

Diversity and Stability of Demersal Species Assemblages in the Gulf of Guinea

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Summary

The structure of demersal fish assemblages on the continental shelf and upper continental slope of the Gulf of Guinea is described. Community structure is determined primarily by depth and type of sediment on the seabed. Changes in the composition of the identified species assemblages over a 25-year period are examined. The dynamics of the assemblages are influenced by physico-chemical parameters of the water masses, mainly temperature, salinity and dissolved oxygen, which are periodically modified by the seasonal coastal upwelling that occurs in the western Gulf of Guinea. Increased industrial trawling in coastal waters and environmental forcing conjointly influenced the changes in the composition and relative importance of species in the assemblages. Irresponsible fishing operations (like the use of explosives) that lead to habitat alteration and other anthropogenic activities like oil and gas exploration which have the potential to cause environmental changes pose a threat to biodiversity in continental shelf waters of the Gulf of Guinea.

Introduction

Knowledge of species aggregation and diversity is an important tenet of the ecosystem management concept and approach that are receiving favourable consideration in recent times in the management of living natural resources. In fisheries, defining the aggregation of species in the ecosystem is the basis for managing species by the management unit approach (Tyler *et al.* 1982).

The structure of species assemblages has been established for several exploited fish populations around the world. In the Gulf of Guinea, Fager and Longhurst (1968) and Longhurst (1969) worked out the assemblage structure of demersal species on the continental shelf using data from the Guinean Trawling Survey of 1963-64 (Williams 1968). Villegas and Garcia (1983) mapped demersal fish communities on the continental shelf of selected countries in the sub-region using data and information from a number of trawl surveys. Assemblage is defined here as “an association of coexisting species with similar environmental tolerance, possibly trophic relationships, but not totally interdependent” (Bianchi 1992).

In the last three decades, significant changes have occurred in the biological and physical components of the Gulf of Guinea marine ecosystem and in nearshore forcing factors that could have affected species associations and status of marine biodiversity in the sub-region (Koranteng 1998). Koranteng (1998) showed that the period between 1963 and 1992 could be broken down into three climatic periods each of which had distinct environmental characteristics in the Gulf of Guinea. In the first period (i.e. 1963 - 1972) sea temperatures (surface and bottom) were relatively high, salinity was low and the thermocline was below its long-term average depth. Between 1972 and 1982 (the second climatic period), there was a global decline in sea temperatures and a rise in salinity. In the final period (1982-1992), temperatures were high and salinity was low and erratic.

The seasonal coastal upwelling of cold, nutrient rich, subthermocline water drives the biology of the continental shelf waters of the Gulf of Guinea, especially off Ghana and Côte d'Ivoire. The duration and intensity of the major upwelling (July-September) and minor upwelling (December-February) that occur annually in the sub-region have changed (Pezennec 1995, Koranteng and Pezennec 1998).

The building of dams on almost all major rivers in the sub-region for hydroelectric and irrigation purposes and the sub-Saharan drought in the 1970s and 1980s have resulted in reduced river discharge and sediment transport into the Gulf of Guinea (Lamb 1982, Mahé 1998).

Furthermore, siltation and draining of many coastal lagoons in the sub-region as a result of urbanisation and depletion of the mangrove cover around these lagoons have undermined their (the lagoons) contribution to the continental shelf ecosystem (Entsua-Mensah 1998). Increased industrial fishing, especially in coastal waters, the use of fishing nets with small-sized meshes and other inappropriate fishing methods like dynamite and other explosives, have led to decline in catch rates of many commercially exploited fish species and virtual extinction of others (Koranteng 1998). According to Longhurst and Pauly (1987) these are some of the principal factors that cause ecological changes in tropical fish communities. Throughout the sub-region, oil and gas exploration and prospecting have been intensified in the last five decades or so. Large-scale drilling for oil is being undertaken on the continental shelf and in the delta areas and occasionally, oil spills occur in the area from these activities (Saenger *et al.* 1998; Shell 1998).

