Study of the structure and dynamics of demersal fish assemblages on the continental shelf and upper slope off Ghana, West Africa

By

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Abstract

Using two-way indicator species analysis and detrended correspondence analysis, species on the continental shelf and upper slope of Ghana were classified into six assemblages. The structure of the assemblages is determined primarily by depth and type of sediment on the seabed. There are clear faunal discontinuities around 30-40 m, 100 m and 200 m depth. The dynamics of the assemblages are influenced by physicochemical parameters of the water masses, mainly temperature, salinity and dissolved oxygen which are periodically modified by the seasonal coastal upwelling that occurs in the area. The observed changes in the composition and relative importance of species in the assemblages can be related to increased fishing activity and environmental forcing.

Keywords: Species assemblages, structure and dynamics, continental shelf and slope, Ghana

Introduction

The structure of species assemblages for several exploited fish stocks around the world has been established. Examples are in the Narragansett Bay, USA (Oviatt and Nixon 1973), Scotian shelf, Canada's Atlantic coast (Mahon 1985), southern Gulf of Mexico (Yáñez-Arancibia *et al.* 1985), Gulf of Carpentaria, Australia (Blaber *et al.* 1994) and Congo, Gabon and Angola in south-west Africa (Bianchi 1992), North-western Indian Ocean and East Africa (Bianchi 1992). 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

(Williams 1968). Caddy and Sharp (1986) pointed out that such studies are necessary to gain a better understanding of multispecies stocks and management of these stocks.

The objectives of this paper are (i) to establish assemblage units of demersal fish species on the continental shelf and upper slope off Ghana, (ii) to establish the factors that determine the structure of these assemblages, and (iii) to assess the impact of environmental forcing and fishing on the structure and dynamics of the assemblages.

Study Area

The study area is the continental shelf and upper slope off Ghana in West Africa (Figure 1). The coastline of Ghana, measuring about 536 km long, stretches from longitude 3° 06′ W to 1° 10′ E and lies between latitudes 4° 30′ and 6° 6′ N. The continental shelf varies in width between about 13 and 80 km (Williams 1968; Koranteng 1998) with the widest point in the middle. The shelf usually drops sharply just after the 75 m depth contour. The area of the continental shelf (to the 200 m depth contour) is 23,700 km² (Koranteng 1984)

The ocean floor on the continental shelf off Ghana has distinct areas of mud, hard rocks and mixed deposits. The is a belt of soft, muddy substrate in shallow waters down to about 30 m deep, followed by a wide area of mixed to hard bottom type (Williams 1968). Generally, the area beyond 75 m deep is not safe for trawling, except towards the western side (Rijavec 1980; Koranteng 1984) where vessels can trawl in waters deeper than 100 m.

Ghana lies in the tropical equatorial belt and experiences high temperatures of between 25 and 35 °C with minimum variation throughout the year and for this reason, the difference in climatic conditions is due mainly to the amount and distribution of rainfall (Biney 1990). During the rainy seasons, the quantity of freshwater reaching the sea through rivers increases considerably thereby lowering the salinity of the surface waters (Binet and Marchal 1993). Several rivers enter the sea along the coast of Ghana either through coastal lagoons or extensive estuaries.

Situated in the western Gulf of Guinea subsystem of the Guinea Current Large Marine Ecosystem (Sherman 1993; Binet and Marchal 1993), the continental shelf waters off Ghana experience two seasonal coastal upwelling (major and minor) each year with differing duration and intensities. During the upwelling, sea surface

temperature (SST) drops, surface salinity increases, and dissolved oxygen is lowered (Mensah and Koranteng 1988). The major upwelling (long cold season) occurs between July and September when SST (usually about 27-29 °C) fall below 25 °C. The minor upwelling (short cold season) normally lasts for only about three weeks (occurring anytime between December and March). In between the cold seasons are warm seasons during which SST is relatively high and a strong thermocline is formed in continental shelf waters.

Materials and Methods

The trawl surveys

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 1988). 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 sets from the GTS (1963-64) and MFRD surveys of 1981-82 (MFRD3) and 1989 (MFRD5) are used in this study. GTS was in two phases; GUINEAN I and GUINEAN II. Off Ghana, GUINEAN I was in September 1963 and GUINEAN II was in March 1964. Two identical vessels each measuring 35 m long and having a gross registered tonnage of 200 were used. A trawling speed of 6.5 km.h⁻¹ was maintained and the survey net had a wing spread (distance between the tips of the net during trawling) of 16.4 m and codend mesh size of 40 mm.

Trawl hauls were taken according to a systematic sampling design that covered 7 transects (each laid perpendicular to the coastline) and placed about 64 km apart. There were 8 sampling stations on each transect located at 15-20, 30, 40, 50, 70-75, 100, 200 and 400-600 m depth.

On reaching the sampling station the net was shot at the pre-determined depth and a trawling time of one hour was maintained. After hauling in the net, the catch was sorted according to species. In some cases the specimen could only be identified to genus level. The total weight and number of each species in the catch were obtained by direct weighing and counting or estimated from sub-samples when the catch was large.

