Vol. 220: 1–12, 2001 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published September 27

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

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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 6 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, 100 and 200 m depth. 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 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.

KEY WORDS: Species assemblages · Structure and dynamics · Continental shelf and slope · Ghana

INTRODUCTION

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). Caddy & Sharp (1986) also pointed out that such studies are necessary to gain a better understanding of multispecies stocks and for the management of these stocks. For such reasons, the structure of species assemblages for several exploited fish stocks around the world has been established. Examples are in the Narragansett Bay, USA (Oviatt & 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), Congo, Gabon and Angola in south-west Africa (Bianchi 1992), and the North-western Indian Ocean and East Africa (Bianchi 1992). In the Gulf of Guinea, West Africa, Fager & Longhurst (1968) and Longhurst (1969) established the assemblage structure of demersal species on the continental shelf using data from the Guinean Trawling Survey (Williams 1968).

In the last 3 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 an effect on species aggregations in the sub-region (Koranteng 1998). The most important recorded changes are the decline and subsequent recovery of the round sardinella *Sardinella aurita* populations (Pezennec 1995), the proliferation and subsequent decline of triggerfish *Balistes capriscus* (Ansa-Emmim 1979, Koranteng 1984, Caverivière 1991) and the increase in abundance of cuttlefish *Sepia officinalis* and globefish *Lagocephalus laevigatus* (Ramos et al. 1990, Koranteng 1998). Studies of fish communities have shown that some natural and anthropogenic factors could induce changes in the structure of species assemblages and affect the general well-being of fishery resources.

The objectives of this paper are to: (1) establish assemblage units of demersal fish species on the continental shelf and upper slope off Ghana; (2) establish the factors that determine the structure of these assem-

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blages; and, (3) assess the impact of environmental forcing and of fishing on the structure and dynamics of the assemblages.

Study area. The study area is the continental shelf and upper slope off Ghana, West Africa (Fig. 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 ~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 km^2 (Koranteng 1984).

The ocean floor on the continental shelf off Ghana has distinct areas of mud, hard rocks and mixed deposits. There is a belt of soft, muddy substrate in shallow waters down to ~30 m depth, followed by a wide area of mixed to hard bottom type (Fig. 1, Williams 1968). Generally, the area beyond 75 m depth is not safe for trawling, except towards the western side (Rijavec 1980, Koranteng 1984) where vessels can trawl in waters deeper than 100 m.

Situated in the western Gulf of Guinea, a subsystem of the Guinea Current Large Marine Ecosystem (Binet & Marchal 1993, Sherman 1993), the continental shelf waters off Ghana experience 2 seasonal periods of 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 decreases (Mensah & Koranteng 1988). The major upwelling (long cold season) occurs between July and September when SST (usually ~27 to 29°C) falls below 25°C. The minor upwelling (short cold season) normally lasts for only about 3 wk (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.

Koranteng (1998) showed that the period between 1963 and 1992 could be broken down into 3 climatic periods, each of which had distinct environmental characteristics in the Gulf of Guinea. In the first period (i.e. before 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, temperatures were high and salinity was low and variable.

MATERIALS AND METHODS

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 1998). The Guinean Trawling Survey (GTS), organised by the Scientific, Technical and Research Commission of the Organisation of African Unity (OAU/STRC) in 1963/4 (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 (1963/4) and MFRD surveys of 1981/2 (MFRD3) and 1989 (MFRD5) are used in this study. The GTS was conducted during the first climatic period described above, MFRD3 and MFRD5

