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Demersal fish assemblages of the Gulf of Salamanca, Colombia (southern Caribbean Sea)

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ABSTRACT: The structure of the demersal fish assemblages of the Gulf of Salamanca, Colombian Caribbean Sea, was studied based on 4 trawl surveys carried out in December 1995, April and August 1996, and February 1997. Multivariate analysis revealed the presence of 2 distinct assemblages, one belonging to the continental shelf (<50 m depth) and the other belonging to the upper slope (>50 m depth). The continental shelf assemblage showed significantly more biomass per tow but not more individuals or species. It is typified by species of interest for the artisanal fishery, like *Lutjanus analis* and *Calamus penna*. *Lutjanus synagris*, however, also of interest for the fishery, typifies the upper slope assemblage. No temporal change was detected in the assemblage structure, at least for the sampling dates in this study, but many species in the assemblages were scarce and rare, indicating high spatial and temporal patchiness. The assemblages found do not fully adjust to existing zonation schemes or assemblages defined in neighboring areas, probably due to the effect of the spatial scale of the studies and the width of the shelf in the Gulf of Salamanca.

KEY WORDS: Demersal fish assemblages · Southern Caribbean Sea · Colombia

INTRODUCTION

The reduction of catch rates and mean size of individuals is a well documented trend in world fisheries (Pitcher 1996). This situation has prompted new approaches to the study of exploited populations, including the study of the fish assemblage structure in relation to environmental variables, and the characterization of seasonal changes for the improvement of management practices (Cady & Sharp 1986).

The present work originated from a similar motivation. The Gulf of Salamanca is used by the artisanal fishery with few restrictions or regulations. Recent trends of reduction of catches by the artisanal fishery on the Caribbean coast of Colombia in the last decade (5886 tonnes landed in 1986 vs 4616 landed in 1995, INPA 1995) have made clear the need for implementing some management measurements, if the fishery is to be sustained and to have any economic importance. For the Gulf of Salamanca, an expansion of the artisanal fishery depth range (now within the 0 to 20 m depth limit) has been proposed.

The study area is also of interest in ecological terms as it shows the potential for strong seasonality as a result of the wind regime that probably causes an upwelling phenomenon in interplay with the rainfall patterns which drive the seasonal entry of freshwater masses to certain areas in the gulf (see 'Study area'). The comparisons of this tropical shelf system with other tropical systems under a similar dynamic pattern might reveal some general trends in the ecology of demersal fish communities.

To our knowledge, there are few multivariate studies of tropical demersal fish assemblages in the Caribbean (excluding coral reef areas, hard banks and coastal lagoons). The study done by Yañes-Arancibia & Sánchez-Gil (1986) can be cited in this context. Lowe-McConnell (1962) studied the demersal fish fauna off Guyana and Bianchi (1992a) did the same for Guyana, Surinam and Venezuela. Multivariate studies in the south Atlantic Bight of the United States have been conducted by Sedberry & van Dolah (1984) and Wenner & Sedberry (1989). The tropical Pacific coast of

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America has been studied by Bartels et al. (1983), Bianchi (1991) and Wolff (1996).

Studies done at several latitudes have highlighted patterns of spatial and temporal variation in composition, abundance and distribution of demersal fish assemblages. These variations have been related to gradients and fluctuations of factors such as depth (Bartels et al. 1983, Bianchi 1991, Gray & Otway 1994), seasonal changes in water salinity and temperature (Allen 1982, Blaber et al. 1989, Watson et al. 1990, Ansari et al. 1995), distance to the coastline (Rainer & Munro 1982), bottom type (Martin et al. 1985) and hydrographic conditions (Bianchi 1991). However, the dominant gradient affecting the distribution of the demersal fish assemblages appears to be depth.

STUDY AREA

The Gulf of Salamanca (Fig. 1) is within 11° 00' and 11° 19' N and 74° 12' and 74° 50 W. The sampled area corresponds to the trawlable area of the gulf between the 10 and 200 m isobaths (Fig. 1) which accounts for 650 km^2, approximately. The trawlable area was defined according to a previous bottom survey performed by the authors and previous trawl experiences (Blanco 1993). Depths less than 10 m were not sampled as they were not accessible to the ships used. Fig. 2 shows the bathymetric profiles of 4 selected sectors in the gulf. As can be seen the continental shelf in the region shows a discrete size with a maximum width of just 16 km and the shelf slope is steep. Stromme & Saetersdal (1989) placed the border of the Colombian Caribbean continental shelf between 50 and 60 m depth in average as is the case in the Gulf of Salamanca (Fig. 2).

The shelf is dominated by litoclastic sand at shallow depths but it becomes muddy toward the shelf edge (Molina 1993) and to the west in the influence area of the Magdalena river (Fig. 1, pers. obs.). In front of the Cienaga Grande de Santa Marta (Fig. 1), fine sand-shell bottoms are dominant. Near the shelf edge a reef-like formation called Las Animas Bank (Blanco et al. 1994) is located, which provides spatial heterogeneity to the sea floor of the gulf but reduces the trawlable area.

The region is dry with an accumulated yearly precipitation that ranges between 400 and 800 mm (Eslava et al. 1986). Rainfall has a bimodal behavior (Fig. 3) generated by the interplay of the trade winds and the displacement of the Intertropical Convergence Zone (ITCZ). Between December and April, there is a

