russelli*	----------1	-------------22-	--132313-4	2--1
Platycephalus spp.	---1-------	----------------	-----111--	1--1
Saurida spp.	-1---------	---1-------1----	2----21-24	--4-
**Nemipterus japonicus*	-----------	---1----1-------	2----11-43	1331
**Saurida tumbil*	-----------	----------------	----------	22-2
Gerres filamentosus	-----------	----------------	---21-----	32-2
**Pomadasys stridens*	-----------	-------1--------	1--4------	2333
Loligo spp.	-----1-1---	---1-1---------1	------12--	22--
**Trichiurus lepturus*	-----------	-----------2--2-	2---------	2321





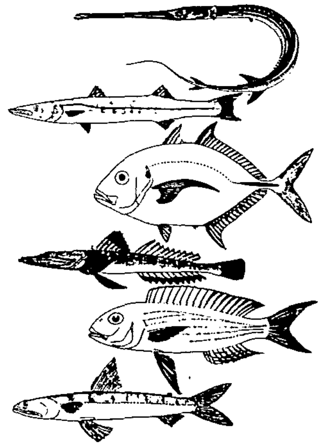


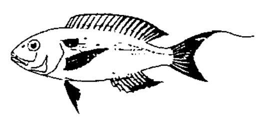


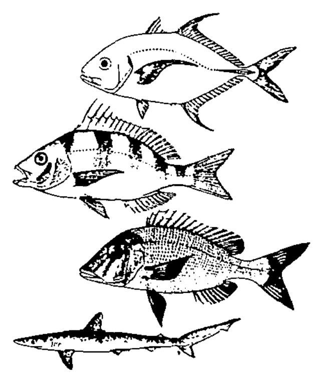


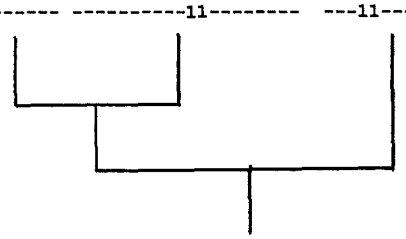
Appendix 2a. Two-way station by species table for Oman resulting from the program TWINSPAN. Values denote categories of abundance: 1: $w < 10$ kg; 2: $10 < w \leq 100$ kg; 3: $100 < w \leq 1{,}000$ kg; 4: $1{,}000 < w \leq 10{,}000$ kg; 5: $w > 10{,}000$ kg. The dendrogram showing the hierarchical relationship between the various groups, substitutes the binary notation produced by the program. a: March 1983 survey; b: November-December 1983 survey

	B	C	A
Depth (m)	18-71(43)	15-104(52)	18-55(40)
Fistularia petimba	-1-11112	-------1--1-1------1	-1-1------1-
**Sphyraena putnamiae*	12112123	--------------------	----------22
Carangoides malabaricus	221-213-	--1----1------------	1-1-----11--
Upeneus sulphureus	----2--2	--------------------	------------
Platycephalus spp.	-1122111	-----------------11-	------------
Lutjanus bengalensis	--1212--	--------------------	------------
Muraenesocidae	---22---	--------------------	------------
Nemipterus bipunctatus	-1-2322-	--------------------	------------
Leiognathus fasciatus	----22--	--------------------	------------
Psettodes erumei	-22-21--	--1----1------------	------------
Pomadasys spp.	22------	--------------------	------------
Loliginidae	--1-1--1	--1------1----------	------------
Carcharhinus spp.	-1-2--1-	---3----------------	------------
Saurida tumbil	1223321-	--11----------------	1-1---------
Gerres filamentosus	12--11--	--12---1------------	------------
Trichiurus lepturus	--11-11-	----2--3------------	------------
Alectis indicus	2-------	-------------------2	------------
Drepane punctata	21------	2------11-----------	------------
Pomadasys opercularis	21------	2---2-1-------------	------------
Gymnura spp.	2-------	--22----------------	------------
Decapterus russelli	---211-4	--11---1--1321--224-	------1-----
Uraspis secunda	----1-1-	1------3-11---------	------------
**Nemipterus japonicus*	--12---2	--21----11-32131232-	------------
Pomadasys stridens	-------2	----31-3111222-1----	------------
Trachurus indicus	--------	--1222--21-3333-----	------------
Sardinella gibbosa	--------	--11--1-----1-------	------------
Lepidotrigla omanensis	--------	------------1----22-	------------
Arius tenuispinis	--------	33-----------1------	------------
Saurida undosquamis	-------3	----------121--12222	--------11--
Pagellus affinis	--------	-------211-33--12111	2----1-1----
Arggyrops spinifer	---2-122	2-1-3-2322-33--2---2	2-22--131-34
Lepidotrigla bentuviae	---21---	2---------111-1-11-1	------113-1-
Epinephelus summana	--------	----1--2---------1--	----------2-
Carangoides equula	--------	-------2--12-------2	11------1---
Epinephelus diacanthus	--------	----------1-2-----22	----1--22---
Cookeolus boops	--------	----------1-------11	--------1---
Arius thalassinus	--------	-2333-31-21-----1---	--2---221222
Scomberomorus commerson	--------	--112---------------	1--1-------1
Alepes vari	1-------	-212-12-------------	1--------2--
Scomberoides commerson.	--------	--32----------------	---------2--
Sepia spp.	11122221	----------2-----1--1	2--3---2----
Lethrinus lentjan	2--1---2	--------------------	22----------
Lutjanus lutjanus	---1-2-1	--------------------	-2-----2----
Gnathanodon speciosus	22------	--------------------	---2--1----2
Argyrops filamentosus	-11-11--	-------------------2	-2-2-222----
**Carangoides chrysophrys*	-1------	--11---21-1---------	1-21123122-2
**Cheimerius nufar*	--------	-------2-1-22------2	-223231331--
Epinephelus gabriellae	--1-----	--------------------	-21-2312----
**Lethrinus nebulosus*	--------	----1--2---2--------	422333222-2-
Epinephelus chlorostigma	--------	-------1------------	-22--2------
Sufflamen fraenatus	--------	--------------------	221----1----
Plectorhinchus schotaf	--------	--------------------	11----22----
Siganus sutor	--------	--------------------	-2-1--1-----
Lutjanus caeruleolin.	--------	--------------------	-1--11-1----
Diagramma pictum	2-------	--------------------	3-3----2--2-
Alutera monoceros	--------	--------------------	---2-2----2-
**Loxodon macrorhinus*	--------	--------------------	2--11-1-1-2-
Lagocephalus spadiceus	--------	--------1-----------	2-2---1-22--
Alectis ciliaris	-1------	--------------------	--11------12
Sphyraena africana	--------	----------11--------	---11-----32



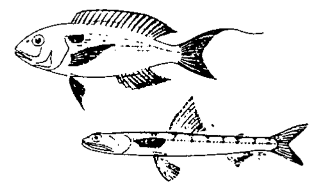


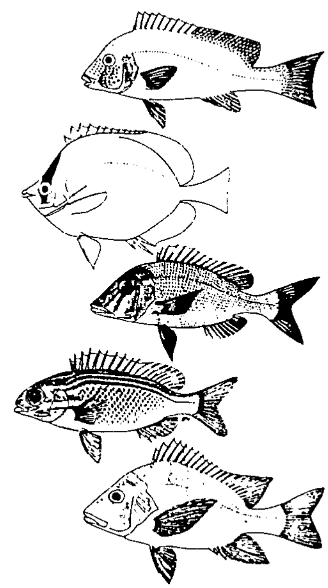


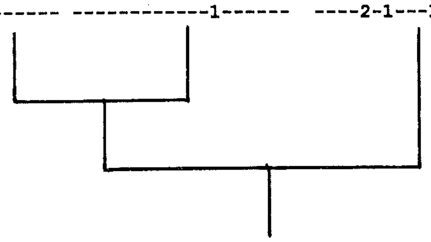


Appendix 2b.

	B	C	A
Depth (m)	16-36 (26)	20-194 (63)	24-93 (41)
Alectis indicus	2-2-1---	-------------------	----------------
Caranx ingnobilis	23------	-------------------	----------------
Psettodes erumei	13--1---	-------------------	----------------
Sphyraena putnamiae	231-1---	--21---------------	----------------
Arius thalassinus	22--1122	----------------13-	----------------
Leiognathus leuciscus	----12--	---------1------122	----------------
Pomadasys maculatum	----1-21	----------------13-	----------------
Upeneus taeniopterus	-----2--	-----------------21	----------------
Loliginidae	1--1111-	----1----1-----12--	1---------------
Stolephorus indicus	----12--	---2-----1---------	----------------
Fistularia petimba	11------	----211------------	-------1------1-
Leiognathus elongatus	1-------	2-1----------------	1---------------
Thenus orientalis	1--1----	----1--11----------	----------------
**Nemipterus japonicus*	12----22	13123222--2---2121-	----------------
**Saurida undosquamis*	12-1222-	------2-11132211---	----------1-----
Sepia faraonis	--22212-	--12--22-1--1---1-2	1---------------
Gazza minuta	1-------	---2-------------12	----------------
Pagellus affinis	--------	1----3--------221-2	----------------
Acropoma japonicum	--------	--------------13---	--------------1-
Trichiurus lepturus	--------	--------------12-2-	----------------
Otolithes ruber	----1---	----------2------3-	----------------
Selar crumenophthalmus	1------1	---22211----------2	----------------
Decapterus russelli	--------	---113221-------1--	1---------------
Upeneus bensasi	--------	1--1-12111-1-1-1---	1---------------
Upeneus moluccensis	--------	---13-21-----------	----------------
Sphyraena obtusata	--------	---1--1---1--1-----	----------1-----
Saurida tumbil	-------2	23-322222-2------2-	--------------1-
Nemipterus bipunctatus	-----1--	----2-2211-1------1	1---------------
Crabs	--------	242---1-------1----	----------------
Trachynocephalus myops	--------	1-1--1-21---11-----	----------1-----
Shrimps	--------	------11----21-----	----------------
Sphoeroides spp.	--------	1-----111----------	1---------------
Gnathanodon speciosus	233-----	-------------------	-2--------------
Scomberomorus commerson	-24----1	--1----------------	---1-------2--1-
Dasyatidae	--3-2---	-------------------	-3--------------
Lagocephalus spadiceus	---11--1	----------2--------	---------2------
Lutjanus bengalensis	1-------	--11----1----------	111-------------
Arothron stellatus	--22----	--------1----------	112-------------
Abalistes stellatus	--1-----	--11-----1---------	12---2----------
Priacanthus blochii	---1----	---11-1------------	--12-----2------
Lethrinus lentjan	1--1----	-------------------	---2-21--2-1-1--
Siganus canaliculatus	--------	------------------2	---1---2-2---1--
Parupeneus cinnabarin.	--------	----1-111---------2	11-1121--1--1-1-
Lethrinus variegatus	--------	--1---------------2	11-1-------1--1-
Scolopsis bimaculatus	--------	------------1-----2	11-2-2-------121
Diagramma pictum	2--2----	-------------------	2331--231-2-----
Lethrinus microdon	--------	------------------1	-22-------------
Lethrinus nebulosus	--------	-------------------	231-212--2------
Lethrinus elongatus	--------	-------------------	222--2222-------
Lutjanus rivulatus	--------	-------------------	2----2-3--------
Epinephelus chlorostig.	--------	-------------------	---------212----
Naso hexacanthus	--------	-------------------	-32--2-22-------
*Chaetodontidae	--------	-------------------	-121111-1-----1-
Heniochus diphreutes	--------	-------------------	-21--112---1--1-
Lutjanus sebae	--------	-------------------	-2222-21--------
Lutjanus bohar	--------	-------------------	-22--223--------
Mulloides flavolineatus	--------	-------------------	-23-------------
Acanthurus bleekeri	--------	-------------------	--2--2-3-----1--
Epinephelus undulosus	--------	-------------------	--21-2----------
Epinephelus multinotat.	--------	-------------------	--2---2-2-------
Lethrinus crocineus	--------	-------------------	-----2232-------
Parupeneus rubescens	--------	-------------------	----2-21------1-
Scolopsis ghanam	--------	------------------1	-211211----1-1--
Parupeneus macronema	--------	------------------1	-1-1-11---1--1--
Stethojulis spp.	--------	-------------------	---1-1-1--1--11-
Pristotis cyanostigma	--------	-------------------	-1-1-------1--21
Sufflamen fraenatus	---1----	-------------------	-----2-1-1-1111-
Odonus niger	--------	-------------------	-----2-1--1-1111
Priacanthus hamrur	--------	------------1------	----2-1---11-2--

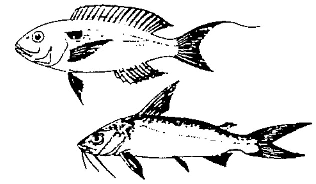


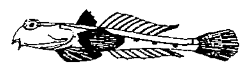


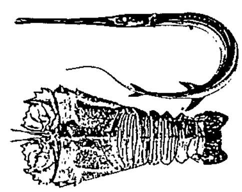


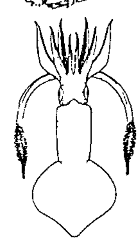
Appendix 3a. Two-way station by species table for South Yemen resulting from the program TWINSPAN. Values denote categories of abundance: 1: w < 10 kg; 2: 10 < w ≤ 100 kg; 3: 100 < w ≤ 1,000 kg; 4: 1,000 < w ≤ 10,000 kg; 5: w > 10,000 kg. The dendrogram showing the hierarchical relationship between the various groups, substitutes the binary notation produced by the program. a: February 1984 survey; b: August 1984 survey

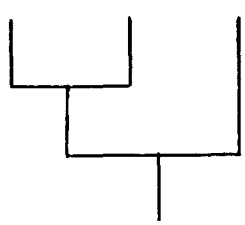
	A	B	C
Depth (m)	20-172 (60)	17-71 (33)	10-61 (34)
Pomadasys stridens	---------------	-12-	---------11
**Nemipterus japonicus*	----111-2------	--44	-11--1-----
Trichiurus lepturus	--------------1	-12-	--1--------
Trachurus indicus	--------------1	--2-	---------1-
**Arius thalassinus*	---------1-----	212-	---------1-
Pomadasys olivaceum	---------------	--2-	-----------
Argyrosomus spp.	---------------	--2-	-----------
Epinephelus tauvina	---------------	--2-	-----------
Epinephelus chlorost.	---------------	--2-	-----------
Sphyraena jello	---------------	--2-	-----------
Acropoma japonicum	-------1----1--	----	-----------
Champsodon spp.	-------11111---	----	-----------
Shrimps	-------2-------	----	-----------
Lepidotrigla bentuviae	----11113----1-	----	-----------
Ariosoma spp.	--------111--1-	----	-----------
Parascolopsis boesem.	--------11-----	----	-----------
Platycephalus spp.	--2-----11-111-	----	-----------
Scorpaenopsis gibbosa	--------1---111	----	-----------
Sufflamen fraenatus	-----------1--1	----	-----------
Parapercis nebulosa	---11-1-1------	----	-----------
Epinephelus diacanthus	--2--11-11-11--	-1--	-----------
**Callionymus marleyi*	234112111---2--	----	-----------
Saurida undosquamis.	----11231-----1	----	-111-1-2---
Psenopsis cyanea	----1--3-------	----	-------3---
Trachynocephalus myops	----1----------	----	-------1---
Sepia faraonis	1----12-1---111	--13	-111---2-2-
Otolithes ruber	---------------	-1--	---------1-
Dussumieria acuta	---------------	--1-	----------1
Scoliodon laticaudus	---------------	--2-	---------3-
Saurida tumbil	---------------	--1-	---------2-
Carangoides malabaric.	---------------	----	---111---1-
**Fistularia petimba*	---------------	----	-1112111---
**Thenus orientalis*	---------------	----	-111112----
Tetrosomus gibbosus	---------------	----	-1111-2----
Priacanthus blochii	---------------	----	-11----1---
**Loligo* spp.	---------------	----	12-122---1-
Pterois russelli	---------------	----	---11------
Synagrops adeni	---------------	----	--2--------
Psettodes erumei	---------------	----	-----1-----
Epinephelus areolatus	---------------	----	2----------
Nemipterus bipunctatus	---------------	----	-1---12----
Abalistes stellatus	---------------	----	--1---1----
Chilomycterus orbicul.	---------------	----	--1---1----
Decapterus russelli	---------------	----	---1--31---
Pagellus affinis	---------------	----	----1-3----
Sardinella longiceps	---------------	----	------213-1
Lutjanus sebae	---------------	----	------1----
Lutjanus sanguineus	---------------	----	------1----
Upeneus moluccensis	---------------	----	------2----
Plotosus lineatus	---------------	----	------21---
Rastrelliger kanagurt.	---------------	----	-----1---1-
Selar crumenophthalmus	---------------	----	---------2-
Plectorhinchus chubbi	---------------	----	---------2-
Pomadasys maculatum	---------------	----	---------2-
Scomberomorus commers.	---------------	----	---------2-
Sphyraena obtusata	---------------	----	---------21





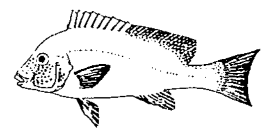


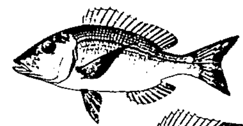


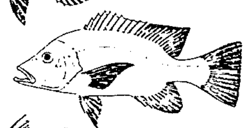


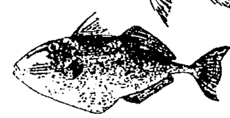
Appendix 3b.