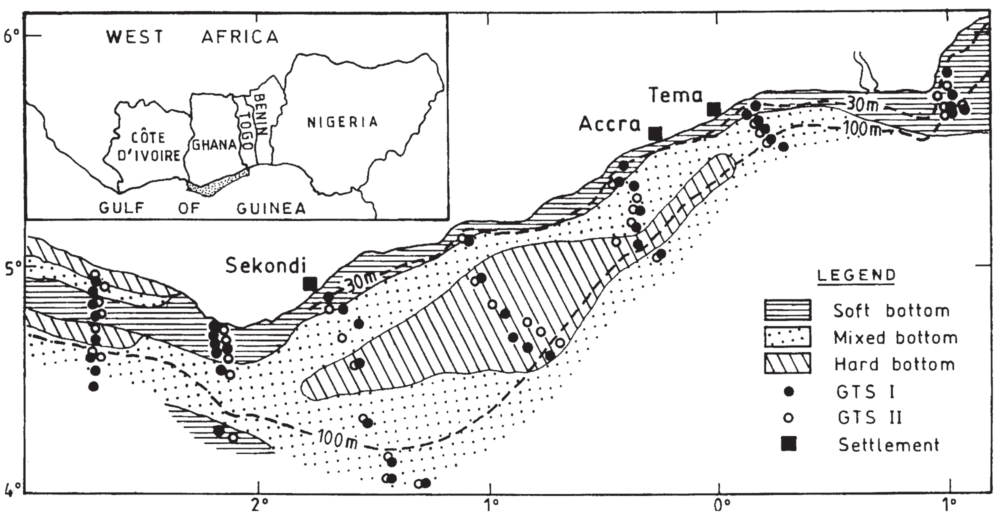

Fig. 1. The Gulf of Guinea, West Africa (inset), showing area surveyed off Ghana. Enlargement shows distribution of bottom sediments and location of hauls in Guinean Trawling Survey (GTS)

were conducted during the second and third climatic periods respectively. The 2 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.

GTS was in 2 phases; GUINEAN I and GUINEAN II. Off the coast of 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) that were 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 1 h 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 to 100 m depth zone. In the MFRD surveys, all stations were sampled during the upwelling periods (Jan, Jul/Aug) and also during the stratified periods (Apr/May, Oct/Nov). The sampling procedures were as those used in the GTS survey except that within the confines of a station, the depth and trawling direction were chosen at random and the duration of tow was 30 min. 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. The same vessel (29 m multipurpose research vessel, trawling speed 5.6 km h^{-1}) was used. The survey net also had a codend mesh of 40 mm and a wing spread of 16.4 m.

Trawl data. 91 hauls from the GTS (64 in waters shallower than 75 m), 70 hauls from MFRD3, and 72 hauls from MFRD5 were included in the analyses. All catch data were input to 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, which were also used to collect water samples for analysis in the laboratory. Salinity and dissolved oxygen were determined from the water samples using a salinometer and Winkler titration method respectively. In the MFRD surveys, sea surface temperature was also recorded with a continuous temperature recorder mounted on the survey vessel.

The hydrographic variables used in the analysis are water temperature, salinity, and dissolved oxygen measured at depths trawled. Other environmental variables 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 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).

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 2 classifications are then used together to obtain an ordered 2-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 sub-divisions of the data is determined inter alia by the length of the gradient, the size of the eigenvalues 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 & Gauch 1980). DCA is a modification of the method of correspondence analysis (CA) and is intended to remove the 2 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 & Hoisæter 1992).

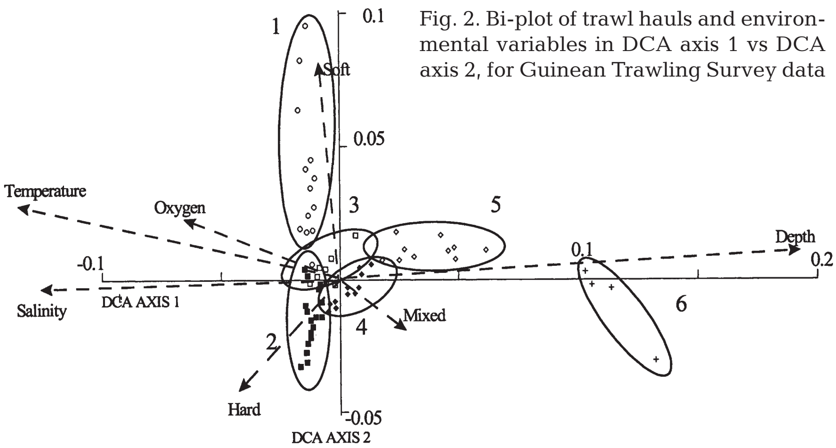

Fig. 2. Bi-plot of trawl hauls and environmental variables in DCA axis 1 vs DCA axis 2, for Guinean Trawling Survey data

