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Demersal assemblages of the continental shelf and slope edge between the Gulf of Tehuantepec (Mexico) and the Gulf of Papagayo (Costa Rica)

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ABSTRACT: The structure of demersal assemblages (fish, crustaceans and cephalopods) of the continental shelf and upper slope between the Gulf of Tehuantepec and the Gulf of Papagayo was studied from data obtained in the course of surveys carried out by the RV 'Dr. F. Nansen' in 1987, by means of an ordination technique, Detrended Correspondence Analysis (DCA) implemented by the program DECORANA, and a classification technique, Two-Way Indicator Species Analysis (TWIA) implemented by the program TWINSPAN. Three major groups of species were identified: those distributed above the thermocline, those within the range of the thermocline and a third group below the thermocline, where oxygen content is extremely low. Highest biomass densities were found below the thermocline, consisting mainly of the galatheid crustacean *Pleuroncodes monodon* (H. Milne Edwards, 1837). Correlation of DCA Axis 1 with depth, temperature, salinity and oxygen showed that depth is the main gradient along which faunal changes occur.

INTRODUCTION

Since 1975 the Norwegian RV 'Dr. F. Nansen' has carried out acoustic and trawl surveys of the continental shelves and upper slopes of many tropical countries. The present study is the first of a series based on material from these surveys, investigating the structure of demersal assemblages in relation to principal environmental variables and geographical location. The taxa included in the analysis are bony and cartilaginous fishes, stomatopods, decapod crustaceans and cephalopods.

As pointed out by Caddy & Sharp (1986), this type of study is a necessary step toward understanding of multispecies stocks. Such work can then be extended to 'descriptive community dynamics' (McManus 1985) in order to find general patterns of which species compositions can be expected under given environmental conditions and fishing effort. Comparison of assemblages from similar ecosystems in different areas might also reveal general trends in the community dynamics of tropical shelves.

In addition, this work could be useful in fisheries management. For example, species composition of trawl catches from a given study area may be roughly anticipated from assemblage maps derived from the analysis, especially for those areas most recently investigated.

Studies of tropical fish community structure by means of multivariate analysis (excluding coral reef areas and lagoon systems) have been carried out in the Gulf of Guinea (Fager & Longhurst 1968), Namibia (Lleonart & Roel 1984), upwelling areas of West Africa (Roel et al. 1985), the Gulf of Nicoya, Costa Rica (Bartels et al. 1983), the Samar Sea, Philippines (McManus 1985), Malaysia (Chan & Liew 1986), northern Australia (Rainer & Munro 1982 and Rainer 1984) and northwestern Australia (Sainsbury 1987).

To the author's knowledge, no other studies of shelf assemblages have covered the area considered in the present work, i.e. the shelf between the Gulf of Tehuantepec and the Gulf of Papagayo. Bartels et al. (1983) described the occurrence, distribution, abundance and diversity of fish assemblages in the Gulf of Nicoya, Costa Rica. Studies on fish community structure in coastal lagoon systems on the Pacific coast of Mexico were carried out by Warburton (1978), Yanez-Arancibia (1978 a, b) and Chavez (1979).

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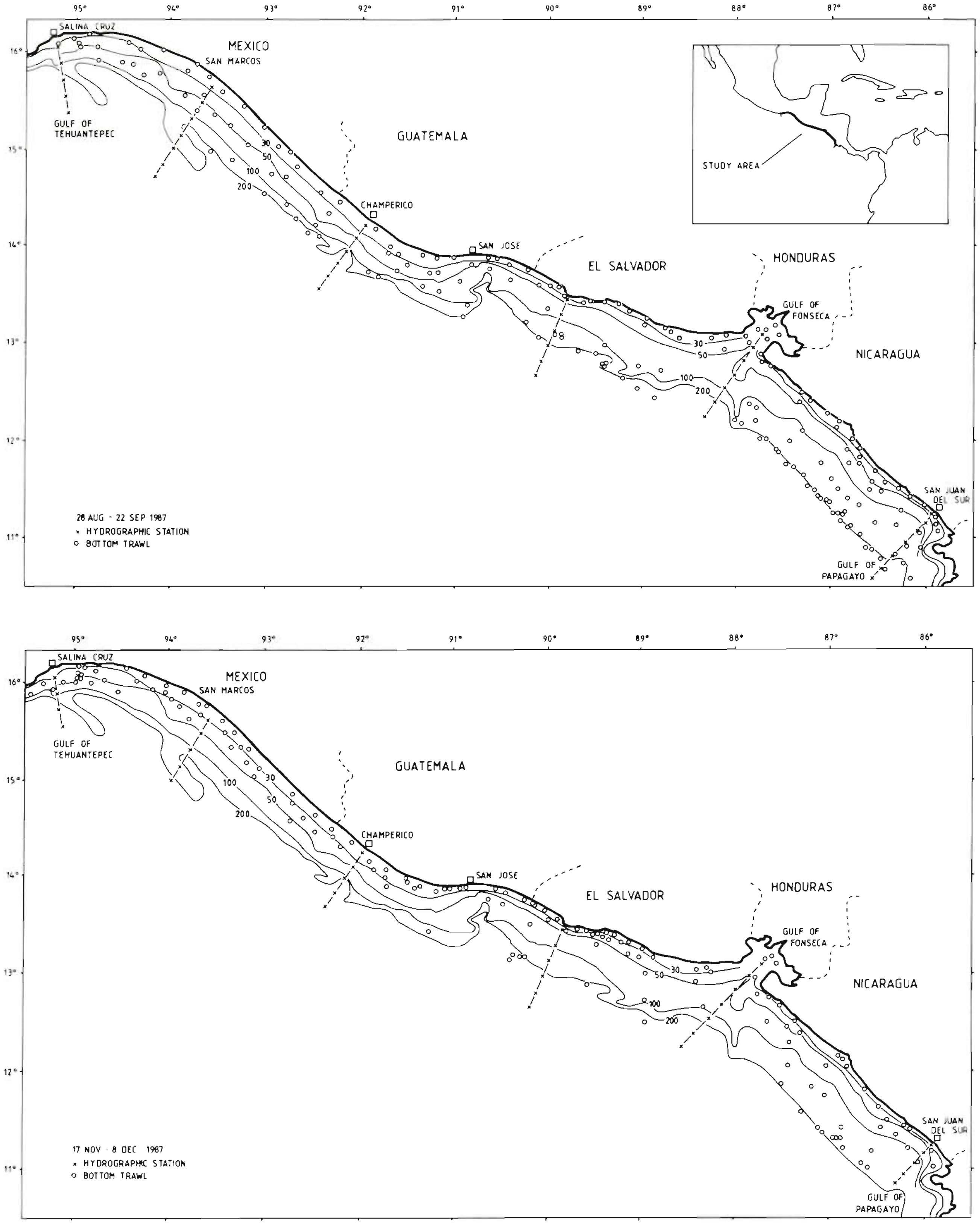


Fig. 1. Position of trawl hauls and hydrographic stations in 1987. Upper: August–September survey; lower: November–December survey. Depth gradients in metres

STUDY AREA

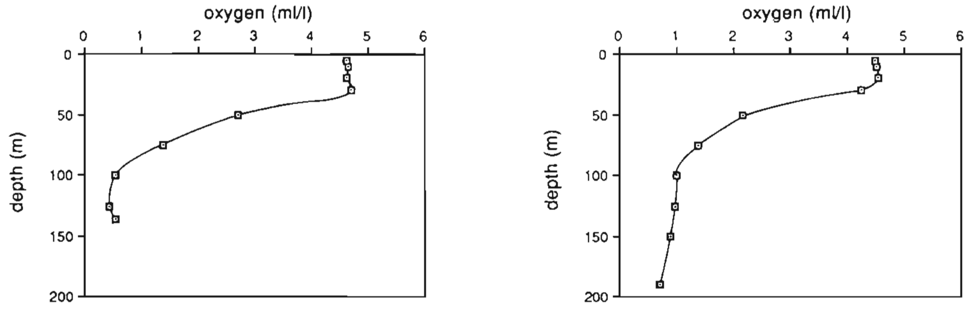
The study area (Fig. 1) included a coastline of about 685 nautical miles, from 95° 30′ W (Mexico) to 85° 50′ W (northern Costa Rica), and an area of about 28 300 square nautical miles (from about 10 to 500 m depth), of which 23 000 represent the shelf area to 200 m depth and about 5300 represent the upper slope (Strømme & Sætersdal 1988). Off Nicaragua and El Salvador the shelf is wide; it narrows off Guatemala and widens again off southern Mexico. The shelf bottom is muddy throughout, but sand and shells are dominant off southern Mexico (Anonymous 1977). The slope to 500 m depth is quite steep off Nicaragua and northwards to Guatemala. Off Mexico it is much wider, with steep and rough bottoms especially in the northwest.

Water masses of the eastern tropical Pacific are comprehensively described by Wyrtki (1967). Hydrographic conditions on the shelf area during the survey period are described in the survey report (Strømme and Sætersdal 1988). The biological oceanography of the eastern tropical Pacific has been reviewed by Blackburn (1966).

The surface offshore circulation of this area is characterized by the Costa Rica Current, i.e. the north branch of the Equatorial Counter Current which splits when approaching Costa Rica. Strongest from June to December, this current flows parallel to the coast and around the Costa Rica Dome and turns westward to feed the North Equatorial Current.

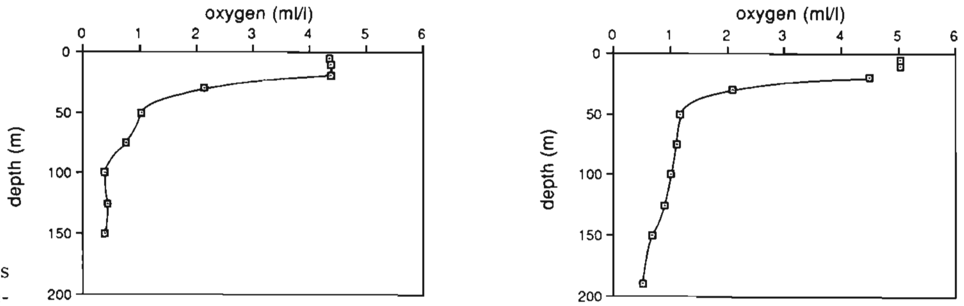
An oxygen-minimum layer more than 1200 m thick characterizes the intermediate water masses off Mexico to Costa Rica; its upper boundary is described as being shallower than 50 m in the coastal and offshore areas from about 9°N (Costa Rica) to 16°N (southern Mexico). This oxygen-minimum layer is a consequence of sluggish water movement in these areas where circulation of the subtropical anticyclones does not penetrate (Wyrtki 1967). In the course of our survey, oxygen levels of 1 ml l^{-1} were observed on the shelf bottom between 50 and 150 m depth, varying with geographical location and season and with a tendency to occur in shallower waters towards the north. In September this level was found between 75 m (Salina Cruz, Mexico) and 125 m (San Juan del Sur, Nicaragua), while in November/December it ascended and was located at about 50 and 75 m respectively. Below the 1 ml l^{-1} isoline, oxygen content decreased and levels of 0.5 ml l^{-1} were found at the edge of the continental shelf or upper slope throughout the year (Strømme & Sætersdal 1988). Fig. 2 shows oxygen profiles at selected stations, for both warm and cold seasons.