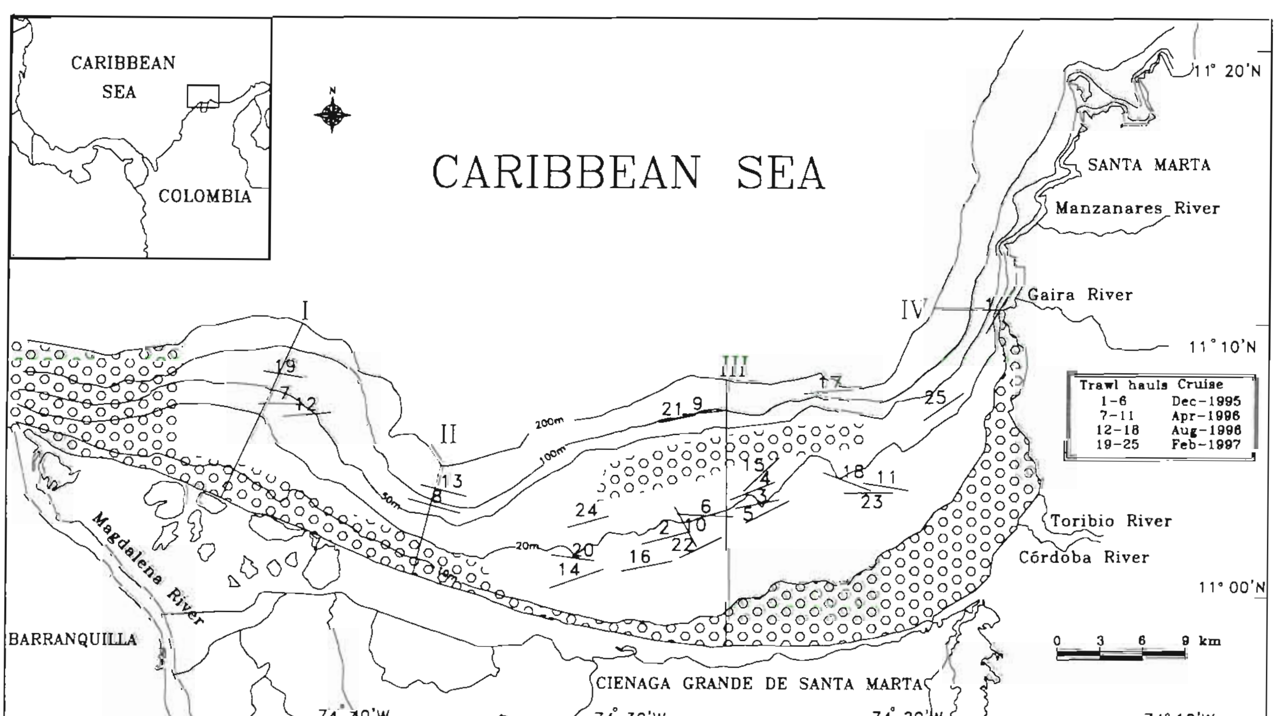

Fig. 1. The Gulf of Salamanca (Colombian Caribbean), showing sampling sites, trawlable area and the non trawlable or not accessible area (shaded), the path of each trawl and the position of the depth transects shown in Fig. 2. The area shaded less than 10 m depth is not accessible to the ships. The non trawlable areas are so due to permanent rough sea conditions (to the east of the Magdalena river) or due to irregular, rough bottom

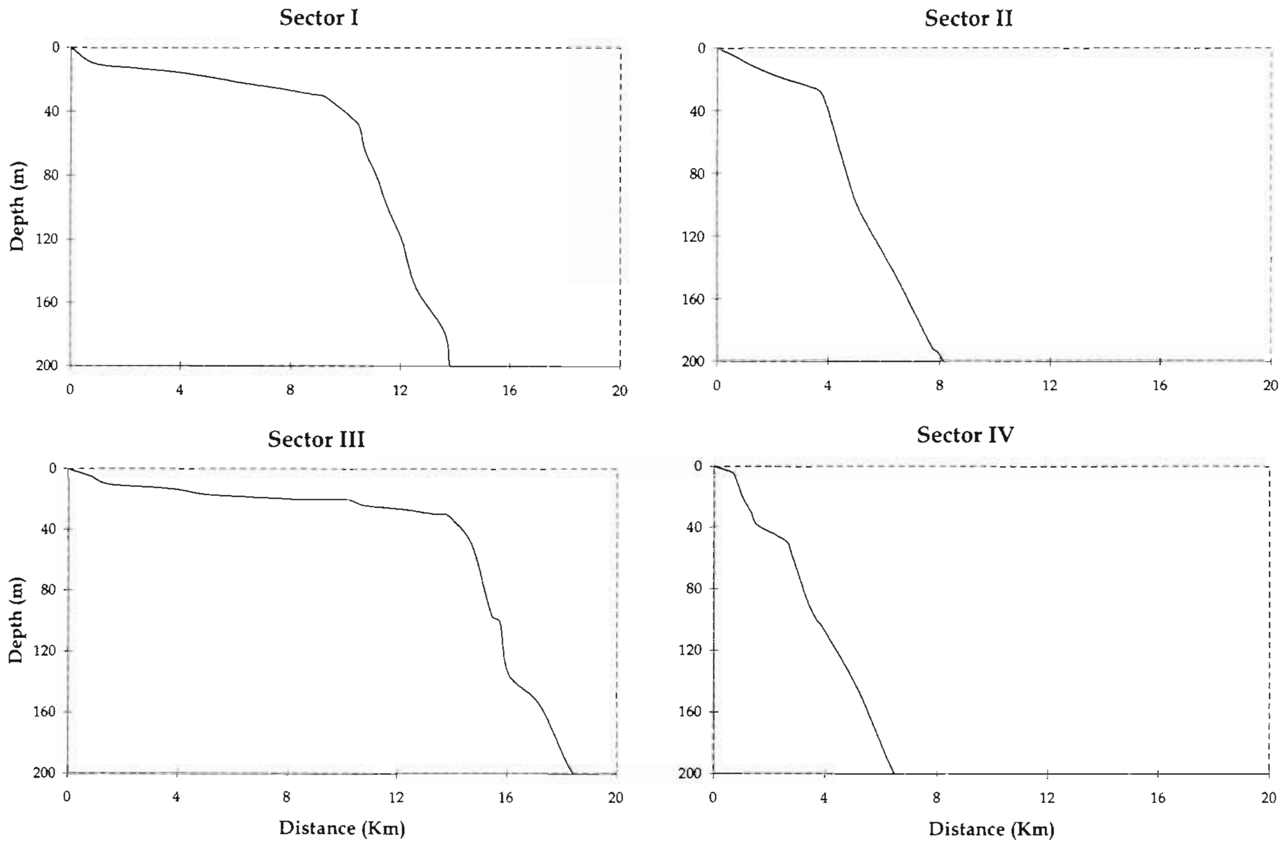

Fig. 2. Depth transects in 4 sectors of the Gulf of Salamanca (Colombian Caribbean) according to nautical chart COL-407

particularly dry period under the direct influence of the trade winds when the ITCZ occupies its southernmost position. In May and June the first rainy period occurs when atmospheric pressure is low, followed by a short dry period called 'veranillo de San Juan' in July-August. The year ends with a period (September to November) of stronger precipitation when the ITCZ is over the region (Marquez 1982, Salzwedel & Müller 1983). Fig. 3 shows that 1996, when most of the sampling campaigns took place, was rainier than average.

The current regime is dependent upon the trade winds. When they are strong (dry season, December to April) they generate the Caribbean Current that runs southwest parallel to the coast. When the trade winds

