

Biogeography of continental shelf and upper slope fishes off El Salvador, Central America

CLAUDIA I. FUENTES^{1,2}, ENZO ACUÑA¹ AND NUMA R. HERNÁNDEZ³

¹Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Casilla 117, Coquimbo, Chile, ²Magister en Ciencias del Mar. Facultad de Ciencias del Mar, Universidad Católica del Norte, Casilla 117, Coquimbo, Chile, ³Centro de Desarrollo de la Pesca y la Acuicultura (CENDEPESCA), Final 1ra. Av. Norte, 13 Calle Poniente y Av. Manuel Gallardo, Santa Tecla, La Libertad, El Salvador

*The present research provides detailed information on the geographic and bathymetric distributional patterns of fishes and describes the main species assemblages of the continental shelf and upper slope off El Salvador. The sampling was based on 673 bottom-trawl tows taken during research surveys from April to November 2003. The data analysis was based on presence-absence matrixes and was conducted with PRIMER 6 software. A total of 148 fish species were recorded during the study period: the families with the highest number of species were Sciaenidae (13) and Carangidae (10), and the highest percentages of occurrence were registered for *Porichthys margaritatus* (40.6%), *Pontinus* sp. (34.8%) and *Monolene dubiosa* (33.1%). The cluster analysis by depth showed three faunistic associations: (1) on the inner and part of the mid continental shelf (20–60 m), (2) one bathymetric stratum on the mid continental shelf (80–100 m), and (3) on the outer continental shelf and upper slope (120–240 m). The cluster analysis by geographic zones showed separation between three zones: Western, Central and Eastern Zones off El Salvador. The Central zone is characterized by a different fish community of mixed habitat, while the main factor that determined the fish assemblages on the continental shelf and upper slope was depth.*

Keywords: Ichthyofauna, bathymetric distribution, spatial distribution, Tropical Eastern Pacific

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INTRODUCTION

The coast of El Salvador is part of the marine biogeographic region known as the Tropical Eastern Pacific (TEP) region which extends from the Pacific coast of Baja California, near Magdalena Bay (~25°N), to the southern shore of the Gulf of Guayaquil (~4°S), and includes the Galápagos Islands and four other isolated oceanic islands and archipelagos: the Revillagigedo group, Clipperton, Cocos and Malpelo (Briggs, 1974; Hastings, 2000; Robertson & Cramer, 2009). The TEP is delimited by thermal gradients to the north and south, by a wide open ocean area (the East Pacific Barrier) to the west, and by the Central American land mass to the east (Hastings, 2000). It is one of the most dynamic coastal environments of any tropical region due to the frequent influence of El Niño events (Glynn & Ault, 2000).

The number and boundaries of biogeographic provinces in TEP have been widely discussed (e.g. Ekman, 1953; Walker, 1960; Briggs, 1974; Boschi, 2000; Hastings, 2000; Spalding *et al.*, 2007; Robertson & Cramer, 2009). Hastings (2000) divided the TEP into four provinces (the Cortez, Mexican, Panamic and Galápagos Provinces), based on the distribution of rocky shore fishes. The stretches of sand and mud shorelines known as the Sinaloa Gap (370 km of shoreline in the SE Gulf of California) and the Central American Gap

(~1000 km of shoreline from the Gulf of Tehuantepec, southern Mexico, to El Salvador) form natural breaks in the distribution of shoreline reef habitats between the mainland provinces (Cortez, Mexican and Panamic). The most recent subdivision of the TEP is based on the distribution of regional endemics and three functional groups of species (reef species, soft-bottom species and pelagic species) (Robertson & Cramer, 2009). According to this subdivision, three provinces are established: the continental coast that contains the Cortez Province (Gulf of California and lower Pacific Baja California), the Panamic Province southward to Ecuador, and the Oceanic Islands Province (including five oceanic island and archipelagos). Robertson & Cramer (2009) noted that the two large gaps have had only small effects at the level of the entire regional fauna.

The TEP has a lower diversity of shorefish fauna compared with the Indo-Malayan global centre of diversity. However, the TEP has the highest rate of endemism (79.3% of the resident shorefishes) among any tropical regions of similar size (Robertson & Allen, 2006). Within the TEP, 1285 shallow-living fish species (found in less than 100 m depth) of coastal and near-shore pelagic habitats have been recorded (Robertson & Allen, 2008). Due to the overlap in ranges of different species, the area with the highest number of species (740–760 spp.) is off Costa Rica and Panama. From this area, the species richness decreases with increasing latitude (Mora & Robertson, 2005a, b).

The Salvadoran coast has a total length of 320 km and its continental shelf comprises a strip between 50 and 80 km wide (Marn & Vimivdu, 2002), with an area of about

Corresponding author:
E. Acuña
Email: eacuna@ucn.cl

17,100 km². Its upper slope area (between 200 and 1000 m) is approximately 3400 km² (Fischer *et al.*, 1995a). This zone is influenced by the Costa Rica Coastal Current, which flows northward along the western margin of Central America into the Gulf of Tehuantepec (México), where its surface current turns south to flow around the south side of the Tehuantepec Bowl (Kessler, 2006). Gierloff-Emdem (1976) reported that branches of the California Current flow southeast, parallel to the Mexican coast, reaching the northwestern coast of El Salvador, however, even with modern data the interconnection of the southeastern branch of the California Current remains unknown (Kessler, 2006; Lavin *et al.*, 2006).

The first available list of marine species of El Salvador was developed by Hildebrand (1925). The study was aimed at investigating the freshwater fishes of El Salvador, but in his results the author includes a list of 13 families and 23 marine fish species obtained from one sampling conducted at Puerto El Triunfo and Puerto Cutuco, in the east of the country. At present, 412 species of marine fish are recorded in Salvadoran waters (Marn & Vimivdu, 2002). However, the knowledge about marine fishes is scarce and most of the information is included in governmental technical reports about artisanal and industrial fisheries. Thus, the studies have been focused on species lists and the determination of catch values of the most abundant marine fishes, captured mainly as bycatch in the shrimp fishery (Ramírez & Miller, 1975; González *et al.*, 1983; Ulloa, 1984a, b; Villegas *et al.*, 1985; López, 1999). The aim of this study is to provide detailed information on geographic and bathymetric distribution patterns of fish and to describe the main species assemblages of the continental shelf and upper slope off El Salvador.

MATERIALS AND METHODS

The area surveyed extends from the Paz River (Guatemalan border) to the Gulf of Fonseca (Nicaraguan border), bathymetrically limited by the 240 m isobath (Figure 1). The continental shelf has a maximum width of 80 km, widening progressively towards the Nicaraguan border. Ninety-one per cent of the total area has deposits of muddy sand, substratum type that further increases in proportion as the shelf approaches the continental slope. The continental slope begins at a depth of about 150 m and descends with a 3–5° angle over a maximum width of 20 km (Villegas *et al.*, 1985). Due to the geographic features present in the area (Gierloff-Emdem, 1976), four zones can be distinguished: (1) The Western Zone (WZ) from the Paz River (13°44'N 90°07'W) to Acajutla (13°34'N 89°50'W), characterized by muddy-sand bottoms with high river inputs (most of them temporary) and estuaries; (2) The Western Central Zone (WCZ) from Acajutla to La Libertad (13°29'N 89°19'W), characterized by rocky bottoms, few river inputs, no large-scale estuaries and a coral reef of approximately 157 km² (Marn & Vimivdu, 2002); (3) The Eastern Central Zone (ECZ) from La Libertad to the Lempa River (13°15'N 88°49'W), characterized mostly by muddy-sand bottoms, high river runoff that provides a large amount of sediments and the Jaltepeque Estuary, the second largest estuary in the country; and (4) The Eastern Zone (EZ), from the Lempa River to the Gulf of Fonseca (13°10'N 87°41'W), which contains the largest estuarine system (Jiquilisco Bay) and a volcanic island system, located in the Gulf of Fonseca, and characterized by rocky, sandy and muddy bottoms (Marn & Vimivdu, 2002).