The thermocline is shallow, located between about 35 and 100 m and present all year round. It appears to be slightly shallower during the cold (upwelling) season (Fig. 3). Coastal upwelling occurs as a consequence of the strong northeast trade winds, from November to April, through the mountain gaps of southern Mexico and southern Nicaragua/northern Costa Rica. Upwelling in the Gulf of Tehuantepec is



a) Salina Cruz (Aug.-Sept. survey)

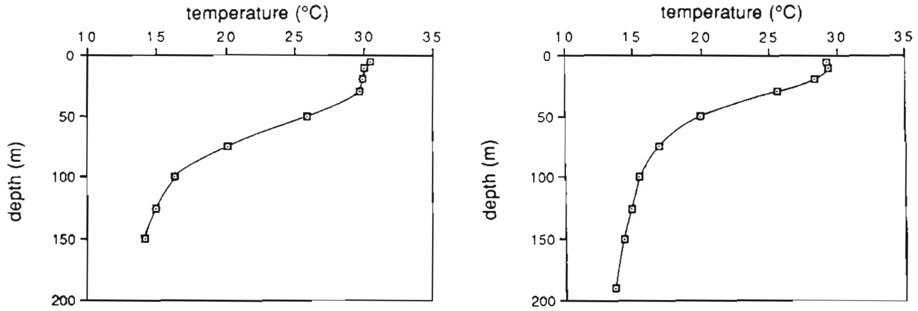
b) San Juan del Sur (Aug.-Sept. survey)



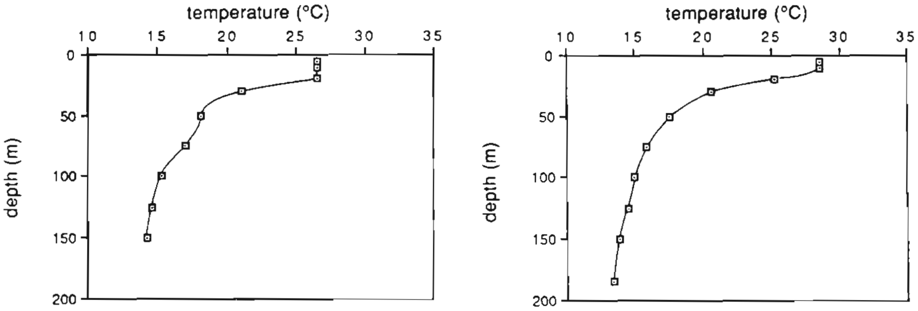
c) Salina Cruz (Nov.-Dec. survey)

d) San Juan del Sur (Nov.-Dec. survey)

Fig. 2. Oxygen concentrations (ml l^{-1}) in relation to depth at selected stations in 1987



a) Salina Cruz (Aug.-Sept. survey) b) San Juan del Sur (Aug.-Sept. survey)



c) Salina Cruz (Nov.-Dec. survey) d) San Juan del Sur (Nov.-Dec. survey)

Fig. 3. Temperature in relation to depth at selected stations in 1987

described by Roden (1961). Upwelling in the Gulf of Papagayo is also a well-known event. Temperatures below 20 °C have been observed in the surface waters near San Juan del Sur (Nicaragua), lasting about 3 mo (January to March; Glynn et al. 1983). Hydrographic observations made with the RV 'Dr. F. Nansen' showed a clear upward trend in depth of the thermocline in the course of Survey 3 (in December 1987). Offshore upwelling has been described for the Costa Rica Dome by Wyrtki (1967), and the associated higher productivity by Blackburn (1966). More detailed studies on phytoplankton and copepod distribution in this area are presented by Sameoto (1986) and Subba-Rao & Sameoto (1988); the latter compared vertical distribution (0 to 1000 m) of phytoplankton inside and outside the Dome area and reported a much higher phytoplankton concentration inside the area, at all depths. Higher concentrations were also found in the aphotic zone originating from the overlying euphotic waters, and this probably plays an important role in the food web of the deep sea.

The shoal thermocline seems also to be a cause of high productivity. Brandhorst (1958) found that in areas of the eastern Pacific where the thermocline was close to the surface (20 to 50 m), standing stocks of chlorophyll and zooplankton were higher than in areas with a deeper thermocline. This is probably due to enrichment from below by wind-mixing and to the significantly higher productivity in the well-lit waters below the mixed layer (Blackburn 1966).

MATERIALS AND METHODS

Trawl data. Material was collected on 2 cruises in 1987 (28 August to 21 September and 17 November to 7 December, respectively). A shrimp and fish trawl was used, with a headline of 31 m, footrope of 47 m, and estimated headline height and distance between wings during towing of 6 and 18–20 m respectively. Mesh size was 2 cm, with double lining in the cod end. Each tow had a standard duration of 30 min. Other details on the gear used may be found in Strømme & Sætersdal (1988). The bottom-trawl stations used in this analysis were randomly set along the cruise track, but in the November–December survey higher effort was concentrated in the inshore areas and at the edge of the continental shelf and upper slope off Nicaragua. The present analysis is based mainly on the August–September survey, with a higher and better-distributed effort, while the November–December survey was used for comparison. A total of 191 and 157 stations were sampled in the course of the 2 surveys respectively (Fig. 1a, b).

Each specimen caught was counted and weighed separately. In cases where identification was possible only to genus or family, provisional names were given and specimens were retained and later identified by experts on the various groups. For the present analysis congeneric species which were difficult to separate were pooled together.

A large collection of bony fishes and crustaceans was deposited at the Senckenberg Museum (Frankfurt, Germany). All station and species data were stored using the B-trieve file system (data available in ASCII format upon request to the author).

Hydrographic data. Samples for temperature, salinity and oxygen measurements were taken with Nansen bottles at standard depths, along fixed transects (Fig. 3a, b). Surface temperature (4 m depth) was continuously recorded by a thermograph. Details on oceanographic data can be found in Strømme & Sætersdal (1988, Vol. 2: Data File).

Temperature, salinity and oxygen data were used in the present analysis to examine relationships of the different species assemblages to the physical environment. For the above variables, values were assigned to each trawl station from the nearest hydrographic station at a similar depth.

Data analysis. The primary objective was to identify major patterns of species associations based on the trawl data, to relate them to the more significant environmental factors and hence to explain the observed patterns. The method traditionally used in fish-community studies to identify groups of species/samples has been cluster analysis, usually using an agglomerative clustering algorithm. This method produces a classification diagram (dendrogram) which also shows the hierarchical relationships between groups. Drawbacks of this method are the production of miscellaneous clusters from 'left-overs' or chaining, i.e. adding objects one-by-one to groups to which they do not really belong. Also, it is quite difficult to relate the sample dendrogram to the species dendrogram and understand which species group corresponds to a given sample cluster.

Two-Way Indicator Species Analysis – TWIA (Hill 1979), implemented by the computer program TWINSPAN – was considered well suited to the main objectives of this work. This method involves a primary ordination of the samples by correspondence analysis (see below) and divisions near the midpoint of each principal axis from each successive analysis, so that each division serves to contrast the most dissimilar object types. The method '. . . constructs a classification of the samples, and then uses this classification to obtain a classification of the species according to their ecological preferences. The two classifications are then used together to obtain an ordered two-way table that expresses the species' synecological relations as succinctly as possible' (Hill 1979). In addition to a hierarchical classification of samples and species, TWIA produces a sorted community table in which stations and species are arranged along the major gradients within the data. Importance values are not used directly but are converted to a scale based on lower class limits (set at 0, 10, 100, 1000 and 10 000 kg in this study, according to catch size by species, which varied from 0 to ca 20 000 kg).

Detrended Correspondence Analysis (DCA; Hill & Gauch 1980), implemented by the computer program DECORANA, was used as a complementary ordination method. This method is particularly useful in ecological studies as it does not assume linear relationships between species abundances and environmental variables. It implicitly assumes a simple unimodal species-response model (ter Braak & Prentice 1988). DCA is a heuristic modification of Correspondence Analysis (CA), developed to eliminate the 'arch effect' and the distortion of relative distances in the ordination which are characteristic of CA. The particular version used in this study (from the program package CANOCO; ter Braak 1987) provides the option of detrending by second-order polynomials (ter Braak & Prentice 1988) instead of by segments as in the original version of the program DECORANA (Hill & Gauch 1980). Detrending by second-order polynomials seems to avoid the inconvenience of destruction of ecologically meaningful information which might occur when detrending by segments (Jongman et al. 1987) and was thus used in the present study.

The above methods are both based on correspondence analysis, which makes it possible to compare their results directly, i.e. the classification from TWINSPAN and the ordination along the first axis of DCA. Comparison is useful, as outliers can affect site classification and can be identified through the ordination results.

The relationship between station groups and environmental variables was analyzed using the DCA application in the program package CANOCO, which also provides the option of correlating the ordination axes with environmental variables (depth, temperature, salinity, and oxygen). This option also produces the mean and SD of the environmental variables for each group.

A table of 'pseudo-*F*' values (ratios of among-group to within-group variances) was constructed to evaluate the degree of conformity of a given species to a site group obtained from the above methods. A formal *F*-test cannot be performed in this case because it would be based on the same data previously used to establish the groups (Green & Vascotto 1978).

In this study biomass (wet weight) was used as a measure of abundance. Biomass is of more relevance to fisheries management and seems ecologically appropriate.

Each weight (x) was converted to $\ln(x+1)$ before DCA and the 'pseudo-*F*' test were performed. This transformation minimizes the dominant effect of anomalous catches. The addition of 1 unit is necessary to avoid problems derived by the presence of values $= 0$ or values < 1. Trials on a small sample of stations showed that this transformation did not affect the results. No transformation is necessary in the case of

TWIA, where abundances are converted to numbers corresponding to different abundance classes (so-called pseudospecies).

Demersal biomass densities (weight per unit area) were calculated using the 'swept area' method, by depth stratum:

$$D_j = C_j / q\, a_j$$

where D_j = density in Stratum j (tonnes per nautical mile), C_j = catch taken in hauls in Stratum j (tonnes), a_j = area of the bottom 'swept' by the trawl hauls in Stratum j (square nautical miles), q = catchability coefficient (= 1, i.e. all fish in the path of the trawl were caught).

Sampling errors and limitations. The research vessel could only operate in waters deeper than 10 to 15 m. Therefore, shallow-water communities were insufficiently sampled.

Bottom trawls are both species- and size-selective, and it was impossible to adjust for this type of selectivity without knowing the behaviour of most species or the real age/size structure of populations. Also, in the case of long tows, the trawl might have artificially blended different assemblages occurring within the path of the trawl.