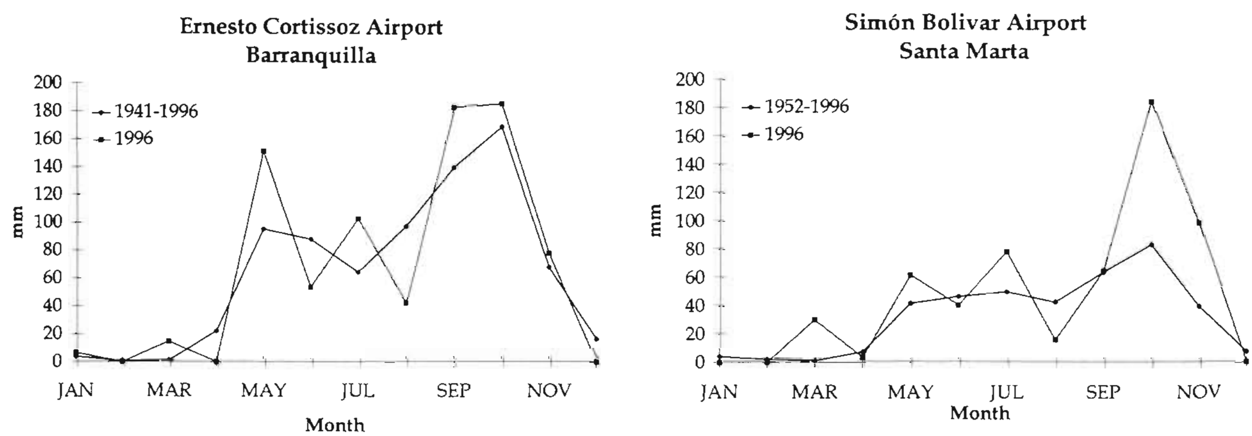

Fig. 3. Multiannual monthly patterns of precipitation and monthly precipitation in the year 1996 as registered at airports in the vicinity to the study area. Source: Instituto de Estudios Ambientales, IDEAM

weaken (rainy season, May to November), the 'Panama' Counter Current, running northeast, eventually reaches the Guajira Peninsula (12° N, Marquez 1982, Molina 1993) but because of the east-west orientation of the Gulf of Salamanca, it presumably does not enter the gulf. As a consequence of this current regime the central part of the Gulf of Salamanca presents oceanic conditions, whereas the western part is seasonally influenced by the Magdalena river plume and the east part is influenced by the Cienaga Grande de Santa Marta and the inflow of other minor rivers. Upwelling waters have been detected up to 75° W, which includes the Gulf of Salamanca, but these waters have been characterized as oligotrophic, causing physical (water cooling) rather than biological effects (Ramirez 1993, Blanco et al. 1994).

MATERIALS AND METHODS

Trawl data. The material was collected on 4 cruises: Cruise 9600 (17 to 19 December 1995, 6 trawls) was done with the RV 'Ancon', Cruises 9601 (10 to 13 April 1996, 5 trawls) and 9602 (8 to 13 August 1996, 7 trawls) were done with the RV 'Malpelo' and finally cruise 9701 (6 to 9 February 1997, 7 trawls) was done again with the RV 'Ancon' For the purposes of this study the February and April cruises were considered representative of the dry season, and the August and December ones representative of the rainy season.

Table 1 shows the characteristics of the fish otter trawls used during the study. Each tow lasted 30 min at an average speed of 3.5 knots. As the number of stations per cruise was limited by the available ship time, the trawlable area (Fig. 1) was divided into 4 subareas around the depth profiles shown in Fig. 1, so as to ensure a complete cover of the Gulf, with the exception of Cruise 9600 where simple random positioning of the trawl stations resulted in an uneven cover (Fig. 1). The actual position of the stations inside a subarea was chosen randomly. Each specimen caught was counted and weighed (wet weight) separately. The biomass and density were estimated by means of the 'swept area' method (Espino & Wosnitza-Mendo 1984). For this calculation, divergence measurements between the 2 cables of the net were done at regular intervals 5 times during each tow. The mean swept area for a trawl in the study was 0.04381 km^2, to which biomass and numbers of individuals are referred.

Table 1 Fishing gear characteristics of the survey ships used in the study

	RV 'Ancón'	RV 'Malpelo'
Headrope (m)	20.60	33.30
Groundrope (m)	25.60	41.60
Trawl length (m)	28.50	38.20
Bridles (m)	50.20	60.00
Mesh size (mm)	45.00	50.80
Mean path width (m)	11.14	19.03

At each station water column and bottom salinity and temperature were measured and sediment samples were taken by means of a van Veen grab. In Cruise 9602, the water temperature was not measured due to a malfunction of the CTD probe.

Data analysis. Since the main purpose of this study was to identify the assemblages of demersal fishes and to relate them to environmental factors, the analysis strategy described by Field et al. (1982) was followed. The trawl stations were ordered on the basis of a biomass matrix by means of a nonmetric multidimensional scaling (NMDS) ordination. The typifying and discriminating species of the clusters of stations revealed by the NMDS were determined using the SIMPER procedure (Clarke 1993). This procedure determines the average contribution of each species to the similarity (typifying species) and dissimilarity (discriminating species) between groups of samples (Clarke 1993).

A relationship to environmental data was obtained by superimposing the environmental data as symbols scaled in size to the data value on the biotic NMDS ordination (Field et al. 1982) and by the BIO-ENV procedure proposed by Clarke & Ainsworth (1993). This procedure measures the match between the similarity matrices underlying both biotic and abiotic NMDS ordination of the samples by means of a rank correlation (Spearman) coefficient (Clarke & Ainsworth 1993).

In order to test the null hypothesis that the demersal fish assemblages do not differ in structure between depth strata, the ANOSIM procedure (Clarke & Green 1988, Clarke 1993) was used. This test is based on the rank similarities between samples in the underlying similarity matrix. A test statistic R is defined as the difference between the average of all rank similarities among replicate samples within groups, and the average of rank similarities arising from all pairs of samples between groups, the groups of samples defined under the null hypothesis. The R statistic is recomputed under permutation of the sample labels. The significance level of the test is found by referring the observed R value to its permutation distribution. If the observed R value looks unlikely to have come from this distribution the null hypothesis can be rejected at a significance level of $100(t+1)/(T+1)\%$, where t is the number of the T simulated R values as large as or larger than the observed R (Clarke & Green 1988, Clarke 1993).

By means of 1-way ANOVAs, the null hypothesis that Hill diversity numbers 1 and 2 (Hill 1973), species

richness, density and biomass per trawl station do not differ between depth strata was tested. In equation form Hill's family of diversity numbers are:

$$NA = \sum_{i=1}^{s} (p_i)^{1/(1-A)}$$

where p_i is the proportion of biomass (in this case) belonging to the ith species, A is the order of these diversity numbers, and s is the number of species.

Biomass dominance patterns were compared between depth strata by means of k-dominance curves (Lambshead et al. 1983) which represent the ranking in percentage of the species in decreasing order of importance. Logging the x (rank) axis allows better visualization of the plot.

The temporal fish assemblage change was tested by the following null hypotheses: the assemblage structure between cruises is not different (ANOSIM procedure, Clarke & Green 1988, Clarke 1993), in this case with the trawl stations grouped by depth stratum in order to control for this factor, and Hill diversity numbers 1 and 2 (Hill 1973), species richness, density and biomass per trawl station do not differ between cruises, in this case regardless of depth stratum.

For all the ANOVA tests normality of the data and homogeneity of variance were tested and data were transformed (number of individuals and biomass, log[x+1]) when necessary. In case of a significant F, a multiple comparisons test was performed (Tukey test, Zar 1984).

RESULTS

Table 2 shows the geographical location, date, time and environmental values of each trawl station. Trawling covered depths between 13 and 154 m. Because the area with depths between 10 and 30 m represented more than 50% of the trawlable area, sampling was concentrated there.