Each weight (x) was converted to log ($x + 1$) in order 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 3 bottom types were treated as 3 levels of 1 nominal variable (bottom type). The CANOCO program package also correlates the ordination axes with the environmental variables. The significance of each correlation was assessed with a Student's *t*-statistic.

The GTS cruises were analysed first. Using the results of TWINSPAN to label the sites/hauls, the DCA scores (from CANOCO) were plotted using the drawing tools available 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 re-analysed using only hauls made between 10 and 75 m depth.

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

Table 1. Community environmental parameters, mean (SD), 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 (‰)	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	*Serlene dorsalis* *Galeoides decadactylus* *Acanthostracion guineensis*	*Balistes forcipatus* *Aluterus punctatus*	*Penaeus notialis* *Brachydeuterus auritus*
	Other important species	*Brachydeuterus auritus* *Ilisha africana* *Pseudotolithus senegalensis*	*Pagellus bellottii* *Brachydeuterus auritus* *Trachurus* spp.	*Pagellus bellottii* *Trachurus* spp. *Raja miraletus*
		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 (‰)	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	*Dentex congoensis* *Boops boops* *Squatina oculata*		*Hymenocephalus italicus*
	Other important species	*Trachurus* spp. *Scomber japonicus* *Ilisha africana*	*Paracubiceps ledanoisi* *Trachurus* spp. *Loligo* sp.	*Squalus fernandus* *Centrophorus uyato* *Hypoclydonia bella*

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

Survey	Variable	Species Axis 1	Species Axis 2	Survey	Variable	Species Axis 1	Species Axis 2
GTS (all hauls)	Hard	–0.13	–0.29**	MFRD3	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 (hauls at ≤ 75 m)	Hard	–0.31**	–0.02	MFRD5	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: (*) $p < 0.05$; (**) $p < 0.01$; (***) $p < 0.001$

$$\mathrm{IRI} = \%\mathrm{W} \times \%\mathrm{F}$$

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 ≥50 in each assemblage were included in a short list of the most important species of the assemblage.

Seasonal (upwelling, stratified) and long-term changes in the assemblages were investigated. For each survey and assemblage, a list of the most important species for the upwelling and stratified seasons was compiled. Thus the species that were present mainly during the upwelling period, those present in the stratified 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 1988) and the 'Similarity Ratio' *Sr* (van Tongeren 1995). For 2 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 2 sites (i and j) is calculated from:

$$Sr_{\mathrm{ij}} = \frac{\sum_k y_{k\mathrm{i}} y_{k\mathrm{j}}}{\sum_k y_{k\mathrm{i}}^2 + \sum_k y_{k\mathrm{j}}^2 - \sum_k y_{k\mathrm{i}} y_{k\mathrm{j}}}$$

where $y_{k\mathrm{i}}$ is the abundance of the k^{th} species at site i, $y_{k\mathrm{j}}$ is its abundance at site j, and $y_{k\mathrm{i}}y_{k\mathrm{j}}$ is the product of the abundance of the k^{th} species occurring at both sites. *Sr* is basically a quantitative equivalent of *Sj* (van Tongeren 1995).

RESULTS

Six groups of stations were identified from the GTS data; salient properties of the 6 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 2 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 2 MFRD surveys.