Species identification often poses serious problems in tropical areas. Unfortunately, no guides such as the F.A.O. Species Identification Sheets for fishery purposes were available for the eastern central Pacific. Although taxonomic work was carried out with the participation of well-trained taxonomists, errors in identification may have occurred because of the participation of less-trained personnel.

Effort (i.e. number of stations) was not uniformly distributed in space or time, and this might have led to biased results. In fact many species, both demersal and pelagic, show important day/night variations in behaviour pattern, but a comparison between day and night catches was not possible because most of the deep-water stations were sampled at night, while stations in shallower water were sampled during the day. This choice was deliberate, based on patterns observed with the echo-integration system indicating that bottom fish tend to be closer to the bottom during daytime while a large number of species move to upper water layers at night. This phenomenon appears to be less pronounced in the deeper part of the shelf and upper slope.

Many typically pelagic species are often caught in bottom trawls. In shallow waters (10 to 20 m), it is quite difficult to differentiate between these 2 groups: small pelagic fish of this zone are also found quite close to the bottom, as some of them feed on bottom detritus and are preyed upon by both demersal and pelagic predators. It seems that in these very shallow waters, demersal and pelagic groups have a much closer relationship than in more offshore waters. For this reason, although this analysis is mainly aimed at demersal communities, pelagic species were included in the analysis whenever they occurred in the bottom trawl. In the deeper part of the shelf and upper slope, some pelagic and mesopelagic species which perform diurnal vertical migrations were caught in bottom trawls during daytime. Even when this occurred the species were included in the analysis, although the results were interpreted in the light of this information.

RESULTS

A total of 230 species comprising 16 004 372 specimens (203 155 kg) were sampled. Table 1 gives a list of the most important species collected and used in the analysis.

Appendix 1 shows the 2-way classification of species and stations obtained with TWINSPAN, while Fig. 4 shows the TWIA dendrogram for station groups. The first dichotomy separates all the stations shallower than 100 m (Groups 1 to 6) from those on the deeper part of the shelf and upper slope (Groups 7 and 8), where oxygen levels are well below 1 ml l^{-1}. At the second division level Group 6 (the intermediate shelf-dwellers, at depths between 50 and 100 m) is separated from Groups 1 to 5, and Group 7 from Group 8. Further divisions of the deeper stations were not considered as they seemed to be mainly due to day/night variations in the catches. At the third division level Group 1 (stations at about 30 to 40 m depth, on sandy/shell bottoms off Guatemala and Mexico) is separated from the very shallow stations (Groups 2 to 4) and from the corresponding depth range in the southern part, off Nicaragua and El Salvador (Group 5). Finally, Group 4, including the Gulf of Fonseca and the adjacent shallow waters, is separated from the remaining shallow coastal waters (Groups 2 and 3) in the fifth division.

Fig. 5 shows the ordination of the stations from the August–September survey on DCA Axes 1 and 2. The eigenvalues of the first 4 axes were 0.92, 0.43, 0.28 and 0.24 respectively. This shows that the gradient represented by the first axis is by far the most important. The 2 largest discontinuities along the first axis (0.42 and 0.63 SD, respectively) produce 3 groups: a first group including stations usually shallower than 50 m, a second group of stations between 50 and 100 m, and a third group in which most stations were deeper than 150 m.

Results from the correlation of DCA Axes 1 and 2 with the environmental variables are presented in Table 2. The first axis was highly correlated with depth, temperature and oxygen, while there was no significant correlation of these variables with Axis 2.

Table 1. Main species collected in 1987 between the Gulf of Tehuantepec (Mexico) and the Gulf of Papagayo (Costa Rica), by major taxonomic groups and families

Cephalopods

- Loliginidae
  - *Loliolopsis diomedeae* (Hoyle)
  - *Lolliguncula panamensis* Berry

Stomatopods

- Squillidae
  - *Squilla biformis* Bigelow
  - *Squilla panamensis* Bigelow

Decapod crustaceans

- Solenoceridae
  - *Solenocera agassizii* Faxon
- Penaeidae
  - *Penaeus brevirostris* Kingsley
  - *Penaeus californiensis* Holmes
  - *Penaeus vannamei* Boone
  - *Xiphopenaeus riveti* Bouvier
- Pandalidae
  - *Heterocarpus* sp.
- Galatheidae
  - *Pleuroncodes monodon* (H. Milne Edwards)
- Calappidae
  - *Mursia gaudichaudii* (H. Milne Edwards)
- Portunidae
  - *Portunus acuminatus* (Stimpson)
  - *Portunus asper* (A. Milne Edwards)

Sharks

- Carcharhinidae
  - *Carcharhinus porosus* (Ranzani)
  - *Nasolamia velox* Gilbert
- Sphyrnidae
  - *Sphyrna lewini* (Cuvier, Griffith & Smith)

Bony fishes

- Albulidae
  - *Albula vulpes* (Linnaeus)
- Muraenidae
- Ophichthidae
- Clupeidae
  - *Neoopisthopterus tropicus* (Hildebrand)
  - *Opisthonema libertate* (Günther)
  - *Opisthopterus dovii* (Günther)
  - *Opisthopterus equitorialis* (Hildebrand)
  - *Pliosteostoma lutipinnis* (Jordan & Gilbert)
- Engraulididae
  - *Anchoa* sp.
  - *Anchoa argentivittata* (Meek & Hildebrand)
  - *Anchoa spinifer* (Valenciennes)
  - *Lycengraulis poeyi* (Kner & Steindachner)
- Ariidae
  - *Arius* spp.
  - *Bagre panamensis* (Gill)
  - *Galeichthys peruvianus* Lütken
- Argentinidae
  - *Argentina aliceae* Cohen
- Synodontidae
  - *Synodus evermanni* Jordan & Bollman
  - *Synodus scituliceps* Jordan & Gilbert
- Myctophidae
- Moridae
- Merlucciidae
  - *Merluccius angustimanus* Garman
- Ophidiidae
  - *Lepophidium pardale* (Gilbert)
- Batrachoididae
  - *Porichthys nautopaedium* Jordan
- Lophiidae
  - *Lophiodes caulinaris* (Garman)
- Ogcocephalidae
  - *Zalieutes elater* (Jordan & Gilbert)
- Scorpaenidae
  - *Pontinus sierra* (Gilbert)
  - *Scorpaena* spp.
- Triglidae
  - *Prionotus horrens* Richardson
  - *Prionotus quiescens* Jordan & Bollman
- Serranidae
  - *Diplectrum euryplectrum* Jordan & Bollman
  - *Diplectrum labarum* Rosenblatt & Johnson
  - *Diplectrum macropoma* (Günther)
  - *Hemanthias signifer* (Garman)
  - *Pronotogrammus eos* Gilbert
- Carangidae
  - *Caranx caballus* Günther
  - *Caranx caninus* Günther
  - *Chloroscombrus orqueta* Jordan & Gilbert
  - *Carangoides ortrynter* (Jordan & Gilbert)
  - *Hemicaranx* spp.
  - *Oligoplites refulgens* Gilbert & Starks
  - *Selar crumenophthalmus* (Bloch)
  - *Selene peruvianus* (Guichenot)
- Lutjanidae
  - *Lutjanus guttatus* (Steindachner)
  - *Lutjanus peru* Nichols & Murphy
- Gerreidae
  - *Diapterus aureolus* (Jordan & Gilbert)
  - *Diapterus peruvianus* (Cuvier)
  - *Eucinostomus gracilis* (Gill)
- Haemulidae
  - *Conodon macrops* Hildebrand
  - *Orthopristis chalceus* (Günther)
  - *Pomadasys axillaris* (Steindachner)
  - *Pomadasys leuciscus* (Günther)
  - *Pomadasys panamensis* (Steindachner)
  - *Xenichthys xanti* (Gill)
- Sciaenidae
  - *Bairdiella* spp.
  - *Cynoscion phoxocephalus* Jordan & Gilbert
  - *Cynoscion reticulatus* (Günther)
  - *Cynoscion stolzmanni* (Steindachner)
  - *Isopisthus altipinnis* (Steindachner)
  - *Larimus acclivis* Jordan & Bristol
  - *Larimus effulgens* Gilbert
  - *Larimus gulosus* Hildebrand
  - *Micropogonias altipinnis* (Günther)
  - *Stellifer* spp.
- Mullidae
  - *Pseudupeneus grandisquamis* (Gill)
- Ephippididae
  - *Chaetodipterus zonatus* (Girard)
  - *Parapsettus panamensis* (Steindachner)
- Sphyraenidae
  - *Sphyraena ensis* Jordan & Gilbert
- Polynemidae
  - *Polydactylus approximans* (Lay & Bennet)
  - *Polydactylus opercularis* (Gill)
- Gobiidae
- Trichiuridae
  - *Trichiurus nitens* Garman
- Scombridae
  - *Scomberomorus sierra* Jordan & Starks
- Stromateidae
  - *Peprilus snyderi* Gilbert & Starks
- Bothidae
  - *Citharichthys platophrys* Gilbert
  - *Cyclopsetta querna* (Jordan & Bollman)
  - *Monolene maculipinna* Garman
- Cynoglossidae
  - *Symphurus* spp.
  - *Symphurus atramentatus* Jordan & Bollman
  - *Symphurus elongatus* (Günther)
- Balistidae
  - *Pseudobalistes polylepis* Steindachner
- Tetraodontidae
  - *Sphoeroides annulatus* (Jordan)
  - *Sphoeroides lobatus* (Steindachner)

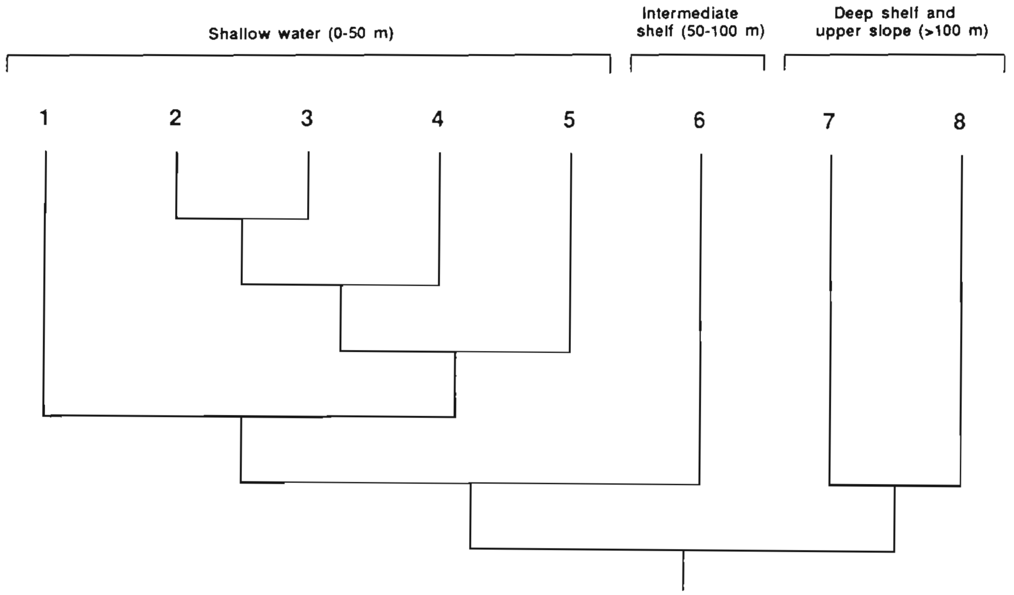


Fig. 4. Dendrogram of station groups (1 to 8) derived from classification with the program TWINSPAN (Hill 1979). See 'Results' for description of each station group

Fig. 6 shows a plot of the station scores on DCA Axis 1 against depth. Although there was a strong correlation between Axis 1 and depth, this correlation was not significant for stations shallower than 50 m and deeper than 150 m.