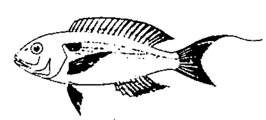
	A	C	B
Depth (m)	30-50(41)	25-86(50)	220-229
Diagramma pictum	--22322--	----2---------	--
Pterocaesio chrysurus	--11--2--	--------------	--
Epinephelus malabaricus	--2-2----	--------------	--
Lutjanus sebae	-22-3----	-----------2--	--
Lethrinus nebulosus	-12-31---	--------------	--
Tetrosomus gibbosus	-111-1---	--------------	--
Parupeneus cinnabarinus	12111----	-----------1--	--
Alutera monoceros	---12----	-----1--------	--
Lutjanus rivulatus	-222-----	--------------	--
Lethrinus elongatus	-1-211---	--------------	--
Gymnocranius griseus	-11111---	---1----------	--
Lethrinus lentjan	-22232---	-1--2------1--	--
Pristipomoides sieboldi	----3----	---2----------	--
Synagrops japonicus	-11------	------------1-	--
Argyrops spinifer	21---1---	---------2-1--	--
Lutjanus argentimaculatus	222-31---	---3-----3----	--
Lutjanus sanguineus	3323312--	---21------2--	--
Abalistes stellatus	-22222---	-1--22-1--11--	--
Carangoides chrysophrys	----22--2	-2---1-1------	--
Nemipterus bipunctatus	2---12112	-2---1--------	--
Rachycentron canadum	---2-23-2	-----1-12-----	--
Selar crumenophthalmus	-11-----1	-------------2	-1
Alepes vari	------122	----31--------	--
Echeneis naucrates	------2-1	----1-1-1-----	--
Upeneus bensasi	------11-	------------11	--
Acropoma japonicum	-1-------	--------------	21
Nemipterus metopias	11-------	------------12	--
Loliginidae	1-11-2111	-2---111-11-12	-1
Dipterygonatus balteatus	--1------	-----------11-	--
Rhizoprionodon oligolinx	--2--1--2	2----12--2--1-	--
Fistularia petimba	1----1-11	--1-1111-111--	--
Thenus orientalis	------1-1	--1111--------	--
Terapon puta	1-1---1--	-121--11-1----	1-
Sphyraena fosteri	---2--1-1	---121111---1-	--
Dasyatidae	-2-------	------3-3-----	--
Leiognathus bindus	--------1	--2----1------	--
Carangoides malabaricus	-1---2--2	12212222-2----	--
Saurida undosquamis	11----111	21-2-121-1222-	--
Atule mate	--------2	33--32-1------	--
Psettodes erumei	1--------	1--11-1-------	--
Terapon jarbua	1--------	-2-----------2	--
Decapterus russelli	-1------1	11-111-------2	--
Priacanthus blochii	----1----	---12-22----1-	-1
Priacanthus hamrur	-11-----1	2-1--1--1222--	--
Sepiidae	11-------	12---2----1-1-	--
*Nemipterus japonicus	1-------1	2-32312123232-	21
*Saurida tumbil	---------	112221112232-2	22
Pomadasys multimaculatum	---------	---13---------	--
Lutjanus lutjanus	---------	---23-1-------	--
Lagocephalus sceleratus	---------	---11-1---1-1-	--
Lagocephalus inermis	---------	-----1-1-1-1--	--
Uraspis secunda	---------	-------211--1-	--
Penaeidae	---------	--22----------	--
Platycephalus spp.	---------	--212---------	--
Arius thalassinus	--1------	-32-----1222--	--
Penaeus semisulcatus	---------	1-2-1-1------2	--
Champsodon spp.	---------	-----------11-	-1
Lepidotrigla bentuviai	---------	--------1-11--	2-
Psenes squamiceps	---------	--------11----	2-
*Nemipteridae	---------	--------------	31

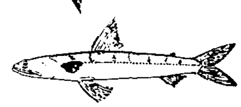


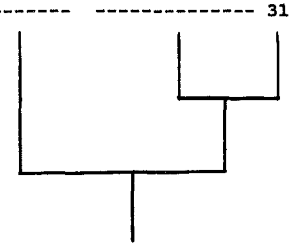






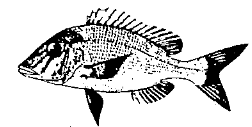
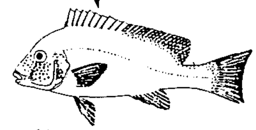


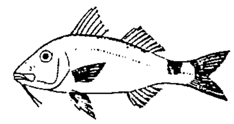




Appendix 4. Two-way station by species table for Ethiopia resulting from the program TWINSPAN. Values denote categories of abundance: 1: $w < 10$ kg; 2: $10 < w \leq 100$ kg; 3: $100 < w \leq 1{,}000$ kg; 4: $1{,}000 < w \leq 10{,}000$ kg; 5: $w > 10{,}000$ kg. The dendrogram showing the hierarchical relationship between the various groups, substitutes the binary notation produced by the program. March 1984 survey

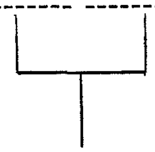
	A	B
Depth (m)	14-81 (45)	28-105 (52)
Priacanthus hamrur	--32----	11------
Scomberoides commersonian.	-----12-	-------2
Mulloidichthys spp.	-22-111-	-1------
Apogonidae	-2--12--	1-------
Rachycentron canadum	---121--	------1-
Lethrinus nebulosus	4--3222-	--------
Diagramma pictum	32-2222-	--------
Pristipomoides filamentos.	--3-----	--------
Parascolopsis eriomma	--3-----	--------
Epinephelus chlorostigma	-12122-1	--------
Argyrops spinifer	--3----1	--------
Cheimerius nufar	--22-1-2	--------
Lutjanus sebae	--22212-	--------
Argyrops filamentosus	---2-222	--------
Lutjanus sanguineus	---22---	--------
Epinephelus tauvina	----222-	--------
Epinephelus undulosus	----222-	--------
Dipterygonatus balteatus	----221-	------1-
Sardinella longiceps	-3----1-	--1-----
Odonus niger	222--1--	1-------
Scolopsis taeniopterus	32-2-1--	1-------
Parupeneus pleurotenia	32212111	1-------
Lethrinus lentjan	321--1--	--------
Sufflamen frenatus	41---1--	--------
Parupeneus indicus	3-------	--------
Scolopsis bimaculatus	31---1--	--------
Scolopsis ghanam	22------	--------
Plectorhynchus fangi	32------	--------
Epinephelus malabaricus	3-------	--------
Siganus canaliculatus	21------	--------
Tetrosomus gibbosus	---1-21-	-----112
Echeneis naucrates	----1-1-	------11
Thenus orientalis	---1-1--	----2---
Scomberomorus commersoni	----2-1-	-----22-
Sphyraena putnamiae	-----1--	-----21-
Boops boops	-3----2-	23------
Pagellus affinis	-2----1-	-321----
Upeneus bensasi	------2-	-2--21--
Nemipterus bipunctatus	---2-11-	13--2-1-
Apistus carinatus	---11---	-1--2---
Scomberomorus tritor	--3-----	1-1-11--
Decapterus russelli	-2-11-1-	213-23--
Saurida undosquamis	---21-1-	232-3--2
Loliginidae	-----11-	2----111
Crabs	--------	---22---
Squid	--------	--212---
Carangoides talamparoides	--------	--4-----
Saurida tumbil	------1-	2--1-31-
Lagocephalus lunaris	--------	----2--2
Carangoides malabaricus	--------	-----3-1

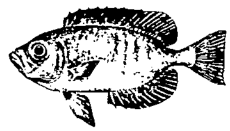



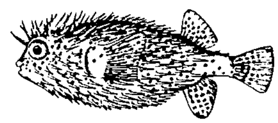


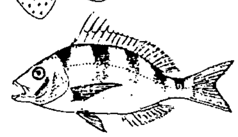
Appendix 5a. Two-way station by species table for Somalia resulting from the program TWINSPAN. Values denote categories of abundance: 1: w < 10 kg; 2: 10 < w ≤ 100 kg; 3: 100 < w ≤ 1,000 kg; 4: 1,000 < w ≤ 10,000 kg; 5: w > 10,000 kg. The dendrogram showing the hierarchical relationship between the various groups, substitutes the binary notation produced by the program. a: March 1984 survey; b: August 1984 survey

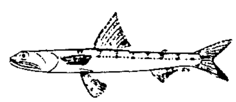
	A	B
Depth (m)	30-81 (54)	23-82 (56)
Tetrosomus gibbosus	---11111-	1--1-----1-
Upeneus sulphureus	2-1----1-	---------21
Odonus niger	321--1132	1-1--12--1-
Carcharinus limbatus	3---2----	---------1-
**Priacanthus hamrur*	2221-1222	11---1--211
Carangoides chrysophrys	22-1221--	---1-1---2-
Lutjanus bengalensis	311------	-----------
Diagramma pictum	2-------1	-----------
Scolopsis ghanam	1-1-----1	-----------
Lethrinus variegatus	2-------1	-----------
Apogonidae	1-1----11	-----------
Lethrinus nebulosus	--2--1---	-----------
Diplodus spp.	2-11-----	-----------
**Diodon* spp.	2----1-11	-----------
**Holohalaelurus* spp.	2-12111--	-1---------
Chaetodon spp.	1--1---1-	-----------
Epinephelus chlorostigma	-------22	----1------
Parupeneus macronema	-------12	-----------
Aetomyleus nichophili	-----21--	-----------
Scolopsis bimaculatus	----1--21	--------1--
Champsodon spp.	----1-1--	1----------
**Cheimerius nufar*	---212-12	1----------
Engyprosopon spp.	---11---1	-------1---
Fistularia petimba	-------11	---1-1-----
Argyrops spinifer	---22--1-	---2-1--2--
Lepidotrigla bentuviai	----1-111	2211----11-
Platycephalus spp.	---11----	21---------
Zeus japonicus	---1---1-	---2-----1-
Loligo spp.	---111121	1-22212211-
Scomber japonicus	1-------1	---------22
Trachurus indicus	-------11	---1-----22
Decapterus russelli	2-----11-	--2---3232-
Sepia spp.	------111	11112--2---
**Saurida undosquamis*	------222	1212222232-
**Pagellus affinis*	232---11-	12124233323
Apistus carinatus	-----1---	3-------1--
Octopus spp.	----1----	111--------
Boops boops	----1--11	----1---321
Shrimp	----1----	21-------1-
Upeneus moluccensis	1-1-1-1--	1-----1322-
Nemipterus japonicus	---------	-2322----2-
Nemipterus bipunctatus	--------1	1----1-22--
Sardinella longiceps	---------	---------24
Decapterus macrosoma	---------	--------222

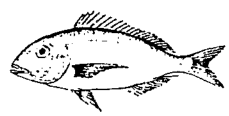












Appendix 5b.

PAPER 7

Zonation of demersal fishes of the East Africa continental shelf. A study based on the surveys of the R/V Dr.'Fridtjof Nansen'(1982-1983)

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Abstract: Bottom trawl stations from the East Africa continental shelf (Kenya to Mozambique, including Madagascar) were analysed by means of multivariate analysis techniques (Detrended Correspondence Analysis and Two-way Indicator species analysis) in order to find patterns of zonation among the demersal megafauna assemblages. Well-defined faunal associations were found in connection with the large-river estuaries and mangrove systems off Mozambique, while the other shelf assemblages appeared to be partly depth-dependent and partly reflected differences in substratum. The shelf assemblages off south and south east Madagascar are closely related to the continental ones, with a few elements from cooler waters and a slightly more depauperate tropical fauna.

INTRODUCTION

The present study is based on trawl surveys carried out by the Norwegian Research vessel 'Dr. Fridtjof Nansen' off East Africa in 1982/1983. Although almost a decade has passed since those surveys, an analysis of the assemblages found at that time still bears some interest. No analysis of this type has been performed earlier in this area. Pauly & Longhurst (1987) have attempted a general description of the fish assemblages of the Indian Ocean, based on various literature, in the lack of comprehensive survey data. Other resources surveys in this area have been performed (e.g. Birkett 1978), but none has been so comprehensive and systematic in approach (Venema 1984). Also, while original data from other surveys are difficult, if not impossible to retrieve, the data collected by the R/V 'Dr. Fridtjof Nansen' are all stored on an easily accessible database.

Furthermore, taxonomic literature for this area has improved in the course of the 1980's, thanks to the compilation of a comprehensive guide based on taxonomically updated works, to cover the fish and invertebrate resources of the Western Indian Ocean (Fischer & Bianchi 1984), which makes the data collected in the 1980' s more reliable.

McManus (1986 and 1989) described zonation of fish assemblages in the Samar Sea (the Philippines) and the southwest shelf of Indonesia, respectively. The present study uses the same analytical methods as those of other works also based on the 'Dr.Fridtjof Nansen' data base, that have covered other tropical continental shelves (Bianchi 1991 and 1992).