Data were collected from 673 bottom-trawl tows made monthly from April to November 2003 (Table 1). A stratified

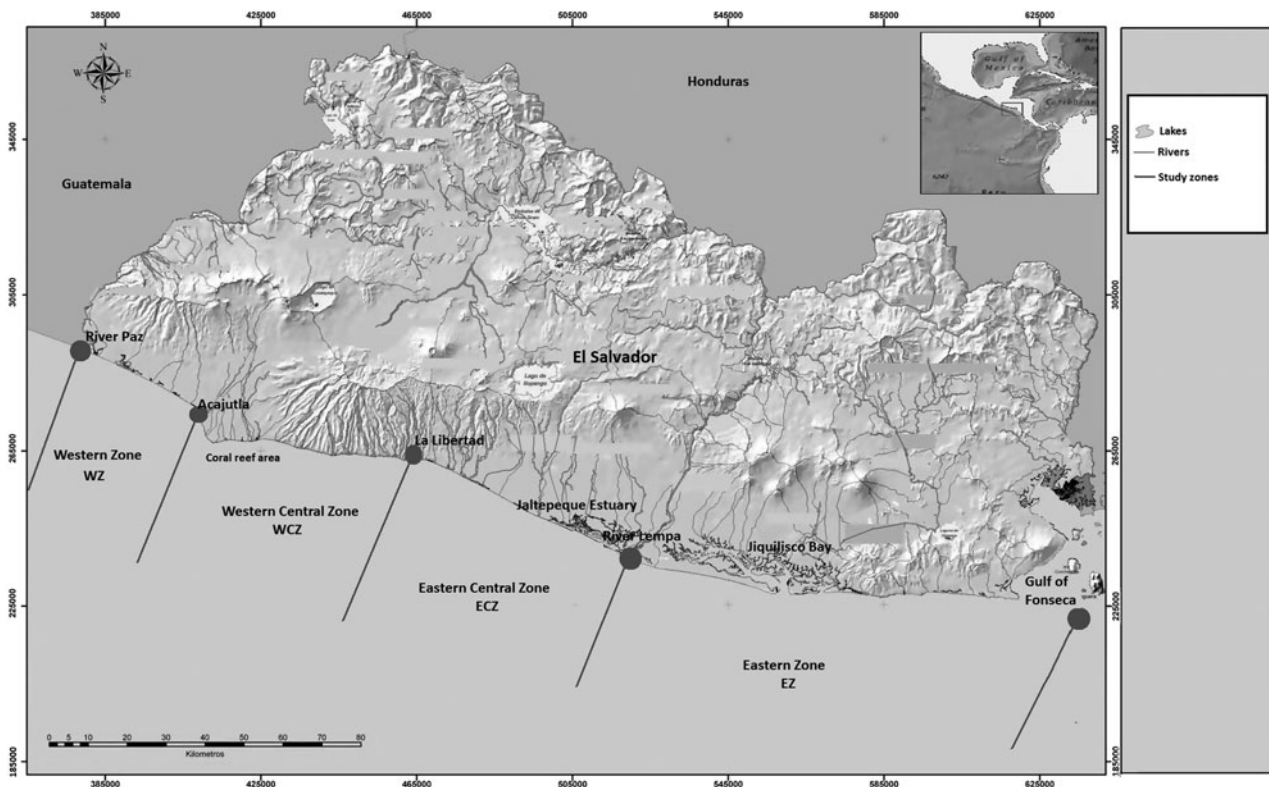


Fig. 1. Map of the study area, with the subdivisions discussed in the text.

Table 1. Dates and number of hauls performed during the eight surveys.

Survey	Dates	Number of hauls
1	11–29.4.2003	81
2	17–28.5.2003	51
3	10–30.6.2003	76
4	11–28.7.2003	87
5	3–22.8.2003	95
6	9–27.9.2003	87
7	4–28.10.2003	100
8	5–24.11.2003	96

sampling was conducted in each of the zones described in Figure 1. Two transects perpendicular to the coast per zone were established, with the exception of the EZ, where four transects were established. At each transect hauls from 20 to 240 m depth were carried out. From 20 to 60 m the hauls were done at 10 m depth intervals and from 60 m onwards, hauls were done at 20 m depth intervals. The samples were obtained during daytime with cod-end twin otter trawls measuring 20.2 m total length with a 3 m vertical opening, approximately 13.4 m wing spread, and 5 cm mesh size. The trawls were performed at a speed of 2.5 knots and the estimated trawling time at depths less than 120 m was 30 min and those deeper were for 15 min. In each haul a random sample of fishes was sampled, ensuring that all species caught were included. The samples were placed in polyethylene bags and stored on ice. Later the samples were frozen at the Aquatic Laboratory of the School of Biology of the University of El Salvador. All fishes in the sample were identified to the lowest possible taxonomic level using the field guides by Chirichigno (1974), Bussing & López (1993), Fischer *et al.* (1995b, c), Amezcua-Linares (1996), Robertson & Allen (2002) and Froese & Pauly (2003). The scientific names used here are those listed in Robertson & Allen (2006) and Eschmeyer (2013). Some sampled fishes were fixed in formalin and preserved in alcohol and catalogued in the fish collection of the School of Biology Museum of the University of El Salvador.

The fish species collected at 13 depth intervals and from the four geographic zones (Table 2) were used to determine similarities among bathymetric strata and geographic zones and thus to define fish assemblages. Species with one occurrence and/or one specimen were excluded from the analysis. The data analysis was based on presence-absence matrices and used PRIMER 6 software (Clarke & Gorley, 2006) for hierarchical cluster analysis using Jaccard's coefficient as an index of similarity and for an Unweighted Pair Group Method analysis using the arithmetic averages aggregation algorithm (UPGMA). The significance of the cluster groups ($P < 0.05$) was tested with the similarity profile (SIMPROF) test included in PRIMER 6 software. The data were analysed in two steps following Macpherson *et al.* (2010). First, a cluster analysis was performed to determine significant faunal similarities between depth intervals, then significant differences in depth assemblage groupings were identified by SIMPROF and these new areas were defined as bathymetric strata. Secondly, the data from each bathymetric stratum were used in a cluster analysis to determine similarities between geographic zones and to define species assemblages. In addition, multidimensional scaling (MDS) ordination analysis was performed using the same configuration as in cluster species analysis.

Table 2. Number of hauls performed by depth and geographic zone.

Depth (m)	Geographic zones				Total
	WZ	WCZ	ECZ	EZ	
20	11	*	15	31	57
30	12	11	15	31	69
40	16	13	16	30	75
50	12	12	13	26	63
60	13	14	10	18	55
80	13	14	13	17	57
100	11	9	12	20	52
120	11	10	7	15	43
140	11	11	7	18	47
160	12	11	3	15	41
180	9	10	**	12	31
200	10	11	**	15	36
220	9	10	**	13	32
240	4	1	**	10	15
Total	154	137	111	271	673

WZ, Western Zone; WCZ, Western Central Zone; ECZ, Eastern Central Zone; EZ, Eastern Zone; (*) sea-bottom was not suitable for trawling; (**) longline fishery zone.