In order to improve the resolution of the shallow-water stations, these were further analysed using DCA. Fig. 7 shows the results after extraction of Group 1, which was better separated from the other shallow-water groups. The first 4 eigenvalues were 0.24, 0.17, 0.13 and 0.10 respectively, showing a low degree of separation of these stations, which were indeed very similar in species composition. Results from the correlation of Axes 1 and 2 with depth, temperature, salinity and oxygen are shown in Table 3. These values clearly show that faunal changes in shallow-water areas must depend on other factors, such as bottom type, connection to river estuaries, etc.

Comparison of the results from classification analysis (TWIA) to those from ordination analysis (DCA) shows that TWIA Groups 1 to 5 correspond to the first group of

Table 2. Pearson product-moment correlation coefficients between sample scores on DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for all stations

Variable	Axis 1	Axis 2
Depth	0.96	−0.10
Temp.	−0.93	0.02
Salinity	0.57	−0.05
Oxygen	−0.85	0.05

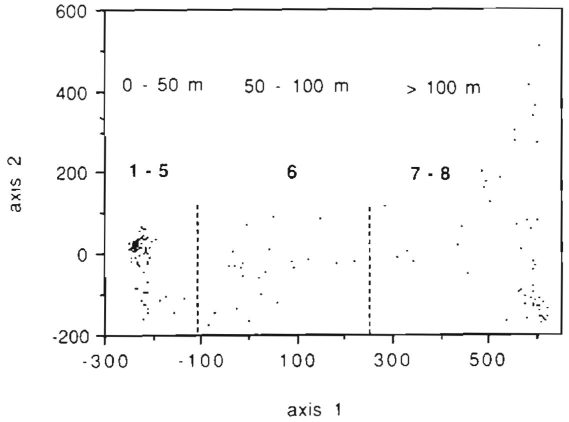


Fig. 5. Detrended correspondence analysis for the August–September survey (SD units × 100). Corresponding TWIA (Two-Way Indicator Species Analysis) groups (1 to 8) and depth ranges also indicated

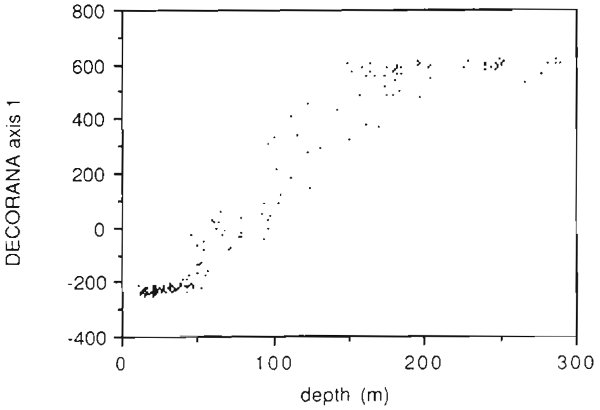


Fig. 6. Plot of station scores on DCA (Detrended Correspondence Analysis) Axis 1 against depth

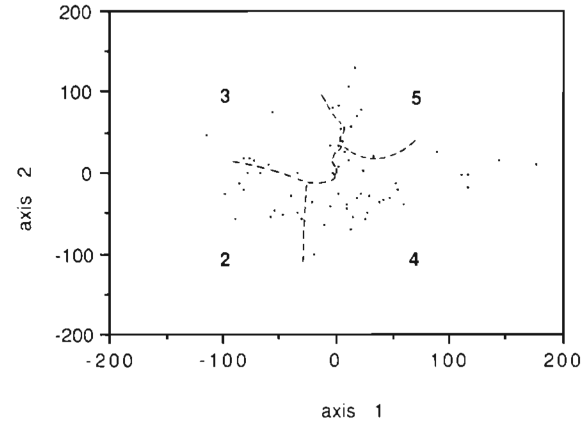


Fig. 7. Detrended correspondence analysis for station Groups 2 to 5 (indicated by numbers) of the August–September survey (SD units × 100)

Table 3. Pearson product-moment correlation coefficients between DCA (Detrended Correspondence Analysis) Axes 1 and 2 and environmental variables for shallow-water stations (Groups 1 to 5)

Variable	Axis 1	Axis 2
Depth	0.13	0.70
Temp.	−0.15	−0.66
Salinity	0.07	0.09
Oxygen	−0.41	−0.56

DCA, TWIA Groups 6 and (partly) 7 correspond to the second DCA group, and TWIA Group 8 coincides with the third DCA group.

Table 4 presents results from the 'pseudo-*F*' test applied to the above groups, together with the average values and standard deviations of the environmental variables. Each station/species group also corresponds to distinct geographical areas, as shown in Fig. 8. Table 5 gives the total weight, numbers and frequency of the main species from each station group.

Fig. 9 shows values of biomass densities obtained with the swept-area method, plotted against depth, for both surveys.

The different groups identified are described as follows:

Group 1: Sandy/shell bottoms off Guatemala and Mexico. This group includes 14 stations and a total of 71 species, located between an area near Salina Cruz (Mexico) and San José (Guatemala), at an average depth of 36 m. This group exhibits a well-defined species composition: it lacks most of the species found in the other shallow-water groups, and is characterized by species whose primary distribution is within this area, including the brassy grunt *Orthopristis chalceus*, the goatfish *Pseudupeneus grandisquamis*, the triggerfish *Pseudobalistes polylepis*, the mojarra *Eucinostomus gracilis*, the jacks *Carangoides ortrynter* and *Caranx caballus*, and the snappers *Lutjanus peru* and

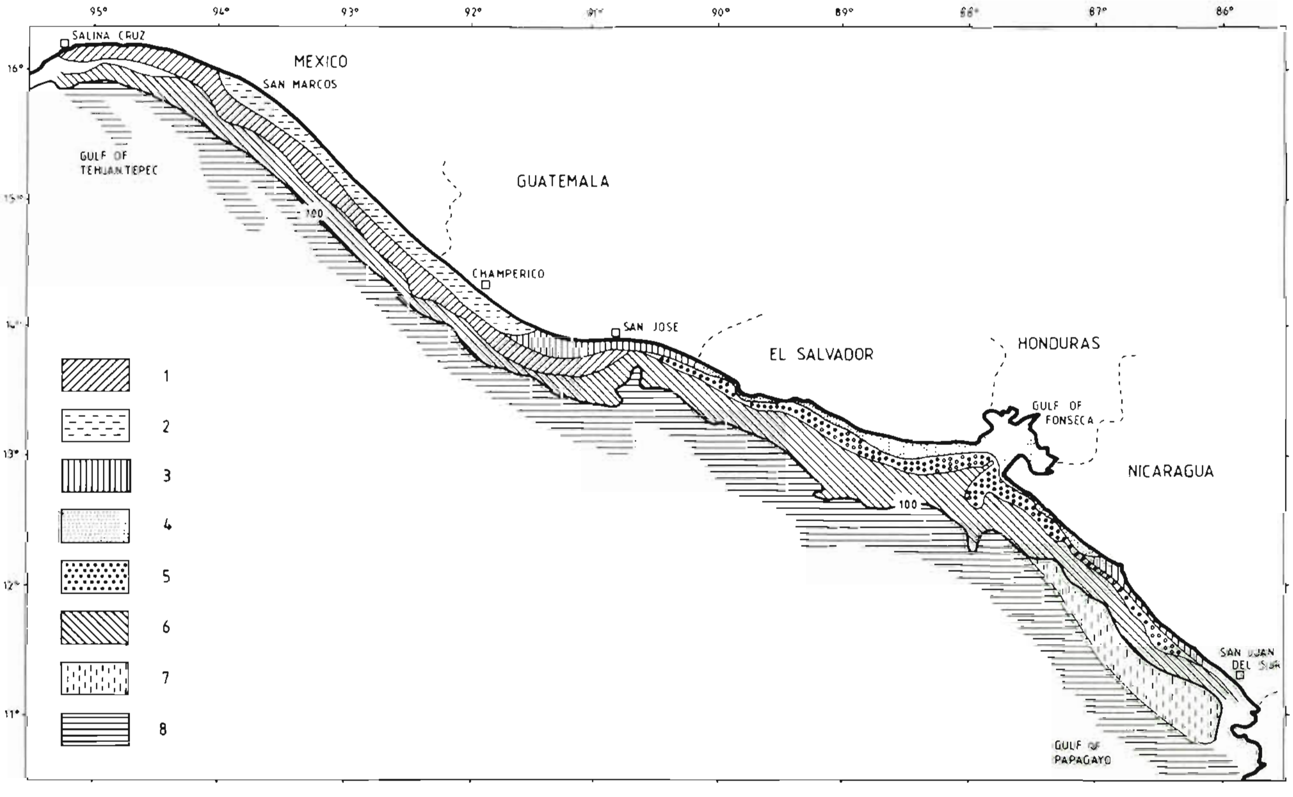


Fig. 8. Subareas corresponding to station groups. Depth gradient in metres

Table 4. Two-way table based on classification and ordination analyses, showing conforming species groups within site groups. Pseudo-*F* (P–*F*) values preceded by an asterisk indicate conformity at a significance of $p = 0.05$ or better. The average biomass value (kg) of a species within each group, converted to ln $(x+1)$, is preceded by an asterisk whenever the 95 % confidence interval for the mean is not overlapping. (****) Indicates that a species is found only in 1 group. Mean values of environmental variables are also shown for each group, with standard deviations in parentheses. Only the most important species are included