The most important recorded changes in fish population in the Gulf of Guinea are the decline and subsequent recovery of the round sardinella (*Sardinella aurita*) populations (Pezennec 1995), the proliferation and subsequent decline of triggerfish (*Balistes capriscus*) (Koranteng 1984, Caverivière 1991) and increase in abundance of cuttlefish (*Sepia officinalis*) and globefish (*Lagocephalus laevigatus*) (Martos *et al.* 1990, Koranteng 1998). The proliferation of triggerfish in the Gulf of Guinea in the 1970s and its total domination of the ecosystem were described by Bakun (1995) as “one of the most phenomenal episodes in the history of fish population dynamics”.

Studies of fish communities have shown that some of these natural and anthropogenic factors could induce changes in the structure of species assemblages, threaten the fish biodiversity and affect the general well-being of fishery resources (Brown *et al.* 1976, Overholtz *et al.* 1985, Greenstreet and Hall 1996).

The primary objective of this study is to examine the structure of demersal species assemblages on the continental shelf and upper continental slope of the Gulf of Guinea and to examine the changes that have occurred in these assemblages in the last three decades. The study also seeks to

isolate the factors that determine fish community structure in the study area and to assess the effects of environmental parameters and anthropogenic activities on the structure and dynamics of the assemblages.

Materials and Methods

Between 1956 and 1992, a number of bottom trawl surveys of the demersal fishery resources on the continental shelf and upper slope off Ghana were conducted (Koranteng 1998). The Guinean Trawling Survey (GTS) organised by the Scientific, Technical and Research Commission of the Organisation of African Unity (OAU/STRC) in 1963-64 (Williams 1968) was the first survey that covered the entire continental shelf of Ghana. From 1969 the Marine Fisheries Research Division (MFRD) of Ghana also conducted a number of bottom trawl surveys in Ghana's marine waters. The data from these surveys, made up of fish catches and measurements of some oceanographic parameters, were used in this study.

Each survey involved cruises in the upwelling and non-upwelling (or thermocline) seasons. The sampling procedures were almost identical in all the surveys. The catch from each haul was sorted according to species. Each species was weighed and the total number of individuals determined by total count or estimation from sub-samples. During the trawl surveys, water temperature was measured using thermometers mounted on Nansen reversing bottles. Salinity was measured using a salinometer and dissolved oxygen by the Winkler titration method.

All catch data were inputted into the NAN-SIS computer program for trawl survey data logging and analysis (Stromme 1992). The GTS catch data were subjected to multivariate statistical analyses to determine the groupings in each data set. A Two-Way Indicator Analysis method implemented by the TWINSPAN computer program (Hill 1979) was used. TWINSPAN uses a divisive cluster analysis algorithm to classify the samples and correspondence analysis (CA) to perform an ordination which is a multivariate statistical method of arranging samples and species in a two-dimensional graph in which similar samples or species are near each other and dissimilar entities are far apart. CA assumes that the response of species to environmental changes follows a unimodal Gaussian curve rather than the linear relationship assumed in other multivariate methods (Digby and Kempton 1987, ter Braak 1991, Jongman *et al.* 1995). Pelagic species occurring in the trawls were included in the analysis as suggested by Longhurst and Pauly (1987) because several fish species classified as pelagic are also common in demersal trawls.

The community ecology program CANOCO (ter Braak 1991) was used to assess the factors that influence the ordination. The hydrographic parameters used in the analysis are water temperature, salinity, and dissolved oxygen measured at depths trawled. Other environmental parameters are the depth sampled and type of bottom sediment at the stations trawled. Bottom type information was obtained from sediment maps produced during GTS and also from Martos *et al.* (1990). Bottom type was classified as follows: Hard (predominantly sand, shell, rock, gravel, grit or coral), Soft (predominantly mud) and Mixed (combination of hard and soft). The three bottom types were treated as three levels of a nominal variable (bottom type). The values of a nominal variable only represent the names of the levels and do not imply any order or magnitude of differences between them.

CANOCO performs a Detrended Correspondence Analysis (DCA) which is an improvement on CA and addresses its defects (Gauch 1994). The influence of each environmental parameter on the ordination, hence assemblage structure was assessed through the significance of the correlation between the environmental parameter and the ordination axes. The DCA scores were plotted using the CANODRAW computer program (Smilauer 1992).