From the 25 trawl stations a total of 6680 individuals weighing 1873.4 kg was collected. A total of 126 species was found distributed in 54 families. Table 3 shows the ranking of these species according to their frequency, accumulated abundance and biomass. A feature of the presence-dominance structure of this demersal fish community was the occurrence of a small group of species that were common and abundant in numbers and biomass throughout the gulf. This background group (defined as those species that appeared at least 3 times and their number or biomass ranked among the first 10, Table 3) included species like *Lutjanus analis*, *Lutjanus synagris*, *Calamus penna*, *Balistes capriscus*, *Selene vomer*, *Selene setapinnis*, *Diodon holacanthus*, *Eucinostomus argenteus*, *Chloroscombrus chrysurus*, *Lutjanus jocu*, *Eucinostomus gula*, *Sciaena trewavasae* and *Holocentrus ascensionis*. The remaining 113 species are scarce or rare (Table 3).

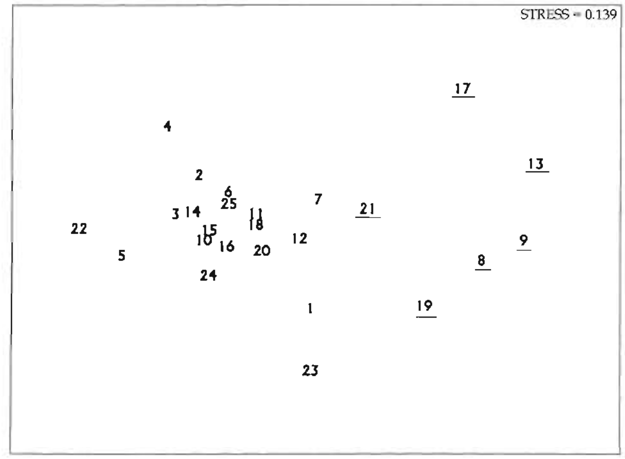

Fig. 4. Ordination (NMDS) of the trawl stations in the Gulf of Salamanca (Colombian Caribbean). Underlined trawl station numbers are stations placed deeper than 50 m

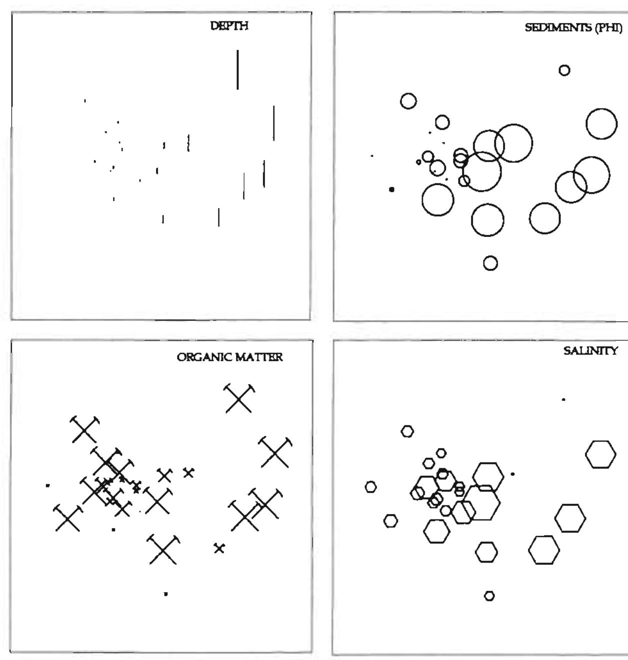

Fig. 5. Superposition of some environmental variables on the trawl stations ordination shown in Fig. 4. Symbol size is in proportion to variable value

Fig. 4 shows the NMDS ordination of the 25 stations of the study. Two clusters of stations along the x axis can be distinguished. Superimposition of the environmental variables (Fig. 5) and the BIO-ENV analysis (Table 4) reveals that depth and, secondarily, median grain size (phi transformation, Buchanan & Kain 1984)

Table 2. Geographical position and environmental variable values of the trawl stations in the Gulf of Salamanca, Colombian Caribbean

Cruise 9600	Stn 1	Stn 2	Stn 3	Stn 4	Stn 5	Stn 6	
Date (mm/dd/yy)	12/16/95	12/18/95	12/18/95	12/19/95	12/19/95	12/19/95	
Initial time (h)	11:00	13:30	16:15	09:10	14:05	15:18	
Final time (h)	11:30	14:00	16:47	09:40	14:37	15:50	
Coordinates, initial: N	11° 09.900'	11° 03.580'	11° 04.430'	11° 05.400'	11° 05.120'	11° 04.210'	
W	74° 15.500'	74° 26.310'	74° 24.680'	74° 23.240'	74° 22.830'	74° 26.790'	
Coordinates, final: N	11° 11.430'	11° 03.120'	11° 04.750'	11° 04.740'	11° 03.900'	11° 03.910'	
W	74° 14.620'	74° 28.090'	74° 23.100'	74° 24.880'	74° 24.300'	74° 24.800'	
Median depth (m)	41.5	17.7	18.5	20.5	16.5	18.5	
Sediments (Φ)	3.94	2.11	2.29	2.96	2.29	2.11	
Organic matter (% dry wt)	15.642	10.701	11.883	10.953	11.883	10.701	
Bottom salinity	36.77	36.70	36.64	36.64	36.64	36.60	
Bottom temperature (°C)	25.68	26.38	26.56	26.36	26.36	26.60	
Cruise 9601	Stn 7	Stn 8	Stn 9	Stn 10	Stn 11		
Date (mm/dd/yy)	4/10/96	4/11/96	4/11/96	4/11/96	4/12/96		
Initial time (h)	20:35	11:24	20:00	06:58	16:05		
Final time (h)	21:05	11:59	20:36	07:30	16:35		
Coordinates, initial: N	11° 07.969'	11° 03.267'	11° 07.043'	11° 03.026'	11° 04.902'		
W	74° 40.504'	74° 34.706'	74° 25.166'	74° 26.078'	74° 20.006'		
Coordinates, final: N	11° 08.003'	11° 03.789'	11° 06.854'	11° 04.481'	11° 04.641'		
W	74° 42.225'	74° 36.635'	74° 27.081'	74° 26.881'	74° 18.341'		
Median depth (m)	32.5	105.5	109.0	17.0	13.0		
Sediments (Φ)	3.85	3.87	4.16	2.11	2.87		
Organic matter (% dry wt)	19.497	19.283	15.739	10.701	9.974		
Bottom salinity	36.08	36.82	36.81	35.58	35.85		
Bottom temperature (°C)	26.55	23.95	23.89	26.95	27.36		
Cruise 9602	Stn 12	Stn 13	Stn 14	Stn 15	Stn 16	Stn 17	Stn 18
Date (mm/dd/yy)	8/8/96	8/9/96	8/10/96	8/10/96	8/10/96	8/13/96	8/13/96
Initial time (h)	11:11	17:25	07:57	12:05	08:01	05:56	10:49
Final time (h)	11:40	17:55	08:33	12:35	08:32	06:25	11:19
Coordinates, initial: N	11° 07.520'	11° 04.250'	11° 03.230'	11° 04.930'	11° 03.010'	11° 08.010'	11° 04.516'
W	74° 41.380'	74° 35.820'	74° 31.750'	74° 24.120'	74° 28.820'	74° 20.490'	74° 19.450'
Coordinates, final: N	11° 07.700'	11° 03.890'	11° 04.210'	11° 06.300'	11° 03.390'	11° 07.910'	11° 05.290'
W	74° 39.520'	74° 34.500'	74° 29.580'	74° 23.090'	74° 26.940'	74° 22.210'	74° 21.500'
Median depth (m)	32.0	137.0	13.5	22.5	15.0	153.5	13.3
Sediments (Φ)	4.32	3.83	2.70	2.96	2.11	2.65	2.87
Organic matter (% dry wt)	22.843	19.232	16.692	11.405	10.701	6.289	9.974
Bottom salinity	36.64	36.81	36.19	36.28	36.19	36.71	35.70
Bottom temperature (°C)	–	–	–	–	–	–	–
Cruise 9701	Stn 19	Stn 20	Stn 21	Stn 22	Stn 23	Stn 24	Stn 25
Date (mm/dd/yy)	2/6/97	2/7/97	2/8/97	2/8/97	2/9/97	2/15/97	2/19/97
Initial time (h)	08:18	17:44	11:40	16:09	09:35	09:18	11:28
Final time (h)	08:48	18:15	12:13	16:40	10:05	09:48	12:04
Coordinates, initial: N	11° 09.201'	11° 03.399'	11° 06.605'	11° 03.235'	11° 04.547'	11° 04.391'	11° 07.189'
W	74° 42.005'	74° 31.498'	74° 27.482'	74° 25.428'	74° 18.900'	74° 30.926'	74° 17.794'
Coordinates, final: N	11° 08.962'	11° 03.187'	11° 06.873'	11° 02.583'	11° 04.535'	11° 04.804'	11° 08.210'
W	74° 40.513'	74° 29.933'	74° 26.178'	74° 26.656'	74° 20.713'	74° 29.416'	74° 16.306'
Median depth (m)	77.0	19.5	73.0	15.3	12.8	24.8	21.5
Sediments (Φ)	3.85	2.70	4.24	2.11	2.87	3.92	2.08
Organic matter (% dry wt)	19.497	16.692	6.672	10.701	9.974	17.297	15.285
Bottom salinity	35.90	35.61	36.10	35.60	35.62	35.60	35.75
Bottom temperature (°C)	25.60	26.20	25.80	26.00	26.10	26.20	26.40