In the MFRD surveys, a stratified semi-random sampling design was used. In this design, the shelf was divided into 3 zones, 9 strata and 10 sectors resulting in 40 trawl stations (Koranteng 1984). The depth range was between 10 and 75 m. The survey area forms about 78 % of the total shelf area of Ghana (Williams 1968). A few hauls were taken in the 75 - 100 m depth zone. The sampling procedures were as used in the GTS survey except that within the confines of a station, the depth and trawling direction were chosen at random. The duration of tow was thirty minutes. The catch was sorted and identified according to keys provided by Blache *et al.* (1970) and Fischer *et al.* (1981). The weight and number of each species were determined as described above for the GTS survey.

For each MFRD survey, there was sampling in the upwelling season as well as the non-upwelling (or thermocline) season. The survey vessel was 29 m long with a trawling speed of 5.6 km.h⁻¹ and the survey net also had a codend mesh of 40 mm and a wing spread of 16.4 m.

Trawl data

Ninety-one hauls from the GTS (64 were in waters shallower than 75 m), 70 hauls from MFRD3 and 72 hauls from MFRD5 were included in the analyses. All catch data were inputted into the NAN-SIS computer program for trawl survey data logging and analysis (Stromme 1992); these were extrapolated to catch-per-hour trawling. All fish names were cross-checked with entries in FISHBASE (FishBase 1998).

Environmental data

At the beginning or end of every haul, water temperature was obtained from thermometers mounted on Nansen reversing bottles. Salinity and dissolved oxygen were determined in the laboratory from water samples collected with the Nansen bottles. In the MFRD surveys, sea surface temperature was also recorded with a continuous temperature recorder mounted on the survey vessel.

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 along the trawling. Bottom type information was obtained from sediment maps produced during GTS and also from Ramos *et al.* (1990); these were 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 one nominal variable (bottom type).

Data analysis

A Two-way Indicator Analysis (TWIA) method implemented by TWINSPAN (Hill 1979) was used to obtain the species groupings in the trawl survey data. In the TWIA method, a classification of the samples is first constructed. This is then used 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). Stations and species are then arranged along the major gradients in the data. The number of subdivisions of the data is determined, *inter alia*, by the length of the gradient, the size of the eigen values obtained from the ordination and presence of suitable indicator species which are representative of the groups.

TWINSPAN uses a divisive cluster analysis algorithm to classify the samples and correspondence analysis (CA) to perform the ordination. The importance values (weights) are converted to a scale based on lower class limits before being used in the analysis. For this work, the class limits were 0, 0.5, 5, 50 and 500 kg.

A further ordination of the data was performed using Detrended Correspondence Analysis (DCA, Hill and Gauch 1980). DCA is a modification of the method of correspondence analysis (CA) and is intended to remove the two defects of CA, namely the 'arch effect' and compression of the ends of the first ordination axis (Gauch 1994). The DCA routine contained in CANOCO (ter Braak 1991), a community ecology computer program, was used in this work. Weights of the catches were used for the analysis (Bianchi and Hoisæter 1992). Each weight (x) was converted to (x + 1) to stabilize the variance as a Gaussian relationship between species abundance and each environmental variable was assumed. The environmental variables included in the analysis were bottom temperature, salinity and dissolved oxygen. Also included were

depth sampled and type of sediment. The CANOCO program package also correlates the ordination axes with the environmental variables. The significance of each correlation was assessed with a student t-statistic.

The GTS cruises were first analysed. Using the results of TWINSPAN to label the sites/hauls, the DCA scores (from CANOCO) were plotted using the drawing tools in the CANODRAW computer program (Smilauer 1992). The MFRD3 and MFRD5 data were similarly analysed. For the results to be comparable, the GTS data were reanalysed using only hauls made between the 10 and 75 m depth.

The most important species in each assemblage were obtained using an index of relative importance (IRI) defined as:

$$IRI = \%Wx \%F$$

where %W is the percentage contribution by weight of each species in the assemblage and %F is the percentage of the number of times that the species occurred in hauls from the assemblage. This index was modified from that of Pinkas *et al.* (1971). Species with IRI values of 50 or more in each assemblage were included in a short list of the most important species of the assemblage.

Seasonal (upwelling and non-upwelling) and long-term changes in the assemblages were investigated. For each survey and each assemblage, a list of the most important species for the upwelling and thermocline seasons was compiled. Thus the species that were present mainly during the upwelling period, those present in the thermocline period and those that were regularly present in the assemblage ('residents') were determined.