To determine the most important species in each assemblage, the index of relative importance (IRI), modified from Pinkas *et al.* (1971) was used. The index is expressed as:

$$IRI = \%W \times \%F$$

where %W is the percentage composition by weight of each species in the assemblage and %F is the percentage frequency of occurrence of the species in hauls from the assemblage. Species with IRI values of 50 or more in each assemblage were considered as the most important species in the assemblage.

Published materials on species assemblages in other parts of the Gulf of Guinea arising from surveys conducted in the sub-region, were examined with a view to comparing the assemblage structures derived from these surveys and the results of this work. The surveys included those conducted off Côte d'Ivoire (Joanny and Menard 1998), Togo and Benin (Crosnier and Berrit 1966), Nigeria (Longhurst 1964) and the Guinean Trawling Survey (GTS) conducted in the entire waters of the Gulf of Guinea (Williams 1968).

The data sets from the GTS (1963-64) and MFRD surveys of 1981-82 (MFRD3) and 1989 (MFRD5) were used in the investigation on possible changes in demersal species assemblages on the continental shelf (depths down to 200 m) and upper continental slope (200 to about 600 m). The GTS was conducted during the first climatic period described above, MFRD3 and MFRD5 were conducted during the second and third climatic periods respectively. The two MFRD surveys were similar in terms of spatial and temporal coverage and in survey methods. The GTS was the only survey of similar spatial coverage conducted in Ghanaian waters during the first climatic period. To obtain data comparable with those of the MFRD surveys, a subset of the GTS data from depths shallower than 100 m were re-analysed.

The first three assemblages on the continental shelf were used to examine fish community dynamics and stability and species diversity in the assemblages. The investigations centred on the nature and pattern of change and the possible factors and causes. For each survey and assemblage, a list of species with IRI>50 was produced for the upwelling and thermocline seasons to determine the species representation at these periods.

The nature and extent of changes at the community level were examined by delineating three depth ranges and following community succession within each depth range over time. The depth ranges are: 10-30, 31-50 and 51-100m. For this analysis, data from trawl surveys conducted in Ghanaian waters in 1963/64, 1969/70, 1973-77 and 1979-90 were used.

In each depth range and climatic period, the following indices were calculated:

$$\text{Shannon Diversity Index, } H'' = - \sum_{i=1}^s \left(\frac{w_i}{w} \right) \ln \left(\frac{w_i}{w} \right),$$

$$\text{Margalef's Richness Index, } R = \frac{s-1}{\ln(w)}, \text{ and}$$

$$\text{Pielou's Evenness Index } J' = \frac{H''}{\ln(s)}$$

where w_i is the sample weight of the i^{th} species, w is total weight and s is the number of species in a sample. Weights of the species were used in the calculations instead of numbers following the suggestion of Wilhm (1968).

The reaction of important species groups to the observed environmental changes was examined. The average density (kg/ha) of each species group in each depth range and climatic period was calculated.

Results

Six species groups (or assemblages) were obtained from the GTS datasets. These groups, corresponding to those named by Longhurst (1969) are:

Group 1: Sciaenid community

Group 4: Sparid community (deep part)

Group 2: Lutjanid community

Group 5: Deep shelf community

Group 3: Sparid community (shallow part)

Group 6: Upper slope community.

Eurybathic or thermocline species (Longhurst 1969) were not isolated in this work as they are generally part of the second assemblage. Also, the estuarine sciaenid community described by Longhurst (1969) was not adequately sampled in the GTS survey.

Figure 1 shows a CANODRAW bi-plot of sites and environmental parameters in the DCA axis 1 / axis 2 plane. Hauls from the same group (assemblage) are indicated by the same symbol and enclosed in an ellipse.

Table 1 gives Pearson's product-moment correlation coefficient r , of species ordination axes 1 and 2 with bottom environmental variables. The significantly high correlation between depth, temperature, salinity and dissolved oxygen and the first two DCA axes show the importance of these parameters in the determination of the structure of the demersal species assemblages in the study area. These physico-chemical parameters are themselves closely related to depth in the oceans and usually change by seasons (Riley and Chester 1971, Mann and Lazier 1996).