Table 3. Species list, frequency (presence in the trawl stations), total numbers and accumulated biomass (g) of the species caught in the study by means of demersal trawls in the Gulf of Salamanca, Colombian Caribbean. Superscripts indicate the top 10 ranked species in number and biomass

Species	Frequency	Number	Biomass	Species	Frequency	Number	Biomass
Lutjanus analis	19	198	252900 [2]	*Dasyatis guttata*	2	3	20530
Lutjanus synagris	16	769 [2]	245965 [3]	*Pomacanthus arcuatus*	2	3	1620
Balistes capriscus	15	870 [1]	310525 [1]	*Pagrus pagrus*	2	3	1620
Calamus penna	15	247 [9]	152680 [4]	*Squatina dumeril*	2	3	1410
Selene vomer	13	57	27090	*Alectis ciliaris*	2	2	1710
Acanthostracion poligonius	9	81	15695	*Ocyurus chrysurus*	2	2	1200
Diodon holacanthus	7	527 [3]	140510 [5]	*Epinephelus niveatus*	2	2	270
Selene setapinnis	7	219	34955 [9]	*Chaetodon capistratus*	2	2	90
Rhomboplites aurorubens	7	35	5735	*Haemulon steindachneri*	1	493 [4]	85960 [6]
Pomacanthus paru	7	15	18925	*Menticirrhus littoralis*	1	37	3550
Balistes vetula	7	15	16120	*Diapterus rhombeus*	1	27	2420
Ogcocephalus cf. *nasutus*	7	13	3100	*Haemulon plumieri*	1	20	10000
Eucinostomus argenteus	6	448 [5]	19490	*Caranx ruber*	1	11	4060
Chaetodipterus faber	6	52	29975	*Eugerres plumieri*	1	11	2225
Trichiurus lepturus	6	13	3830	*Saurida brasiliensis*	1	11	160
Chloroscombrus chrysurus	5	306 [7]	17490	*Cynoscion jamaicensis*	1	10	1200
Opisthonema oglinum	5	36	4590	*Trachinotus carolinus*	1	8	13720
Caranx crysos	5	17	7680	*Macrodon ancylodon*	1	6	2000
Acanthostracion quadricornis	5	15	2685	*Pristipomoides macrophthalmus*	1	6	1160
Caranx bartholomei	5	8	11150	*Lutjanus cyanopterus*	1	6	360
Anisotremus virginicus	5	7	2060	*Mustelus* cf. *canis*	1	5	2500
Eucinostomus gula	4	238 [10]	9815	*Chaetodon ocellatus*	1	5	400
Ctenosciaena gracilicirrhus	4	91	8530	*Calamus calamus*	1	4	2280
Sphyraena guachancho	4	35	11215	*Prionotus punctatus*	1	4	400
Lutjanus jocu	4	33	51215 [8]	*Scyacium micrurum*	1	3	190
Rhinesomus bicaudalis	4	24	9100	*Diapterus auratus*	1	2	950
Priacanthus arenatus	4	5	2340	*Raja cervigoni*	1	2	540
Narcine brasiliensis	4	5	2000	*Hemicaranx amblyrhynchus*	1	2	230
Scorpaena plumieri	4	5	1795	*Prionotus stearnsi*	1	2	220
Sciaena trewavasae	3	380 [6]	34910 [10]	*Pomadasys crocro*	1	2	160
Holocentrus ascensionis	3	263 [8]	63440 [7]	*Diodon histrix*	1	1	5500
Pristipomoides aquilonaris	3	142	11880	*Caranx falcatus*	1	1	2100
Micropogonias furnieri	3	92	17460	*Rhinobatos perceles*	1	1	800
Haemulon aurolineatum	3	73	3465	*Lagocephalus laevigatus*	1	1	800
Serranus atrobranchus	3	39	330	*Lutjanus vivanus*	1	1	750
Haemulon boschmae	3	33	6800	*Echeneis naucrates*	1	1	750
Albula vulpes	3	26	13890	*Epinephelus itajara*	1	1	700
Lutjanus apodus	3	20	11685	*Aluterus monoceros*	1	1	700
Selar crumenophthalmus	3	17	4010	*Calamus* sp.	1	1	520
Upeneus parvus	3	15	860	*Umbrina broussonnettii*	1	1	480
Caranx hippos	3	14	6435	*Sparisoma rubiprinne*	1	1	460
Anisotremus surinamensis	3	13	10675	*Trachinotus goodei*	1	1	450
Acanthurus chirurgus	3	12	5200	*Caulolatilus guppyi*	1	1	420
Trachinotus falcatus	3	9	16045	*Gymnothorax ocellatus*	1	1	300
Fistularia tabacaria	3	9	3070	*Prionotus roseus*	1	1	220
Scomberomorus brasiliensis	3	8	3030	*Synodus foetens*	1	1	200
Bagre marinus	3	8	1690	*Scorpaena brasiliensis*	1	1	200
Saurida normani	3	8	730	*Polydactylus* sp.	1	1	200
Lutjanus purpureus	3	6	6960	*Acanthurus bahianus*	1	1	200
Fistularia petimba	3	6	1860	*Haemulon chrysargyreum*	1	1	120
Steindachneria argentea	2	154	1340	*Dactylopterus volitans*	1	1	120
Porichthys plectrodon	2	86	1190	*Larimus breviceps*	1	1	80
Selene brownii	2	22	3205	*Cynoponticus savanna*	1	1	80
Synagrops trispinosus	2	16	285	*Prionotus arenatus*	1	1	40
Calamus pennatula	2	15	9745	*Lutjanus bucanella*	1	1	30
Albula nemoptera	2	11	4760	*Apogon quadrisquamatus*	1	1	25
Diaphus cf. *dumerili*	2	11	30	Paralepididae	1	1	20
Neoepinnula orientalis	2	6	450	*Lepophidium aporrhox*	1	1	20
Lutjanus mahogoni	2	5	900	*Synodus poeyi*	1	1	15
Eucinostomus sp.	2	5	220	*Cytharichthys* cf. *dinoceros*	1	1	10
Dasyatis americana	2	4	5810	*Chaetodon sedentarius*	1	1	10
Haemulon album	2	4	1940	*Paraconger* sp.	1	1	5
Pseudopeneus maculatus	2	4	220				