Similarities in the composition of the various assemblages were assessed using the Jaccard Index, Sj (Southwood 1978) and the Similarity Ratio, Sr (van Tongeren 1995). For two sampled sites (1 and 2), Sj is calculated as

$$Sj = \frac{c}{A + B - c}$$

where c is the number of species common to both sites, and A and B are the total number of species at the first and second sites respectively. To be adapted for use in this work, all stations in each assemblage were grouped and the assemblage treated as a 'site'. Following the notation of van Tongeren (1995), the Similarity Ratio for the comparison of two sites (i and j) is calculated from:

$$Sr_{ij} = \frac{\sum_{k} y_{ki} y_{kj}}{\sum_{k} y_{ki}^{2} + \sum_{k} y_{kj}^{2} - \sum_{k} y_{ki} y_{kj}}$$

where y_{ki} is the abundance of the kth species at site i, y_{kj} is its abundance at site j, and $y_{ki}y_{kj}$ is the product of the abundance of the kth species occurring at both sites. Sr is basically a quantitative equivalent of the Sj (van Tongeren 1995).

Results

Six groups of stations were identified from the GTS data; salient properties of the six groups are presented in Table 1. The table gives the number of trawl stations that make up the group, average values of each environmental parameter, the indicator species and some of the other important species of each assemblage. Each level of the nominal variable (bottom type) was scaled from 0 to 1 where 0 denotes non-existence and 1 is a predominance of the type of bottom. Table 2 gives the Pearson's product-moment correlation coefficient of the first two axes with temperature, salinity, dissolved oxygen, depth and bottom type. The significance of each correlation is indicated. The table also gives corresponding information for the subset of GTS data and the two MFRD surveys.

Figure 2 (for the complete GTS data) is an example of the CANODRAW biplots of sites and environmental parameters in the DCA axis 1 against DCA axis 2 plane. Hauls in the same group (assemblage) are indicated by the same symbol and enclosed in an ellipse. To be able to compare the plots for the various surveys, the axes are scaled to lie between -1 and +1. The bi-plot gives an indication of the environmental parameters that separate the groups and characteristics of each group are also indicated in Table 2. For example, Group 1 is a shallow water assemblage on soft bottom, Group 2 is also in shallow waters but on hard bottom, Groups 3 and 4 (at mid depths) are separated mainly by bottom type (3 towards soft and 4 towards mixed bottom) and Groups 5 and 6 are separated from the others mainly by depth. Figure 3 is a dendrogram showing the order of grouping and relationships between the six GTS groups.

The list of species with IRI value of 50 or more in each of the six groups

identified from the GTS data is given in Table 3. In this table, W is total weight caught in the survey, %W is percentage of total weight contributed by a particular species and F is the number of hauls in which the species was caught throughout the survey. The listed species form 77-92 % of the total catch in each group. As species were not placed exclusively in one group or the other, a number of species occur in more than one group. The occurrence of the bigeye grunt (*Brachydeuterus auritus*) and the sparid (*Sparus caeruleostictus*) in all three groups in shallow water is noticeable. Groups 5 and 6 share only a few species with the other groups.

Tables 4.1 - 4.3 give the list of the most important species found in each of the two main seasons (upwelling and non-upwelling). With the GTS data, only hauls in depth less than 75 were included in this analysis. In the tables, the names in bold type face are for species found in both seasons (hereafter referred to as 'resident' species). The species above the 'resident' species are present mainly during the upwelling period and those below are present mainly during the non-upwelling period. In the third group *B. auritus* was always found only during the non-upwelling period. This is one of the species describe by Longhurst (1969) as eurybathic.

Calculated values of the Jaccard Index and Similarity Ratio are presented in Tables 5 and 6 respectively. These were computed for both upwelling and thermocline seasons. Figures above shaded diagonal are for the upwelling period, and those below are for the non-upwelling period.

Discussion

From the GTS data the six groups identified in this work correspond to the following assemblages (as named by Longhurst 1969):

Group 1: Sciaenid Group 2: Lutjanid Group 3: Sparid (shallow part)

Group 4: Sparid (deep part) Group 5: Deep shelf Group 6: Upper slope.

The group of species referred to as eurybathic or thermocline species by Longhurst (1969) is not isolated in this work; these are generally included in the second assemblage. Also the estuarine sciaenid community described by Longhurst (1969) is

not represented in these results considering the range of depths (especially the minimum depth) covered in the surveys used in this study.

The first pair of assemblages (the sciaenid and lutjanid) is found in waters shallower than 40 m (Table 1). This is less than the average depth of the thermocline off Ghana which is given as about 41 m (Koranteng 1998). The second pair is in 40-100 m depth and the last pair in waters deeper than 100 m. The two sparid communities (groups 3 and 4) originate from within the thermocline depth and stretch seaward into deeper waters and the deep shelf and upper slope assemblages lie well below the thermocline layer.

The significantly high correlation between depth, bottom temperature, bottom salinity and bottom dissolved oxygen and the first DCA axis and between sediment type and the second axis, for the GTS data (Table 2), shows the importance of these parameters in the determination of the structure of the demersal species assemblages in the study area. Depth appears to be the most important variable in the ordination. It is followed by bottom temperature, salinity and dissolved oxygen. These physicochemical parameters are themselves closely related to depth in the oceans and usually change by seasons. Thus the upwelling, which appears to change the properties of water masses may also have effect on the structure of demersal species assemblages.