STUDY AREA

The study area covers the trawlable grounds of the East Africa continental shelf from Kenya to Mozambique (from about 2 to 21 °S), and south and southeast Madagascar (Fig. 1). The continental shelf is mostly very narrow except off northern Kenya, off Tanzania, in correspondence with Zanzibar and Mafia islands, off Mozambique (Sofala Bank) and the

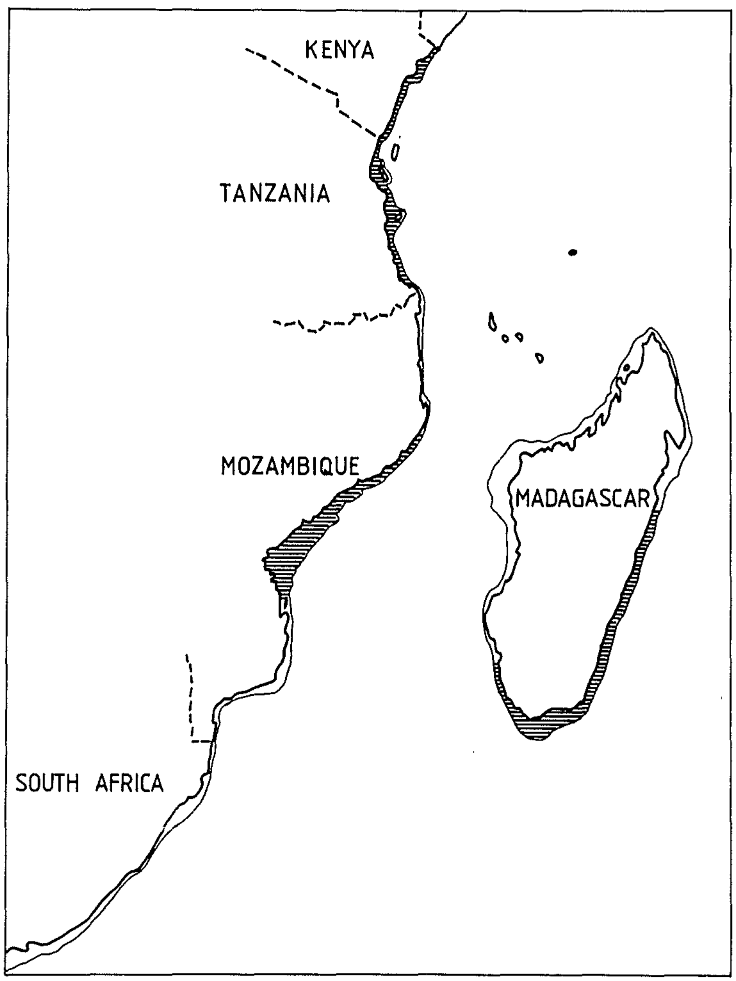

Fig. 1. Study area

Southern plateau off southern Madagascar. The shelf is very shallow, sloping from 30-60 metres to 200 m rather abruptly almost throughout. Coral reefs fringe the coast, except in correspondence with river outlets where mangrove areas are usually found. The bottom is mainly sandy, with shell, dead corals and fine sand throughout (Anon. 1980). Mud bottoms occur in shallow waters, originating from sedimentation of soil particles and detritus from river runoffs.

A description of the shelf off south and southeast Madagascar can be found in the cruise report (Anon. 1983). The south west shelf is very narrow and mostly untrawlable. The southern plateau is trawlable at depths shallower than 130 m and otherwise very steep. In the western part of the plateau however, the presence of sponges made trawling very difficult. The eastern coast is characterized by the presence of fringing coral reefs and a very steep bottom outside the reef area and mostly unsuitable for trawling.

The general physical oceanography of the Indian Ocean was described by Wyrtki (1973), based on the results of the International Indian Ocean Expedition (1959-1965). The waters of the area under study are part of the southern subtropical gyre. The South Equatorial Current flows westward toward East Africa and branches off at the northern tip of Madagascar. One branch flows along the east coast of Madagascar, while the main branch splits into the northward-flowing East Africa Coastal Current and the southward-flowing Mozambique Current. A marked hydro-chemical front is found at about 10 °S (off southern Tanzania), in subsurface waters, separating low-oxygen and high nutrient waters of the northern Indian Ocean from those of high oxygen content but nutrient-poor waters of the southern subtropical gyre. During the south east monsoon period (April-May and October-November) the East Africa Coastal Current continues northward into the Somali Current while during the north east monsoon, meets a southward flowing current off Somalia to form the Equatorial Counter Current.

The following description of the hydrographic conditions at the time of the surveys is based on the reports of the R/V 'Dr. Fridtjof Nansen'. In the period June-September 1982 and May-June 1983, a series of hydrographic stations were sampled along tracks perpendicular to the coast (Fig. 2 to 5). During the south-west monsoon period (August-September 1982), coastal waters, to 100 m depth, had high temperature and oxygen concentrations throughout ($T > 25$ °C and $O_2 > 4$ ml l^{-1}), but lower temperatures and higher oxygen values (23 °C and 5 m l_{-1} respectively) were recorded off Mozambique. Salinities were about 35 ‰ or slightly below off Kenya and Tanzania, while the pattern off Mozambique was more complex. Two types of shelf water were found: one type characterized by low salinity values (as low as 34 ‰), the presence of which is possibly related to the major rivers runoffs and high salinity water with increasing salinity values

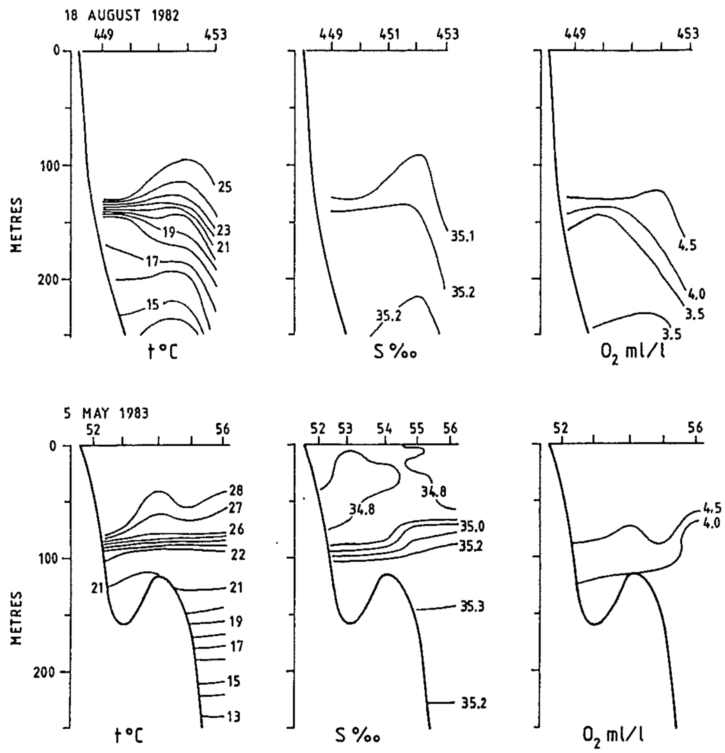

Fig. 2. Hydrographic profiles for temperature, salinity and oxygen at selected places, Kenya

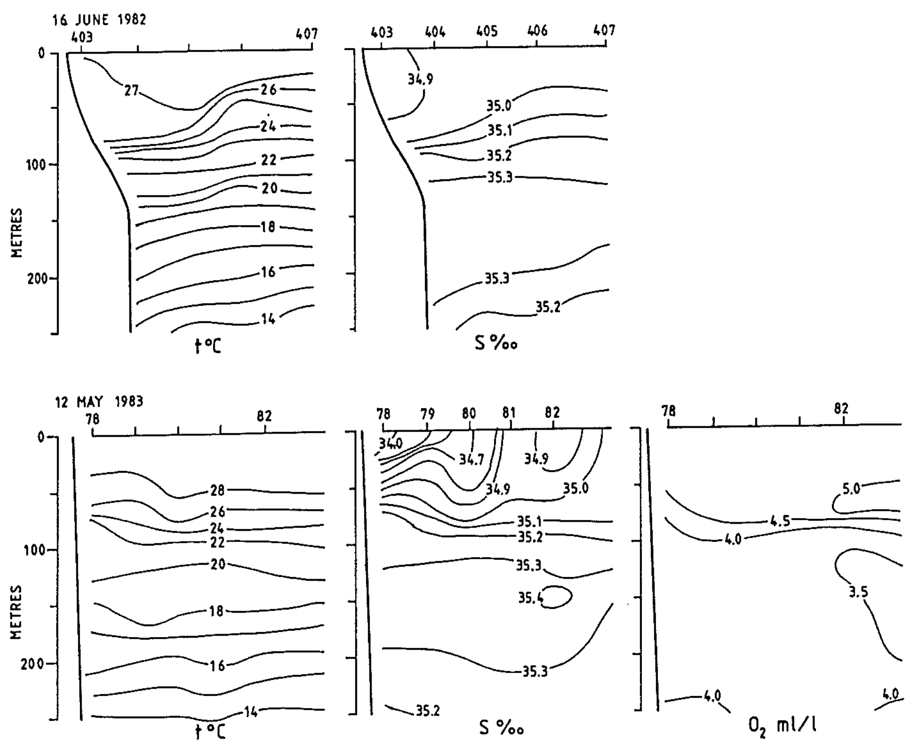

Fig. 3. Hydrographic profiles for temperature, salinity and oxygen at selected places, Tanzania

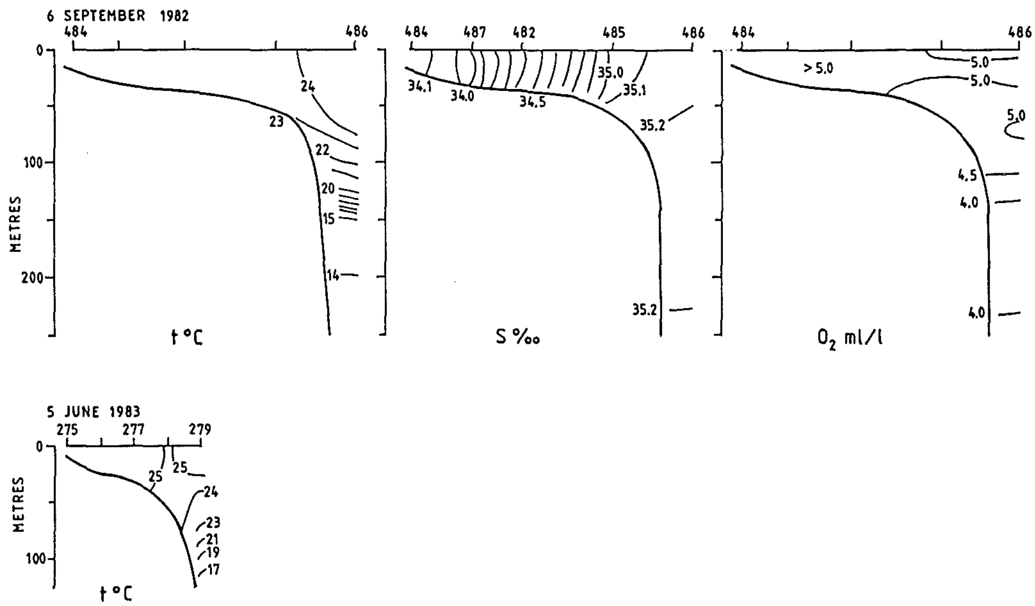

Fig. 4. Hydrographic profiles for temperature, salinity and oxygen at selected places, Mozambique

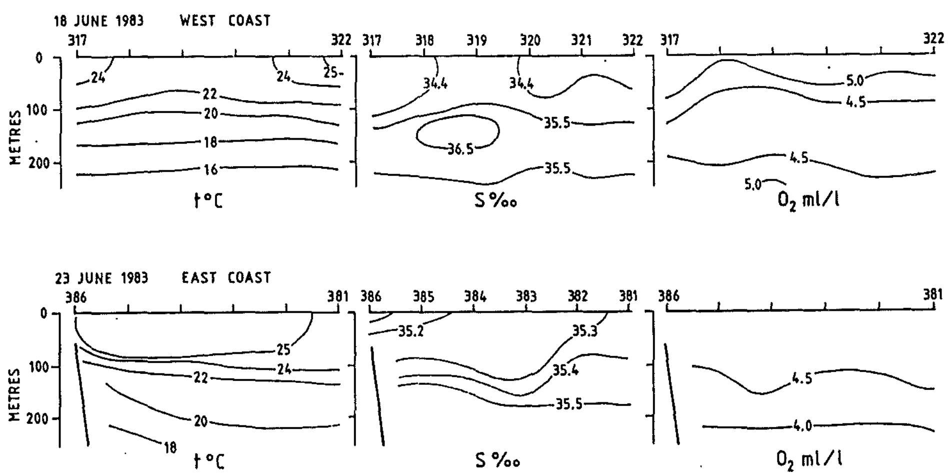

Fig. 5. Hydrographic profiles for temperature, salinity and oxygen at selected places, Madagascar

toward the shore, located in the southern part of Sofala Bank and partly related to the inundation of the mangrove areas followed by evaporation, concentration of salt and eventual flushing back into the sea (Brinca et al. 1982). This area is unfortunately mostly untrawlable and only a few samples are available.

During the north east monsoon period (May-June 1983) surface waters were warmer while salinities appeared lower in coastal waters because of the increased rainfall and river runoff. Very small fluctuations were otherwise observed in the values of temperature and oxygen concentrations. Slightly higher oxygen concentrations and lower temperatures were again found off Mozambique and south and southeast Madagascar (June 1983). The eastern shelf of Madagascar is dominated, to 75 m depth, by the Equatorial surface Water transported southward by the east Madagascar Current and characterized by temperatures above 25 °C and salinities between 35.2 and 35.3 ‰. Lower temperatures (22 to 25 °C) and higher salinities (to 35.6 ‰) characterized the southern and southwest shelves (Anon. 1983).

MATERIAL AND METHODS

The surveys of the R/V 'Dr. Fridtjof Nansen' involve bottom and pelagic trawling, acoustic registrations and water sampling for hydrographic studies. The analysis presented here utilizes bottom trawl data and hydrographic samples.

Two sets of surveys were included in this study, one covering the shelves of Kenya, Tanzania and Mozambique (June-September 1982, Figs. 6 and 7) and another including the above areas as well as the south and southeast coasts of Madagascar (May-June 1983, Figs. 8 and 9). The number of stations included, by country and survey period with depth ranges are given in Table 1. The overall depth range of the stations included in the analysis is 7 to 77 m. All the bottom trawl stations were performed during daytime. The shallow depth range of the stations has to be related to the bottom topography.

Table 1. Number of stations included in the analyses, by country and survey period

	June-Sept 1982	Depth range (m)	May-June 1983	Depth range (m)
Kenya	18	(7 - 50)	14	(10 - 55)
Tanzania	44	(11 - 63)	42	(10 - 77)
Mozambique	57	(7 - 60)	46	(8 - 37)
Madagascar	--		27	(22 - 75)
Total	119		129	

The main objective of this study was to detect the presence of large-scale trends in the occurrence of fish, cephalopods and mobile invertebrates in the trawl catches and from this possibly infer zonation among those groups. The methods used include Two-Way Indicator Analysis (TWIA, Hill 1979) and an ordination technique, Detrended Correspondence Analysis, DCA, Hill & Gauch 1980), implemented by the program DECORANA. These methods, originally developed for floristic studies, have proven to be very useful also in marine faunistic studies (Bianchi 1991 and 1992; Fosså & Brattegard 1990; Buhl-Jensen & Fosså, in press; McManus 1986 and 1989).