An example of the CANODRAW bi-plots of sites and environmental parameters in the DCA axis 1 against DCA axis 2 plane for the complete GTS data is given in Fig. 2. Hauls in the same group (i.e. assemblage) are indicated by the same symbol and enclosed in an ellipse. To be able to compare the plots for the various

Table 3. Total weight (W, kg), percentage weight (%W), and frequency of occurrence (F, no. of stations) of main species in each group of stations; Guinean Trawling Survey, 1963–64

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

Species	W (kg)	% W	F
Group 4 (26 stations)			
Trachurus sp.	3145	18.7	24
Dentex congoensis	2237	13.3	24
Scomber japonicus	2263	13.5	22
Priacanthus arenatus	1210	7.2	24
Pagelus bellottii	1179	7.0	21
Dentex angolensis	820	4.9	22
Sardinella aurita	1370	8.2	10
Boops boops	529	3.1	21
Epinephelus aeneus	550	3.3	19
Paracubiceps ledanoisi	601	3.6	15
Dentex gibbosus	179	1.1	19
Total	14084	83.8	
Total (all stations)	16812		
Group 5 (11 stations)			
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)			
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		

surveys, the axes are scaled between –1 and 1. The biplot 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. A dendrogram showing the order of grouping and relationships between the 6 GTS groups is given in Fig. 3.

The list of species with IRI value ≥50 in each of the 6 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 species listed form 77 to 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 >1 group. The occurrence of the bigeye grunt *Brachydeuterus auritus* and the sparid *Sparus caeruleostictus* in all 3 groups in shallow water is noticeable. Groups 5 and 6 share only a few species with the other groups.

Table 4 gives the list of the most important species found in each of the 2 main seasons (upwelling, stratified). With the GTS data, only hauls in depth <75 m were included in this analysis. In the tables, the names in bold are for species found in both seasons ('resident' species). The species above these are present mainly during the upwelling period and those below are present mainly during the stratified period. In the third group, *Brachydeuterus auritus* was always found only during the stratified period. This is one of the species described by Longhurst (1969) as eurybathic.

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

DISCUSSION

From the GTS data the 6 groups identified in this work correspond to the following assemblages (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.

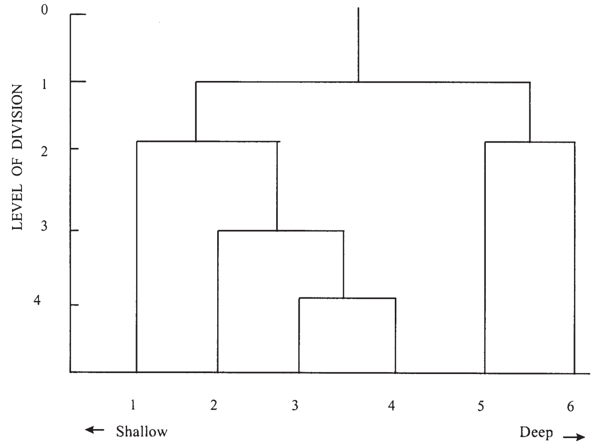

Fig. 3. Dendrogram showing clustering order of groups of stations for Guinean Trawling Survey data analysed with TWINSPAN

The first pair of assemblages (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 ~41 m (Koranteng 1998). The second pair is in 40 to 100 m depth and the last pair in waters deeper than 100 m. The 2 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.

For the GTS data (Table 2), the significantly high correlation between the first DCA axis and depth, bottom temperature, bottom salinity and bottom dissolved oxygen, and also between sediment type and the second axis, the importance of these variables in the determination of the structure of demersal species assemblages in the study area is shown. Depth appears to be the most important variable in the ordination, followed by bottom temperature, salinity and dissolved oxygen. These physico-chemical variables 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 an effect on the structure of demersal species assemblages.

Sediment type then follows in importance, being highly significant ($p < 0.01$) 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 considered.