The number of fish species caught during each cruise of the three surveys and classified according to assemblage, is given in Table 2. The number varied between 47 in the first assemblage obtained from the data of the May 1982 cruise and 150 for the second assemblage of the September cruise of the GTS (1963). As an example of differences that occur in species abundance during the two seasons, the with IRI values greater than 50 in the sciaenid assemblage derived from the data in the three surveys (GTS - 1963/64, MFRD3 - 1981/82 and MFRD5 - 1989) are presented in Table 3. The table shows species that are present mainly during the upwelling season, those in the thermocline season and those that are available all the time in the assemblage (referred to as resident species).

The calculated Shannon Diversity Index (H'), Margalef's Richness Index (R) and Pielou's Evenness Index (J') for the three depth ranges and different climatic periods are presented in Table 4. The table shows a decline in species diversity between the first and second climatic periods in the 10-30 and 31-50 m depth ranges and a slight increase in the 51-100 m depth range. Species diversity increased in all three depth ranges in 1982-92. Species richness and evenness also showed some variation as indicated in Table 4.

The pie charts in Figure 2 show percentage composition by weight of three important groups of species (lutjanids, sciaenids, sparids) and triggerfish in the total weight of the four groups only. The other species caught in the survey were ignored in these comparisons. There is one pie chart for each climatic period and depth range.

Discussion

Structure of demersal fish communities in the Gulf of Guinea

The continental shelf of the Gulf of Guinea has distinct biotopes comprising mud, hard rocks and mixed deposits (Longhurst 1964, Crosnier and Berrit 1966, Williams 1968, Martos *et al.* 1990). Off Ghana the shelf is characterised by a belt of soft, muddy substrate in shallow waters down to about 30 m depth, followed by a wide area of mixed to hard bottom type.

The demersal fauna is quite similar in the entire Gulf of Guinea (Williams 1968, Longhurst 1969), however, the occurrence of isolated patches of rocky bottoms, estuaries and lagoons result in some differences in the distribution and abundance of demersal fish species. Similar species assemblages occur over similar biotopes and water depths throughout the region (Longhurst 1964, Crosnier and Berrit 1966, Longhurst 1969, Williams 1968, Villegas and Garcia 1983, Longhurst and Pauly 1987, Koranteng 1998, Joanny and Menard 1998). Longhurst (1969) noted the remarkable degree of agreement between the various authors of earlier works with regard to the organisation of the assemblages.

The six principal species assemblages were named by Longhurst (1969) as sciaenid, lutjanid, sparid (shallow component), sparid (deep component), deep shelf and upper slope assemblages. The species assemblages occurring throughout the Gulf of Guinea are described below.

- i. The sciaenid assemblage occurs in shallow-waters (15 - 50 m) on soft, sandy and muddy bottoms and close to estuaries. Very extensive sciaenid assemblages occur off Côte d'Ivoire, eastern part of Ghana, Nigeria and Togo-Benin. The characteristic members include *Brachydeuterus auritus*, *Galeoides* spp., *Pseudolithus* spp., *Arius* spp., *Selene dorsalis* and *Ilisha africana*.
- ii. The lutjanid assemblage is usually found next to the sciaenid assemblage on mixed to hard bottoms. It could also occur close to shore, as is the case off Togo-Benin, or alternate with the sciaenid assemblage as the first assemblage encountered from shore (e.g. off Nigeria-Cameroon). The lutjanid assemblage is very prominent off Liberia. Some of the important members of the assemblage are *Lethrinus atlanticus*, *Lutjanus* spp., *Acanthurus monroviae*, *Balistes forcipatus*, *Pagellus bellottii*, *Brachydeuterus auritus* and *Trachurus* sp.