RESULTS

A total of 148 fish species, comprising 15 Chondrichthyes (9 genera of 7 families) and 133 Osteichthyes (79 genera of 47 families), were recorded. The families with the highest number of species were the chondrichthyan Family Urotrygonidae (3 species) and the osteichthyan families Sciaenidae (13 species) and Carangidae (10 species). Three bony fish species were identified only to the genus level (*Pontinus* sp., *Citharichthys* sp. and *Bollmannia* sp.). The highest percentages of occurrence were recorded for *Porichthys margaritatus* (40.6%), *Pontinus* sp. (34.8%) and *Monolene dubiosa* (33.1%) (Table 3). According to the habitat categories described by Froese & Pauly (2003), most of the species captured were demersal fishes (83), followed by reef associated (23), pelagic (21), benthopelagic (18), bathydemersal (2) and bathypelagic (1) species.

Most species showed higher occurrences at depths less than 60 m (Figure 2), but 15 species showed a wide distributional range: *Gymnothorax phalarus*, *Synodus evermanni*, *Merluccius angustimanus*, *Porichthys margaritatus*, *Lophiodes caulinaris*, *Lophiodes spilurus*, *Zalieutes elater*, *Pontinus* sp., *Prionotus stephanophrys*, *Diplectrum euryplectrum*, *Cynoscion nannus*, *Bollmannia* sp., *Trichiurus nitens*, *Peprilus snyderi* and *Monolene dubiosa*. Only 11 species exceeded the 200 m depth limit: *Merluccius angustimanus*, *Cherublemma emmelas*, *Lophiodes caulinaris*, *Lophiodes spilurus*, *Pontinus* sp., *Cynoscion nannus*, *Kathetostoma averruncus*, *Trichiurus nitens*, *Peprilus snyderi*, *Citharichthys* sp. and *Monolene dubiosa*.

The cluster analysis among depth strata showed three faunistic associations: one on the inner and part of the mid continental shelf (20–60 m) containing 4 bathymetric strata, the second in a single bathymetric stratum on the mid continental shelf (80–100 m), and the third on the outer continental shelf and upper slope (120–240 m) comprising 4 bathymetric strata (SIMPROF, $P < 0.05$) (Figure 3). A decrease in species richness with increasing depth was observed below the 30–40 m bathymetric stratum (Table 4).

Table 3. Fish species captured on the shelf and upper slope off El Salvador during April to November 2003, including the habitat, the total number of occurrences, the percentage of total occurrence and geographic zones.

Taxa	Acronym	H	Occurrence		Geographic zones				
			Total	%	WZ	WCZ	ECZ	EZ	
Class CONDRICHTHYES									
Order CARCHARHINIFORMES									
Family SPHYRNIDAE									
1	<i>Sphyrna lewini</i> (Griffith & Smith, 1834)	Sphlew	P	4	0.6	0.0	25.0	50.0	25.0
2	<i>Sphyrna media</i> Springer, 1940	Sphmed	D	6	0.9	0.0	0.0	33.3	67.3
Family NARCINIDAE									
3	<i>Narcine entemedor</i> Jordan & Starks, 1895	Narent	D	4	0.6	50.0	25.0	25.0	0.0
4	<i>Narcine vermiculatus</i> Breder, 1928	Narver	D	50	7.4	48.0	24.0	24.0	4.0
Order RAJIFORMES									
Family RHINOBATIDAE									
5	<i>Rhinobatos leucorhynchus</i> Günther, 1867	Rhileu	D	30	4.5	50.0	23.3	20.0	6.7
6	<i>Rhinobatos planiceps</i> Garman, 1880	Rhipla	D	1	0.1	0.0	100.0	0.0	0.0
7	<i>Zapteryx xyster</i> Jordan & Evermann, 1896	Zapxys	R	5	0.7	40.0	40.0	20.0	0.0
Family DASYATIDAE									
8	<i>Dasyatis dipterura</i> (Jordan & Gilbert, 1880)	Dasdip	D	37	5.5	43.2	35.1	13.5	8.1
9	<i>Dasyatis longa</i> (Garman, 1880)	Daslon	R	4	0.6	50.0	0.0	50.0	0.0
Family GYMNURIDAE									
10	<i>Gymnura marmorata</i> (Cooper, 1864)	Gymmar	D	1	0.1	0.0	100.0	0.0	0.0
Family MYLIOBATIDAE									
11	<i>Aetobatus narinari</i> (Euphrasen, 1790)	Aetnar	B	2	0.3	0.0	0.0	50.0	50.0
12	<i>Rhinoptera steindachneri</i> Evermann & Jenkins, 1891	Rhiste	R	2	0.3	0.0	0.0	100	0.0
Family UROTRYGONIDAE									
13	<i>Urotrygon chilensis</i> (Günther, 1872)	Urochi	D	2	0.3	0.0	100.0	0.0	0.0
14	<i>Urotrygon munda</i> Gill, 1863	Uromun	D	1	0.1	0.0	0.0	0.0	100.0
15	<i>Urotrygon rogersi</i> (Jordan & Starks, 1895)	Urorog	D	13	1.9	15.4	46.2	7.7	30.8
Class ACTINOPTERYGII									
Order ALBULIFORMES									
Family ALBULIDAE									
16	<i>Albula esuncula</i> (Garman, 1899)	Albesu	D	6	0.9	16.7	16.7	66.7	0.0
17	<i>Albula nemoptera</i> (Fowler, 1911)	Albnem	D	3	0.4	0.0	0.0	66.7	33.3
Order ANGUILIFORMES									
Family MURAENIDAE									
18	<i>Gymnothorax equatorialis</i> (Hildebrand, 1946)	Gymequ	D	5	0.7	0.0	20.0	0.0	80.0
19	<i>Gymnothorax phalarus</i> Bussing, 1998	Gympha	D	6	0.9	66.7	16.7	16.7	0.0
Family OPHICHTHIDAE									
20	<i>Callechelys cliffi</i> Böhlke & Briggs, 1954	Calcli	D	1	0.1	0.0	0.0	0.0	100.0
21	<i>Ophichthus remiger</i> (Valenciennes, 1837)	Ophrem	D	1	0.1	0.0	0.0	0.0	100.0
22	<i>Ophichthus triserialis</i> (Kaup, 1856)	Ophtri	D	2	0.3	50.0	0.0	0.0	50.0
Family MURAENESOCIDAE									
23	<i>Cynoponticus coniceps</i> (Jordan & Gilbert, 1882)	Cyncon	D	59	8.8	20.3	11.9	10.2	57.6
Order CLUPEIFORMES									
Family CLUPEIDAE									
24	<i>Lile stolidifera</i> (Jordan & Gilbert, 1882)	Lilsto	P	21	3.1	0.0	4.8	19.0	76.2
25	<i>Opisthonema libertate</i> (Günther, 1867)	Opilib	P	35	5.2	17.1	5.7	37.1	40.0
26	<i>Opisthonema medirastre</i> Berry & Barrett, 1963	Opimed	P	1	0.1	0.0	100.0	0.0	0.0
Family ENGRAULIDAE									
27	<i>Anchoa lucida</i> (Jordan & Gilbert, 1882)	Ancluc	P	1	0.1	0.0	0.0	100	0.0
28	<i>Anchoa panamensis</i> (Steindachner, 1876)	Achpan	P	1	9.2	0.0	100.0	0.0	0.0
39	<i>Anchoa spinifer</i> (Valenciennes, 1848)	Ancspin	P	62		17.7	11.3	22.6	48.4
30	<i>Anchoa walkeri</i> Baldwin & Chang, 1970	Achwal	P	44	6.5	9.1	9.1	29.5	52.3
31	<i>Anchoa macrolepidota</i> (Kner, 1863)	Ancmac	P	1	0.1	0.0	0.0	0.0	100.0
Family PRISTIGASTERIDAE									
32	<i>Odontognathus panamensis</i> (Steindachner, 1876)	Odopan	P	33	4.9	21.2	6.1	27.3	45.5
Order SILURIFORMES									
Family ARIIDAE									
33	<i>Bagre panamensis</i> (Gill, 1863)	Bagpan	D	6	1.2	0.0	0.0	50.0	50.0
34	<i>Bagre pinnimaculatus</i> (Steindachner, 1876)	Bagpin	D	9	1.3	0.0	0.0	0.0	100.0
35	<i>Cathorops dasycephalus</i> (Günther, 1864)	Catdas	D	20	3.0	0.0	5.0	35.0	60.0
36	<i>Notarius kessleri</i> (Steindachner, 1876)	Notkess	D	1	0.1	0.0	0.0	100	0.0