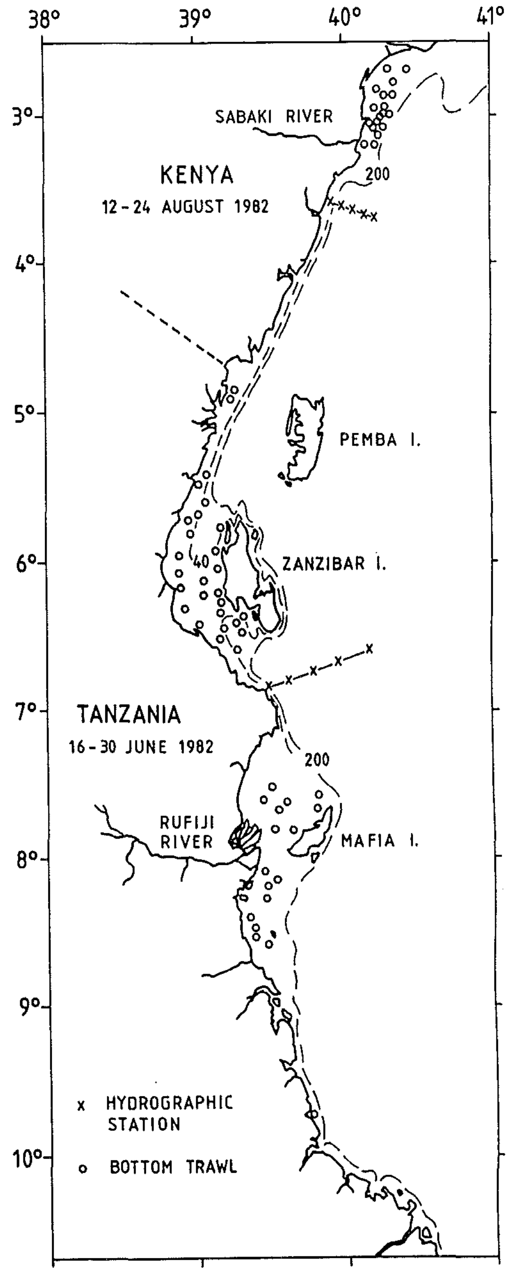

Fig. 6. Position of trawl hauls and hydrographic stations off Kenya and Tanzania (June-August 1982)

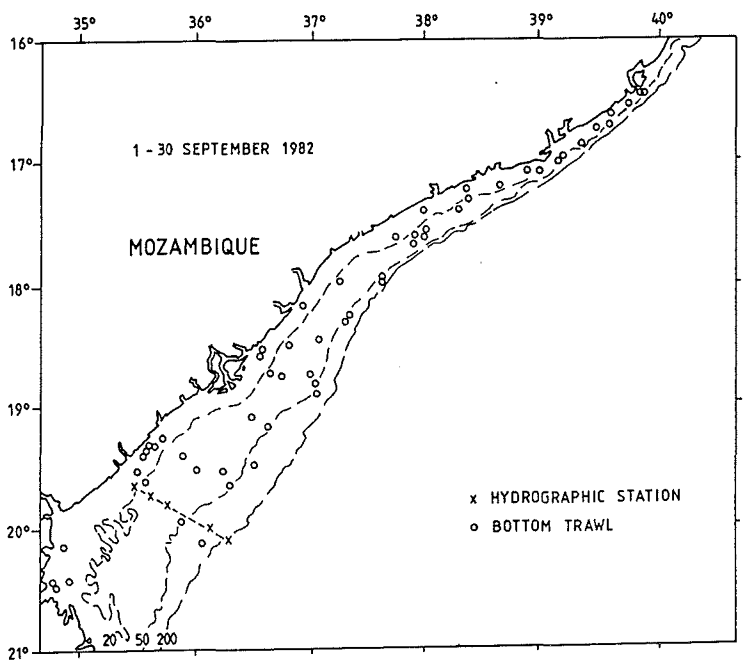

Fig. 7. Position of trawl hauls and hydrographic stations off Mozambique (September 1982)

In this study biomass (wet weight) was used as a measure of abundance. Biomass seems to be ecologically appropriate and can be more relevant for practical applications as for example in fishery management. Also, as shown in Bianchi & Høisæter (in press), main ecological typification is not affected by the abundance measure used in the case of DCA and TWIA when analysing data covering long gradients.

Each weight ($\underline{x}$) was converted to $\ln(\underline{x}+1)$ before analysis with DCA. This transformation minimizes the dominant effect of anomalous catches. The addition of 1 unit is necessary to avoid problems derived by the

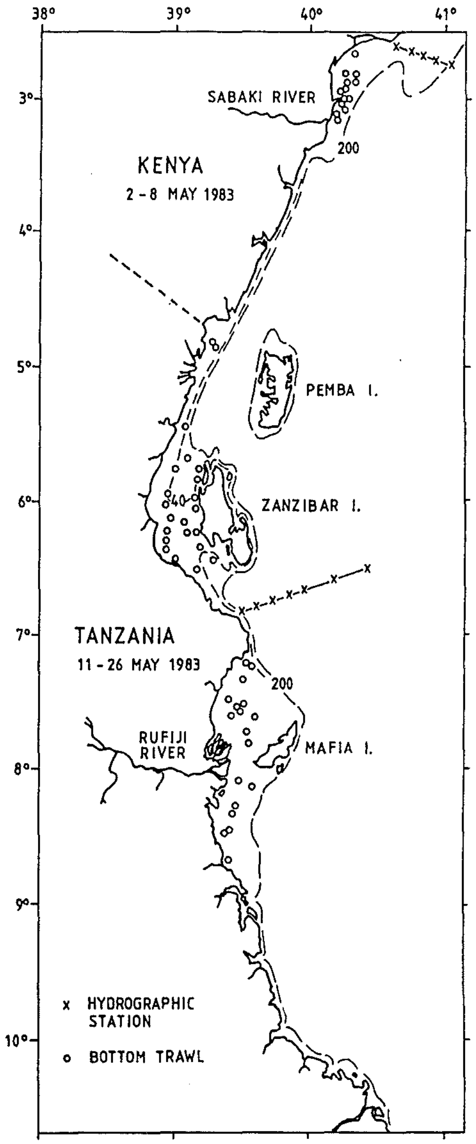

Fig. 8. Position of trawl hauls and hydrographic stations off Kenya and Tanzania (May 1983)

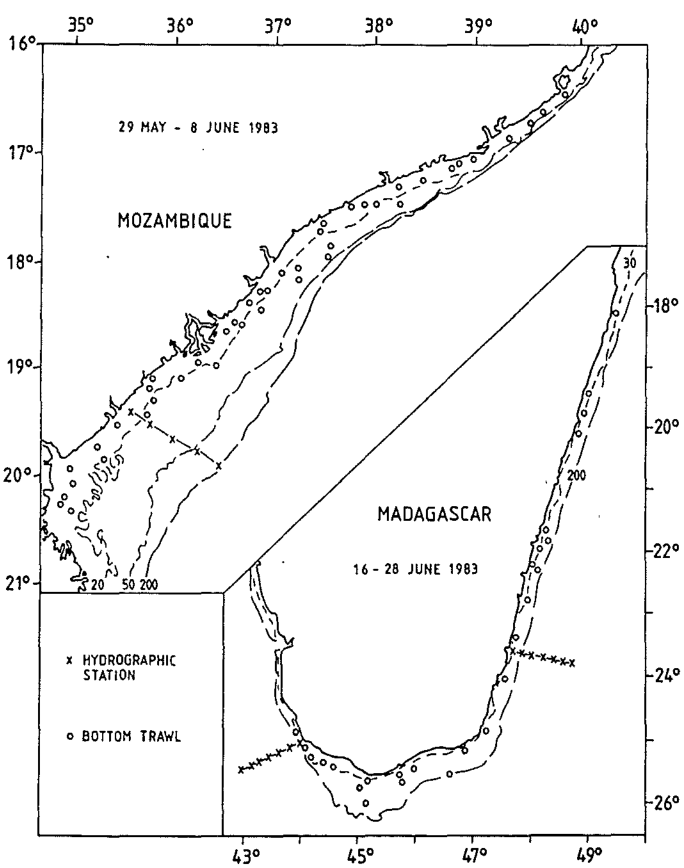

Fig. 9. Position of trawl hauls and hydrographic stations off Mozambique and Madagascar (May-June 1983)

presence of values = 0 or values < 1. No transformation is necessary in the case of TWIA, where abundances are converted to numbers corresponding to different abundance classes (pseudospecies). In this study 5 'pseudospecies' were used, corresponding to classes with lower limits set at 0, 0.5, 5, 50 and 500. These cut levels are lower than those used in other studies (Bianchi, 1991 and 1992) but they are more appropriate as they reflect the lower abundances of the southwest Indian Ocean as compared with the areas covered by those studies.

RESULTS

Appendix 1 shows the station by species output resulting from the programme TWINSPAN for the 1982 surveys off Kenya, Tanzania and Mozambique. The first division separates the shallowest groups, with average depths of 16, 12 and 21 m, from the deeper ones with 36, 36 and 31 m respectively.

At the second division level groups 1 and 2 (mainly stations from Mozambique) separate from group 3, a number of slightly deeper stations from northern Mozambique, Tanzania and Kenya while a group of stations from southwest Zanzibar (Group 6) separates from the stations at similar depth off Tanzania, Kenya and Mozambique. At the third division, only the further fractioning of the largest groups was interpreted as meaningful. The separation of the shallow water stations off Mozambique into two components was found of interest: the stations closer to the major river deltas (mainly in the southern half of the coast) and the others, in the northern half. Also ,the separation of the deeper stations of Tanzania (Group 4) from those off Mozambique (Group 5).

The plot of DCA Axes 1 and 2 is shown in Fig. 10. The eigenvalues were 0.70, 0.56, 0.42 and 0.34 respectively. The gradient of the first axis was 6.9 standard deviations. Considering that the range of a species' occurrence is on average 4 to 6 standard deviation units, the stations found at the extreme left and right of the plot (stations from southwest Zanzibar and shallow-water stations from Mozambique respectively) do not have any species in common (Jongman et al. 1987). The correlation between DCA Axis 1 and depth was significant, though not very strong (-0.57, $p > 0.05$). Fig. 11 shows the plot of DCA axis 1 and depth for each of the stations. Apart from the rightmost stations (shallow water from Mozambique) all the other groups include stations with a wide depth range. This variable was not significantly correlated with any of the other axes.

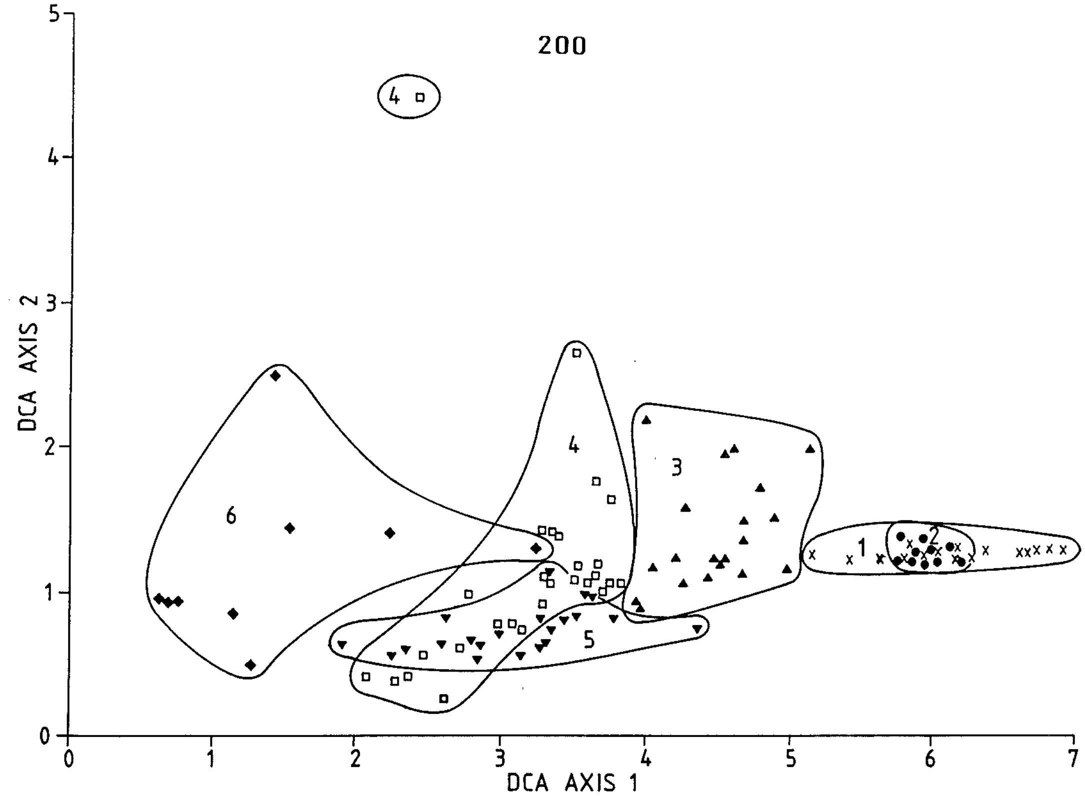

Fig. 10. Detrended correspondence analysis of bottom-trawl stations of the June-September survey 1982 (SD units x 100). Corresponding TWIA (Two-Way Indicator species analysis) Groups 1 to 6 are indicated by the different symbols and encircling lines

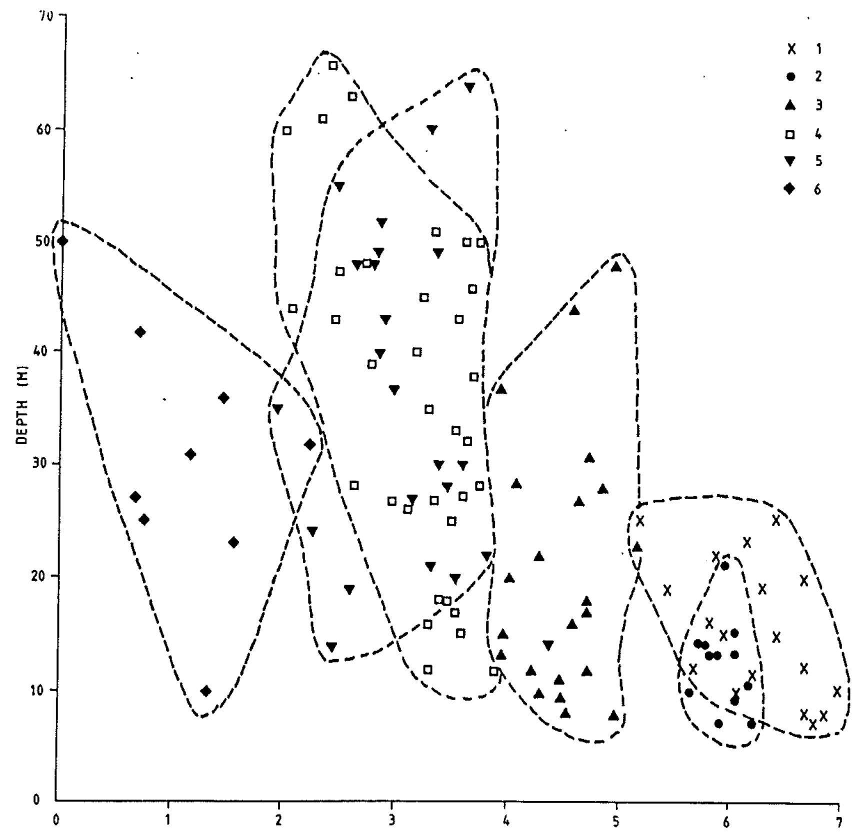

Fig. 11. Plot of station scores on DCA Axis 1 and corresponding depth values (June-September 1982 survey)

The survey in 1983 covered the south and south east coast of Madagascar as well, with stations from 22 to 75 m depth. Appendix 2 shows the output from TWINSPAN. The first division results into two groups, the rightmost including only stations from Madagascar. At the second division level the stations from south west Zanzibar and Mafia Islands separate from a group including mainly stations from Zanzibar and Mafia Channels and a group of stations from Mozambique typified by Scomberomorus commerson and Decapterus russelli. It is interesting to note that although the number and position of the sampling stations was different in the two survey periods, corresponding groups can be identified. Figs. 12 and 13 show the DCA plots of Axes 1 and 2 for the data without the Madagascar stations and with those stations respectively. The eigenvalues of the analysis without the Madagascar stations were 0.67, 0.45, 0.42 and 0.29 and the length of gradient was 6.0 SD. The eigenvalues were 0.78, 0.62, 0.53 and 0.41 for Axes 1 to 4 respectively and the length of gradient of the first axis was 7.4 SD for the ordination of all stations (including Madagascar). The correlation of DCA Axis 1 and depth were -0.56 and 0.64 respectively.