- iii. The sparid assemblage comprises shallow and deep parts. The former is found within 15 and 70 m water depth on soft/mixed bottoms and extends into very shallow waters during some parts of the year. *Penaeus notialis*, *Brachydeuterus auritus*, *Balistes capriscus*, *Trachurus* sp., *Raja miraletus* and *Pagellus bellottii* are some of the indicator species of the shallow part. The deep part prefers mixed to hard bottoms and may be found in water depths down to 200 m. *Dentex* spp., *Boops boops*, *Squatina oculata*, *Trachurus* sp., *Scomber japonicus*, *Pagellus bellottii*, *Pseudupeneus prayensis*, *Epinephelus* spp. and *Lagocephalus laevigatus* represent this assemblage.
- iv. The deep continental shelf assemblage is found at water depths of 200 m or more on mixed/soft bottoms and have *Paracubiceps ledanoisi*, *Trachurus* sp., *Loligo* sp. as some of its important members.
- v. The upper continental slope assemblage usually found on mixed/soft bottoms at depths of 400 m or more has *Peristedion cataphractum*, *Antigonia capros*, *Chlorophthalmus* spp., *Epigonus* spp., *Trigla* spp., *Centrophorus uyato* as the representative species.

Variability and trends in fish community structure in the Gulf of Guinea

There were some differences in the composition of the assemblages between surveys and seasons. Certain species occurred repeatedly in some assemblages over the 25-year period examined in this work. These included *Brachydeuterus auritus*, *Galeoides decadactylus* and *Sparus caeruleostictus* in the sciaenid assemblage, *Dentex canariensis*, *Pagellus bellottii*, *Priacanthus arenatus*, *Pseudupeneus prayensis* and *Sparus caeruleostictus* in the lutjanid assemblage, and *Epinephelus aeneus* and *P. bellottii* in the sparid assemblage.

The pie charts in Figure 2 display clearly, significant shifts in relative importance of the various groups between the climatic periods and depth ranges. At 10 -30 m, Sparidae accounted for 69 % of the total density recorded for the three families (Sparidae, Sciaenidae and Lutjanidae) and *Balistes capriscus* in 1963-71. This was followed by Lutjanidae (26 %), Sciaenidae (3 %) and *B. capriscus* (2 %). Between 1972 and 1982 when the population of *B. capriscus* increased in the Gulf of

Guinea, the contribution of Sparidae in the 10 -30 m depth range reduced substantially to 16 %; Lutjanidae accounted for 7 %, Sciaenidae 1 % and *B. capriscus*, 76 %. In 1982 - 1990, the *Balistes capriscus* stock declined and accounted for only 4 % of the total catch of the species and the other three groups. The percentage composition of Sparidae increased to 52 %, Lutjanidae to 40 %, and Sciaenidae to 2 %.

In the 31 - 50 m depth range, the percentage composition of all three families reduced from the first climatic period to the second (81 to 20 % for Sparidae; 11 to 4 % for Lutjanidae and 2 to 1 % for Sciaenidae). On the other hand *B. capriscus* increased in percentage composition from 6 to 75 %. In 1982 - 1990, the situation changed to become similar to that in 1963-71, with the percentage contribution of *B. capriscus* substantially reduced and that of the other families increased.

In the 51-100 m depth range, the effect of *B. capriscus* was least shown. The percentage contribution of the species increased from 0 % in 1963-71 to 15 % in 1972-82. The contributions of the three families changed only slightly to accommodate this modest rise and subsequent decline of *Balistes capriscus*. In the third climatic period, the contribution of the species reduced to 3 %.

Accounting for 52-89 % of catches of the four groups, Sparidae were the most important fishes at all depths for the three study periods, except between 1972 and 1982 where *Balistes capriscus* was dominant in the 10-30 m and 31-50 m depth ranges.

Possible factors affecting fish community structure in the Gulf of Guinea

The significantly high correlation between depth, bottom temperature, bottom salinity and bottom dissolved oxygen and the first ordination axis and between sediment type and the second ordination axis, show the importance of these parameters in the determination of the structure and dynamics of the demersal species assemblages in the study area. It has been observed that changes could occur in the structure and composition of species assemblages as a result of differential reaction of species to seasonal environmental changes (Villegas and Garcia 1983, Overholtz and Tyler 1985). Thus the upwelling, which appears to change the properties of water masses could affect the structure and dynamics of demersal species assemblages and species diversity. Similarly, pollution which could arise from large-scale oil spillage, or chemical effluents from land-based sources, could have similar

effect. Reduced river input into coastal waters due to the building of dams affect salinity regimes in coastal waters and could also affect the stability of the sciaenid assemblage.