				Site groups					P–*F*
	2	3	4	5	1	6	7	8	
Environmental variables									
Depth (m)	20(5)	25(8)	23(8)	39(6)	37(8)	66(17)	134(33)	205(43)	
Temp. (°C)	29(1)	27(2)	28(2)	24(2)	27(2)	22(4)	15(1)	13(1)	
Salinity (‰)	33.1(0.3)	33.7(0.5)	33.5(0.5)	33.2(0.5)	33.8(0.4)	34.3(0.3)	34.7(0.2)	34.8(0.0)	
Oxygen (ml l^{-1})	4.5(0.4)	3.6(0.7)	3.6(0.7)	2.5(0.5)	3.1(1.0)	1.8(0.9)	0.7(0.1)	0.4(0.1)	
Species									
Anchoa spinifer			*0.836						****
Bairdiella spp.	0.191	0.228	*1.558	0.561					*17.5
Lycengraulis poeyi		0.279	*0.948	0.439					*17.4
Xiphopenaeus riveti	0.243		*1.376	0.203					*20.2
Polydactylus opercularis	1.449	1.382	0.994	1.685		0.022			*17.5
Penaeus vannamei	*1.520	0.474	0.800	0.611	0.174				*22.5
Sphyraena ensis	2.779	*4.326	2.745	2.934	0.591	0.066			*57.5
Hemicaranx spp.	0.872	1.193	1.073	0.244	0.026	0.011			*11.3
Opisthonema libertate	1.794	2.393	2.407	1.287	0.518	0.054			*26.0
Opisthopterus dovii	0.698	0.390	0.595	0.396					* 7.2
Pliosteostoma lutipinnis	1.991	0.473	1.563	0.937					*26.4
Polydactylus approximans	1.700	2.379	1.800	1.589	0.034	0.031			*33.8
Anchoa spp.	1.827	1.457	*2.210	0.331					*30.1
Isopisthus altipinnis	1.006	0.671	0.964	0.754					*14.2
Oligoplites refulgens	0.882	0.157	0.796	0.024					*14.0
Anchoa argentivittata	0.258	*1.349	0.384	*3.280	0.183	0.049			*22.6
Larimus acclivis	1.019	*1.791	0.863	0.325	0.087	0.052			*14.4
Scomberomorus sierra	1.462	*2.835	1.022	1.193	0.189	0.052			*31.7
Diapterus peruvianus	3.098	3.314	1.690	1.265	0.285				*32.6
Stellifer spp.	*1.207		0.111						*16.3
Selene peruvianus	2.083	*3.858	2.010	2.734	1.014	0.211		0.006	*32.6
Pomadasys panamensis	0.034	1.421	0.672	*2.420	0.631	0.136			*14.3
Chloroscombrus orqueta	3.537	4.390	1.592	0.513	2.299	0.019			*57.3
Pomadasys axillaris	*3.044	0.598			0.495				*50.8
Diapterus aureolus	0.342	*1.541	0.168	1.326	0.224	0.167			*13.1
Bagre panamensis	2.122	2.541	1.230	2.232	1.059	0.466			*20.5
Carangoides ortrynter			0.006	0.199	*1.099			0.043	*16.3
Selar crumenophthalmus		0.925	0.067	0.081	*1.184				*13.7
Caranx caballus	0.361	0.631	0.267	0.114	0.763	0.030			* 5.0
Eucinostomus gracilis	0.266	0.846	0.212	0.526	1.330	0.247			* 9.0
Pseudupeneus grandisquamis	0.283	0.497	0.176	0.454	*1.307	0.106			*11.4
Orthopristis chalceus	1.136	1.505			*3.150	0.979			*19.3
Cyclopsetta querna		0.563	0.166	*2.356	0.013	0.469			*24.1
Pseudobalistes polylepis					*1.614	0.244			*19.0
Scorpaena spp.						0.674			****
Peprilus snyderi	1.368	2.702	2.149	3.214	0.607	1.028	2.060	0.146	*13.4
Trichiurus nitens		0.079	0.535	0.071		0.191	*1.160	0.708	* 2.9
Loliolopsis diomedeae	0.069		0.166	0.334		0.806	0.383	0.033	* 3.8
Porichthys nautopaedium	0.004		0.083	0.077		*1.269	0.641	0.041	*14.3
Penaeus brevirostris						*1.035	0.125		*15.0
Lepophidium pardale						0.219	*0.624	0.070	* 3.8
Gobiidae				0.088		0.029	*1.764	0.020	*24.2
Citharichthys platophrys			0.034			0.272	*1.168		*14.3
Prionotus quiescens			0.051			*0.862	*3.426	0.134	*16.3
Synodus evermanni	0.139		0.078	0.045	0.259	0.625	*1.248	0.070	* 5.8
Zalieutes elater						0.301	0.329	0.184	1.9
Pontinus sierra						0.009	1.844	1.548	*14.9
Squilla biformis			0.056			0.024	0.655	*2.522	*12.3
Monolene maculipinna						0.015	0.264	*1.513	*14.7
Pleuroncodes monodon							*1.661	*5.721	*63.3
Merluccius angustimanus							0.442	*1.628	*10.9
Heterocarpus vicarius								*1.120	****
Argentina aliceae							0.868	*2.045	* 8.6
Diplectrum macropoma								*1.420	****

Table 5. Total weight (W, in kg), numbers (N) and frequency (F: no. of stations where found in the respective group) of main species from station Groups 1 to 8

Species	W	(%)	N	(%)	F
Group 1 (14 stations)					
Chloroscombrus orqueta	2 027	(35)	36 204	(47)	11
Orthopristis chalceus	897	(16)	10 550	(14)	14
Lutjanus peru	564	(10)	2 968	(4)	5
Bagre panamensis	247	(4)	2 008	(3)	6
Pseudobalistes polylepis	186	(3)	1 058	(1)	10
Eucinostomus gracilis	171	(3)	5 590	(7)	12
Lutjanus guttatus	158	(3)	204	(0)	6
Albula vulpes	140	(2)	372	(1)	6
Pseudupeneus grandisquamis	100	(2)	1 460	(2)	10
Selar crumenophthalmus	93	(2)	804	(1)	8
Selene peruvianus	87	(2)	4 042	(5)	9
Caranx caballus	47	(1)	274	(0)	7
Carangoides ortrynter	39	(1)	142	(0)	8
Pomadasys panamensis	18	(0)	130	(0)	7
Total	4 774	(83)	65 806	(85)	
Total (all species)	5 764		77 674		
Group 2 (14 stations)					
Chloroscombrus orqueta	830	(12)	14 754	(2)	14
Selene peruvianus	680	(10)	10 732	(2)	13
Sphyraena ensis	629	(10)	5 410	(1)	13
Diapterus peruvianus	527	(8)	7 726	(1)	14
Pomadasys axillaris	490	(7)	9 880	(1)	14
Opisthonema libertate	477	(7)	5 889	(1)	12
Anchoa spp.	443	(7)	402 400	(57)	11
Orthopristis chalceus	392	(6)	4 814	(1)	6
Pliosteostoma lutipinnis	275	(4)	198 282	(28)	11
Peprilus snyderi	209	(2)	1 130	(0)	7
Bagre panamensis	177	(3)	1 892	(0)	12
Polydactylus approximans	167	(3)	2 604	(0)	13
Polydactylus opercularis	106	(2)	866	(0)	9
Stellifer spp.	93	(1)	2 980	(0)	9
Scomberomorus sierra	76	(1)	262	(0)	10
Larimus acclivis	68	(1)	1 852	(0)	7
Penaeus vannamei	65	(1)	1 660	(0)	14
Isopisthus altipinnis	57	(1)	1 028	(0)	9
Total	5 761	(87)	674 161	(96)	
Total (all species)	6 640		704 308		
Group 3 (11 stations)					
Chloroscombrus orqueta	2 442	(22)	34 372	(16)	11
Sphyraena ensis	1 655	(15)	11 082	(5)	11
Selene peruvianus	1 075	(10)	26 290	(13)	11
Diapterus peruvianus	746	(7)	2 538	(1)	10
Peprilus snyderi	730	(7)	3 842	(2)	8
Opisthonema libertate	435	(4)	4 972	(2)	9
Bagre panamensis	338	(3)	1 000	(0)	10
Scomberomorus sierra	328	(3)	790	(0)	10
Anchoa argentivittata	254	(2)	71 376	(34)	6
Orthopristis chalceus	251	(2)	2 890	(1)	6
Polydactylus approximans	228	(2)	2 280	(1)	10
Hemicaranx spp.	209	(2)	1 348	(1)	5
Pomadasys panamensis	158	(1)	702	(0)	5
Diapterus aureolus	140	(1)	4 604	(2)	8
Anchoa spp.	97	(1)	32 333	(15)	6
Larimus acclivis	95	(1)	934	(0)	9
Polydactylus opercularis	86	(1)	438	(0)	6
Eucinostomus gracilis	25	(0)	292	(0)	6
Isopisthus altipinnis	23	(0)	182	(0)	5
Penaeus vannamei	13	(0)	192	(0)	4
Pseudupeneus grandisquamis	11	(0)	122	(0)	5
Total	9 349	(83)	202 579	(96)	
Total (all species)	11 205		210 926		

Table 5 (continued)

Species	W	(%)	N	(%)	F
Group 4 (29 stations)					
Sphyraena ensis	903	(10)	10 101	(2)	27
Opisthonema libertate	879	(10)	12 557	(3)	26
Diapterus peruvianus	722	(8)	2 729	(1)	18
Selene peruvianus	577	(6)	18 159	(4)	29
Peprilus snyderi	543	(6)	6 388	(1)	24
Anchoa spp.	468	(5)	234 000	(48)	26
Bairdiella spp.	383	(4)	23 164	(5)	21
Polydactylus approximans	254	(3)	4 310	(1)	25
Chloroscombrus orqueta	253	(3)	8 303	(2)	25
Xiphopenaeus riveti	207	(2)	40 795	(8)	21
Pliosteostoma lutipinnis	204	(2)	53 707	(11)	26
Larimus acclivis	204	(2)	4 382	(1)	16
Cynoscion phoxocephalus	202	(2)	2 880	(1)	11
Hemicaranx spp.	192	(2)	1 846	(0)	19
Pomadasys panamensis	138	(2)	2 575	(1)	9
Bagre panamensis	125	(1)	3 220	(1)	22
Scomberomorus sierra	125	(1)	306	(0)	17
Galeichthys peruvianus	120	(1)	453	(0)	11
Polydactylus opercularis	117	(1)	1 097	(0)	18
Parapsettus panamensis	116	(1)	1 480	(0)	10
Anchoa spinifer	101	(1)	8 565	(2)	18
Isopisthus altipinnis	95	(1)	4 450	(1)	20
Oligoplites refulgens	74	(1)	1 040	(0)	18
Lycengraulis poeyi	71	(1)	1 403	(0)	25
Penaeus vannamei	71	(1)	3 104	(1)	18
Trichiurus nitens	43	(1)	2 198	(0)	15
Total	7 187	(80)	452 789	(93)	
Total (all species)	9 040		487 172		
Group 5 (9 stations)					
Peprilus snyderi	838	(17)	5 943	(2)	8
Sphyraena ensis	722	(15)	7 567	(3)	8
Anchoa argentivittata	610	(12)	217 932	(76)	8
Selene peruvianus	354	(7)	9 321	(3)	9
Bagre panamensis	250	(5)	854	(0)	6
Pomadasys panamensis	246	(5)	1 004	(0)	7
Cyclopsetta querna	158	(3)	1 025	(0)	8
Diapterus peruvianus	111	(2)	320	(0)	4
Polydactylus opercularis	110	(2)	698	(0)	7
Polydactylus approximans	90	(0)	770	(0)	5
Pliosteostoma lutipinnis	62	(0)	18 088	(6)	4
Opisthonema libertate	56	(0)	1 014	(0)	7
Diapterus aureolus	47	(0)	2 078	(1)	6
Scomberomorus sierra	44	(0)	65	(0)	5
Isopisthus altipinnis	19	(0)	210	(0)	4
Penaeus vannamei	10	(0)	261	(0)	6
Total	3 727	(76)	267 150	(93)	
Total (all species)	4 935		287 095		
Group 6 (31 stations)					
Loliolopsis diomedeae	906	(22)	204 320	(65)	12
Orthopristis chalceus	412	(10)	7 281	(2)	13
Peprilus snyderi	281	(7)	2 651	(1)	15
Porichthys nautopaedium	182	(5)	16 644	(5)	26
Penaeus brevirostris	153	(4)	8 297	(3)	20
Cynoscion reticulatus	128	(3)	135	(0)	3
Prionotus quiescens	122	(3)	2 218	(1)	17
Synodus scituliceps	112	(3)	1 826	(1)	18
Prionotus horrens	88	(2)	422	(0)	6
Synodus evermanni	86	(2)	3 122	(1)	11
Squilla panamensis	85	(2)	6 612	(2)	8
Diplectrum labarum	68	(2)	1 926	(1)	11
Scorpaena spp.	64	(2)	4 380	(1)	16
Solenocera florea	39	(1)	12 708	(4)	5
Muraenidae	21	(1)	248	(0)	11
Zalieutes elater	20	(1)	1 472	(1)	11
Total	2 767	(69)	274 262	(87)	
Total (all species)	4 036		316 257		