Continued

Table 3. Continued

Taxa	Acronym	H	Occurrence						
			Total	%	Geographic zones				
					WZ	WCZ	ECZ	EZ	
37	<i>Sciades dowii</i> (Gill, 1863)	Scidow	D	3	0.4	0.0	0.0	67.7	33.3
38	<i>Sciades guatemalensis</i> (Günther, 1864)	Scigua	D	30	4.5	10.0	6.7	46.7	36.7
39	<i>Sciades seemanni</i> (Günther, 1864)	Scisee	D	5	0.7	0.0	0.0	60.0	40.0
Order AULOPIFORMES									
Family SYNODONTIDAE									
40	<i>Synodus evermanni</i> Jordan & Bollman, 1890	Syneve	D	50	7.4	22.0	20.0	26.0	32.0
41	<i>Synodus scituliceps</i> Jordan & Gilbert, 1882	Synsci	D	59	8.8	28.8	13.6	22.0	35.6
42	<i>Synodus sechurae</i> Hildebrand, 1946	Synsec	D	11	1.6	27.3	0.0	18.2	54.5
Order GADIFORMES									
Family MERLUCCIIDAE									
43	<i>Merluccius angustimanus</i> Garman, 1899	Merang	BaP	130	19.3	33.6	10.0	18.5	36.9
Order OPHIDIIFORMES									
Family OPHIDIIDAE									
44	<i>Brotula clarkae</i> Hubbs, 1944	Brocla	B	1	0.1	0.0	0.0	100	0.0
45	<i>Cherublemma emmelas</i> (Gilbert, 1890)	Cheemm	BaD	3	0.4	66.7	0.0	0.0	33.3
46	<i>Lepophidium pardale</i> (Gilbert, 1890)	Leppar	D	9	1.3	0.0	33.3	22.2	44.4
47	<i>Lepophidium prorates</i> (Jordan & Bollman, 1890)	Leppro	D	57	8.5	36.8	5.3	21.1	36.8
Order BATRACHOIDIFORMES									
Family BATRACHOIDIDAE									
48	<i>Batrachoides waltersi</i> Collette & Russo, 1981	Batwal	D	41	6.1	29.3	0.0	17.1	53.7
49	<i>Porichthys greeni</i> Gilbert & Starks, 1904	Porgre	D	2	0.3	0.0	0.0	0.0	100.0
50	<i>Porichthys margaritatus</i> (Richardson, 1844)	Pormar	D	273	40.6	23.8	20.9	20.9	34.4
Order LOPHIIFORMES									
Family LOPHIIDAE									
51	<i>Lophiodes caularis</i> (Garman, 1899)	Lopcau	D	70	10.4	27.1	17.1	15.7	40.0
52	<i>Lophiodes spilurus</i> (Garman, 1899)	Lopspi	D	45	6.7	28.9	26.7	8.9	35.6
Family ANTENNARIIDAE									
53	<i>Fowlerichthys avalonis</i> (Jordan & Starks, 1907)	Fowava	D	2	0.3	0.0	0.0	50.0	50.0
Family OGCOEPHALIDAE									
54	<i>Zalieutes elater</i> (Jordan & Gilbert, 1882)	Zalela	D	9	1.3	0.0	11.1	11.1	77.8
Order SYNGNATHIFORMES									
Family FISTULARIIDAE									
55	<i>Fistularia commersonii</i> Rüppell, 1838	Fiscom	R	5	0.7	0.0	60.0	0.0	40.0
56	<i>Fistularia corneta</i> Gilbert & Starks, 1904	Fiscor	P	9	1.3	22.2	22.2	22.2	33.3
Family SYNGNATHIDAE									
57	<i>Hippocampus ingens</i> Girard, 1858	Hiping	R	1	0.1	0.0	100.0	0.0	0.0
Order SCORPAENIFORMES									
Family SCORPAENIDAE									
58	<i>Pontinus</i> sp.	Ponsp	D	234	34.8	18.4	24.8	15.0	41.9
59	<i>Scorpaena russula</i> Jordan & Bollman, 1890	Scorus	D	28	4.2	25.0	25.0	28.6	21.4
Family TRIGLIDAE									
60	<i>Prionotus birostratus</i> Richardson, 1844	Pribir	D	3	0.4	0.0	0.0	66.7	33.3
61	<i>Prionotus horrens</i> Richardson, 1844	Prihor	D	42	6.2	35.7	11.9	14.3	38.1
62	<i>Prionotus ruscarius</i> Gilbert & Starks, 1904	Prirus	D	58	8.6	37.9	22.4	17.2	22.4
63	<i>Prionotus stephanophrys</i> Lockington, 1881	Priste	D	47	7.0	25.5	10.6	17.0	46.8
Order PERCIFORMES									
Family CENTROPOMIDAE									
64	<i>Centropomus medius</i> Günther, 1864	Cenmed	D	2	0.3	0.0	0.0	50.0	50.0
65	<i>Centropomus robalito</i> Jordan & Gilbert, 1882	Cenrob	P	15	2.2	26.7	0.0	20.0	53.3
66	<i>Centropomus viridis</i> Lockington, 1877	Cenvir	D	4	0.6	25.0	0.0	25.0	50.0
Family SERRANIDAE									
67	<i>Diplectrum eumelum</i> Rosenblatt & Johnson, 1974	Dipeum	D	10	1.5	10.0	0.0	10.0	80.0
68	<i>Diplectrum euryplectrum</i> Jordan & Bollmann, 1890	Dipeur	D	76	11.3	23.7	19.7	23.7	32.9
69	<i>Diplectrum labarum</i> Rosenblatt & Johnson, 1974	Diplab	D	5	0.7	20.0	20.0	60.0	0.0
70	<i>Epinephelus analogus</i> Gill, 1863	Epiana	R	3	0.4	33.3	0.0	0.0	66.7
71	<i>Hyporthodus acanthistius</i> (Gilbert, 1892)	Hypaca	D	15	2.2	26.7	0.0	33.3	40.0
72	<i>Hyporthodus exsul</i> (Fowler, 1944)	Hypexs	D	7	1.0	28.6	42.9	0.0	28.6
73	<i>Rypticus nigripinnis</i> Gill, 1861	Rypnig	R	1	0.1	0.0	0.0	0.0	100.0
Family PRIACANTHIDAE									
74	<i>Pristigenys serrula</i> (Gilbert, 1891)	Priser	R	11	1.6	27.3	9.1	36.4	27.3