Koranteng (1998) showed that during the first (1963-71) and third (1983-90) climatic periods the species assemblages were relatively easy to identify using ordination techniques, but in the second period (1972 - 1982), the assemblages were difficult to separate (especially the lutjanid and sparid assemblages). The author noted that the apparent disorganisation of the assemblages during the second climatic period could be attributed mainly to the sudden increase in abundance of *Balistes capriscus*. During that period, the continental shelf waters were relatively cold and more saline; an environment preferred by the sparid community to which *B. capriscus* belongs (Gulland and Garcia 1984). It is possible also that irresponsible fishing methods like the use of dynamite could also alter fish assemblage structure as it destroys habitats of the fish. For example, lutjanid species the abundance of which appears to have declined in the study area, have been associated with corals (Longhurst 1969) and is possible that these corals have been destroyed by dynamite or large industrial trawlers over the years.

It is important to note, however, that whereas environmental forcing could lead to temporal disruption of assemblages, habitat destruction could result in permanent change. However, it is often difficult, if not impossible, to separate fluctuations due to natural factors from those caused by anthropogenic factors.

Diversity of continental shelf species assemblages in the Gulf of Guinea

An analysis of variance showed that H'' was significant ($p < 0.02$) between the climatic periods (Koranteng 1998). Species richness and evenness also changed within the study period (Table 4). In 1963-71, the Margelef's Richness Index (R) was relatively higher in 10-30 and 31-50 m, but these reduced significantly between 1972 and 1982. R increased again in both depth ranges between 1982 and 1990. The direction of change of R in the 51-100 m depth range was opposite that in the shallow areas, increasing between the first and second climatic periods but decreasing slightly after

1982. Pielou's Evenness Index J' also decreased between 1963-71 and 1972-82 but increased in 1983-90.

Because of differential reaction of individual species to environmental and ecosystem changes and to exploitation, species diversity is likely to change as a result of changes in the environment and/or exploitation. The recorded changes in the fish diversity index could be due to changes in the marine ecosystem relating to the environment, decline of the sardinella resources and proliferation of triggerfish. In the 10-30 and 31-50 m depth ranges, the diversity index was lowest during 1972-82. In the 51-100 m depth range the diversity increased throughout the period under investigation. The increase of H'' in this depth range, especially in 1972-82, may have been due to migration of species predominantly from 31-50 m depth which had quite similar sediment type. This is confirmed by the corresponding increase in species richness (R) at these depths during 1972-82. This situation further explains why assemblage discrimination was difficult during the 1972-82 period. The drastic reduction of evenness in 1972-82 at depths where triggerfish initially occupied is a further evidence of the effect of the proliferation of the species on the ecosystem.

It has been argued that diversity indices can be used to indicate the general 'health' of an ecosystem (Magurran 1991); thus the decline in H'' in the 1970s can be seen as an indication that the shelf ecosystem in the Gulf of Guinea was stressed at that time. The stress may be due to the declining temperature, increased salinity, changes in other near-shore forcing factors, increased exploitation, the 'invasion' of triggerfish, decrease of the *Sardinella aurita* stock in the western Gulf of Guinea or the combined effects of these. The invasion by triggerfish is perhaps a more likely cause considering the aggressive behaviour of the species. The magnitude of change in biomass recorded in the Gulf of Guinea, especially involving a comparatively hardy species like triggerfish, could induce structural changes in species assemblages.

Persistence in fish species assemblages

Long-term changes in fish assemblages have been attributed to a number of factors including over-exploitation of some species within the assemblage (Brown *et al.* 1976, Overholtz and Tyler 1985) and climatic variations (Sutcliffe and Muir 1977). Dominance or decline of some species in the

assemblage may result from exploitation or differential response to changes in environmental forcing factors (Gulland and Garcia 1984, Macpherson and Gordo 1992). Similarly, spatial changes in the assemblage can occur with the whole assemblage performing inshore-offshore temporal migrations in response to environmental forcing and pollution (e.g. Macdonald *et al.* 1984, Gomes *et al.* 1995).