Sediment type then follows in importance being highly significant (1 % level) on the second DCA axis (Table 2). This shows the importance of this feature, which like depth, is invariant with time (at least within the time frame under consideration).

In the MFRD surveys, sediment type appears to be the most important factor determining assemblage structure. All levels of this variable are highly significant on the first DCA axis (Table 2). The second axis is dominated by depth and then temperature, dissolved oxygen and salinity. These results are rather different from the GTS results and which seem to imply that with a long depth gradient, as was the case in the GTS, sediment type becomes secondary to depth as the principal factor influencing assemblage structure. From these data sets, it appears that when the depth range is not wide, then the most important factor affecting community structure is the type of sediment on the seabed, relegating depth to a secondary position. This appears to be a fractal problem whereby, on some gradients the grain size could be an important factor

in assemblage formation (e.g. Mahon et al. 1984).

From the plot of DCA axis 1 versus DCA axis 2 (Figure 2), it appears that the first two species assemblages derived from the GTS data, are separated mainly by sediment type - the first on soft bottom and the second on hard bottom. Assemblages 3 and 4 are separated by both sediment type and depth. The last two assemblages are separated from the others mainly by depth. Consequently, it may be sufficient to regard depth and bottom sediment type as the principal forcing factors determining the structure of fish assemblages on the continental shelf and upper slope off Ghana. As temperature and dissolved oxygen also then become important on the second axis in case of short depth gradient, it appears, therefore, that these physico-chemical parameters are important in the dynamics of the assemblages.

The information on the site-environmental parameters bi-plots (Figure 2) correspond with the habitat preferences of various species in the assemblages as described by Longhurst (1969), Williams (1968), Blache *et al.* (1970) and Schneider (1990).

The results obtained in this study, in one way or the other, corroborate those of similar studies undertaken elsewhere. For example, it has been shown by several authors (including Fager and Longhurst 1968; Mahon *et al.* 1984; Yáñez-Arancibia *et al.* 1985; Bianchi 1992) that depth is the most important gradient along which faunal changes occur. Working on the entire GTS data collected from Guinea Bissau to Congo, Fager and Longhurst (1968) attributed assemblage boundaries in the Gulf of Guinea to thermal discontinuity and sediment type the latter of which also changes with depth.

The analyses carried out in this work on temporal and spatial patterns of community structure (using the first three assemblages and the three surveys) only shows subtle seasonal and temporal differences in assemblage structure. The calculated values of the Jaccard Index and Similarity Ratio (Tables 5 and 6) indicate that assemblages 2 and 3 showed closest resemblance to each other during the upwelling season and 1 and 2 in the non-upwelling season. The first situation could be due to fishes in assemblage 3 moving closer inshore during the upwelling and the second perhaps, due to assemblage 1 fishes moving away from shallow areas during the warm season (Koranteng 1998). It could also be due to seasonal inshore-offshore movement

of fishes in assemblage 2.

In general, the properties of the derived assemblages in the MFRD surveys are quite similar to each other and different from the GTS. This is true in both the upwelling and thermocline periods. Differences in assemblage structure have been attributed to differential response to changes in environmental forcing factors (Gulland and Garcia 1984; Overholtz and Tyler 1985; Macpherson and Gordoa 1992) or fishing (Brown *et al.* 1976; Overholtz and Tyler 1985). Koranteng (1998) showed that the period between 1963 and 1992 could be broken down into three time blocks each of which had distinct environmental characteristics in the Gulf of Guinea. In the first and third time blocks (i.e. before 1972 and after 1982 respectively) 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 environmental time block), there was a global decline in sea temperatures and a rise in salinity. The peak of the changing events was between 1975 and 1979. Thus, the observed change may be as a consequence of these environmental perturbations.

The Guinea Trawling Survey was conducted 17 years before MFRD3 and at a time when commercial trawling on the continental shelf of Ghana and neighbouring countries was much less intense than was the case at the time of the MFRD surveys. For example, the number of days fished by large industrial trawlers in Ghana's waters increased from 500 days in 1974 to 5500 days in 1990 (Koranteng 1998). This increase in fishing effort was partly due to the deployment of Ghanaian-registered vessels in home waters as several countries declared 200 nautical miles of exclusive economic zone in accordance with the third United Nations Convention on the Law of the Sea (UNCLOS III). These vessels were acquired principally to fish in more productive distant waters.

Differences in the assemblages could also be a consequence of the proliferation of triggerfish (*Balistes capriscus*) in this ecosystem between 1972 and 1988 (Ansa-Emmim 1979; Koranteng 1998). It appears that these factors conjointly or singly, affected the nature of species assemblages in Ghana's coastal waters. Koranteng (1998) showed that the increased abundance of triggerfish also destabilised the shallow water assemblages, especially the lutjanid and sparid (shallow part).