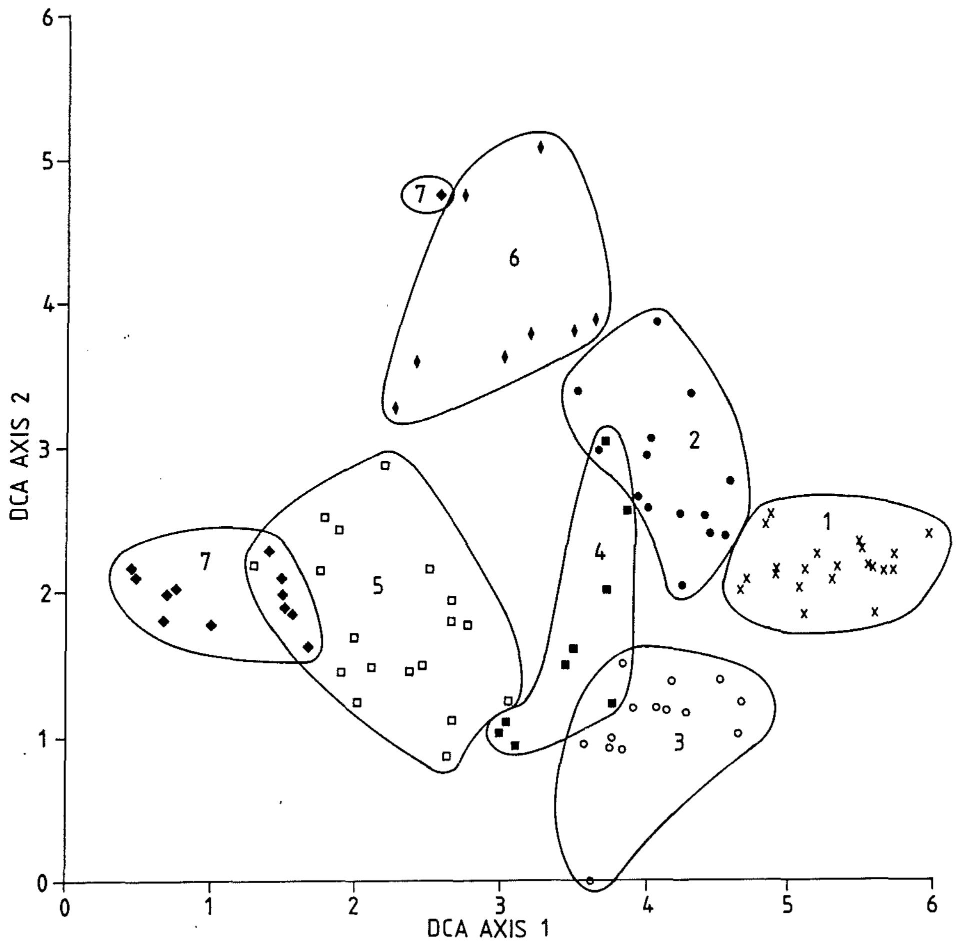

Fig. 12. Detrended correspondence analysis of bottom-trawl stations for Kenya, Tanzania and Mozambique (May-June survey, 1983) (SD units x 100). Corresponding TWIA (Two-Way Indicator species analysis) Groups 1 to 7 are indicated by the different symbols and encircling lines

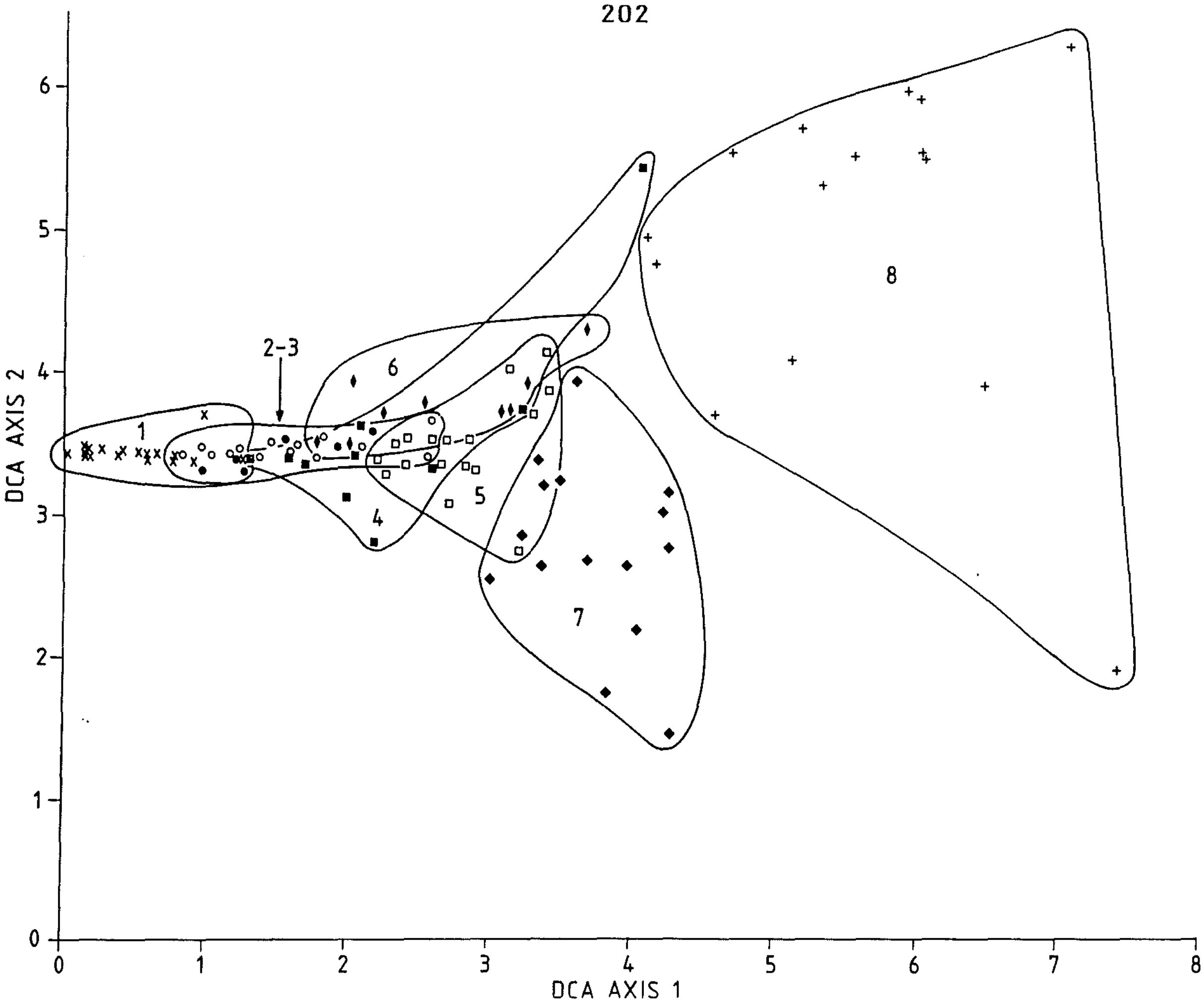

Fig. 13. Detrended correspondence analysis of bottom-trawl stations for Kenya, Tanzania, Mozambique and Madagascar (May-June survey, 1983) (SD units x 100). Corresponding TWIA (Two-Way Indicator species analysis) Groups 1 to 8 are indicated by the different symbols and encircling lines

Station groups were arranged in a similar way along Axis 1 as for the plot of the 1982 data set: from the shallow waters off Mozambique (extreme right) to the deeper, hard/sandy bottoms off southwest Zanzibar and Mafia Islands. There is however a stronger overlap along axis 1 of the shallow water stations off Mozambique with the slightly deeper stations of groups 3 and 4 for the 1983 stations. The various groups derived from the 1983 data set are more overlapping along axis 1 than those derived from the 1982 data set.

Below is a description of the main groups produced by TWIA. Tables 2 and 3 present the total caches, within each group, by species, for the 1982 and 1983 surveys respectively.

Table 2. Total weight (W), numbers (N) and frequency (F) (F: number of stations where found in each of the respective groups) of main species from station groups 1 to 6 (Kenya to Mozambique, June-September 1982)

Group 1 (18 stations)

	W	(%)	N	(%)	F
Thryssa vitrirostris	637	(16)	35 564	(30)	17
Johnius dussumieri	355	(9)	12 135	(10)	16
Pellona ditchela	328	(8)	11 055	(9)	16
Otolithes ruber	270	(7)	3 688	(3)	16
Trichiurus lepturus	224	(6)	5 670	(5)	17
Sardinella gibbosa	206	(5)	3 684	(3)	7
Polynemus sextarius	182	(5)	5 020	(4)	15
Upeneus vittatus	173	(4)	6 454	(5)	13
Leiognathus equulus	149	(4)	3 667	(3)	7
Metapeneus monoceros	114	(3)	4 465	(4)	18
Pomadasys commersonni	113	(3)	2 828	(2)	10
Terapon jarbua	82	(2)	2 323	(2)	11
Pomadasys maculatus	63	(2)	808	(1)	8
Penaeus indicus	61	(2)	1 875	(2)	17
Cynoglossus spp.	59	(1)	1 962	(2)	9
Secutor insidiator	55	(1)	3 621	(3)	8
Crabs	22	(1)	470	(0)	6
Penaeus monodon	7	(0)	104	(0)	10
Total	3 100	(79)	107 120	(89)	
Total (all species)	3 945		119 535		
Average catch rate	219		6 640		

Group 2 (13 stations)

	W	(%)	N	(%)	F
Pellona ditchela	777	(31)	33 368	(38)	13
Thryssa vitrirostris	495	(20)	24 770	(28)	10
Sardinella gibbosa	222	(9)	5 058	(6)	3
Johnius dussumieri	102	(4)	5 233	(6)	10
Trichiurus lepturus	94	(4)	2 498	(3)	12
Leiognathus equulus	72	(3)	4 470	(5)	11
Scomberoides tol	66	(3)	1 144	(1)	8
Pomadasys maculatus	64	(3)	1 776	(2)	10
Metapenaeus monoceros	45	(2)	2 125	(2)	10
Otolithes ruber	42	(2)	1 467	(2)	12
Penaeus indicus	41	(2)	1 084	(1)	10
Secutor insidiator	39	(2)	2 532	(3)	9
Alepes djeddaba	37	(2)	138	(0)	8
Megalaspis cordyla	37	(2)	99	(0)	9
Scomberomorus commerson	35	(1)	83	(0)	7
Terapon jarbua	26	(1)	448	(0)	8
Rastrelliger kanagurta	25	(1)	520	(1)	5
Polynemus sextarius	8	(0)	56	(0)	6
Total (all species)	2 531		88 359		
Average catch rate	195		6 797		

Group 3 (22 stations)

	W	(%)	N	(%)	F
Secutor insidiator	2 430	(19)	189 196	(36)	18
Leiognathus equulus	1 993	(15)	111 995	(21)	17
Gazza minuta	1 200	(9)	47 483	(9)	8
Upeneus vittatus	547	(4)	18 542	(4)	12
Sphyraena obtusata	545	(4)	3 659	(1)	12
Pellona ditchela	440	(3)	15 486	(3)	9
Pomadasys commerson	272	(2)	285	(0)	9
Scomberomorus commerson	207	(2)	92	(0)	10
Scomberoides commers.	200	(2)	44	(0)	6
Gerres filamentosus	164	(1)	4 528	(1)	8
Sardinella gibbosa	162	(1)	5 606	(1)	13
Carangoides malabar.	150	(1)	5 630	(1)	6
Rastrelliger kanag.	140	(1)	1 234	(0)	7
Terapon jarbua	133	(1)	3 198	(1)	8
Pomadasys maculatus	133	(1)	2 839	(0)	11
Carangoides armatus	99	(1)	598	(0)	5
Polynemus sextarius	77	(1)	1 782	(0)	11
Saurida undosquamis	27	(0)	404	(0)	9
Total	8 918	(69)	412 601	(78)	
Total (all species)	12 940		527 891		
Average catch rate	588		23 995		

Group 4 (33 stations)

	W	(%)	N	(%)	F
Leiognathus leuciscus	2 997	(19)	193 746	(33)	16
Upeneus vittatus	1 522	(10)	66 258	(11)	17
Gerres filamentosus	853	(5)	18 757	(3)	18
Secutor insidiator	741	(5)	56 424	(10)	11
Atule mate	530	(3)	6 328	(1)	15
Gazza minuta	509	(3)	23 788	(4)	16
Decapterus russelli	500	(3)	16 440	(3)	23
Sardinella gibbosa	421	(3)	25 124	(4)	14
Carangoides malabar.	411	(3)	7 704	(1)	14
Leiognathus equulus	285	(2)	10 642	(2)	8
Saurida undosquamis	263	(2)	5 008	(1)	25
Rastrelliger kanagurta	198	(1)	2 732	(0)	22
Abalistes stellatus	145	(1)	144	(0)	18
Scomberoides commers.	139	(1)	102	(0)	10
Scomberomorus commerson	99	(1)	46	(0)	12
Nemipterus japonicus	91	(1)	2 003	(0)	13
Stolephorus spp.	88	(1)	622	(0)	8
Sphyraena forsteri	82	(1)	588	(0)	21
Nemipterus bipunctatus	73	(0)	1 066	(0)	11
Carangoides armatus	47	(0)	446	(0)	14
Nemipterus metopias	30	(0)	602	(0)	10
Sphyraena obtusata	28	(0)	664	(0)	6
Apogonidae	16	(0)	1 596	(0)	12
Total	10 068	(65)	480 830	(75)	
Total (all species)	15 664		580 763		
Average catch rate	475		17 598		

Group 5 (24 stations)

	W	(%)	N	(%)	F
Leiognathus elongatus	1 135	(20)	283 660	(64)	9
Decapterus macrosoma	959	(17)	94 740	(21)	8
Decapterus russelli	795	(14)	24 534	(6)	15
Scomberomorus commerson	372	(7)	139	(0)	18
Upeneus bensasi	231	(4)	9 686	(2)	11
Nemipterus bipunctatus	191	(3)	2 826	(1)	16
Rastrelliger kanagurta	155	(3)	1 530	(0)	10
Carangoides malabaricus	88	(2)	1 383	(0)	12
Loliginidae	53	(1)	3 738	(1)	11
Saurida undosquamis	47	(1)	513	(0)	16
Crabs	23	(0)	28	(0)	12
Scyllaridae	16	(0)	74	(0)	10
Total	4 066	(72)	422 851	(95)	
Total (all species)	5 666		444 341		
Average catch rate	236		18 514		

Group 6 (9 stations)