Table 4. Seasonal membership of assemblages; species listed in **bold** are 'resident' species found in both seasons; those above were found in the upwelling season only; those below were found in the stratified season only

Group 1	Group 2	Group 3
GTS (only stations of depth 75 m or less)		
Drepane africana	*Decapterus* spp.	*Dentex gibbosus*
Epenephelus aeneus	*Fistularia villosa*	*Raja miraletus*
Ilisha africana	*Lutjanus dentatus*	*Sardinella aurita*
Loligo sp.	*Pomadasys incisus*	*Boops boops*
Pomadasys jubelini	*Lutjanus dentatus*	*Scomber japonicus*
Pseudotolithus brachygnathus	*Trachinocephalus myops*	
Pseudotolithus typus	*Acanthurus monroviae*	***Sparus caeruleostictus***
Sparus caeruleostictus	*Balistes forcipatus*	***Priacanthus arenatus***
	Loligo sp.	***Epenephelus aeneus***
Brachydeuterus auritus	*Lutjanus agennes*	***Pagellus bellottii***
Galeoides decadactilus	*Lutjanus fulgens*	***Dentex congoensis***
Pagellus bellottii	*Raja miraletus*	***Trachurus* sp.**
Raja miraletus	*Scomber japonicus*	***Pseudupeneus prayensis***
Trichiurus lepturus	Turtles	***Dentex angolensis***
Pseudotolithus senegalensis		
Pteroscion peli	***Brachydeuterus auritus***	*Brachydeuterus auritus*
	Dactylopterus volitans	*Sphyraena* sp.
Sphyraena sp.	***Dentex canariensis***	*Pentheroscion mbizi*
	Epenephelus aeneus	*Sardinella maderensis*
	Pagellus bellottii	
	Priacanthus arenatus	
	Pseudupeneus prayensis	
	Sparus caeruleostictus	
	***Trachurus* sp.**	
	Sardinella aurita	
MFRD3 1981–82		
Decapterus rhonchus	*Balistes capriscus*	*Acanthurus monroviae*
Pagellus bellottii	*Boops boops*	*Boops boops*
Pomadasys incisus	*Brachydeuterus auritus*	*Chaetodon luciae*
Priacanthus arenatus	*Chromis lineatus*	*Dactylopterus volitans*
Pseudupeneus prayensis	*Dentex angolensis*	*Distodon speciosus*
Sepia sp.	*Dentex congoensis*	*Fistularia villosa*
	Dentex gibbosus	*Lutjanus fulgens*
Balistes capriscus	*Paracubiceps ledanoisi*	*Lutjanus goreensis*
Brachydeuterus auritus	*Rhizoprionodon acutus*	*Rhizoprionodon acutus*
Chloroscombrus chrysurus	*Trachurus* sp.	*Trigla* sp.
Dentex canariensis	*Umbrina canariensis*	
Epenephelus aeneus		***Balistes capriscus***
Galeoides decadactylus	***Dactylopterus volitans***	***Dentex canariensis***
Selene dorsalis	***Dentex canariensis***	***Dentex gibbosus***
Sparus caeruleostictus	***Epenephelus aeneus***	***Epenephelus aeneus***
	Fistularia villosa	***Pagellus bellottii***
Elops senegalensis	***Pagellus bellottii***	***Priacanthus arenatus***
Engraulis encrasicolus	***Priacanthus arenatus***	***Pseudupeneus prayensis***
Ilisha africana	***Pseudupeneus prayensis***	***Sepia* sp.**
Pseudotolithus senegalensis	***Sparus caeruleostictus***	***Sparus caeruleostictus***
Pseudotolithus sp.	*Acanthostracion guineensis*	
Pteroscion peli	*Acanthurus monroviae*	*Brachydeuterus auritus*
Scyacium micrurum	*Balistes forcipatus*	*Chloroscombrus chrysurus*
Sphyraena sphyraena	*Chaetodon* sp.	*Chromis lineatus*
	Chloroscombrus chrysurus	*Decapterus rhonchus*
	Decapterus sp.	*Lepidotrigla* sp.
	Lagocephalus laevigatus	*Pomadasys incisus*
	Lethrinus atlanticus	*Raja miraletus*
	Lutjanus fulgens	*Sardinella aurita*
	Scyacium micrurum	*Selene dorsalis*
	Sepia sp.	