Table 4. BIO-ENV combination of the environmental variables ranked according to the match of biotic and abiotic similarity matrices. 1: depth; 2: sediment Φ; 3: organic matter; 4: bottom salinity; 5: bottom temperature; 6: northern coordinate; 7: western coordinate; 8: rainfall; 9: sampling date

	r	1	2	3	4	5	6	7	8	9
Cruise 9600										
1	0.804	x								
2	0.797	x	x							
3	0.797	x	x	x						
4	0.720	x	x	x			x			
5	0.660	x	x	x		x	x			
6	0.665	x	x	x		x	x	x		
7	0.604	x	x	x	x	x	x	x		
Cruise 9601										
1	0.955	x			x	x	x			
2	0.946	x	x		x	x	x			
3	0.924	x								
4	0.924	x				x				
5	0.924	x			x	x				
6	0.862	x	x		x	x	x	x		
7	0.753	x	x	x	x	x	x	x		
Cruise 9602										
1	0.749	x								
2	0.694	x			x					
3	0.637	x		x	x					
4	0.568	x		x	x		x			
5	0.450	x		x	x		x	x		
6	0.359	x	x	x	x		x	x		
Cruise 9701										
1	0.437	x								
2	0.435	x				x				
3	0.314	x		x		x				
4	0.249	x		x	x	x				
5	0.228	x	x	x	x	x				
6	0.175	x		x	x	x	x	x		
7	0.166	x	x	x	x	x	x	x		
Study total										
1	0.610	x								
2	0.519	x	x							
3	0.498	x	x		x					
4	0.494	x	x		x		x			
5	0.479	x	x		x		x			x
6	0.464	x	x	x	x		x			x
7	0.408	x	x	x	x		x		x	x
8	0.387	x	x	x	x		x	x	x	x

were the variables that better fit the biological ordination. The *x* axis in the biological ordination represents a depth gradient with shallow trawl stations (less than 50 m depth) clustering to the left and deep stations (more than 50 m depth) clustering to the right. As the 50 m depth limit can be taken to represent the border of the continental shelf in the Gulf of Salamanca (see Fig. 2 and Stromme & Saeterdsal 1989) this result suggests the existence of 2 distinct assemblages: one belonging to the continental shelf and the other belonging to the upper slope.

Table 5. Percentage contributions of typifying species (over 5%) and discriminating species (over 2%) to within-group similarity and between-group dissimilarity, respectively, identified by SIMPER analysis examining between the 2 demersal fish assemblages found in the Gulf of Salamanca. S: shelf; U.SL.: upper slope

Typifying species	S. (<50 m)	U.SL. (>50 m)
Lutjanus analis	31.77	–
Calamus penna	19.54	–
Balistes capriscus	14.79	–
Diodon holacanthus	6.68	–
Selene vomer	5.92	–
Chaetodipterus faber	5.04	
Lutjanus synagris	7.17	37.19
Rhomboplites aurorubens	–	15.32
Ctenosciaena gracilicirrhus	–	9.54
Pristipomoides aquilonaris	–	9.40
Pagrus pagrus	–	5.93
Sciaena trewavasae	–	5.18
Within-group similarity	29.29	14.83
Discriminating species	**S. vs U.SL.**	
Lutjanus analis	10.07	
Balistes capriscus	7.98	
Calamus penna	8.27	
Lutjanus synagris	6.26	
Diodon holacanthus	5.02	
Sciaena trewavasae	3.10	
Pristipomoides aquilonaris	2.48	
Chaetodipterus faber	2.27	
Ctenosciaena gracilicirrhus	2.23	
Selene vomer	3.26	
Selene setapinnis	2.00	
Rhomboplites aurorubens	2.00	
Lutjanus jocu	2.26	
Between-group dissimilarity	93.90	

The ordination of the 25 trawl stations exhibits a marginal relation with the bottom salinity, sampling date, northern and western coordinates as shown by the BIO-ENV analysis (Table 4). This result suggested that the composition and distribution of the demersal fish assemblages in the Gulf of Salamanca was weakly dependent upon seasonal changes (at least for our sampling dates) and the only spatial gradient of importance was the one associated with depth. The secondary importance level of other variables was confirmed when the BIO-ENV analysis per cruise was considered. In Table 4 it can be seen that variables like bottom salinity and temperature ranked always in second place or first in one case but in combination with the depth.