Conclusion

The analyses of community structure resulted in six species assemblages on the continental shelf and upper slope off Ghana. The first two, namely the sciaenid and lutjanid assemblages, are predominantly supra-thermocline whilst the two sparid assemblages begin at the thermocline depth of about 40 m and extend offshore. The last two (deep shelf and upper slope) assemblages occur well below the thermocline.

Associated with the soft, muddy substrate which is found in shallow waters (generally less than 40 m deep), is the sciaenid community made up mainly of species of the *Pseudotolithus* and *Galeoides* genera. Lying beyond this belt is a wide area of mixed-to-hard bottom associated with which are the lutjanid and the sparid assemblages (shallow and deep parts). There are clear faunal discontinuities around 30-40 m, 100 m and 200 m depth. The first ecotone is closely related with depth and the thermocline, the second to a steep shelf drop, and the third to significant division between shelf and slope assemblages.

The structure of the assemblages is determined primarily by depth and sediment type the latter of which is more important when considering a restricted depth gradient as in the MFRD surveys. The dynamics of the assemblages, including seasonal movements of component species, are influenced by physico-chemical properties of the water masses, mainly temperature, salinity and dissolved oxygen. Therefore, the seasonal coastal upwelling that occurs in the western Gulf of Guinea and which changes the characteristics of the water masses on the continental shelf, would have effect on the dynamics of the species assemblages.

The observed change in assemblage structure may also be due to increased industrial trawling and proliferation of triggerfish (*Balistes capriscus*) in Ghana's continental shelf waters.

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Table 1: Summary (mean) of community environmental parameters and indicator species.

| Survey | Variable | Group 1 | Group 2 | Group 3 |
|--------|------------------------------|-----------------|---------------|---------------|
| GTS | No. of stations | 16 | 25 | 9 |
| | Hard | | 0.4 | |
| | Mixed | 0.4 | 0.6 | 0.4 |
| | Soft | 0.6 | | 0.6 |
| | Depth (m) | 28 (8) | 37 (10) | 49 (10) |
| | Temperature (°C) | 20.8 (1.0) | 19.8 (1.3) | 19.4 (1.2) |
| | Salinity (% ₀) | 35.85 (0.09) | 35.82 (0.12) | 35.88 (0.09) |
| | Oxygen (ml l ⁻¹) | 3.13 (0.74) | 2.98 (0.62) | 2.44 (0.70) |
| | Indicator species | S. dorsalis | B. forcipatus | P. notialis |
| | | G. decadactylus | A. punctatus | B. auritus |
| | | | A. guineensis | |
| | Other important | B. auritus | P. bellottii | P. bellottii |
| | species | I. africana | B. auritus | Trachurus sp. |
| | | P. senegalensis | Trachurus sp. | R. miraletus |
| Survey | Variable | Group 4 | Group 5 | Group 6 |
| GTS | No. of stations | 26 | 11 | 4 |
| | Hard | 0.3 | | |
| | Mixed | 0.6 | 0.7 | 0.8 |
| | Soft | 0.1 | 0.3 | 0.2 |
| | Depth (m) | 87 (32) | 217 (43) | 411 (23) |
| | Temperature (°C) | 17.5 (1.3) | 14.0 (1.4) | 11.0 (3.0) |
| | Salinity (% ₀) | 35.74 (0.09) | 35.41 (0.15) | 35.37 (0.46) |
| | Oxygen (ml l ⁻¹) | 2.74 (0.54) | 2.23 (0.54) | 2.07 (0.65) |
| | Indicator species | D. congoensis | | H. italicus |
| | | B. boops | | |
| | | S. oculata | | |
| | Other important | Trachurus sp. | P. ledanoisi | S. fernandus |
| | species | S. japonicus | Trachurus sp. | C. uyato |
| | | I. africana | Loligo sp. | H. bella |

Table 2: Pearson's product-moment correlation coefficient r, of species axes 1 - 4 with bottom environmental variables.

| Survey | Variable | Species | Species | 1 [| Survey | Variable | Species | Species |
|-------------|-------------|----------|----------|-----|--------|-------------|----------|----------|
| | | Axis 1 | Axis 2 | | | | Axis 1 | Axis 2 |
| | Hard | -0.13 | -0.29** | | MFRD3 | Hard | -0.49*** | 0.09 |
| GTS | Mixed | 0.13 | -0.14 | | | Mixed | 0.30** | 0.01 |
| (all hauls) | 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 | Hard | -0.31** | -0.02 | | MFRD5 | Hard | -0.29** | -0.30** |
| (hauls at | Mixed | -0.11 | -0.29* | | | Mixed | 0.16 | 0.12 |
| ≤ 75 m) | 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 3: Total weight (W kg), percentage weight (%W) and frequency of occurrence (F, number of stations) of the main species in each group of stations; Guinean Trawling Survey, 1963-64.