Table 4 (continued)

Group 1	Group 2	Group 3
MFRD5 1989		
Lagocephalus laevigatus	*Acanthurus monroviae*	*Anthias anthias*
Pagellus bellottii	*Boops boops*	*Boops boops*
Pentheroscion mbizi	*Decapterus rhonchus*	*Chromis* sp.
Pomadasys incisus	*Pomadasys incisus*	*Decapterus* sp.
Priacanthus arenatus	*Trachurus* sp.	*Dentex canariensis*
Pteroscion peli	*Trachurus trecae*	*Dentex gibbosus*
Rhizoprionodon acutus		*Sardinella aurita*
Trachinocephalus myops	***Balistes forcipatus***	*Scomber japonicus*
Trachurus trecae	***Brachydeuterus auritus***	
	Chloroscombrus chrysurus	***Dactylopterus volitans***
Brachydeuterus auritus	***Dentex canariensis***	***Dentex congoensis***
Galeoides decadactilus	***Fistularia villosa***	***Epenephelus aeneus***
Penaeus notialis	***Lagocephalus laevigatus***	***Fistularia villosa***
Pomadasys jubelini	***Lutjanus fulgens***	***Pagellus bellottii***
Pseudupeneus prayensis	***Pagellus bellottii***	***Pseudupeneus prayensis***
Sepia officinalis	***Priacanthus arenatus***	***Rhizoprionodon acutus***
Selene dorsalis	***Pseudupeneus prayensis***	***Sparus caeruleostictus***
Sparus caeruleostictus	***Sepia officinalis***	***Trichiurus lepturus***
	Sparus caeruleostictus	*Balistes forcipatus*
Chilomycterus spinosus		*Brachydeuterus auritus*
Chloroscombrus chrysurus	*Apsilus fuscus*	*Chloroscombrus chrysurus*
Dasyatis sp.	*Balistes capriscus*	*Lagocephalus laevigatus*
Dentex canariensis	*Chaetodon* sp.	*Lepidotrigla* sp.
Drepane africana	*Chromis lineatus*	*Priacanthus arenatus*
Elops senegalensis	*Dactylopterus volitans*	*Raja miraletus*
Epenephelus aeneus	*Decapterus* sp.	*Scyacium micrurum*
Eucinostomus melanopterus	*Epinephelus aeneus*	*Sepia officinalis*
Grammoplites gruveli	*Lethrinus atlanticus*	*Selene dorsalis*
Lutjanus fulgens	*Sphyraena sphyraena*	*Serranus accraensis*
Sardinella maderensis	*Trigla* sp.	*Sphyraena sphyraena*
Sphyraena sphyraena		*Trachurus* sp.
Torpedo sp.		*Umbrina* sp.

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, which seems to imply that with a wide depth range, 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 (Fig. 2), it appears that the first 2 species assemblages derived from the GTS data are separated mainly by sediment type—the first on soft bottom and the sec-

Table 5. Jaccard's index of similarity between pairs of assemblages for the same survey. *Italics*: upwelling period; **bold**: stratified period

Group	GTS			MFRD3			MFRD5		
	1	2	3	1	2	3	1	2	3
1	1	*0.27*	*0.35*	1	*0.45*	*0.37*	1	*0.43*	*0.33*
2	**0.45**	1	*0.35*	**0.36**	1	*0.35*	**0.45**	1	*0.37*
3	**0.40**	**0.41**	1	**0.36**	**0.46**	1	**0.39**	**0.46**	1

Table 6. Within-survey Similarity Ratios among the 3 assemblages. *Italics*: upwelling period; **bold**: stratified period