The literature is rather inconsistent with respect to the persistence of fish species assemblages through time. One school of thought holds the view that marine fish communities are in constant motion and hold no memory that will enable them to return to a previous state (Tyler *et al.* 1982, Beddington 1984). On the other side of the argument, Longhurst and Pauly (1987) are of the view that "...one can assume that given sensitive management, or the relaxing of fishing pressure for some reason, tropical fish communities would tend to revert to the natural state...". McGlade (1989) also believes that "...natural systems do recover from large environmental perturbations". Greenstreet and Hall (1996) noted that differences in fish species assemblages over time are subtle and most apparent in the dominance structure. This was further underlined in an analysis of the effects of the industrial fisheries on the North Sea ecosystem (Robertson *et al.* 1996).

The results of this study appear to confirm the theory that the proliferation of *B. capriscus* seriously disrupted the assemblage structure and behaviour of demersal fish species on the continental shelf of the Gulf of Guinea. Towards the end of the observation period when the species had almost disappeared from this ecosystem, the assemblages appeared similar to those before the dominance of *B. capriscus*. However, it is uncertain whether the system was returning or had already returned to its original or 'natural' state.

Conclusion

The structure of species assemblages on the continental shelf in the Gulf of Guinea is determined primarily by depth and sediment type and the dynamics are influenced by physico-chemical parameters of the water masses. Structural changes in the assemblages and in species diversity in the area were probably due mainly to the sudden increase in abundance of *Balistes capriscus* and also environmental forcing. The relative importance of sciaenids, lutjanids and sparids on the continental shelf, as well as species richness, evenness and diversity changed in response to these alterations in the ecosystem. It appears that activities that lead to habitat alteration could bring about permanent changes in fish species assemblages, whereas temporal environmental changes could lead to short-term changes in the structure and dynamics of the assemblages.

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Table 1:

Pearson's product-moment correlation coefficient r , of species ordination axes 1 and 2 with bottom environmental variables.

Survey	Variable	Species Axis 1	Species Axis 2	Survey	Variable	Species Axis 1	Species Axis 2
GTS 1963/64 (all hauls)	Hard	-0.13	-0.29**	1981/82	Hard	-0.49***	0.09
	Mixed	0.13	-0.14		Mixed	0.30**	0.01
	Soft	-0.02	0.43**		Soft	0.30**	0.13
	Depth	0.95**	0.01		Depth	-0.29**	0.79***
	Temperature	-0.81**	0.10		Temperature	0.23*	-0.65***
	Salinity	-0.64**	-0.01		Salinity	-0.02	0.28
	Oxygen	-0.34**	0.11		Oxygen	0.13	-0.54***
	Eigenvalues	0.68	0.50		Eigenvalues	0.40	0.34
GTS 1963/64 (hauls at ≤ 100 m)	Hard	-0.31**	-0.02	1989	Hard	-0.29**	-0.30**
	Mixed	-0.11	-0.29*		Mixed	0.16	0.12
	Soft	0.44**	0.37**		Soft	0.20*	0.26**
	Depth	-0.51***	-0.71***		Depth	-0.42***	0.60***
	Temperature	0.47***	-0.47***		Temperature	0.18	-0.54***
	Salinity	0.18*	-0.07		Salinity	0.08	-0.07
	Oxygen	0.21*	-0.19		Oxygen	-0.02	-0.47***
	Eigenvalues	0.54	0.40		Eigenvalues	0.46	0.36

r significant at * 5% level, ** at 1% level, *** at 0.1 % level.

Table 2:

Number of species and species groups recorded during surveys in thermocline and upwelling seasons. Species are not limited exclusively to one assemblage or the other.

Survey	Season	Number of species in assemblage		
		Sciaenid	Lutjanid	Sparid
1963/64	Upwelling	110	150	93
	Thermocline	143	110	83
1981/82	Upwelling	81	51	48
	Thermocline	47	65	77
1989	Upwelling	69	80	63
	Thermocline	55	74	51

Table 3:
The Sciaenid assemblage in the Gulf of Guinea at different periods.