Continued

Table 3. Continued

Taxa	Acronym	H	Occurrence						
			Total	%	Geographic zones				
					WZ	WCZ	ECZ	EZ	
Family CARANGIDAE									
75	<i>Carangoides vinctus</i> (Jordan & Gilbert, 1882)	Carvin	P	7	1.0	0.0	0.0	57.1	42.9
76	<i>Caranx caballus</i> Günther, 1868	Carcab	P	9	1.3	22.2	33.3	22.2	22.2
77	<i>Caranx caninus</i> Günther, 1867	Carcan	P	10	1.5	20.0	20.0	30.0	30.0
78	<i>Chloroscombrus orqueta</i> Jordan & Gilbert, 1883	Chlorq	B	76	11.3	17.1	7.9	23.7	51.3
79	<i>Selene brevoortii</i> (Gill, 1863)	Selbre	B	143	21.2	20.3	12.6	24.5	42.7
80	<i>Selene orstedii</i> Lütken, 1880	Selors	B	5	0.7	40.0	20.0	20.0	20.0
81	<i>Selene peruviana</i> (Guichenot, 1866)	Selper	B	51	7.6	21.6	13.7	21.6	43.1
82	<i>Trachinotus kennedyi</i> Steindachner, 1876	Traken	D	1	0.1	0.0	0.0	100	0.0
83	<i>Trachinotus paitensis</i> Cuvier, 1832	Trapai	B	1	0.1	0.0	0.0	100	0.0
84	<i>Trachinotus rhodopus</i> Gill, 1863	Trarho	R	5	0.7	20.0	0.0	40.0	40.0
Family LUTJANIDAE									
85	<i>Lutjanus argentiventris</i> (Peters, 1869)	Lutarg	R	4	0.6	75.0	25.0	0.0	0.0
86	<i>Lutjanus colorado</i> Jordan & Gilbert, 1882	Lutcol	R	1	0.1	0.0	0.0	0.0	100.0
87	<i>Lutjanus guttatus</i> (Steindachner, 1869)	Lutgut	R	56	8.3	30.4	12.5	25.0	32.1
88	<i>Lutjanus peru</i> (Nichols & Murphy, 1922)	Lutper	R	1	0.1	0.0	0.0	0.0	100.0
Family LOBOTIDAE									
89	<i>Lobotes pacificus</i> Gilbert, 1898	Lobpac	B	1	0.1	0.0	0.0	100	0.0
Family GERREIDAE									
90	<i>Diapterus aureolus</i> (Jordan & Gilbert, 1882)	Diaaur	B	5	0.7	20.0	20.0	40.0	20.0
91	<i>Diapterus brevirostris</i> (Sauvage, 1879)	Diabre	D	69	10.3	15.9	8.7	26.1	49.3
92	<i>Eucinostomus currani</i> Zahuranec, 1980	Euccur	D	75	11.1	24.0	9.3	14.7	46.7
Family HAEMULIDAE									
93	<i>Haemulon sexfasciatum</i> Gill, 1862	Haesex	R	6	0.9	0.0	16.7	66.7	16.7
94	<i>Haemulopsis elongatus</i> (Steindachner, 1879)	Haeelo	D	20	3.0	35.0	0.0	45.0	20.0
95	<i>Pomadasys branickii</i> (Steindachner, 1879)	Pombra	D	1	0.1	0.0	0.0	100	0.0
96	<i>Pomadasys macracanthus</i> (Günther, 1864)	Pommac	B	60	8.9	26.7	8.3	35.0	30.0
97	<i>Pomadasys panamensis</i> (Steindachner, 1876)	Pompan	D	153	22.7	24.2	15.0	14.4	46.4
Family SCIAENIDAE									
98	<i>Cynoscion nanus</i> Castro-Aguirre & Arvizu-Martínez, 1976	Cynnan	B	128	19.0	19.5	31.3	11.7	37.5
99	<i>Cynoscion phoxocephalus</i> Jordan & Gilbert, 1882	Cynpho	D	1	0.1	0.0	0.0	0.0	100.0
100	<i>Cynoscion squamipinnis</i> (Günther, 1867)	Cynsqu	B	1	0.1	0.0	0.0	0.0	100.0
101	<i>Larimus acclivis</i> Jordan & Bristol, 1898	Laracc	P	98	14.6	22.4	2.0	42.9	32.7
102	<i>Larimus argenteus</i> (Gill, 1863)	Lararg	P	5	0.7	40.0	0.0	40.0	20.0
103	<i>Larimus pacificus</i> Jordan & Bollman, 1890	Larpac	P	122	18.1	41.8	12.3	18.9	27.0
104	<i>Micropogonias altipinnis</i> (Günther, 1864)	Micalt	B	18	2.7	16.7	11.1	16.7	55.6
105	<i>Nebris occidentalis</i> Vaillant, 1897	Nebocc	B	35	5.2	11.4	0.0	20.0	68.6
106	<i>Ophioscion scierus</i> (Jordan & Gilbert, 1884)	Ophsci	D	4	0.6	0.0	0.0	0.0	100.0
107	<i>Ophioscion strabo</i> Gilbert, 1897	Ophstr	D	90	13.4	25.6	5.6	22.2	46.7
108	<i>Paralonchurus petersi</i> Bocourt, 1869	Parpet	D	24	3.6	20.8	12.5	29.2	37.5
109	<i>Paralonchurus rathbuni</i> (Jordan & Bollman, 1890)	Parrat	B	6	0.9	0.0	0.0	0.0	100.0
110	<i>Stellifer fuerthii</i> (Steindachner, 1876)	Stefue	D	1	0.1	0.0	0.0	0.0	100.0
Family POLYNEMIDAE									
111	<i>Polydactylus approximans</i> (Lay & Bennett, 1839)	Polapp	D	118	17.5	21.2	11.0	23.7	44.1
112	<i>Polydactylus opercularis</i> (Gill, 1863)	Polope	D	16	2.4	31.3	0.0	18.8	50.0
Family MULLIDAE									
113	<i>Pseudupeneus grandisquamis</i> (Gill, 1863)	Psegra	D	35	5.2	34.3	0.0	28.6	37.1
Family CHAETODONTIDAE									
114	<i>Chaetodon humeralis</i> Günther, 1860	Chahum	R	1	0.1	0.0	0.0	100	0.0
Family MUGILIDAE									
115	<i>Mugil curema</i> Valenciennes, 1836	Mugcur	B	1	0.1	0.0	0.0	0.0	100.0
Family URANOSCOPIDAE									
116	<i>Kathetostoma averruncus</i> Jordan & Bollmann, 1890	Katave	BaD	3	0.4	0.0	33.3	33.3	33.3
Family CALLIONYMIDAE									
117	<i>Synchiropus atrilabiatus</i> (Garman, 1899)	Synatr	D	6	0.9	16.7	16.7	33.3	33.3
Family GOBIIDAE									
118	<i>Bollmannia</i> sp.	Bolsp	D	55	8.2	5.5	12.7	21.8	60.0
Family EPHIPPIDAE									
119	<i>Chaetodipterus zonatus</i> (Girard, 1858)	Chazon	R	19	2.8	21.1	5.3	15.8	57.9
120	<i>Parapsettus panamensis</i> (Steindachner, 1876)	Parpan	D	27	4.0	14.8	3.7	29.6	51.9