Table 5 (continued)

Species	W	(%)	N	(%)	F
Group 7 (13 stations)					
Pleuroncodes monodon	22 583	(66)	2 935 558	(90)	5
Prionotus quiescens	8 480	(25)	170 114	(5)	11
Trichiurus nitens	285	(1)	8 036	(0)	8
Pontinus sierra	275	(1)	9 454	(0)	9
Gobiidae	256	(1)	27 357	(1)	8
Peprilus snyderi	219	(1)	6 844	(0)	11
Synodus evermanni	161	(1)	9 050	(0)	8
Lepophidium pardale	71	(0)	1 952	(0)	8
Argentina aliceae	59	(0)	2 778	(0)	5
Diplectrum euryplectrum	56	(0)	1 464	(0)	6
Citharichthys platophrys	56	(0)	5 792	(0)	11
Porichthys nautopaedium	35	(0)	3 970	(0)	8
Zalieutes elater	12	(0)	1 444	(0)	8
Monolene maculipinna	8	(0)	1 224	(0)	5
Penaeus brevirostris	2	(0)	72	(0)	5
Total	32 543	(95)	3 184 647	(98)	
Total (all species)	34 209		3 258 052		
Group 8 (55 stations)					
Pleuroncodes monodon	72 499	(55)	7 910 418	(74)	51
Argentina aliceae	15 406	(12)	780 158	(7)	25
Squilla biformis	12 235	(9)	661 894	(6)	31
Diplectrum macropoma	11 126	(8)	610 184	(6)	25
Heterocarpus vicarius	2 295	(2)	249 071	(2)	18
Merluccius angustimanus	1 339	(1)	45 308	(0)	29
Trichiurus nitens	1 101	(1)	38 273	(0)	16
Pontinus sierra	937	(1)	58 091	(1)	36
Monolene maculipinna	789	(1)	75 034	(1)	36
Total	117 727	(89)	10 428 431	(97)	
Total (all species)	132 326		10 736 293		

L. guttatus (see Appendix 1). The biomass of most of these species is also highest here, as shown in Table 4. The Pacific bumper *Chloroscombrus orqueta* and the Peruvian moonfish *Selene peruvianus*, the most widely distributed shallow-water species, are also found here, the former species accounting for 35 % in weight and 47 % in abundance of the total catches for this group (Table 5). Sea charts (Anonymous 1977) report mud/sand, sandy bottoms with shells and shingle in this area, and some of the above species, for example *L. peru* and *L. guttatus*, are in fact known to prefer hard bottoms (Allen 1985).

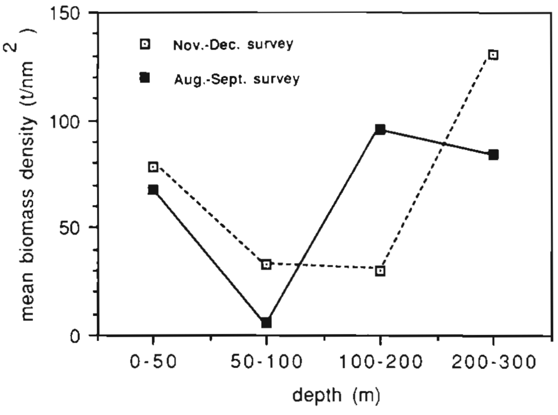


Fig. 9. Plot of mean biomass density (tonnes per square nautical mile) by depth stratum against depth for the August–September and November–December surveys. Both pelagic and demersal species included for the depth stratum 1–50 m

Groups 2, 3, 4 and 5 have several species in common: *Selene peruvianus*, *Chloroscombrus orqueta*, the threadfins *Polydactylus opercularis* and *P. approximans*, the whiteleg shrimp *Penaeus vannamei*, the barracuda *Sphyraena ensis*, the bluntnose jacks *Hemicaranx* spp., the thread herring *Opisthonema libertate*, the weakfish *Isopisthus altipinnis*, the anchovies *Anchoa* spp., the catfish *Bagre panamensis* and the butterfish *Peprilus snyderi*. However, these groups are typified by other species and occupy distinct geographical areas (Fig. 8).

Group 2: Shallow-water stations from near San Marcos (Mexico) to northern Guatemala. This group includes 14 stations, at an average depth of 20 m, with 73 species. A very high bottom temperature (29.2 °C) and high oxygen content (always above 4 ml l^{-1}) characterize this area. Typical species are the grunt

Pomadasys axillaris, *Penaeus vannamei* and the drums *Stellifer* spp. The Peruvian mojarra *Diapterus peruvianus* and *Chloroscombrus orqueta* are most abundant here and in Group 3 (Table 4). Table 5 shows that the small clupeoids, *Anchoa* spp. and the yellowfin herring *Pliosteostoma lutipinnis*, account numerically for about 85 % of the catches in that area. Also, because of their high frequency, they appear as important elements in the food chain, certainly representing an important food item for predators such as *Sphyraena ensis* and *Selene peruvianus*. The coastal zone where this group is located is characterized by a series of lagoons which probably serve as nursery grounds for the shrimp (*Penaeus vannamei*). An important fishery for this species already exists in this area (Holthuis 1980). A more complete list of the species in this group is given in Appendix 1.

Group 3: Shallow waters off Nicaragua and Guatemala. This group is very similar to Group 2, and their separation possibly artificial. Group 3 consists of 11 stations with 77 species. This group is characterized by high concentrations of *Sphyraena ensis* and the Spanish mackerel *Scomberomorus sierra*, voracious predators, and *Selene peruvianus* and *Chloroscombrus orqueta*, possibly among the prey, with catches often above 1000 kg h^{-1}. The mojarras *Diapterus aureolus* and *D. peruvianus*, *Peprilus snyderi*, *Polydactylus approximans* and *Bagre panamensis* were also almost constantly present in the catches (see Tables 4 & 5 and Appendix 1).

Group 4: Gulf of Fonseca and adjacent shallow waters of El Salvador and Nicaragua. This group is well defined and extends from the border between El Salvador and Guatemala to about 12° 20′ N (Nicaragua), including the Gulf of Tehuantepec. It includes 29 stations and 123 species and exhibited a mean depth of 23 m and high temperature and oxygen levels. *Sphyraena ensis*, *Opisthonema libertate*, *Selene peruvianus* and *Diapterus peruvianus* are the dominant species, as they are in almost all the other shallow-water Groups 2 to 4. A number of species are, however, more typical of Group 4: the sabretooth anchovy *Lycengraulis poeyi*, the croakers *Bairdiella* spp., *Anchoa spinifer* and other *Anchoa* species and the Pacific seabob *Xiphopenaeus riveti* (Tables 4 & 5). The soft and muddy bottom as well as the connection to a major river in the southern part of the Gulf explains the presence of the above species. *Lycengraulis poeyi* is a large anchovy (to 23 cm total length) and is known to prey on the smaller (to about 7 cm) anchovies of the genus *Anchoa* (Whitehead et al. 1988). The smaller anchovies are the only plankton feeders among the most widespread shallow-water species. These small fishes, because numerous and ubiquitous, must play a significant role in the food chain, and they certainly represent an important food item for the larger predatory species.

Group 5: Deeper shallow waters off Nicaragua and El Salvador. This group, with 9 stations (average depth 39 m) and 83 species, can be considered as corresponding to Group 1 (sandy/shell bottoms off Guatemala and Mexico), but is located in the southern part of the area. Most of the widespread shallow-water species missing in Group 1 are present here, particularly *Peprilus snyderi*, *Sphyraena ensis* and *Selene peruvianus* (Appendix 1). Also, the environmental conditions are slightly different, with lower oxygen and temperature levels and a bottom with a much lower sand component. Species most characteristic are *Anchoa argentivittata*, *Pomadasys panamensis* and the toothed flounder *Cyclopsetta querna* (Table 4). This latter species is known to prefer soft bottoms (Chirichigno et al. 1982).

Group 6: Upper intermediate shelf-dwellers. With an average depth of 66 m, much lower oxygen content (1.8 ml l^{-1}) and lower temperatures (21.7 °C), this group appears to be within the range of the thermocline (35 to 100 m). It includes 31 stations with 127 species. The apparently high number of species is due to the fact that some of the shallow-water species which typify the groups above are also found in the shallower stations of this group, and at the same time, species with a deeper depth range appear in the deepest stations. However, all the above species are present in very small quantities as compared to their respective primary areas of distribution (Table 4). Only 2 species show a clear preference for this area: the small toadfish *Porichthys nautopaedium* and the crystal shrimp *Penaeus brevirostris*, with higher biomass than in the other areas. Other species found here were the dart squid *Loliolopsis diomedeae*, *Peprilus snyderi*, the searobin *Prionotus quiescens*, the lizardfishes *Synodus scituliceps* and *S. evermanni* and the scorpionfishes *Scorpaena* spp. (Table 5).

Group 7: Lower intermediate shelf-dwellers. This group is found only on the wide shelf off Nicaragua. The 13 stations exhibit average depth, temperature and oxygen values of 114 m, 15 °C and 0.7 ml l^{-1} respectively. Group 7 contains a total of 54 species; the dominant ones are also found in Group 6 (*Peprilus snyderi*, *Porichthys nautopaedium*, *Prionotus quiescens*, *Synodus evermanni*, the batfish *Zalieutes elater* and the sanddab *Citharichthys platophrys*) or in the deeper shelf and upper slope, such as the scorpionfish *Pontinus sierra* and the squat lobster *Pleuroncodes monodon*. This latter species constitutes 66 % by weight and 90 % by number of individuals of the total catch for the stations in this group (Table 5). However, its value in Table 4 is not the highest, because logarithmic transformation reduces the dominant effect of the 2 very large catches which account for the high value of the total catch.