| Group 1 (16 stations) | | | | | | | |
|-----------------------------|-------|--------------|--------------|-------------------------|------------------|----------|----|
| ~ . | | | _ | Group 3 (9 stations) | | | |
| Species | W | % *** | \mathbf{F} | g • | *** | 0/ | |
| Dug alandantamia annitria | kg | W | 15 | Species | W | % | F |
| Brachydeuterus auritus | 2616 | 34.2 | 15 | Cramia agamilaagiatus | kg 569 | W | 0 |
| Serlene sorsalis | 544 | 7.1 | 13 | Sparus caeruleostictus | | 17.0 | 9 |
| Galeoides decadactylus | 565 | 7.4 | 11 | Brachydeuterus auritus | 771 | 23.1 | 6 |
| Pseudotolithus senegalensis | 586 | 7.7 | 10 | Trachurus spp. | 444 | 13.3 | 7 |
| Ilisha africana | 620 | 8.1 | 7 | Raja miraletus | 155 | 4.6 | 7 |
| Sparus caeruleostictus | 313 | 4.1 | 9 | Priacanthus arenatus | 124 | 3.7 | 7 |
| Pagellus bellottii | 235 | 3.1 | 10 | Epinephelus aeneus | 81 | 2.4 | 6 |
| Drepane africana | 221 | 2.9 | 9 | Pseudupeneus prayensis | 88 | 2.6 | 5 |
| Raja miraletus | 149 | 2.0 | 12 | Sparus caeruleostictus | 62 | 1.9 | 5 |
| Trichiurus lepturus | 152 | 2.0 | 10 | Lepidotrigla cadmani | 59 | 1.8 | 4 |
| Loligo sp. | 250 | 3.3 | 6 | Loligo sp. | 32 | 0.9 | 6 |
| Pomadasys jubelini | 100 | 1.3 | 8 | Dentex congoensis | 58 | 1.7 | 3 |
| Pteroscion peli | 132 | 1.7 | 6 | Cynoglossus canariensis | 34 | 1.0 | 5 |
| Epenephelus aeneus | 88 | 1.2 | 8 | Penaeus notialis | 22 | 0.7 | 7 |
| | | | | Sardinella aurita | 39 | 1.2 | 4 |
| Total | 6571 | 85.9 | | Dentex angolensis | 38 | 1.1 | 4 |
| Total (all species) | 7646 | | | | | | |
| | | | | Total | 2576 | 77.1 | |
| Group 2 (25 stations) | | | | Total (all species) | 3343 | | |
| Species | W | % | F | | | | |
| | kg | \mathbf{W} | | | | | |
| Pagelus bellottii | 1926 | 16.5 | 25 | Group 4 (26 stations) | | | |
| Brachydeuterus auritus | 1394 | 12.0 | 17 | | | | |
| Trachurus spp. | 1008 | 8.6 | 18 | Species | \mathbf{W} | % | F |
| Sparus caeruleostictus | 746 | 6.4 | 24 | | kg | W | |
| Pseudupeneus prayensis | 585 | 5.0 | 23 | Trachurus sp. | 3145 | 18.7 | 24 |
| Priacanthus arenatus | 420 | 3.6 | 24 | Dentex congoensis | 2237 | 13.3 | 24 |
| Dentex canariensis | 352 | 3.0 | 20 | Scomber japonicus | 2263 | 13.5 | 22 |
| Sardinella aurita | 432 | 3.7 | 16 | Priacanthus arenatus | 1210 | 7.2 | 24 |
| Epinephelus aeneus | 339 | 2.9 | 19 | Pagelus bellottii | 1179 | 7.0 | 21 |
| Scomber japonicus | 364 | 3.1 | 16 | Dentex angolensis | 820 | 4.9 | 22 |
| Dactylopterus volitans | 224 | 1.9 | 23 | Sardinella aurita | 1370 | 8.2 | 10 |
| Decapterus sp. | 381 | 3.3 | 11 | Boops boops | 529 | 3.1 | 21 |
| Loligo sp. | 196 | 1.7 | 20 | Epinephelus aeneus | 550 | 3.3 | 19 |
| Lutjanus agennes | 207 | 1.8 | 17 | Paracubiceps ledanoisi | 601 | 3.6 | 15 |
| Lutjanus fulgens | 184 | 1.6 | 18 | Dentex gibbosus | 179 | 1.1 | 19 |
| Balistes forcipatus | 153 | 1.3 | 21 | | | | |
| Sphyraena sp. | 230 | 2.0 | 14 | Total | 14084 | 83.8 | |
| Acanthurus monroviae | 162 | 1.4 | 18 | Total (all stations) | 16812 | | |
| Lethrinus atlanticus | 98 | 0.8 | 18 | | | | |
| Raja miraletus | 66 | 0.6 | 23 | | | | |
| Total | 9467 | 81.2 | | | | | |
| Total (all species) | 11657 | 01.2 | | | | | |
| Total (all species) | 11057 | | | | | | |