Continued

Table 3. Continued

Taxa	Acronym	H	Occurrence						
			Total	%	Geographic zones				
					WZ	WCZ	ECZ	EZ	
Family SPHYRAENIDAE									
121	<i>Sphyraena ensis</i> Jordan & Gilbert, 1882	Shyens	P	37	5.5	21.6	16.2	29.7	32.4
Family TRICHIURIDAE									
122	<i>Trichiurus nitens</i> Garman, 1899	Trinit	B	46	6.8	8.7	2.2	21.7	67.4
Family SCOMBRIDAE									
123	<i>Scomberomorus sierra</i> Jordan & Starks, 1895	Scosie	P	9	1.3	22.2	0.0	44.4	33.3
Family STROMATEIDAE									
124	<i>Peprilus snyderi</i> Gilbert & Starks, 1904	Pepsny	B	147	21.8	9.5	15.6	25.9	49.0
Order PLEURONECTIFORMES									
Family PARALICHTHYDAE									
125	<i>Ancyclosetta dendritica</i> Gilbert, 1890	Ancden	D	2	0.3	50.0	0.0	0.0	50.0
126	<i>Citharichthys platophrys</i> Gilbert, 1891	Citpla	D	24	3.6	0.0	41.7	4.2	54.2
127	<i>Citharichthys</i> sp.	Citsp	D	105	15.6	18.1	20.0	23.8	38.1
128	<i>Cyclosetta panamensis</i> (Steindachner, 1876)	Cycpan	D	41	6.1	22.0	17.1	22.0	39.0
129	<i>Cyclosetta querna</i> (Jordan & Bollman, 1890)	Cycque	D	155	23.0	26.5	17.4	18.7	37.4
Family BOTHIDAE									
130	<i>Engyophrys sanctilaurentii</i> Jordan & Bollman, 1890	Engsan	D	1	0.1	0.0	100.0	0.0	0.0
131	<i>Monolene dubiosa</i> Garman, 1899	Mondub	D	223	33.1	25.6	28.7	10.8	35.0
Family ACHIRIDAE									
132	<i>Achirus klunzingeri</i> (Steindachner, 1880)	Achklu	D	4	0.6	0.0	0.0	0.0	100.0
133	<i>Achirus mazatlanus</i> (Steindachner, 1869)	Achmaz	D	57	8.5	29.8	24.6	3.5	42.1
134	<i>Achirus scutum</i> (Günther, 1862)	Achscu	D	9	1.3	22.2	0.0	22.2	55.6
135	<i>Trinectes fimbriatus</i> (Günther, 1862)	Trifim	D	16	2.4	6.3	0.0	43.8	50.0
136	<i>Trinectes fonsecensis</i> (Günther, 1862)	Trifon	D	7	1.0	14.3	0.0	14.3	71.4
Family CYNOGLOSSIDAE									
137	<i>Symphurus melasmatotheca</i> Munroe & Nizinski, 1990	Symm	D	58	8.6	17.2	10.3	19.0	53.4
Order TETRAODONTIFORMES									
Family BALISTIDAE									
138	<i>Balistes polylepis</i> Steindachner, 1876	Balpol	R	2	0.3	100.0	0.0	0.0	0.0
Family MONACANTHIDAE									
139	<i>Aluterus monoceros</i> (Linnaeus, 1758)	Alumon	R	2	0.3	0.0	100.0	0.0	0.0
140	<i>Aluterus scriptus</i> (Osbeck, 1765)	Aluscr	R	1	0.1	0.0	0.0	100.0	0.0
Family TETRAODONTIDAE									
141	<i>Arothron hispidus</i> (Linnaeus, 1758)	Arohis	R	1	0.1	0.0	100.0	0.0	0.0
142	<i>Sphoeroides annulatus</i> (Jenyns, 1842)	Sphann	R	26	3.9	19.2	19.2	23.1	38.5
143	<i>Sphoeroides lobatus</i> (Steindachner, 1870)	Sphlob	D	13	1.9	46.2	0.0	30.8	23.1
144	<i>Sphoeroides sechurae</i> Hildebrand, 1946	Sphsec	D	7	1.0	28.6	0.0	42.9	28.6
145	<i>Sphoeroides trichocephalus</i> (Cope, 1870)	Sphtri	D	37	5.5	27.0	5.4	37.8	29.7
Family DIODONTIDAE									
146	<i>Diodon eydouxi</i> Brisout de Barneville, 1846	Dioeyd	P	1	0.1	100.0	0.0	0.0	0.0
147	<i>Diodon holocanthus</i> Linnaeus, 1758	Diohol	R	13	1.9	30.8	38.5	23.1	7.7
148	<i>Diodon hystrix</i> Linnaeus, 1758	Diohys	R	8	1.2	12.5	62.5	25.0	0.0

H, habitat; D, demersal; R, reef associated; P, pelagic; B, benthopelagic; BaD, bathydemersal; BaP, bathypelagic; DWZ, Western Zone; WCZ, Western Central Zone; ECZ, Eastern Central Zone; EZ, Eastern Zone.

The cluster analysis among geographic zones showed separation between the WCZ and the other three zones. Within the three other zones, the WZ and the Eastern Zones (ECZ and EZ) clustered separately ($P < 0.05$) (Figure 4). The highest number of species was recorded in the Eastern Zones, with 136 species collected (Table 4).

Classification and ordination of the fish fauna showed four main groupings (Figure 5), three of which were separated by depth: one represented a single species, *Cherublemma emmelas*, limited to 200–220 m; the second comprised a group associated with the depth range of 80–240 m, including *Gymnothorax phalarus*, *Merluccius angustimanus*, *Lophiodes caulinaris*, *Lophiodes spilurus*, *Zalieutes elater*, *Pontinus* sp., *Cynoscion nannus*, *Kathetostoma averruncus*, *Synchiropus atrilabiatu*s, *Citharichthys*

sp. and *Monolene dubiosa*; the third comprised a group of 132 species associated with the depth range of 20–80 m, some of which were also recorded over a wide bathymetric distribution (*Synodus evermanni*, *Porichthys margaritatus*, *Prionotus stephanophrys*, *Diplectrum euryplectrum*, *Trichiurus nitens* and *Peprilus snyderi*). The last group comprised species that were only found in the WCZ, i.e. *Urotrygon chilensis*, *Opisthonema medirastre*, *Anchoa panamensis* and *Aluterus monoceros*.

DISCUSSION

The 148 species recorded in this study are fewer than previously reported for other latitudes of the TEP that used