The analysis of similarity (ANOSIM) revealed that the demersal fish assemblage of the shelf differed in structure from the assemblage of the upper slope ($p < 0.05$). Table 5 shows the species found by the SIMPER procedure to typify and discriminate the trawl station

Table 6. Comparisons of the mean biomass, density, number of species, and Hill numbers 1 and 2 per trawl station between the 2 demersal fish assemblages found in the study and between cruises. Mean values ± standard error. S.: shelf; U.SL.: upper slope

	S. (<50 m)	U.SL. (>50 m)	9600	9601	9602	9701
Biomass (kg)	87.50 ± 15.24	14.60 ± 3.19	82.36 ± 25.87	64.59 ± 18.98	86.20 ± 34.10	47.09 ± 22.50
Density (ind./0.04381 km^2)	276.43 ± 71.63	135.58 ± 73.98	204.57 ± 107.29	398.98 ± 92.29	339.71 ± 171.64	102.25 ± 41.06
Number of species	14.80 ± 1.48	12.17 ± 3.63	11.39 ± 1.50	22.4 ± 1.50	15.29 ± 2.58	11.28 ± 2.63
Hill 1	6.68 ± 0.56	4.62 ± 0.75	5.44 ± 0.90	7.39 ± 0.87	6.84 ± 1.02	5.31 ± 1.00
Hill 2	5.56 ± 0.54	4.14 ± 1.06	4.53 ± 0.77	6.03 ± 1.11	5.67 ± 1.11	4.78 ± 0.98
n	19	6	6	5	7	7

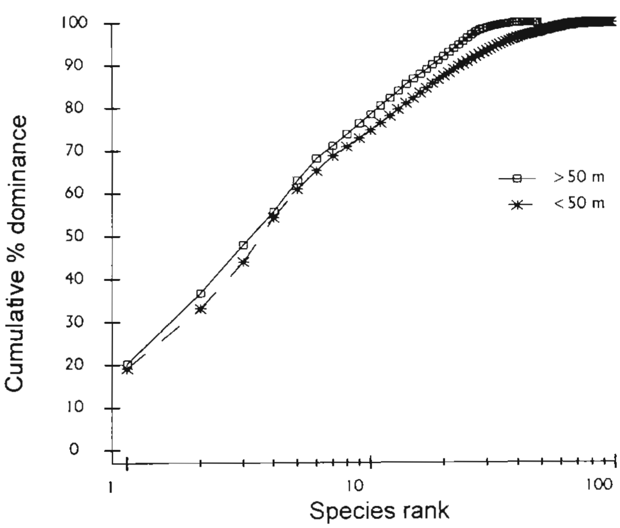

Fig. 6. Comparison of biomass dominance patterns between the continental shelf assemblage trawl stations and the continental slope assemblage trawl stations by means of k-dominance curves

groupings according to the depth strata. *Lutjanus synagris* showed a general distribution and high abundance, and is important both as a typifying species inside the depth strata assemblages, although it typifies the upper slope assemblage particularly well (Table 5), and as a discriminating species. The discriminating species that ranked higher belonged to the shelf assemblage (Table 5), suggesting that their distribution was more restricted to their depth range than the distribution of the upper slope species.

Table 6 presents the mean values of biomass, density, species number, and Hill numbers 1 and 2 per trawl station by depth strata and for each cruise. The ANOVA showed that biomass per trawl station did differ between depth strata ($p < 0.05$), with the continental shelf showing a higher biomass concentration (Table 6). The ANOVA revealed no difference in the number of individuals per trawl station between depth strata as was also the case for number of species and Hill numbers 1 and 2 ($p > 0.05$).

Fig. 6 shows the k-dominance curves for both depth strata in the study based on biomass data. The shelf assemblage exhibited less dominance than the upper slope assemblage, i.e. in the shelf the distribution of the biomass among species is more even than in the upper slope.

The analysis of similarity (ANOSIM) between cruises by depth strata did not detect significant differences in assemblage structure ($p > 0.05$), i.e. the abundance, distribution and association patterns of the background species remained roughly the same in time, at least for the dates of the cruises.

The ANOVA revealed that biomass, density, and Hill numbers 1 and 2 per trawl station did not differ statistically between cruises ($p > 0.05$), whereas the number of species per trawl station did ($p < 0.05$). Tukey test showed that Cruise 9601 (April 1996, RV 'Malpelo') had significantly ($p < 0.05$) more species per trawl (Table 6) than Cruise 9701 (February 1997, RV 'Ancon'). The other pairwise cruise comparisons were not significant ($p > 0.05$).

DISCUSSION

While density and biomass values were standardized to area swept, the use of 2 different trawls in the survey left the number of species per trawl station as the main source of bias. Indeed, a significant difference was found between Cruises 9601 (RV 'Malpelo', with a mean swept area of 0.0701 km^2) and 9701 (RV 'Ancon', with a mean swept area of 0.0327 km^2) which were 10 mo apart, with Cruise 9601 having more species per trawl station. However, no other pairwaise comparison resulted in statistical differences, i.e. Cruise 9601 differed only from one of the 2 RV 'Ancon' cruises and Cruise 9602 (RV 'Malpelo') was not different in species number from any of the other cruises. Thus, the results of the study seem to be not unduly influenced by the different fishing gears.

The presence-dominance pattern found here seems not to be uncommon in demersal fish communities. Similar pictures can be found, for instance, in Bianchi

(1992b, c) and Wenner & Sedberry (1989). As the resource availability in the benthos can be thought to be at a premium for the fish, there seems to be a strong hierarchical organization in the demersal fish assemblages where a few species tend to preempt wide use of the resources by the rest. On the other hand, the mechanisms responsible for the maintenance of the rich demersal fish species diversity (an average of 5 new species resulted in each tow) are worth investigating. Even though the sedimentary bottom may look structurally simple, the presence of Las Animas Bank, of mangrove forest on the coastline, the seasonal influence of continental run off and winds, and the oceanographic regime may explain this demersal fish species richness.

Two distinctive demersal fish assemblages clearly associated with the topography of the gulf emerge from the analysis: a shallow assemblage reaching the 50 m depth limit which represents the continental shelf, and a deep assemblage beyond that depth which represents the upper slope. The first assemblage exhibits greater biomass and contains species of larger size and commercial interest (for instance, *Lutjanus analis* and *Calamus penna*); the second one is characterized by the presence of species like *Porichthys plectrodon*, *Sciaena trewavasae* and *Steindachneria argentea*, which are small and non-commercial species, although the dominance of snappers of median size (*L. synagris*, *Rhomboplites aurorubens* and *Pristipomoides aquilonaris*) make it of interest for fishing (Table 5). The finding that biomass declines with depth is in accordance with reports elsewhere in the world (Darcy & Gutherz 1984, Pauly 1988, Gonzalez-Sansón et al. 1997).

As shown in this study the main determining bottom feature associated with the structure of the demersal fish assemblages is the depth as it reflects the change from the continental shelf to the continental slope. Other bottom and oceanographic factors do play a role, however. Thus, with the exception of Cruise 9600 (December 1995) when grain size in combination to depth scores second in the BIO-ENV correlation, in the other 3 cruises bottom temperature and salinity (always in combination with depth) scored first or second, i.e. the distribution pattern of bottom salinity and temperature, for a given period, seems to show enough contrast to influence the configuration of the assemblages as has been detected in other studies in particular in relation to temperature (Bianchi 1991, 1992b, c, Gonzalez-Sansón et al. 1997).