	W	(%)	N	(%)	F
Dasyatis pastinaca	160	(21)	4	(0)	1
Pomacentrus spp.	86	(11)	6 799	(33)	3
Stegostoma spp.	80	(10)	2	(0)	1
Arothron stellatus	56	(7)	16	(0)	5
Scolopsis bimaculatus	51	(7)	1 500	(7)	6
Parupeneus cinnabarinus	39	(5)	1 020	(5)	5
Lethrinus mahsena	29	(4)	886	(4)	5
Nemipterus bipunctatus	27	(4)	506	(2)	8
Diagramma pictum	13	(2)	10	(0)	2
Saurida undosquamis	11	(1)	344	(2)	7
Atule mate	10	(1)	84	(0)	4
Thenus orientalis	9	(1)	38	(0)	6
Gymnocranius griseus	5	(1)	170	(1)	5
Total	576	(75)	11 379	(54)	
Total (all species)	777		20 509		
Average catch rate	86		2 278		

Table 3. Total weight (W) and frequency (F) (F: number of stations where found in each of the respective groups) of main species from station groups 1 to 8 (Kenya to Madagascar, May-June 1983)

	W (%)	N (%)	F
Group 1 (21 stations)			
Pellona ditchela	3 625 (30)	171 756 (28)	20
Thryssa vitrirostris	1 303 (11)	82 961 (13)	19
Trichiurus lepturus	583 (5)	17 078 (3)	18
Sardinella gibbosa	546 (5)	10 782 (2)	12
Johnius dussumieri	541 (5)	27 329 (4)	18
Otolithes ruber	421 (4)	5 624 (1)	18
Secutor insidiator	384 (3)	27 576 (4)	14
Penaeus indicus	267 (2)	6 701 (1)	18
Polynemus sextarius	244 (2)	8 714 (1)	16
Pomadasys maculatus	243 (2)	9 116 (1)	13
Caridean shrimps	236 (2)	159 484 (26)	10
Arius spp.	199 (2)	3 086 (0)	9
Parastromateus niger	160 (1)	746 (0)	13
Alepes djeddaba	139 (1)	2 184 (0)	9
Megalaspis cordyla	118 (1)	1 158 (0)	15
Upeneus vittatus	110 (1)	4 488 (1)	10
Cynoglossus spp.	88 (1)	4 286 (1)	14
Terapon jarbua	77 (1)	2 456 (0)	11
Metapeneus monoceros	73 (1)	6 374 (1)	18
Scomberoides tol	65 (0)	1 724 (0)	16
Thryssa setirostris	58 (0)	2 278 (0)	16
Gazza minuta	45 (0)	2 620 (0)	14
Penaeus monodon	25 (0)	300 (0)	8
Total	9 550 (80)	558 821 (87)	
Total (all species)	11 879	613 646	
Average catch rate	566	29 221	
Group 2 (14 stations)			
Upeneus vittatus	955 (36)	33 408 (41)	11
Carangoides malabar.	281 (11)	4 854 (6)	13
Secutor insidiator	260 (10)	16 334 (20)	12
Pellona ditchela	226 (9)	7 924 (10)	8
Leiognathus equulus	67 (2)	1 822 (2)	6
Rastrelliger kanagurta	42 (2)	418 (0)	10
Terapon jarbua	33 (1)	426 (0)	9
Saurida undosquamis	31 (1)	350 (0)	8
Loliginidae	*24 (1)*	*622 (1)*	*11*
Scomberoides tol	11 (0)	226 (0)	9
Total	1 930 (73)	66 384 (82)	
Total (all species)	2 638	81 502	
Average catch rate	188	5 821	
Group 3 (16 stations)			
Pellona ditchela	1 328 (22)	66 262 (31)	15
Gazza minuta	913 (15)	29 428 (14)	12
Leiognathus equulus	487 (8)	15 795 (7)	12
Secutor insidiator	434 (7)	20 066 (9)	10
Trichiurus lepturus	298 (5)	1 086 (0)	9
Upeneus taeniopterus	134 (2)	4 932 (2)	10
Leiognathus fasciatus	115 (2)	1 834 (1)	6
Leiognathus daura	113 (2)	3 164 (1)	11
Drepane punctata	94 (1)	289 (0)	12
Leiognathus spp.	93 (1)	31 678 (15)	9
Gerres filamentosus	86 (1)	2 190 (1)	10
Upeneus sulphureus	85 (1)	3 344 (1)	11
Sphyraena obtusata	69 (1)	1 116 (0)	12
Pomadasys maculatus	70 (1)	1 100 (0)	9
Polynemus sextarius	51 (1)	696 (0)	12
Chirocentrus dorab	45 (1)	102 (0)	11
Terapon teraps	42 (1)	874 (0)	12
Otolithes ruber	37 (1)	182 (0)	8
Pomadasys commersonni	28 (0)	127 (0)	7
Arius spp.	19 (0)	80 (0)	8
Total	4 541 (74)	184 345 (85)	
Total (all species)	6 138	215 693	
Average catch rate	384	13 480	
Group 4 (16 stations)			
Gazza minuta	1 292 (24)	58 121 (20)	13
Secutor insidiator	737 (14)	61 665 (21)	11
Leiognathus equulus	444 (8)	23 666 (8)	9
Upeneus taeniopterus	195 (4)	8 410 (3)	8
Leiognathus leuciscus	128 (2)	10 274 (3)	6
Sphyraena obtusata	98 (2)	1 243 (0)	10
Saurida undosquamis	63 (1)	884 (0)	12
Gerres filamentosus	57 (1)	1 138 (0)	13
Loliginidae	40 (1)	1 608 (0)	10
Total	3 054 (58)	167 009 (57)	
Total (all species)	5 274	293 115	
Average catch rate	330	18 319	
Group 5 (21 stations)			
Leiognathus leuciscus	2 657 (23)	209 780 (58)	16
Upeneus taeniopterus	1 513 (13)	46 497 (13)	12
Atule mate	400 (4)	3 526 (1)	9
Decapterus russelli	394 (4)	13 250 (4)	14
Saurida undosquamis	394 (4)	8 293 (2)	13
Gazza minuta	331 (3)	12 925 (3)	9
Nemipterus japonicus	233 (2)	3 900 (1)	15
Gerres filamentosus	188 (2)	3 488 (1)	11
Gerres oyena	185 (2)	3 252 (1)	8
Scomberomorus commerson	93 (1)	70 (0)	9
Upeneus bensasi	63 (0)	3 612 (1)	13
Abalistes stellatus	55 (0)	64 (0)	10
Loliginidae	36 (0)	1 540 (0)	13
Total	6 542 (57)	310 197 (85)	
Total (all species)	11 559	364 245	
Averaga catch rate	550	17 345	
Group 6 (9 stations)			
Scomberomorus commerson	93 (26)	38 (1)	7
Atule mate	32 (9)	802 (24)	3
Decapterus russelli	28 (8)	962 (29)	6
Crangoides malabaricus	17 (5)	162 (5)	4
Scomberomorus plurilin.	14 (4)	8 (0)	2
Loliginidae	13 (4)	283 (9)	8
Total	197 (56)	2 255 (68)	
Total (all stations)	355	3 337	
Average catch rate	39	370	
Group 7 (15 stations)			
Saurida undosquamis	93 (9)	2 722 (11)	12
Decapterus russelli	85 (8)	1 574 (6)	2
Upeneus bensasi	78 (8)	5 360 (21)	10
Loliginidae	78 (8)	237 (1)	10
Nemipterus bipunctatus	59 (6)	826 (3)	13
Lethrinus mahsena	35 (3)	776 (3)	8
Pomacentrus spp.	33 (3)	1 532 (6)	6
Scolopsis bimaculatus	26 (3)	405 (2)	9
Echeneis naucrates	13 (1)	34 (0)	7
Gymnocranius griseus	10 (1)	156 (1)	5
Fistularia petimba	9 (1)	56 (0)	9
Labridae	6 (1)	140 (1)	7
Total	525 (52)	13 818 (55)	
Total (all species)	1 009	25 077	
Average catch rate	67	1 538	

Table 3. Continued

	W (%)		N (%)		F
Group 8 (15 stations)					
Trachurus delagoae	485	(14)	12 972	(35)	3
Argyrosomus regius	479	(14)	36	(0)	1
Carcharinidae	240	(7)	6	(0)	2
Scolopsis bimaculatus	147	(4)	164	(0)	4
Parupeneus spp.	146	(4)	4 652	(12)	12
Pagellus natalensis	133	(4)	3 479	(9)	4
Teixerichthys jordani	133	(4)	4 736	(13)	8
Cheimerius nufar	122	(3)	72	(0)	5
Priacanthus spp.	51	(1)	902	(2)	6
Sepiidae	37	(1)	240	(1)	8
Aprion virescens	34	(1)	18	(0)	4
Parupeneus fraterculus	22	(1)	184	(0)	7
Loliginidae	11	(0)	142	(0)	8
Apogonidae	9	(0)	1 808	(5)	5
Total	2 048	(59)	29 411	(79)	
Total (all species)	3 472		37 256		
Average catch rate	231		2 484		

Groups 1 and 2. Shallow waters off Mozambique (Sofala Bank). The shallow water stations of the Sofala Bank (Fig. 14) form a quite homogeneous and well defined group, with consistent catches of a number of shrimps (mainly Metapenaeus monoceros and Penaeus indicus), accompanied by small pelagic species like the thread herring Thryssa vitrirostris and Pellona ditchela, larger fish species, typically fish predators, as croakers (Otolithes ruber and Johnius dussumieri/amblycephalus), hairtail Trichiurus lepturus or more bottom feeders and crustacean predators (Polynemus sextarius and Pomadasys commersonni). There is some difference between the northern and southern parts of the Sofala Bank (Groups 1 and 2, respectively, Appendix 1). Although the average depth is comparable, the stations found in the former zone are characterized by Upeneus vittatus, Penaeus monodon and Cynoglossus spp., while they seem to lack the carangids Scomberoides tol, Alepes djeddaba and Megalaspis cordyla found in the latter zone in the course of the 1982 surveys. Fifty per cent of the catches of group 2 consist of Pellona ditchela and Thryssa vitrirostris. In the course of the 1983 survey (Fig. 15), although two main groups can still be distinguished, some changes have occurred and the species that had typified groups 1 and 2 are now co-occurring. Group 2 of the 1983 survey seems to represent stations with a slightly deeper depth range. Furthermore, catch rates are much higher (Table 3), mainly because of the increase of Pellona ditchela and Thryssa vitrirostris, and associated predators (i.e. Sphyraena obtusata) especially in the southern area. Both the above clupeoids are highly euryhaline and widely distributed in the Indo-Pacific area. They feed on a variety of small crustaceans and zoae larvae. Their increase can be related to the season (just after the main rainy season, which also coincides with the maximum discharge from the Zambesi and Save Rivers).

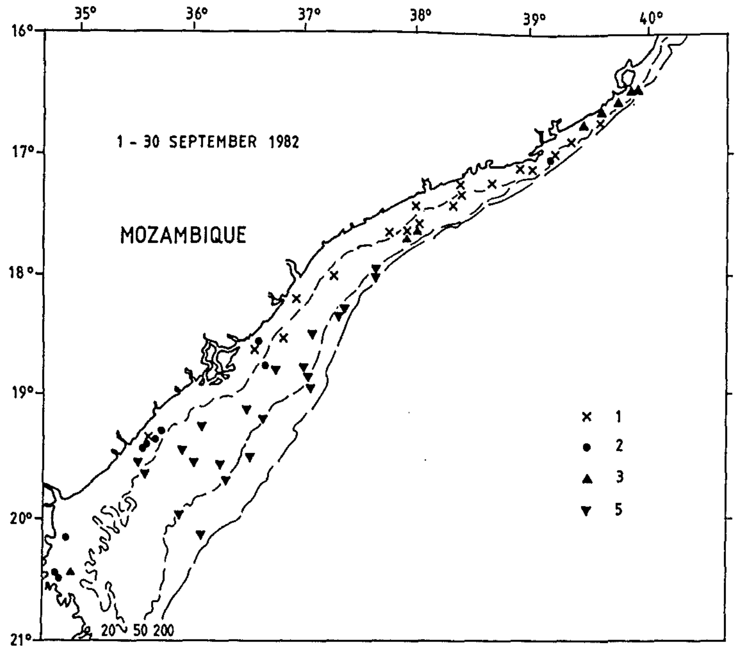

Fig. 14. Position of trawl hauls off Mozambique (September 1982) after being assigned to the different groups

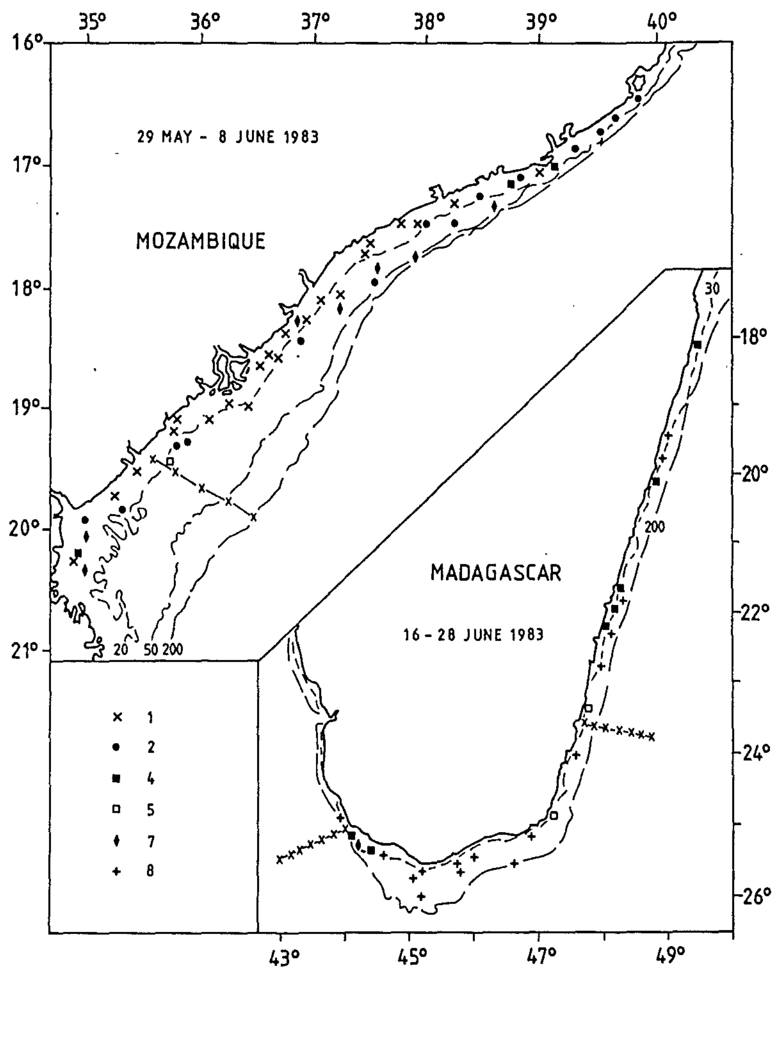

Fig. 15. Position of trawl hauls off Mozambique and Madagascar (May-June 1983) after being assigned to the different groups

This type of environment also exists along the Tanzanian coast (see for example the Rufiji River system) but the sampling in shallow waters was not as intensive off Tanzania.

The other groups of the first TWINSPAN division are slightly deeper but are well distinguished by lacking the typical estuarine group of the shallow waters of Mozambique (Appendix 1). Similar environments, although not so extensive, are present along the East African coast (i.e. Rufiji delta) but they were not sampled in both surveys and therefore do not appear in this study.