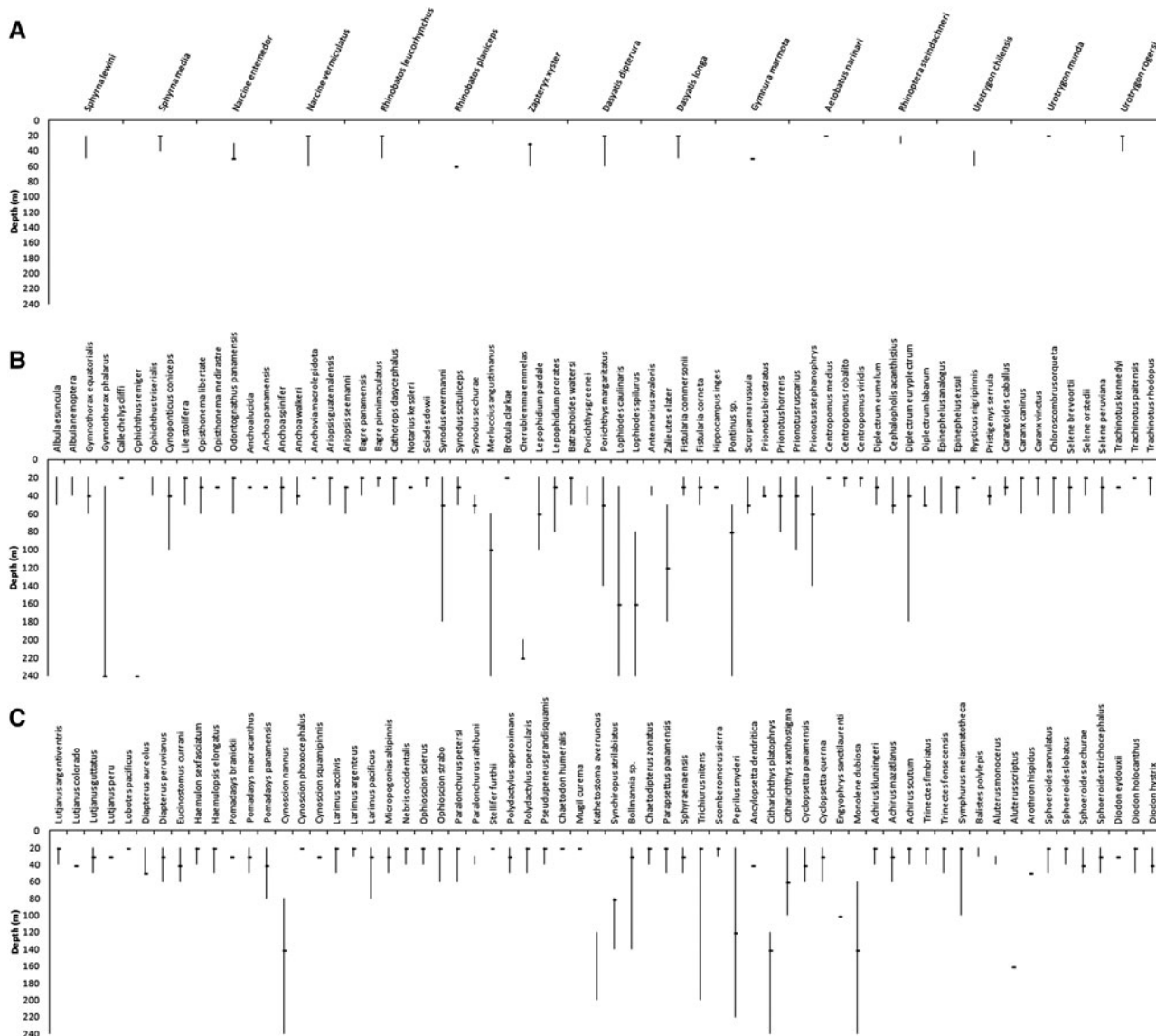


Fig. 2. Bathymetric distribution of fish species recorded on the continental shelf and upper slope off El Salvador–Central America, April to November 2003. (A) Class CONDRICHTHYES, (B) Class ACTINOPTERYGII, Fam. ALBULIDAE-CARANGIDAE, (C) Class ACTINOPTERYGII, Fam. LUTJANIDAE-DIODONTIDAE.

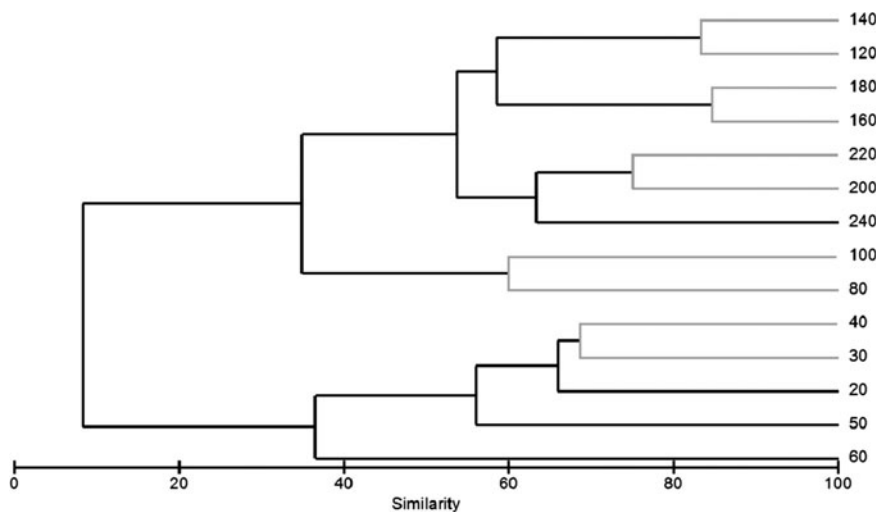


Fig. 3. Similarity dendrogram among depth using Jaccard's coefficient as similarity index and UPGMA analysis. The significance of the groups ($P < 0.05$) was tested with the similarity profile (SIMPROF); non-significant cells in grey.

Table 4. Number and percentage of families, genera and species of fishes captured on the shelf and upper slope off El Salvador (by bathymetric strata and geographic zone), April to November 2003.

	Families	Genera	Species
Bathymetric strata			
20	43 (80%)	70 (80%)	103 (70%)
30–40	45 (83%)	69 (78%)	119 (80%)
50	36 (67%)	51 (58%)	72 (49%)
60	27 (50%)	38 (43%)	45 (30%)
80–100	19 (35%)	21 (24%)	25 (17%)
120–140	17 (31%)	17 (19%)	18 (12%)
160–180	12 (22%)	12 (14%)	13 (9%)
200–220	11 (20%)	11 (13%)	12 (8%)
240	8 (15%)	8 (9%)	9 (6%)
Geographic zone			
Western Zone (WZ)	43 (80%)	64 (73%)	93 (63%)
Western Central Zone (WCZ)	44 (81%)	62 (70%)	87 (59%)
Eastern Zones (ECZ-EZ)	51 (94%)	83 (94%)	136 (92%)
Total	54	88	148

similar sampling gears. Northward, in the Central Pacific of Mexico (off Nayarit, Michoacán and Guerrero), 215 fish species have been recorded (Amezcu-Linares, 1996) and off the coast of the Gulf of Tehuantepec (off Oaxaca and Chiapas) 166 species have been reported (Tapia-García *et al.*, 1995). According to Robertson & Cramer (2009), species-richness peaks at the centre of the Panamic Province (Costa Rica and Panamá), but is fairly high throughout most of the mainland of the TEP, except in the northern part of the Gulf of California and in the Sinaloan and Central American Gap, including the coast of El Salvador, where species richness was significantly lower. Their study included all records of all shorefishes, and despite the fact that the Central American Gap contained fewer species than the adjacent Mexican and Panamic Provinces, their measure of the species richness included about 500–600 fish species. Our count of 148 species for the Salvadoran part of the province is primarily due to the sampling methodology, which is not directly comparable with other studies. Species of shallow, brackish, estuarine habitats and rocky or coral reef habitats could not be captured, since trawling did not sample the

0–10 m and 20 m depths and avoided underwater hazards (e.g. rocky outcrops). In addition, the 8-month duration and the relatively large mesh size (5 cm) of the sampling gear, which excluded smaller fish species, probably also led to the lower number of species recorded.

The dominance of the families Sciaenidae and Carangidae is consistent with studies in Mexico (Tapia-García *et al.*, 1995; Amezcu-Linares, 1996), which noted the dominance in diversity, frequency and abundance of these families. Nevertheless, the numerical dominance of *Porichthys margaritatus*, *Pontinus* sp. and *Monolene dubiosa*, was not reported in those studies. These three species are characterized by their presence in all four zones and their wide depth distribution, demersal habitat (Froese & Pauly, 2003) and carnivorous feeding habits (Robertson & Allen, 2006). *Pontinus* sp. has been reported as the third most abundant species off El Salvador, after *Cynoscion nannus* and *Peprilus snyderi* (Del Río, 2010).

Three species are recorded only to the genus level in this study: *Pontinus* sp., *Bollmannia* sp. and *Citharichthys* sp. Three *Citharichthys* species are presently documented to occur in Salvadoran waters, i.e. *C. gilberti*, *C. platophrys* and *C. mariajoriseae*. *Citharichthys gilberti* is limited to shallow water habitats, thus the *Citharichthys* flatfishes sampled in this study likely include both *C. platophrys* and *C. mariajoriseae*.

Faunal associations by depth may be determined by the effect of temperature. In El Salvador, sea surface temperature averages from 28 to 30°C throughout the year (JICA, 2002) and the thermocline is between 50 and 75 m (Strømme & Sætersdal, 1988). Hence, the three main groupings of fish species found in this study may be a result of the sharp thermocline, although there are limited records of environmental parameters in the region.