Group 8: Deeper shelf and upper slope. This group includes 55 stations and 55 species and is characterized by extremely low oxygen levels, ranging from 0.3 to 0.8 ml l^{-1} (average 0.4 ml l^{-1}). Most stations in this group are from the deeper shelf and upper slope of Nicaragua and El Salvador. *Pleuroncodes monodon*, known in Central and South America as 'langostino', dominates this part of the surveyed area and was caught at extremely high rates (up to 20 t h^{-1}) off Nicaragua, while it seemed to be less abundant in the northern part. Biomass of this species, as well as numbers and frequency, was far higher than that of any other species (Table 5). Other species in this group are *Pontinus sierra*, the deepwater Pacific flounder *Monolene maculipinna*, the hake *Merluccius angustimanus*, the argentine *Argentina aliceae*, the cagua seabass *Diplectrum macropoma*, the mantis shrimp *Squilla biformis* and the nylon shrimp *Heterocarpus vicarius*. Most of these species were not consistently caught at all stations. *Argentina aliceae* and the cutlassfish *Trichiurus nitens* were only caught in the daytime hauls.

DISCUSSION

Species assemblages

The sharpest changes in species composition occur along the depth gradient, and 3 major zones of the continental shelf can be identified. The upper zone (to about 50 m depth), with oxygen values usually well above 2 ml l^{-1}, is rich in number of species (well over 200) and exhibits relatively high biomass densities. The intermediate zone (to about 100 m), widely influenced by the thermocline and thus displaying rapid changes and short-term fluctuations in physical characteristics of the water masses, still contains a high number of species (about 160), but most of them have their optima in the water layers above and below this level, and biomass densities are in fact very low here. The deeper zone has an extremely low oxygen content (usually < 1 ml l^{-1}), which is probably the main factor, together with bottom type, explaining the type of fauna found. A single species, *Pleuroncodes monodon*, dominates the environment, together with *Squilla biformis* and *Heterocarpus vicarius*, present in much smaller quantities. It seems that the above crustaceans, particularly *P. monodon*, are well suited to live in hypoxic conditions. Of the few fish species found here in considerable quantities – *Trichiurus nitens*, *Argentina aliceae* and *Diplectrum macropoma* – the first 2 are known to perform daily vertical migrations.

Analysis of the November–December survey broadly confirms the results obtained from the August–September survey. However, faunal discontinuities along the depth gradient are less clear. The largest gap on DCA Axis 1 separates the stations deeper than 150 m from the others. This seems to be due mainly to the migration of *Pleuroncodes monodon* to slightly greater depths.

Further separation of groups, within each depth stratum, is less marked. Of the shallow-water stations, Groups 1 to 5, only Group 1 (found on sandy/shell bottoms of southern Mexico) is quite distinct. The remaining groups display a very similar species composition, although with significant differences in those species' relative abundances (Table 4). Group 4 (Gulf of Fonseca and adjacent coastal areas) is also distinguished by a number of species (*Lycengraulis poeyi*, *Anchoa spinifer*, *Xiphopenaeus riveti* and *Cynoscion phoxocephalus*) highly characteristic for this area.

Most of the studies on demersal fish assemblages on continental shelves have indicated that the main faunal changes occur along the depth gradient (Fager & Longhurst 1968, Lleonart & Roel 1984, McManus 1985, Roel 1987). Physical characteristics of water masses, as well as bottom type, light intensity, pressure, etc., are mostly depth-dependent, and depth obviously reflects the combined effects of these factors. Fager & Longhurst (1968) found that separation between different assemblages in the Gulf of Guinea was related to the thermal discontinuity layer as well as to sediment type (which also changed with depth). McManus (1985) studied fish assemblages of the Samar Sea (Philippines) from 20 to 90 m depth and found a depth-dependent faunal distinction between 30 and 40 m, independent of season and substrate type. Lleonart & Roel (1984) identified structures in species composition associated with depth and latitude when analysing demersal communities of fishes and crustaceans of the Namibian coast. Roel (1987) also concluded that composition of the demersal fauna in the upwelling region off South West Africa was related mainly to depth. In this respect, he found a main boundary between the slope fauna and the shelf fauna at about 380 m depth. The area corresponding to the shelf community could be further subdivided into 5 subareas. Two of these extended over the whole shelf and did not seem to be subject to seasonal variations. The remaining 3 corresponded to the inner shelf; their extent varied between summer and winter and appeared to be independent of depth.

The above studies, as well as the present one, indicate that when the depth range is wide enough to include areas where different water layers impinge on the shelf slope, the greatest changes in species composition are depth-related. However, within each water layer, other factors – such as presence of river mouths, type of substratum, etc. – become more relevant.

Biomass

The highest biomass densities are found along the continental shelf-slope boundary. Longhurst & Pauly (1987) indicate that the distribution of benthic biomass on tropical continental shelves reflects the importance of inshore primary production and/or enrichment from rivers, and that highest benthic biomass values correspond to the inshore mixed layer. Here, regeneration of nutrients from the bottom can be directly utilized for phytoplankton production. This is the case, for example, in the tropical Atlantic (Guinea–Sierra Leone), where Longhurst (1959) found highest benthic biomass in shallow inshore waters and a minimum at the bottom of the thermocline (50 to 100 m). Rowe (1971) found an inverse relationship between biomass and depth in temperate regions, such as the north temperate Atlantic, in tropical regions such as the Gulf of Mexico, and in the upwelling area of the Pacific off Peru. However, the conclusions apply to a wide depth range (shelf to over 5000 m depth), and a high variance was found in waters shallower than 1000 m in the upwelling area off Pisco (Peru). Here the influx of organic material is so high as to cause oxygen depletion, and stressful conditions for life and maximum biomass densities are found offshore of the oxygen-poor depths. The conditions found in the area under study seem to represent another case of deviation from the general trend of biomass decreasing with depth. As shown in Fig. 9, highest biomass densities are found below 100 m depth, consisting mainly (80 %) of *Pleuroncodes monodon*. The survey report (Strømme & Sætersdal 1988) gives identical catch rates for both daytime and nighttime hauls, which suggests a strictly demersal behaviour for this species.

The reason for this apparent deviation can be deduced from the fact that the region under study, although geographically tropical, is characterized by singular hydrographic conditions. High productivity results from the processes described above (seasonal upwelling and shallow thermocline; see 'Study area') and, possibly under-utilized by pelagic herbivores, is deposited by sedimentation on the bottom. Haedrich et al. (1976) as cited by Rowe (1981) also reported highest densities of large benthic organisms (megafauna) along the continental shelf/slope boundary off northern West Africa, and they related this finding to a prominent shelf-break upwelling. It seems evident that the inverse relationship between depth and benthic biomass is to be considered a general trend but that local hydrographic conditions may introduce deviations from this pattern.

Mass occurrences of anomouran crustaceans have been reported from other regions, usually highly eutrophic, like the California Current and the Humboldt Current. The dominance of this group seems to be due mainly to their wide range of feeding mechanisms and their ability to live in oxygen-deficient waters. Benthic mass aggregations tend to occur in areas below diatom blooms and at depths corresponding to those where the oxygen-minimum layer meets the continental shelf/slope (Longhurst 1968). Low oxygen content may be responsible for a lower number of taxa and, because of reduced competition, for high densities. *Pleuroncodes monodon*, in particular, is also very abundant off central Chile, where it occurs on the deeper shelf together with another galatheid (*Cervimunida johni*) and the shrimp *Heterocarpus reedi* (Longhurst 1968). Here the environmental conditions are similar to those found in the area of the present study – i.e., oxygen-deficient waters and high productivity. However, these are not so pronounced as to produce practically anoxic conditions with a rich fauna of sulphur bacteria, such as those further north off northern Chile and Peru, where 'semiabiotic' regions can be found between the deeper shelf and upper slope areas (about 100 and 500 m depth) (Rowe 1971).

Taxonomic note

The *Pleuroncodes* species found in this area has usually been identified as *P. planipes* Stimpson (Vidal 1971, Orellana & Escoto 1981 and others). This species typifies the Baja California upwelling region, while *P. monodon* (H. Milne Edwards) has been considered to be the southern-hemisphere congener. Highest concentrations of this species are found off central Chile, at depths between 125 and 200 m (Longhurst 1968). However, Boyd (1963), as cited by Longhurst (1968), had already reported the occurrence of *P. monodon* off the west coast of Mexico and hypothesized that this species possibly occurs off Central America. This was later confirmed by Longhurst & Seibert (1971), who found young stages of *P. monodon* in micronekton nets during eastern tropical Pacific expeditions.

Pleuroncodes planipes are known to occasionally form large pelagic swarms as adults, while most species belonging to the same family (Galatheidae) are exclusively benthic. In the course of the RV 'Dr. F. Nansen' surveys *Pleuroncodes* sp. was caught only in the bottom trawl. Also, none of the pelagic acoustic recordings was attributed to this species. No significant differences were found in the catches between night and day, confirming the strictly demersal nature of the population found off Central America.

Specimens collected off Nicaragua in the course of the RV 'Dr. F. Nansen' survey programme were recently analysed by M. Türkay (Senckenberg Museum, Frankfurt, Germany), who found (pers. comm.)

that the species in fact fits the description of *Pleuroncodes monodon*, i.e. displays slightly flattened and bare pereiopods, compared to the extremely flattened and ciliated pereiopods of *P. planipes*.

I believe that the population off central America is in fact *Pleuroncodes monodon* and that the appellation *'planipes'* has been erroneously used in this area.