Group 5 (11 stations)

| Species | \mathbf{W} | % | \mathbf{F} |
|----------------------------|--------------|--------------|--------------|
| _ | kg | \mathbf{W} | |
| Paracubiceps ledanoisi | 1567 | 26.4 | 10 |
| Trachurus spp. | 1188 | 20.0 | 4 |
| Antigonia capros | 431 | 7.3 | 8 |
| Loligo sp. | 435 | 7.3 | 7 |
| Pentheroscion mbizi | 333 | 5.6 | 7 |
| Smaris macrolepidotus | 327 | 5.5 | 7 |
| Chlorophthalmus atlanticus | 119 | 2.0 | 7 |
| Paragaleus pectoralis | 265 | 4.5 | 3 |
| Paracubiceps multisquamis | 98 | 1.7 | 5 |
| Priacanthus arenatus | 88 | 1.5 | 5 |
| Dentex angolensis | 101 | 1.7 | 4 |
| Dentex congoensis | 66 | 1.1 | 5 |
| Total | 5019 | 84.6 | |
| Total (all stations) | 5933 | | |

Group 6 (4 stations)

| Species | \mathbf{W} | % | \mathbf{F} |
|----------------------------|--------------|--------------|--------------|
| | kg | \mathbf{W} | |
| Squalus fernandus | 501 | 47.5 | 2 |
| Hypoclydonia bella | 116 | 11.0 | 2 |
| Centrophorus uyato | 134 | 12.7 | 1 |
| Paracubiceps multisquamis | 44 | 4.2 | 3 |
| Chlorophthalmus sp. | 41 | 3.9 | 2 |
| Chlorophthalmus atlanticus | 71 | 6.7 | 1 |
| Carcharhinus signatus | 31 | 2.9 | 2 |
| Paracubiceps ledanoisi | 32 | 3.0 | 1 |
| | | | |
| Total | 970 | 92.0 | |
| Total (all species) | 1055 | | |
| | | | |

Tables 4.1 - 4.3

Table indicating seasonal membership of species in the various assemblages; names in bold type face are for species found in both seasons (resident) in the indicated assemblage, those at the top were found in the upwelling season only and those below were found in the thermocline season only.

Table 4.1: GTS (only stations of depth 75 m or less)

| Group 1 |
|------------------------------|
| Drepane africana |
| Epenephelus aeneus |
| Ilisha africana |
| Loligo sp. |
| Pomadasys jubelini |
| Pseudotolithus brachygnathus |
| Pseudotolithus typus |
| Sparus caeruleostictus |

Brachydeuterus auritus Galeoides decadactilus Pagellus bellottii Raja miraletus Trichiurus lepturus Pseudotolithus senegalensis Pteroscion peli

Sphyraena sp.

Group 2

Decapterus spp.
Fistularia villosa
Lutjanus dentatus
Pomadasys incisus
Lutjanus dentatus
Trachinocephalus myops
Acanthurus monroviae
Balistes forcipatus
Loligo sp.
Lutjanus agennes
Lutjanus fulgens

Raja miraletus

Turtles

Scomber japonicus

Brachydeuterus auritus
Dactylopterus volitans
Dentex canariensis
Epenephelus aeneus
Pagellus bellottii
Priacanthus arenatus
Pseudupeneus prayensis
Sparus caeruleostictus
Trachurus sp.

Sardinella aurita

Group 3

Dentex gibbosus Raja miraletus Sardinella aurita Boops boops Scomber japonicus

Sparus caeruleostictus
Priacanthus arenatus
Epenephelus aeneus
Pagellus bellottii
Dentex congoensis
Trachurus sp.
Pseudupeneus prayensis
Dentex angolensis

Brachydeuterus auritus Sphyraena sp. Pentheroscion mbizi Sardinella maderensis

Group 1

Decapterus rhonchus
Pagellus bellottii
Pomadasys incisus
Priacanthus arenatus
Pseudupeneus prayensis
Sepia sp.

Balistes capriscus
Brachydeuterus auritus
Chloroscombrus chrysurus
Dentex canariensis
Epenephelus aeneus
Galeoides decadactylus
Selene dorsalis
Sparus caeruleostictus

Elops senegalensis
Engraulis encrasicolus
Ilisha africana
Pseudotolithus senegalensis
Pseudotolithus sp.
Pteroscion peli
Scyacium micrurum
Sphyraena sphyraena

Group 2

Balistes capriscus
Boops boops
Brachydeuterus auritus
Chromis lineatus
Dentex angolensis
Dentex congoensis
Dentex gibbosus
Paracubiceps ledanoisi
Rhizoprionodon acutus
Trachurus sp.
Umbrina canariensis

Dactylopterus volitans
Dentex canariensis
Epenephelus aeneus
Fistularia villosa
Pagellus bellottii
Priacanthus arenatus
Pseudupeneus prayensis
Sparus caeruleostictus

Acanthostracion guineensis
Acanthurus monroviae
Balistes forcipatus
Chaetodon sp.
Chloroscombrus chrysurus
Decapterus sp.
Lagocephalus laevigatus
Lethrinus atlanticus
Lutjanus fulgens
Scyacium micrurum
Sepia sp.