Patterns in the depth distributions of marine species and the negative relationship between depth of occurrence and depth range have been pointed out by numerous authors working on marine biogeography (Macpherson, 2003). Our findings, which show that most species have high occurrences at depths less than 60 m and only a few of those exceed 200 m, are consistent with Stevens (1996), who documented that there are very few species with broad depth ranges at low latitude or near the surface of the ocean. Pineda (1993) also shows

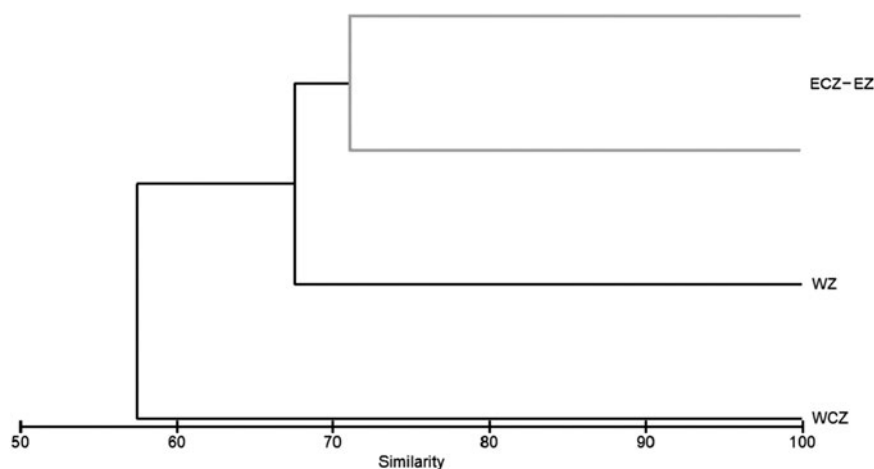


Fig. 4. Similarity dendrogram among geographic zones using Jaccard's coefficient as similarity index and UPGMA analysis. The significance of the groups ($P < 0.05$) was tested with the similarity profile (SIMPROF); non-significant cells in grey. WZ, Western Zone; WCZ, Western Central Zone; ECZ, Eastern Central Zone; EZ, Eastern Zone.

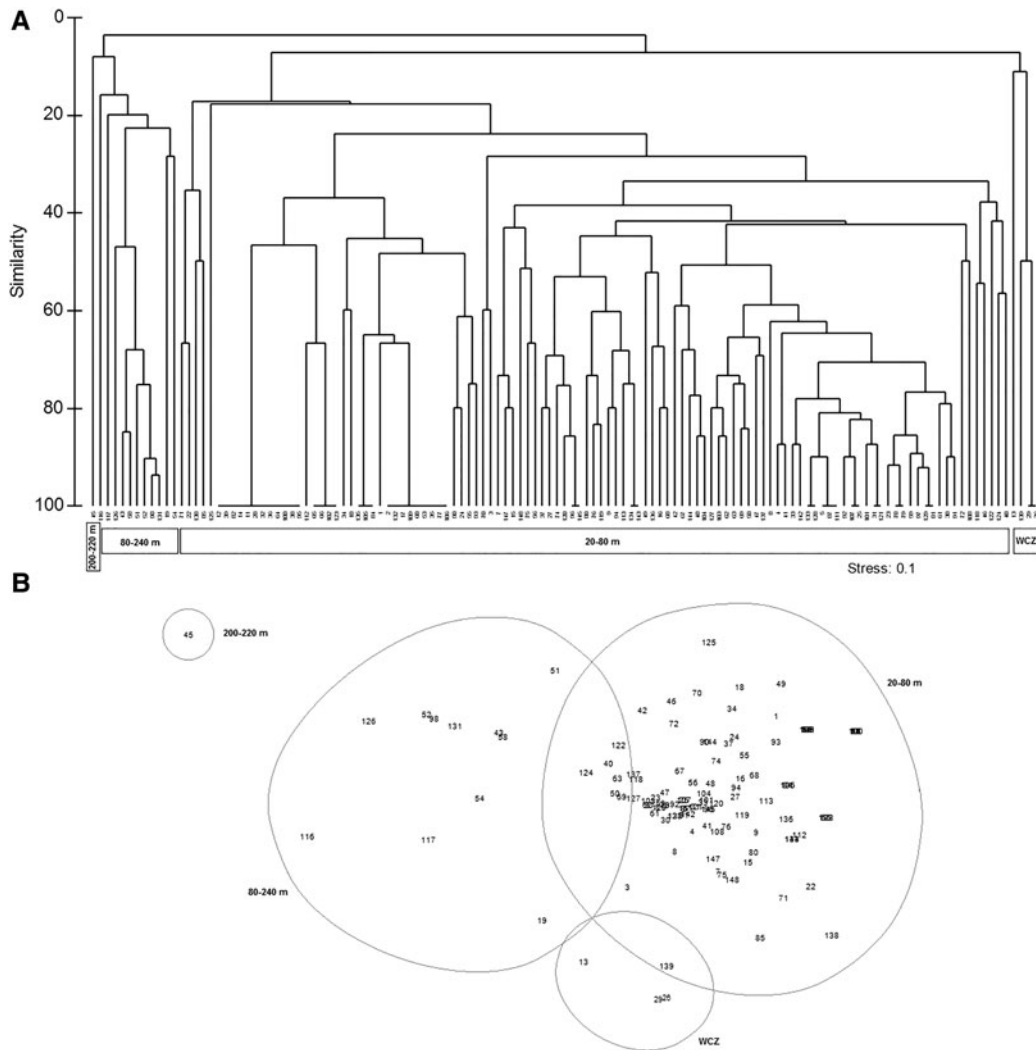


Fig. 5. Classification (A) and ordination (B) of the continental and upper slope fishes off El Salvador, using Jaccard's coefficient as a similarity index.

that species subject to higher environmental fluctuations (coastal species) have smaller depth ranges, while species dwelling in less variable environments (slope/rise species) have larger depth ranges.

The decrease in species richness with increasing depth is consistent with the results reported by Bianchi (1991), who found the highest number of species in the upper zone of the continental shelf (to about 50 m depth), a considerable number of species in the intermediate zone (to about 100 m depth) and only few species in the deeper zone; this variation is attributed to changes in dissolved oxygen in the water column ($>2 \text{ ml l}^{-1}$ on the upper zone and $<1 \text{ ml l}^{-1}$ in deeper waters).

The boundaries between geographic provinces tend to coincide with upwelling areas, river discharges, main currents and oceanographic fronts where there are pronounced changes in the oceanographic features of the waters such as temperature, salinity and productivity (Macpherson, 2003). This explains the separation of the eastern zones (ECZ and EZ) (Figure 4), where the Lempa River mouth (the largest in the country) is located, creating a barrier between the Eastern and Western zones. The Eastern Zones are characterized by the presence of the largest estuaries (Jaltepeque and Jiquilisco) and the Gulf of Fonseca, probably the most

productive zone of El Salvador. However, the species richness found in this zone is likely a result of many factors.

Moreover, faunal associations by biogeographic zone show that the WCZ is distinct from the other three zones. This zone includes the Protected Natural Area Complejo Los C6banos, which contains volcanic rocky bottoms and coral formations at 0–30 m depth (Gierloff-Emdem, 1976; Orellana, 1985), making it quite different from the rest of the Salvadoran coast. At Los C6banos, 49 species of reef-associated fishes have been reported (Orellana, 1985), of which 37 were not recorded in this study.

The vast majority of the TEP shallow-water habitat occurs along the continental coastline, which has a very narrow continental shelf (Zapata & Robertson, 2007). We observed that the fish assemblages were determined by depth rather than geographic areas; the three groups determined by depth are limited by the 20–80, 80–240 and 200–220 m depth strata. Macpherson (2003) mentioned that boundaries between depth provinces are usually related to environmental variations and these depth boundaries define a coastal domain ($\sim <100 \text{ m}$), a continental shelf and slope domain ($\sim 100\text{--}1000 \text{ m}$), typically with a boundary in the vicinity of the shelf break ($\sim 300 \text{ m}$) and a slope/rise domain ($>1000 \text{ m}$); but the extent of these domains changes with latitude.

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Correspondence should be addressed to:

E. Acuña

Departamento de Biología Marina, Facultad de Ciencias del Mar

Universidad Católica del Norte, Casilla 117, Coquimbo

email: eacuna@ucn.cl