Group	GTS			MFRD3			MFRD5		
	1	2	3	1	2	3	1	2	3
1	1	*0.09*	*0.01*	1	*0.17*	*0.10*	1	*0.20*	*0.06*
2	**0.18**	1	*0.23*	**0.16**	1	*0.10*	**0.60**	1	*0.12*
3	**0.01**	**0.28**	1	**0.30**	**0.07**	1	**0.01**	**0.04**	1

ond on hard bottom. Assemblages 3 and 4 are separated by both sediment type and depth. The last 2 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 the case of short depth range, it appears, therefore, that these physico-chemical parameters are important in the dynamics of the assemblages.

The information on the site-environmental variables bi-plots (Fig. 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 & 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 & 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 3 assemblages and the 3 surveys, only shows subtle seasonal and temporal differences in assemblage structure. The calculated values of the Jaccard Index and Similarity Ratio (Tables 5 & 6) indicate that closest resemblance was found for assemblages 2 and 3 during the upwelling season and assemblages 1 and 2 in the stratified 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 stratified periods. Differences in assemblage structure have been attributed to a differential response to changes in environmental forcing factors (Gulland & Garcia 1984, Overholtz & Tyler 1985, Macpherson & Gordoa 1992). Thus, the differences may be as a consequence of the environmental perturbations observed during the climatic periods. For example, Gulland & Garcia (1984) noted that the Sparid assemblage has affinity for the low temperature, high salinity environment that prevailed in the Gulf of Guinea during the second climatic period (1972 to 1982).

Differences in the assemblages during the period in question could also be a consequence of the proliferation of triggerfish *Balistes capriscus*, a species of the Sparid assemblage, and associated ecological changes in the Gulf of Guinea between 1972 and 1988 (Ansa-Emmim 1979, Koranteng 1998). Koranteng (1998) showed that the increased abundance of triggerfish also destabilised the shallow water assemblages, especially the Lutjanid and the shallow part of the Sparid.

Changes in the pattern and intensity of fishing could well induce changes in the structure of demersal assemblages (Brown et al. 1976, Overholtz & Tyler 1985). GTS was conducted 17 yr 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 d in 1974 to 5500 d 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 n mile of exclusive economic zone in accordance with the Third United Nations Convention on the Law of the Sea.

It appears that natural and anthropogenic factors, conjointly or singly, affected the nature of species assemblages in Ghana's coastal waters. It is acknowledged, however, that it is often difficult, if not impossible, to separate natural fluctuations from those caused by anthropogenic factors such as exploitation (Cushing 1980, Sissenwine et al. 1982).

CONCLUSION

The analyses of community structure identified 6 species assemblages on the continental shelf and upper slope off Ghana. The first 2, namely the Sciaenid and Lutjanid assemblages, are predominantly suprathermocline whilst the 2 Sparid assemblages begin at the thermocline depth (~40 m) and extend offshore. The last 2 (deep shelf and upper slope) assemblages occur well below the thermocline.

The Sciaenid community is associated with the soft, muddy substrate found in shallow waters generally <40 m deep, and is made up mainly of species of the *Pseudotolithus* and *Galeoides* genera. Lying beyond this belt is a wide area of mixed-to-hard bottom, with which the Lutjanid and the Sparid assemblages (shallow and deep parts) are associated. There are clear faunal discontinuities around 30–40, 100 and 200 m depth. The first ecotone is closely related to bottom depth and the presence and depth of 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 being 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 an 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. However, it is difficult from this study, to separate fluctuations due to long-term environmental changes from those caused by anthropogenic factors such as fishing.

Acknowledgements. I am grateful to Professor Jacqueline McGlade, Dr Gabriella Bianchi and the reviewers for their constructive criticism and comments that have undoubtedly improved this paper.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: May 30, 2000; Accepted: February 20, 2001
Proofs received from author(s): September 7, 2001