Group 3

Acanthurus monroviae
Boops boops
Chaetodon luciae
Dactylopterus volitans
Distodon speciosus
Fistularia villosa
Lutjanus fulgens
Lutjanus goreensis
Rhizoprionodon acutus
Trigla sp.

Balistes capriscus
Dentex canariensis
Dentex gibbosus
Epenephelus aeneus
Pagellus bellottii
Priacanthus arenatus
Pseudupeneus prayensis
Sepia sp.
Sparus caeruleostictus

Brachydeuterus auritus
Chloroscombrus chrysurus
Chromis lineatus
Decapterus rhonchus
Lepidotrigla sp.
Pomadasys incisus
Raja miraletus
Sardinella aurita
Selene dorsalis

Group 1

Lagocephalus laevigatus
Pagellus bellottii
Pentheroscion mbizi
Pomadasys incisus
Priacanthus arenatus
Pteroscion peli
Rhizoprionodon acutus
Trachinocephalus myops
Trachurus trecae

Brachydeuterus auritus
Galeoides decadactilus
Penaeus notialis
Pomadasys jubelini
Pseudupeneus prayensis
Sepia officinalis
Selene dorsalis
Sparus caeruleostictus
Trichiurus lepturus

Chilomycterus spinosus
Chloroscombrus chrysurus
Dasyatis sp.
Dentex canariensis
Drepane africana
Elops senegalensis
Epenephelus aeneus
Eucinostomus melanopterus
Grammoplites gruveli
Lutjanus fulgens
Sardinella maderensis
Sphyraena sphyraena
Torpedo sp.

Group 2

Acanthurus monroviae Boops boops Decapterus rhonchus Pomadasys incisus Trachurus sp. Trachurus trecae

Balistes forcipatus
Brachydeuterus auritus
Chloroscombrus chrysurus
Dentex canariensis
Fistularia villosa
Lagocephalus laevigatus
Lutjanus fulgens
Pagellus bellottii
Priacanthus arenatus
Pseudupeneus prayensis
Sepia officinalis
Sparus caeruleostictus

Apsilus fuscus
Balistes capriscus
Chaetodon sp.
Chromis lineatus
Dactylopterus volitans
Decapterus sp.
Epinephelus aeneus
Lethrinus atlanticus
Sphyraena sphyraena
Trigla sp.

Group 3

Anthias anthias
Boops boops
Chromis sp.
Decapterus sp.
Dentex canariensis
Dentex gibbosus
Sardinella aurita
Scomber japonicus

Dactylopterus volitans
Dentex congoensis
Epenephelus aeneus
Fistularia villosa
Pagellus bellottii
Pseudupeneus prayensis
Rhizoprionodon acutus
Sparus caeruleostictus

Balistes forcipatus
Brachydeuterus auritus
Chloroscombrus chrysurus
Lagocephalus laevigatus
Lepidotrigla sp.
Priacanthus arenatus
Raja miraletus
Scyacium micrurum
Sepia officinalis
Selene dorsalis
Serranus accraensis
Sphyraena sphyraena
Trachurus sp.
Umbrina sp.

Table 5: Jaccard's index of similarity between pairs of assemblages for the same survey. Figures above shaded diagonal are for the upwelling period, and those below are for the thermocline period.

| | | GTS | | MFRD3 | | | | | | |
|-------|------|------|------|-------|------|------|------|------|------|-------|
| Group | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | Group |
| 1 | 1 | 0.27 | 0.35 | 1 | 0.45 | 0.37 | 1 | 0.43 | 0.33 | 1 |
| 2 | 0.45 | 1 | 0.35 | 0.36 | 1 | 0.35 | 0.45 | 1 | 0.37 | 2 |
| 3 | 0.40 | 0.41 | 1 | 0.36 | 0.46 | 1 | 0.39 | 0.46 | 1 | 3 |
| | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | |

Table 6: Within survey Similarity Ratios among the three assemblages. Figures above shaded diagonal are for the upwelling period, and those below are for the thermocline period.

| | | GTS | | MFRD3 | | | | | | |
|-------|------|------|------|-------|------|------|------|------|------|-------|
| Group | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | Group |
| 1 | 1 | 0.09 | 0.01 | 1 | 0.17 | 0.10 | 1 | 0.20 | 0.06 | 1 |
| 2 | 0.18 | 1 | 0.23 | 0.16 | 1 | 0.10 | 0.60 | 1 | 0.12 | 2 |
| 3 | 0.01 | 0.28 | 1 | 0.30 | 0.07 | 1 | 0.01 | 0.04 | 1 | 3 |
| | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | |

Legends to Figures

- Figure 1: Map of the Gulf of Guinea, West Africa, showing the location of Ghana
- Figure 2: Bi-plot of trawl hauls and environmental parameters in DCA axis 1 versus axis 2 for the GTS data
- Figure 3: Dendrogram showing clustering order of groups of stations for the GTS data analysed with TWINSPAN