Group 3. Shallow waters (Kenya, Tanzania, Mozambique). Twenty-two stations located off Mozambique (off the Angoche area), off Tanzania (only 3 stations outside the Rufiji delta) and in the deeper part of Ungama Bay (Kenya)(Figs. 14 and 15). The average depth is 21 m (range 11 to 44). It appears as an intermediate group between the very shallow waters associated to mangrove areas and the deeper shelf waters (Appendix 1). Dominating species are the slipmouths Secutor insidiator, Leiognathus equulus and Gazza minuta contributing to 43 % of the catches in biomass (Table 2). In the 1983 survey (Appendix 2 and Figs.15 and 18) this group corresponds to groups 3 and 4, consisting of stations from the whole survey area, including Madagascar and identifiable by the same dominating species. In 1983 however, because of the different coverage, the presence of a few stations from Madagascar and better availability of a number of species, 2 groups may be distinguished on the basis of different depth ranges and the occurrence of shallow-water preferential in Group 3 and deeper water preferential in group 4.

Group 4. Assemblages of the Zanzibar and Mafia Channels. There are 33 stations in this group, mostly from the Zanzibar and Mafia Channels, with an average depth of 36 m, range 12 to 66 (Appendix 1). Also in this group a slipmouth, Leiognathus leuciscus, is most abundant, accounting for 20 % of the catches, followed by the goatfish Upeneus vittatus (10%). The round scad Decapterus russelli, the lizardfish Saurida undosquamis and the Indian mackerel Rastrelliger kanagurta had highest frequencies. This group seems to represent the intermediate shelf environment, where the connection to the coastline, and especially to mangrove areas, is not present. The dominating species of groups 1 and 2 are practically absent. This group can easily be identified also in the 1983 survey (Group 5, Appendix 2), with the same dominating species and average depth (Figs. 16 and 17).

Group 5. Intermediate shelf off Mozambique. The average depth of the 24 stations of this group is 36 m, exactly as the corresponding Group 4 off Tanzania. The main difference seems to be the presence of a few dominating species in this group as compared to the one from Tanzania. Thus more 50 % of the catches consist of three species, the slipmouth Leiognathus elongatus, and the round scads Decapterus macrosoma and D. russelli.

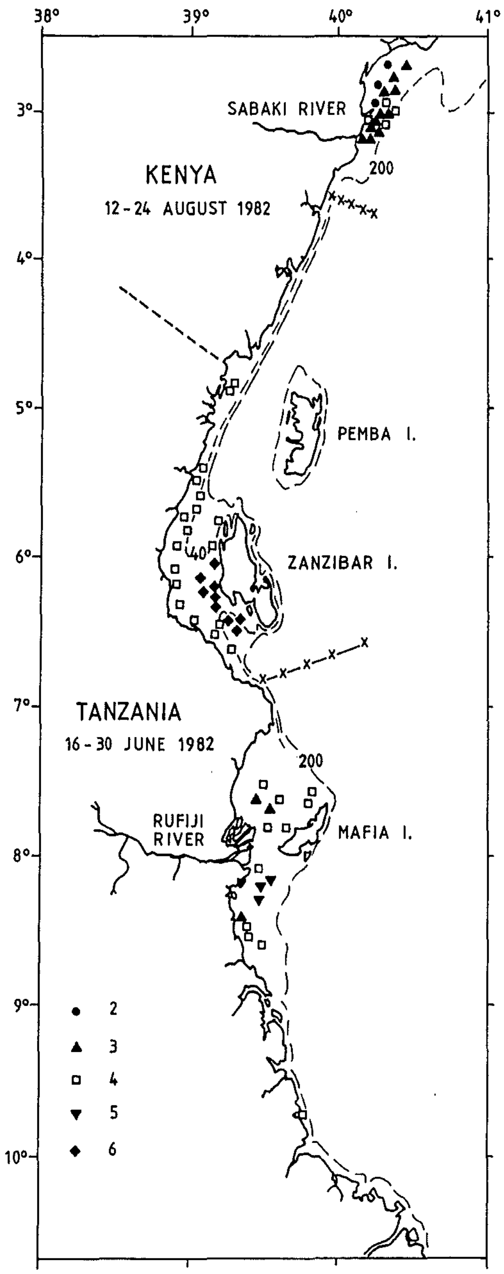

Fig. 16. Position of trawl hauls off Kenya and Tanzania (June-August 1982) after being assigned to the different groups

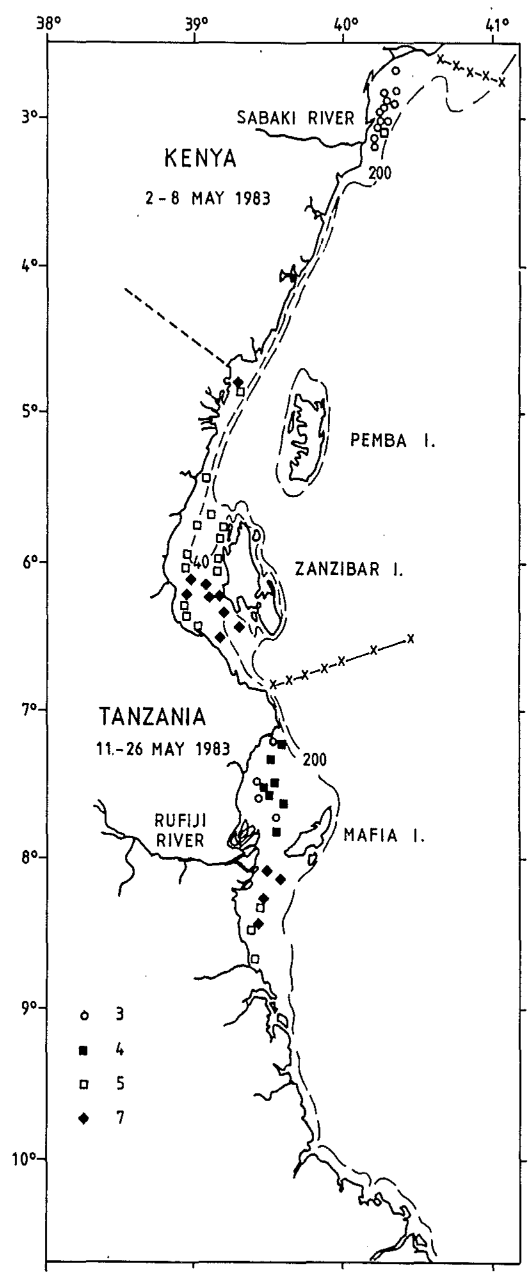

Fig. 17. Position of trawl hauls off Kenya and Tanzania (May 1983) after being assigned to the different groups

Most frequent were the Spanish mackerel Scomberomorus commerson and the threadfin Nemipterus bipunctatus (= N. delagoae). In the 1983 survey, a few stations forming a group linked to the deeper Tanzania stations, appears as extremely poor both in number of species and total abundance. They are characterized by the almost constant appearance of squid (Loliginidae) together with Scomberomorus commerson (Group 6, Appendix 2). In 1983 very few stations were sampled in the same area (Figs. 14 and 15).

Group 6. Southwest Zanzibar. Although the average depth of 31 m (range 16 to 50) is comparable to the two groups above, this group seems to be well differentiated from 4 and 5 (Table 2). Dominating species (in frequency of occurrence in the catches) are Nemipterus bipunctatus, Saurida undosquamis, Scolopsis bimaculatus, Thenus orientalis, Lethrinus mahsena, Arothron stellatus and Parupeneus cinnabarinus. The stingray Dasyatis pastinaca dominates the catches but was caught only ones while small pomacentrids (Pomacentrus spp.), making up 29 % of the catches, were more common.

The same group is found in the 1983 survey, but also included the corresponding area off Mafia Island (Figs. 16 and 17). The most remarkable feature of this group is perhaps the lack of leiognathids that have instead been the dominating species in the other groups and the presence of species typically around coral reef areas. Another remarkable difference is the extremely low average catch rate (86 kg h^{-1} and 67 kg h^{-1}, for the two surveys respectively) as compared to the other groups (this might however also be due to lower efficiency of the gear in the case coral outcrops were encountered).

Madagascar. Most of the stations from Madagascar (Fig. 15) are included in Group 8 (Appendix 2 and Table 3) and are separated at the first TWINSPAN division level. A number of new species appear while most of the others are missing. The depth range is higher and a direct comparison with the continental groups is not possible. A non identified Parupeneus species is the most frequent taxon. The other species are known to occur also along the east African coast. Cheimerius nufar (abundant in the Arabian Sea and known to occur throughout the western Indian Ocean to South Africa) was not caught off Kenya to Mozambique but this is probably due to the shallow depth range of the sampled stations.

DISCUSSION

Although depth appears as the dominant gradient affecting the distribution of the assemblages identified, there is evidence of non-depth-related zonation. Furthermore, as already indicated by other works (Bianchi 1991 and 1992) depth is a spurious variable and often obscures other more meaningful ecological parameters. Although the first TWIA subdivision of the 1982 stations seems to be clearly related to depth, average 16, 12 and 21 m versus 36, 36 and 31 m for the groups of the first and second TWIA division respectively, the main differences should probably be related to the special ecological conditions found in proximity of mangrove areas. DCA axis 1 is significantly correlated with depth, but examination of the plot of DCA Axis 1 against depth (Fig. 11) shows that only groups 1 and 2 have consistent depth values while the other groups show a high degree of variation in the depth ranges. The shallow depths, however, also reflect the presence of extensive mangrove areas and the clear zonation observed is due to the presence of this particular ecosystem. Here the main source of nutrients comes from detritus and detritus-feeders (shrimps) and their predators typify the system. The top species of Groups 1 and 2 of both surveys (including the shallow water stations in proximity of mangrove areas and river estuaries off Mozambique) consist of pelagic species feeding on zooplankton, mainly crustaceans and zoae larvae (Pellona ,Thryssa, Alepes djeddaba) and their predators (Trichiurus and Otolithes), bottom feeders (Cynoglossus and Johnius) and detritus feeders (Penaeus and Metapenaeus). Shrimp, together with other detritus-feeder invertebrates, are at the base of the trophic chain of these environments. Larvae and juvenile shrimp, mostly in shallow brackish waters, are the preferred item of euryhaline small pelagics (Thryssa and Pellona). Adult shrimp is also a preferred item of a number of demersal perciformes. Shrimp forms also the basis of the most lucrative fisheries in these areas and fish bycatch is usually discarded at sea. Some proposals aimed at saving the fish part of the catches include excluding devices where either the fish part of the catch is rejected before being brought on deck or the fish is scared off (see for example Sternin & Allsop 1981). If the assemblage structure described above is taken into account, the implementation of such devices would tend to lead, other things being equal, to an increase in the biomass of the predators in relation to the shrimp stocks with obvious negative consequences for the latter.

A second type of assemblage is the one of the intermediate shelf on sandy bottoms, where dominating species include leiognathids and pelagic taxa. Ursin (1984) argues that in the tropics, because of the lack of the marked seasonality associated with higher latitudes, production is more constant throughout the year and the more efficient utilization of the primary production leaves little for benthos to feed on. For this reason real bottom fauna consists mostly of animals seeking shelter or rest on the bottom and real demersal fish (i.e. feeding on bottom animals) are practically absent. It is indeed quite striking that the species dominating the intermediate shelf groups are leiognathids (Groups 3 and 4 of Appendix 1 and 3, 4 and 5 of Appendix 2). It seems that the stable levels of primary production have allowed a typically demersal family (Leiognathidae) to specialize in feeding both in the water column and on small organisms on the bottom. The mouth shape of the leiognathids, strongly upward protrucible (Secutor), forward or downward protrucible (Leiognathus), toothed and not strongly protrucible (Gazza) suggests a specialization within this family to optimally exploit different trophic niches, i.e. zooplankton and small bottom invertebrates (Fischer & Bianchi 1984), making this group one of the most successful in typically tropical open shelves throughout the Indo-Pacific. Other dominating species in the catches are, besides larger predators (i.e. Scomberomorus, Sphyraena, Saurida) semi-pelagic forms (i.e. Decapterus and other carangids). Rastrelliger and some of the more pelagic species are probably caught in the upper water layers when the trawl is hauled in. The presence of a high percentage of pelagic or semi-pelagic species in the bottom trawl catches again fits with the general description given by Ursin (1984) '..demersal catches in the tropics are based to a large extent on species feeding more or less pelagically..'. It should be added that the designation 'tropics' includes shelves with a stable structure of the water masses and should not be applied in a geographical sense.

A third type of assemblage is represented by the stations off south west Zanzibar and Mafia (Group 6 in the 1982 survey and Group 7 in the 1983 survey). This group has nothing in common with the estuarine/mangrove-associated groups, lack leiognathids and associated larger predators (Sphyraena, Scomberomorus, Scomberoides). Most common species (in terms of frequency of occurrence) in both surveys were Nemipterus bipunctatus and Saurida undosquamis. This reflects the position of these stations in proximity of areas with many coral outcrops and small islands, and the lack of major rivers. The trawlable areas here are more an extension of the reef environment which might explain the difference with groups 4 and 5, with stations located in more open shelf.

The Madagascar stations are deeper then the continental ones and therefore not directly comparable. The dominating species are widely distributed in the Indian Ocean. Tachurus delagoae however, belongs to a more temperate regime and is mainly distributed off South Africa. The appearance of this species indicates the proximity of a zoogeographic boundary.

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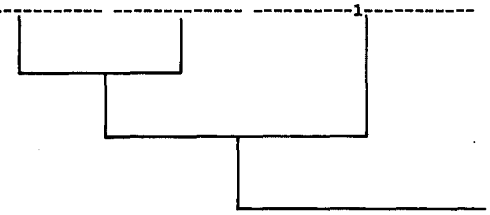
Appendix 1. Two-way station by species table for Kenya, Tanzania, Mozambique (June-September 1982) resulting from the program TWINSPAN. Values denote categories of abundance: 1: w < 0.5 kg; 2: 0.5 < w ≤ 5 kg; 3: 5 < w ≤ 50 kg; 4: 50 < w ≤ 500 kg; 5: w > 500 kg. The dendrogram showing the hierarchical relationship between the various groups, substitutes the binary notation produced by the program.