As depth (topography), sediment grain size and organic content can be considered as fixed or very conservative features, assemblage temporal change must be associated with variables such as salinity and temperature as they are expected to show more temporal variability. The ANOSIM procedure, however, did not detect temporal change in the overall assemblage structure between cruises as was also the case, in general, with the ANOVA analysis of univariate community aspects. These findings suggested that temporal change in the assemblage composition was weakly associated with seasonal change, at least for our cruise dates. This is not to say that the assemblages did not change with time. The spatial patchiness is matched by temporal patchiness of a vast number of species (Table 3).

The dominance pattern found here partly corresponds to a scheme proposed by Longhurst (1969) for western tropical Africa. Longhurst (1969) suggested 3 demersal fish groups based on the dominant species. The first group occurred in warm estuaries or coastal clear waters above the thermocline, on muddy or sandy bottoms and was dominated by the family Sciaenidae; the second group appeared in colder waters under the thermocline, on hard or sandy bottoms and was dominated by the families Sparidae and Lutjanidae; the third group was present at the border of the continental shelf and beyond, and was dominated by merluccids and related species.

As samples from depths shallower than 10 m were not collected (see 'Materials and methods'), Longhurst's first group had no equivalent in this study. There is a coincidence between Longhurst's second group and the shelf assemblage as defined here, where Lutjanidae and Sparidae showed dominance, but partially so with Longhurst's third group (border of the continental shelf) as the upper slope assemblage in the Gulf of Salamanca is dominated by small snappers and sciaenids (Table 5), although *Steindachneria argentea*, a merlucid, was important in depths of more than 50 m in Cruise 9601 and a representative of the genus *Synagrops* (*S. trispinosus*), one of the Longhurst's 'related species', also occurred in 2 deep stations.

The scheme proposed by Lowe-McConnell (1962) for the shelf off Guyana consisted of 'brown' (catfishes, rays), 'golden' (sciaenids), 'silver' (carangids, grunts) and 'red' (snappers) fish zones, from the shallow to the deep shelf. This scheme does not seem to fit the dominance pattern found in the Gulf of Salamanca. For instance, its 'red' fish zone is found between 80 and 120 m depth, whereas the snappers are typical species in the full depth range of this study (Table 5). The demersal fish assemblages in the Gulf of Salamanca would resemble a mixture of Lowe-McConnell's 'golden', 'silver' and 'red' fish zones.

Bianchi (1992a), by means of quantitative multivariate methods, described 12 assemblages for the shelf off Venezuela, Guyana and Surinam, 6 for the dry/windy climatic condition (May) and 6 for the rainy/calm cli-

matic condition (August) which, as is the case here, primarily responded to a depth gradient. At the species level, in terms of dominance patterns, none of these 12 assemblages seems to correspond with the assemblages of the Gulf of Salamanca (compare Tables 7 & 8, p. 131 to 134, in Bianchi 1992a with Table 5 in this study), although both areas share many species. The same is true at the family level: in Bianchi's assemblages the families Sparidae and Balistidae are never of importance whereas their representatives typify the assemblages in the Gulf of Salamanca (Table 5). Representatives of the families Clupeidae and Trichiuridae are typifying species in Bianchi's (1992a) assemblages but not in this study. On the other hand, both studies have in common that representatives of the families Lutjanidae, Sciaenidae and Carangidae are among the most important typifying species in the assemblages.

Strong temporal change was a notorious feature in the assemblages described by Bianchi (1992a). The assemblages found in the May cruise got reorganized in the August cruise in terms of their dominance patterns and spatial coverage. Bianchi (1992a) attributes this to uneven sampling effort in the 2 cruises and to the migration of a number of species from deep waters to shallow waters and vice versa. This contrasts with the situation found in the Gulf of Salamanca where temporal change was not strong enough to alter the basic dominance pattern from one cruise to the next, although many species were very patchy in time (Table 3).

The comparison with the zonation schemes by Longhurst (1969) and Lowe-McConnell (1962) and with the assemblages of Bianchi (1992a) are obscured by the great difference in spatial scale. Our study area, including the non-trawlable area and the area less than 10 m depth (see 'Materials and methods'), is 955 km^2 which, for instance, is 125 times smaller than the study area of Bianchi (1992a), which was 120000 km^2, approximately (calculated from her Fig. 1, p. 119). A second great difference is the width of the continental shelf. While in Bianchi (1992a) the shelf spreads 180 km from the coast, in the Gulf of Salamanca the continental shelf just reaches to 16 km from the coast. A third difference refers to the sampling density. Whereas in this study, in the cruise with fewer stations (Table 2), a station was placed every 191 km^2 on average, in Bianchi (1992a), in the cruise with more stations (May, 94 trawl stations), a station was placed every 1276 km^2 on average.

The narrow shelf in the Gulf of Salamanca probably precludes a vertical zonation of the demersal assemblages, other than the zonation described in this study, i.e. shelf versus upper slope. The small area in the Gulf of Salamanca probably allows for the manifestation of the effects of local habitats, for instance, the Animas Bank, on the composition and dynamics of the demersal fish fauna, effects that are obscured in studies covering bigger areas. Thus it is an open question whether Bianchi's (1992a) demersal assemblages and their temporal change have an ecological meaning or whether they are an artifact of the low sampling density, i.e. if new surveys were to be conducted under the same conditions and time of the year would the same assemblages emerge? Likewise only repeated sampling in the Gulf of Salamanca will tell to what extent the demersal fish assemblages identified are predictable.

Another general factor that makes comparisons and the search for general descriptions in demersal assemblages a difficult task is the fishery regime. In all the cases discussed here the shelves are subject to substantial fishery pressure, except the Gulf of Salamanca in depths more than 50 m. Clearly there is a distortion of the natural condition by this mortality source which is difficult to assess.

It is of interest to note that *Balistes capriscus*, which belongs to the background species in the Gulf of Salamanca (Table 3), appeared also as dominant in the Gulf of Guinea, which is characterized by a strong upwelling (Bianchi 1992b). According to Longhurst & Pauly (1987) and Bianchi (1992b) this species had increased its abundance since the seventies as a result of fishing of competitors. As mentioned, *B. capriscus* is to date of no commercial interest for fishermen in the Gulf of Salamanca and is discarded, which may contribute to its survival. An open question is then whether a similar situation to that found in the Gulf of Guinea may be occurring in the Gulf of Salamanca.

Among the background species we found *Lutjanus analis*, *L. synagris* and *Calamus penna* (Table 3), 3 of the more interesting fishes for commercial purposes in the Caribbean area. This may emphasize the importance of the Gulf of Salamanca as an area to be managed with special care. The case of *Balistes capriscus*, normally ignored by fishermen, may require the development of an educational campaign as this fish has a general acceptance and is consumed in various tropical American countries including Mexico and Venezuela.

The overall picture gained here on the demersal fish communities in the Gulf of Salamanca stresses once more the multispecies character of the tropical fisheries. Management effort should take into account this fact as the fishing taking place in the gulf is not species selective. On the other hand, the ecological interdependence should be assessed as the impact of exploitation and of potential management measures on the demersal fish assemblages is unclear.

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