1963/64	1981/82	1989
<p>Upwelling season species</p> <p><i>Drepane africana</i> <i>Epenephelus aeneus</i> <i>Ilisha africana</i> <i>Loligo</i> sp. <i>Pomadasys jubelini</i> <i>Pseudolithus brachygnathus</i> <i>Pseudolithus typus</i> <i>Sparus caeruleostictus</i></p>	<p>Upwelling season species</p> <p><i>Decapterus rhonchus</i> <i>Pagellus bellottii</i> <i>Pomadasys incisus</i> <i>Priacanthus arenatus</i> <i>Pseudupeneus prayensis</i> <i>Sepia</i> sp.</p>	<p>Upwelling season species</p> <p><i>Lagocephalus laevigatus</i> <i>Pagellus bellottii</i> <i>Pentheroscion mbizi</i> <i>Pomadasys incisus</i> <i>Priacanthus arenatus</i> <i>Pteroscion peli</i> <i>Rhizoprionodon acutus</i> <i>Trachinocephalus myops</i> <i>Trachurus trecae</i></p>
<p>Resident species</p> <p><i>Brachydeuterus auritus</i> <i>Galeoides decadactilus</i> <i>Pagellus bellottii</i> <i>Raja miraletus</i> <i>Trichiurus lepturus</i> <i>Pseudolithus senegalensis</i> <i>Pteroscion peli</i></p>	<p>Resident species</p> <p><i>Balistes capriscus</i> <i>Brachydeuterus auritus</i> <i>Chloroscombrus chrysurus</i> <i>Dentex canariensis</i> <i>Epenephelus aeneus</i> <i>Galeoides decadactylus</i> <i>Selene dorsalis</i> <i>Sparus caeruleostictus</i></p>	<p>Resident species</p> <p><i>Brachydeuterus auritus</i> <i>Galeoides decadactilus</i> <i>Penaeus notialis</i> <i>Pomadasys jubelini</i> <i>Pseudupeneus prayensis</i> <i>Sepia officinalis</i> <i>Selene dorsalis</i> <i>Sparus caeruleostictus</i> <i>Trichiurus lepturus</i></p>
<p>Thermocline season species</p> <p><i>Sphyraena</i> sp.</p>	<p>Thermocline season species</p> <p><i>Elops senegalensis</i> <i>Engraulis encrasicolus</i> <i>Ilisha africana</i> <i>Pseudolithus senegalensis</i> <i>Pseudolithus</i> sp. <i>Pteroscion peli</i> <i>Scyacium micrurum</i> <i>Sphyraena sphyraena</i></p>	<p>Thermocline season species</p> <p><i>Chilomycterus spinosus</i> <i>Chloroscombrus chrysurus</i> <i>Dasyatis</i> sp. <i>Dentex canariensis</i> <i>Drepane africana</i> <i>Elops senegalensis</i> <i>Epenephelus aeneus</i> <i>Eucinostomus melanopterus</i> <i>Grammoplites gruvelli</i> <i>Lutjanus fulgens</i> <i>Sardinella maderensis</i> <i>Sphyraena sphyraena</i> <i>Torpedo</i> sp.</p>

Table 4:

Calculated values of Shannon Diversity Index, Margalef's Richness Index and Pielou's Evenness Index at different depths and climatic periods

Period	Shannon Diversity Index				Margalef's Richness Index				Pielou's Evenness Index			
	10-30	51-50	51-100	Mean	10-30	51-50	51-100	Mean	10-30	51-50	51-100	Mean
1963-71	2.69	3.04	2.59	2.77	12.23	12.47	6.97	10.56	0.64	0.66	0.64	0.65
1972-82	2.16	2.03	2.63	2.27	8.14	8.77	8.47	8.46	0.54	0.47	0.62	0.54
1983-90	2.80	3.21	2.92	2.98	8.75	9.90	7.89	8.85	0.68	0.74	0.70	0.71

List of captions for the figures

Figure 1: Plot of DCA axis 1 versus axis 2 for the Guinean Trawl Survey data. Co-ordinates of environmental parameters in the ordination plane are also shown (with original scale reduced by 1/5).

Figure 2: Percentage composition of sciaenids, lutjanids, sparids and *B. capriscus* at three depth ranges and time periods.