Group	1	2	3
Geog. position	Mozambique		Kenya, Tanz., Moz.
Average depth (m)	16	12	21
Metapenaeus monoceros	122333333333312122	1111322233---	---2--22--------------
Penaeus indicus	23233222222-222231	1122222233---	----------------------
Penaeus monodon	12221-1221------2-	-------1-----	----------------------
Johnius dussumieri	3-344323332322332-	-1223324-3-32	----------------------
Otolithes ruber	323333233333323-3-	22222223-3333	-----------------122-3
Thryssa vitrirostris	3333333323443244-3	4322333344---	------------1---------
Cynoglossus spp.	--323133332-------	---1---------	---2-1----------------
Pellona ditchela	22333334-233-24323	3322444444333	--------4---23333--122
Trichiurus lepturus	33322333323222333-	3332333-23333	---21-----3-2---2--1--
Polynemus sextarius	2-2--1222223224333	221----22--2-	--------3322--3312222-
Pomadasys commersonni	----3--3-33332333-	--3-323--2233	3--3-3--32--3-342-----
Terapon jarbua	2-22-2--2---124323	222--22232---	--2--13-3323--3-------
Pomadasys maculatus	2------222---2-233	332--22322-23	-21-114-3--2-----2212-
Alepes djeddaba	21-----------1----	3321-222----1	--332-----------------
Scomberoides tol	------2-----------	22-1-23233---	--2-2---3-------------
Megalaspis cordyla	-1--------2-2-----	222132-3--12-	------3-----1---3-----
Leiognathus equulus	-----3-222--3-2--4	33--233322233	3-13124-54432444---232
Sphyraena obtusata	-------2---3-----4	-2-----------	3---1-3-33242442--2---
Secutor insidiator	-1----2----33223-3	322-222333---	2343334-4533-452-1221-
Sardinella gibbosa	21---------3-2432-	--------432--	133333---43------11122
Upeneus vittatus	2-----232333223233	--2--------1-	142433433---2-33------
Crabs	-----222323-------	2------------	------32--------------
Scyllaridae	----------2------2	2-----1------	------3-------------2-
Scomberomorus commer.	-----2--------3---	32-221--33---	---3-3-3-3-2333-3----2
Scomberoides commers.	------------------	-------------	-----3---4-4-333------
Gazza minuta	122---------------	-------------	3-13----543----32-----
Gerres filamentosus	----------------3-	-------------	---312--432------33---
Stolephorus spp.	------------------	-------------	---2----312--------1--
Rastrelliger kanagur.	------------------	-2--223-3----	------4--3-31133------
Carangoides armatus	------------------	-------------	----23-----3-33-------
Carangoides malabar.	------------------	-1-----2-----	--2-23--4-33----------
Saurida undosquamis	--------2--32---32	-------3-----	2--2---33--2-----2111-
Leiognathus elongatus	------------------	-------------	----------2------33---
Abalistes stellaris	------------------	-----------32	---------2--3-----1-2-
Loliginidae	------------------	-------------	-2--------------------
Nemipterus bipunctat.	------------------	-------------	----------------------
Upeneus bensasi	------------------	----3--------	----------------------
Arothron stellatus	------------------	-------------	--------------------2-
Scolopsis bimaculatus	------------------	-------------	----------------------
Parupeneus cinnabar.	------------------	-------------	----------------------
Lethrinus mahsena	------------------	-------------	----------------------
Thenus orientalis	------------------	-------------	----------------------
Atule mate	------------------	-------------	---------3------------
Decapterus russelli	------------------	-------------	----------------------
Nemipterus japonicus	------------------	-------------	---------3------------
Nemipterus metopias	------------------	-------------	----------------------
Leiognathus leuciscus	------------------	-------------	--------34------------
Sphyraena fosteri	------------------	-------------	--------3-------------
Apogonidae	------------------	-------------	----------1-----------



4 Tanzania 36	5 Mozambique 36	6 South-West Zanzibar 31
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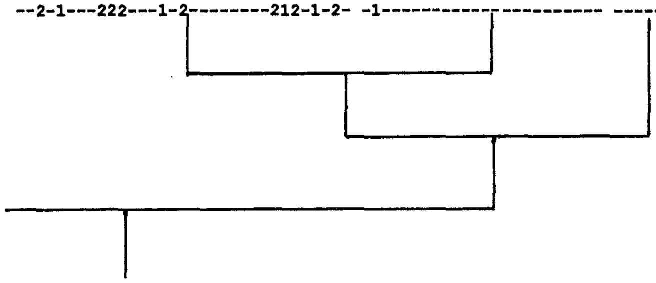
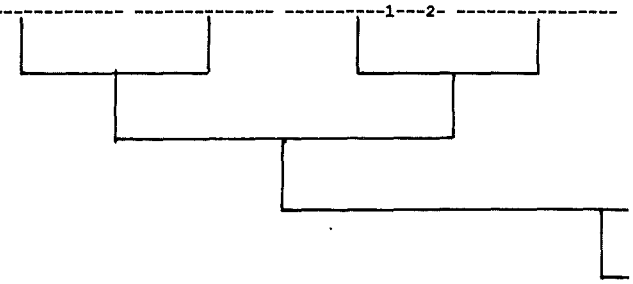
-2-------------------------------	-------------- -------2--	---------
---------2-----------------------	-------------- ----------	---------
------3--------------------------	-------------- ----------	---------
--------221------------1---------	-------------- ----------	---------
----2----------------------------	-------------- -------33-	---------
-2-------------------------------	-----2-----2-- ------2---	---------
----2-3--------------------------	-------------- --1--1--3-	---------
------------2-2------------------	-------------- -----2----	---------
-2321-4-44-----------113---------	-------------- -------23-	---------
------------1-323----23----------	----2--2------ --------23	---------
-21---4434---21-2---3--2---------	-----4-------2 --23------	---------
-----4343-332---32-3---331-1-----	21-------2---- ----1-----	---------
-1313-3-----133443344-5-----3-2--	----------1--2 --------4-	-2-------
---------------------------------	-----2-2--2222 22221-2---	---------
1--------------------------------	--2-2-12-231-- -121------	---------
-----2--3---3322-223---3----3--3-	323334-3---3-3 33333233-3	---------
----3-3333---332--23-------------	-------------- ----------	---------
-12-1-4-341114-222--33-2---------	-------------- ----------	-----1---
-24-22423-31232-333433-----------	-------------- ----------	-------1-
-1--4---2---2---23---1---1-------	-------------- ----------	---------
---1233-3--222332-2332222222--2--	----324-33---- -1-1-1-23-	2--------
-2-12-3--2--112-1-1--23---1-1----	----------2--- -----223-2	---------
------3-43-123333324-3-4---------	21--332212---- ---2-22--2	---------
-1---2313333221332-3334--3333122-	-23-3-22--2-22 2--2122232	-2122222-
----3---333--------------1--11---	4--5------2--2 2-22-12---	---------
33---23233-23-32--2-2-1-3-3-22---	322----------- ---------4	---------
--3--3---2122-1---2------2322-2--	212--3--13-13- 32-2------	11--11--2
-22--3------------------13223232-	243-3--1133322 -----32334	22-223222
-1-------4--13------32--3323-----	32-4433312---- -----1---3	--2-22-2-
--------------------3------------	-------3------ ----------	--33333--
-1-------------------------------	-2------------ ---------2	323332---
-1-----------------------1-11-2--	-------------- --------2-	32332----
-2----------------------2--------	31------------ ----------	32212----
-1----------------232-------2-2--	-------------- ------1---	21222---2
-23--2343-3-23-21224----2--------	-2-3-3-------- ---3-1----	222----2-
--3--4-34-2312-32--3223342311224-	23334443333--- 2----2--32	---------
-------1333232--32--2----332-----	-------------- ----------	---------
-----23-------32---------2-21222-	-------------- ----------	----1----
-1----44---34433444454-----22----	-------------- ----------	---------
--3-322-3-32-232223222----21-212-	3------------- ------2---	---------
--2-1---222---1-2--------212-1-2-	-1------------ ----------	---------



Group	1	2	3	4
Geog. pos.	Mozambique		Tanz, Kenya	Mad,Tanz,Moz
Average depth (m)	13	17	20	32
Thryssa vitrirostris	23233343343-34343-444	222--12--1----	----34----------	-111------------
Megalaspis cordyla	332-332-2-23-232223--	211--2----3---	2----2-------1--	------3---2-----
Thryssa setirostris	--122312-3222222-223-	112-----------	-------32------2	-121------------
Alepes djeddaba	----23-3-32-1--2---34	3222----3222--	-------------1--	-----21---------
Terapon jarbua	--1212--2-1-----13323	2222--223--3-1	----------------	----------------
Upeneus vittatus	121-------1--232124--	222343335-43--	----------------	---3----------1-
Parastromateus niger	422-2332-22--2-22--3-	2--3----------	----------------	----------------
Scomberoides tol	--2-232223222-2222-33	22222-22-2---1	----------------	-----1---------2
Penaeus monodon	3-1322-121-----------	1-------------	----------------	----------------
Metapeneus monoceros	2-22323333222-1223-22	11111---21--2-	----------------	----------------
Johnius dussumieri	33333334431---1213234	-1------------	----------------	----------------
Penaeus indicus	2222232333--122321-44	-1------------	----------------	----------------
Cynoglossus spp.	22322233332--2---3-3-	----21-2----11	----------------	--------------11
Caridean shrimp	13-3333443------1----	--------------	----------------	----------------
Pellona ditchela	33333444343-444443545	2212-44--1-2--	222323354434-333	-313---2---2----
Polynemus sextarius	3-322-221-2--22224324	2133--11------	3223222--323-2-2	-212-2-----2----
Pomadasys commersonni	32-13--3---------22--	--2----2------	322233--2-------	----------------
Trichiurus lepturus	34-33333342-33333-333	-22--------222	23244-3-4-2----1	23-33-----2-----
Arius spp.	33--33-33------2--3-4	------------2-	---2-22-322--2-2	-3----1--3------
Scomberomorus pluril.	-32-222-3-2----2-----	2-23---------3	-----3--33-3----	----------3---33
Dussumieria acuta	--2222--231-1--11--2-	3323-12----3--	-------2---2--2-	----2---32------
Pomadasys maculatus	332-------22122213-34	2224---4--2---	2--2---33332-2-2	---3--1----2----
Otolithes ruber	43233333332--1322-344	-122---------1	2223---32-2----3	-2-3------------
Secutor insidiator	-2----12-34-233334434	32133324-222-1	----33-334-43232	---33-134543-312
Terapon theraps	3------21-----2-----4	-1-----2----2-	322222--2213-2-2	---2--3----3----
Chirocentrus dorab	23-----------3--2--3-	--22----------	--22-3-3232-2223	-----3-2222-----
Leiognathus equulus	-2------------2---334	1-2-3--42-1---	-433-3-334-31123	---321344343----
Leiognathus daura	---------------------	--------------	----11-432121122	------2---------
Leiognathus spp.	---------------------	--------------	3----233332-1-2-	----------------
Sphyraena obtusata	----------2---22-3--5	12132--3-----1	1--233-22213-233	323333123-3-----
Drepane africana	322-----2-12--1--2---	-11---------1-	3222-2-323-2232-	---2--2---------
Gazza minuta	-21-2-32-22212-1-322-	12-2---3------	--2-33-445342333	24334-14444412--
Upeneus sulphureus	-----------2--2------	-1--11--------	222333-3--22-2-2	-33---2--34--4--
Nemipterus japonicus	---------------------	--------------	2--232-3---3----	--2-2-21--23----
Gerres filamentosus	-----------------2---	--2-3-22------	----22-2341232-2	2--222333-131122
Psettodes erumei	-------------------3-	------2------1	2---3-----------	------3323-2----
Rastrelliger kanag.	--1--2----2-2----2324	332222--3121--	-----------3---2	22-2-2---3------
Sardinella gibbosa	--22242-331---1-1--44	22-----2-----2	-----------4232-	---------43-1--1
Carangoides malabar.	--------------3--2-3-	222333234-3323	----------------	-----2--------2-
Lethrinus mahsena	---------------------	--------------	----------------	----------------
Nemipterus bipunctat.	------2--------------	--------------	1---------------	----------------
Pomacentrus spp.	---------------------	--------------	--1-------------	----------------
Decapterus russelli	--------------------2	------------22	----------------	--2-2-----------
Atule mate	-----2-------1-------	--------3-2--4	----------------	------2--------1
Leiognathus leuciscus	---------------------	--------------	----2-----------	------243323----
Saurida undosquamis	-2-------------------	222-2-22--23--	-----------3-2--	-2332--23332-211
Scomberomorus commer.	----------3-3-2-----3	2-----3--3--23	--------33------	32-33----23---22
Upeneus bensasi	----------2------33--	1123------1---	-------3-32-----	-----2----------
Gerres oyena	---------------------	--------------	-------3--------	----------------
Loliginidae	---1--2---2--21-2-22-	22--2222-22222	----3-23--12212-	-2---112-322221-
Abalistes stellaris	---------------------	--------------	---------3-2-2--	---------2------
Upeneus taeniopterus	-----------------2---	-------2--1--1	1---32--342312-2	2-3332-34--3----
Parupeneus spp.	---------------------	--------------	--------------2-	2---------------
Cheimerius nufar	---------------------	--------------	----------------	----------------
Priacanthus spp.	---------------------	--------------	----------------	2---------------
Parupeneus cinnabar.	---------------------	--------------	----------------	------------2---
Teixerichthys jordani	---------------------	--------------	----------------	----------------
Trachurus delagoae	---------------------	--------------	----------------	----------------
Sepiidae	-3-22-23-31---22---2-	-------2-----1	--------------2-	----------------
Siganus canaliculat.	---------------------	--------------	----------------	2---------------
Scolopsis bimaculat.	---------------------	--------------	1-----2---------	----------------
Labridae	---------------------	--------------	----------1---2-	----------------



5	6	7		8
Tanzania	Mozambique	South-west	Zanzibar, Mafia	Madagascar
37	24	28		51
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-----------------2---	---------	---	------------	----------------
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-------------33------	---------	---	------------	----------------
-----2---------------	---------	---	------------	-----2----------
-----2--3-----3-3-3--	---------	---	------------	----------------
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-----1--------33-3---	---------	---	------------	----------------
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-----3--3-------4----	---------	---	------------	----------------
-----1-------2-------	---------	---	------------	----------------
---------------2-----	---------	---	------------	----------------
-----3-----1---------	-1-------	---	------------	----------------
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14---2---------------	---------	---	-----1------	-------------2--
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122--422------334----	---------	---	------------	----1-----------
--------3-1--3-------	---------	---	------------	----------------
----2333233333333-2-3	------22-	3-2	2---1-------	----------------
-2---2-3-32333334----	---------	---	------------	----------------
------22222-----2-3--	---------	---	------------	----------------
----2---2--1--33----3	------2--	---	----------3-	-----1----------
----1---2-13---43----	---------	--2	------1---2-	----------------
-----------2-34333--3	-212-3---	---	1-----------	----------------
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---21-21-------------	---------	333	321212-22-31	----------------
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13--3---1-2333334-333	--1-22322	---	----2-----4-	----------------
------222--2-34433---	-232-----	---	------------	----------------
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23-2-13233--4433233-2	11-------	233	31-2223222--	-----1111-------
--33---3-223--2-23---	3-33-3333	---	2--2--------	----32----------
---2--22221233222-2--	-----122-	233	31-1-1333---	-------------2--
--22-----32-34-34----	---------	---	-2----2---1-	-------------2--
2-2323322---1-3--22-2	222-22221	2-2	12--22--1222	212-22-2-2--2--1
---2-2223-----3-2-333	---------	---	--2---1-2-3-	23--------------
243223--3---34544----	----3----	---	-22----3-33-	----12-1-1--2---
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---------------------	---------	---	------------	---3---333---2--
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---------------------	---------	---	------------	--11--13---2-23-
---------------------	---------	---	------------	--13--33-1334---
14-------------------	---------	---	------------	---2--------43--
2-------21--13---23--	----2----	2--	1----2--1---	33----21-232-2--
-----------2---------	---------	---	-1-2-22-----	---2---------3--
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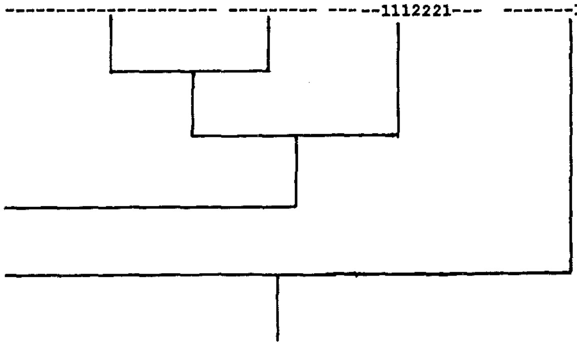

Appendix 2. Two-way station by species table for Kenya, Tanzania, Mozambique and Madagascar (May-June 1983) resulting from the program TWINSPAN. Values denote categories of abundance: 1: $w < 0.5$ kg; 2: $0.5 < w \leq 5$ kg; 3: $5 < w \leq 50$ kg; 4: $50 < w \leq 500$ kg; 5: $w > 500$ kg. The dendrogram showing the hierarchical relationship between the various groups, substitutes the binary notation produced by the program.