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Appendix 1. Two-way station-by-species table produced by the program TWINSPAN (Hill 1979). Values denote categories of abundance (in weight, W): (1) W < 10 kg; (2) 10 < W ≤ 100 kg; (3) 100 < W ≤ 1000 kg; (4) 1000 < W ≤ 10 000 kg; (5) W > 10 000 kg. Vertical lines separate station groups; station numbers along top margin (arranged vertically under group numbers). Hierarchy shown in binary notation along the bottom and right margins of the table for stations and species respectively

```
                                 1              2            3                    4
                           1111111111111|11111111111111|11     1111|           1111111111        |
                          42257347882678|33334455666679|38455571223|45555778888000000111347777788|
                          78254059191652|67843749027910|28515739393|63689283467123456346964567901|

Cynoscion phoxocephalus   --------------|--------------|--2--------|-2---1--1-------1-2---2-21211|
Opisthopterus spp.        --------------|--------------|---2-------|22--22----------------2-----2|
Lycengraulis poeyi        --------------|--------------|------2----|1111-1111111-11111111-11-1111|
Bairdiella spp.           --------------|---1----1-----|----1-1----|2--2-11-1111-2-1211--21222212|
Anchoa spinifer           --------------|--------------|-----------|---1--11-111-11111---11-22111|
Xiphopenaeus riveti       --------------|-11----1-2--1-|-----------|---1---11-11-2112121112222211|
Parapsettus panamensis    -----1--------|-1--1---------|--11-2-1---|--1--1------111-----1-2122---|
Polydactylus opercularis  --------------|21-12-111-12--|2-2--22-1-2|21-21-111111--111----2-1-12-2|
Penaeus vannamei          ----1-----1---|11111111121111|-1-1--11---|2111-1-1--12-111112-111-----1|
Sphyraena ensis           --1-2-----2-1-|11-22321321312|23222333212|222222232211222322221111-121-|
Hemicaranx spp.           ------1-------|---111112--11-|-2-132--1--|1--121-11111--122-21-11---111|
Opisthonema libertate     --2-2---------|111331--111111|23-1222121-|2112311221221231211-2211-121-|
Opisthopterus dovii       --------------|1---11-1-1-1-1|-----1-2---|------111111-1111-------2--1-|
Pliosteostoma lutipinnis  --------------|1121311222---1|---111-----|211221111-111211122122112-11-|
Polydactylus approximans  ------------1-|1221121112-112|222121221-2|-122-22-111112121-11222121111|
Isopisthus altipinnis     --------------|-1-12--1121-11|--1-1-111--|11-2-1-1-111-11111-111111---1|
Opisthopterus equitorialis--------------|---1--1111--1-|--1-1-----1|--12---11---111-1---11---22--|
Anchoa spp.               ------------1-|1112311221--1-|--22--2221-|22-232221121-11211212222-2211|
Oligoplites refulgens     --------------|---1111-1-2111|---1-------|-11221-1111-12111---11-1--1--|
Pomadasys leuciscus       --------------|------1-------|1--1---2-1-|--2--21--1---1------1--1-----|
Neoopisthopterus tropicus --------------|----1------1-1|-------11--|--------------121211---------|
Anchoa argentivittata     ----------2---|------11---1-2|--1-32-2-11|-11------1---2-11------------|
Larimus acclivis          ------------1-|112---1-2-1--1|-12121121-2|1111-11--111-1--11--1-21----3|
Scomberomorus sierra      ------1---1---|1--1-2121-1211|2322222221-|-21121-1111-211--11111-------|
Larimus gulosus           --------------|-2-------2----|--2-1------|--1-----1------11------------|
Diapterus peruvianus      ---------1--2-|21221211232213|222-2231222|23223211222-1-1--11-12-------|
Xenichthys xanti          ------------1-|--------------|2-11-1----2|--1--11---1--1---1-----------|
Conodon macrops           ---1----------|-1---11-11-1-1|1-1-1------|--------11-----------1-------|
Stellifer spp.            --------------|111-12-1-21--1|-----------|----------------1---111------|
Larimus effulgens         --------------|---212-1---2-2|2----------|---------------------1-------|
Lutjanus guttatus         31----1-1--12-|--------------|--21122---1|222----1-1-1-1---1----1-----2|
Albula vulpes             21------1-2-22|--------------|-1-----1122|---------1-------------------|
Selar crumenophthalmus    --212---111-11|--------------|22----1---2|-11------11------------------|
Caranx caballus           -1-----1211-12|----11-----1--|12------1--|----1---------------211------|
Selene peruvianus         -1--11111-2-22|213312111111-1|23322222213|12221131111111111111213112112|
Pomadasys panamensis      -111--1---11-1|--------1-----|--122-22---|--12---12--1---1-12---------2|
Caranx caninus            22------------|----------1-1-|22---------|--1----2-------1-------------|
Chloroscombrus orqueta    --214212-11212|22322221221322|33222332234|11121111111212211--1112112-1-|
Chaetodipterus zonatus    ------1-----11|---1----11-1--|-1----2----|--1--11-------------1-1------|
Sphyrna lewini            ---2--1---2---|11-----------1|-------2---|---2-2-1111--122-------------|
Pomadasys axillaris       ---1---3-1----|22322211221212|-2------2--|--------------------1--------|
Diapterus aureolus        ----------1--1|111--11-1-----|-2111-121-2|-----------1----------------2|
Cynoscion reticulatus     ----------1---|11--2-1-1--1-1|-21111-31-2|-1----2------11-11111-1--1---|
Micropogonias altipinnis  --------------|---1-1--1---11|--2----1--2|--1---1----2---12----1-------|
Bagre panamensis          ---23-----2111|22-12121221-12|12-12222112|2112--2--11111-1111-11-221111|
Arius spp.                ---1----1-----|11-----1--1-1-|2----------|2----------------------------|
Carcharhinus porosus      -1---2----1---|--------------|---122-----|---1--2-2--------------------|
Lolliguncula panamensis   ----------1---|----11--1----1|----11-1-11|-111--1-1-1--1111----111-111-|
Carangoides ortrynter     -1---11-1112-1|--------------|-----------|-----------------1--1--------|
Eucinostomus gracilis     -1211113-21111|111---------1-|---1--11111|1-----2---11-1------1-1------|
Galeichthys peruvianus    -21---1-11----|---1-2---1---1|---1-----1-|---1-12-------1--1--112-12--1|
Pseudupeneus grandisquamis-1222111111---|-12-----------|-1-1---111-|------1--1111--1-------------|
Orthopristis chalceus     22231222122222|-231221-------|2211----2-3|----------------------------1|
Cyclopsetta querna        ------1-------|--------------|----2-21---|1-1-----1--1----1------------|
Lutjanus peru             331-2--1------|--------------|-----------|-----------------------------|
Nasolamia velox           22----2-------|--------------|-----------|---------------1-------------|
Sphoeroides annulatus     --------------|-1---1-----1-1|-----------|------2----1-1-1---------1---|
Portunus acuminatus       ----1---------|---1----1-1-1-|----------1|-------------------1---------|
Pseudobalistes polylepis  -1-21-1-112222|--------------|-----------|-----------------------------|
Scorpaena spp.            --------------|--------------|-----------|-----------------------------|
Prionotus horrens         --1-----------|--------------|-----------|---1-------1----------------1|
Penaeus californiensis    1-------------|--------------|-----------|-----------1----------------1|
Sphoeroides lobatus       --1-11--1-----|--------------|-----------|----------------------1------|
Synodus scituliceps       ----1---------|-1------11--1-|---1-------|--1-----11--1----------------|
Peprilus snyderi          --1-1--1--2--1|21-1-2312-----|331-2-321-2|-2-2-223111212222221112--2212|
Portunus asper            --------------|112-----------|---1---1---|---1------1----11------------|
Muraenidae                -----1--------|--------------|-----------|-----------1-----------------|
Diplectrum labarum        --------------|--------------|-----------|-----------------------------|
Loliolopsis diomedeae     --------------|-------1-1----|--1--------|-------1--1------1111--------|
Porichthys nautopaedium   --------------|111-----------|-----------|-----1-----1---------------11|
Penaeus brevirostris      --------------|--------------|-----------|-----------------------------|
Ophichthidae              --------------|-11-----------|-----------|-------------------1---------|
Squilla panamensis        --------------|--------------|---1-------|-----------------------------|
Symphurus atramentatus    --------------|-----1--------|-----------|-----------------------------|
Lepophidium pardale       --------------|--------------|-----------|-----------------------------|
Gobiidae                  --------------|--------------|-----------|--------1-------------------1|
Citharichthys platophrys  --------------|1-------------|-----------|1----------1-----------------|
Prionotus quiescens       --------------|--------------|-----------|----------------------------1|
Synodus evermanni         --11------1---|-----1--------|-----------|-----------1------1----------|
Symphurus spp.            --------------|1------1--1-1-|-----------|----------------1---11-----1-|
Symphurus elongatus       --------------|-1---1---1----|-----------|-----------------------------|
Diplectrum euryplectrum   --------------|--------------|-----------|-----------------------------|
Zalieutes elater          --------------|--------------|-----------|-----------------------------|
Lophiodes caulinaris      --------------|--------------|-----------|-----------------------------|
Solenocera agassizii      --------------|--------------|-----------|-----------------------------|
Pronotogrammus eos        --------------|--------------|-----------|-----------------------------|
Cynoscion stolzmanni      --------------|--------------|-----------|-----------------------------|
Mursia gaudichaudii       --------------|--------------|-----------|-----------------------------|
Moridae                   --------------|--------------|-----------|-----------------------------|
Pontinus sierra           --------------|--------------|-----------|-----------------------------|
Diplectrum macropoma      --------------|--------------|-----------|-----------------------------|
Hemanthias signifer       --------------|--------------|-----------|-----------------------------|
Monolene maculipinna      --------------|--------------|-----------|-----------------------------|
Pleuroncodes monodon      --------------|--------------|-----------|-----------------------------|
Merluccius angustimanus   --------------|--------------|-----------|-----------------------------|
Myctophidae               --------------|--------------|-----------|-----------------------------|
Heterocarpus vicarius     --------------|--------------|-----------|-----------------------------|
Argentina aliceae         --------------|--------------|-----------|-----------------------------|
Squilla biformis          --------------|--------------|-----------|-----------1----1--1--------1|
Trichiurus nitens         --------------|--------------|----1--1---|---1-11----1-11-1--1--2111111|

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134452278 85032883675134745880101 90187201  8992187413167 3510285463369956989645028050126516096570247015748243492

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11-----12 ----------------------- --------  ------------- -------------------------------------------------------  000100
222-2111- --1-------------------- --------  ------------- -------------------------------------------------------  000100
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122233-21 -1--------------------- ---11---  ------------- -------------------------------------------------------  000100
-1-1----1 ------------1---------- ----1---  ------------- -------------------------------------------------------  000100
-1112111- -11-------------------- 1--11---  ------------- -------------------------------------------------------  000100
-11-1---- ----------------------- --------  ------------- -------------------------------------------------------  000100
-212-1--- ----------------------- --------  ------------- -------------------------------------------------------  000100
-22212--- ----------------------- -1--1---  ------------- -------------------------------------------------------  000100
-111-1--- ----------------------- --------  ------------- -------------------------------------------------------  000100
---2--1-- ----------------------- --------  ------------- -------------------------------------------------------  000100
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-----1-1- -1--------------------- --------  ------------- -------------------------------------------------------  000100
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21-1---11 ----1------------------ --------  ------------- -------------------------------------------------------  000101
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---2-121- ----------------------- --------  ------------- -------------------------------------------------------  000101
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23212-1-2 --2---1---------------- 1-------  ------------- -------------------------------------------------------  001001
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-----1-21 ---1------------------- --------  ------------- -----------------------------------------1-------------  001001
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21212221- 211---------1--111-1--- 11--1---  ------------- -------------------------------------------------------  010100
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3222321-1 --111------------221122 1121--21  2211113211-2- ------------------------------------2-22---------------  011
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000000111      001111100011000111 00011                 0 1111110000000000000000111111110000011111111 000111
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