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Demersal crustacean assemblages along the Pacific coast of Costa Rica: a quantitative and multivariate assessment based on the Victor Hensen Costa Rica Expedition (1993/1994)

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Abstract: During the first cruise leg with the RV Victor Hensen to the Pacific coast of Costa Rica in December 1993 (end of the rainy season) the crustacean fauna found in the demersal collections revealed an unexpected species richness and biomass. The Crustacea collections were analyzed qualitatively and quantitatively during the fourth leg (February 1994, dry season) in the three study areas Golfo Dulce (GD), Bahía Coronado in the Sierpe-Térraba-estuary (ST) and Golfo de Nicoya (GN). Qualitative data were available for comparison from the first leg in december 1993. A total of 24 beamtrawl and ten ottertrawl sample collections were done on an area of 860.000 m² yielding a total of 119 species with a biomass of 37,8 kg (10275 specimens). Despite the smaller area covered by the beamtrawl, it collected a higher number of species and more biomass than the ottertrawl due to the smaller mesh size (0,8 cm). Judging from the shape of the species -per-area-curves, the crustacean fauna appeared as representatively sampled for the study area. As compared with the GN (biomass 0,36 g ± 0,26, SR = 97) and the ST (0,41 g ± 0,27, SR = 59) and according to the results of the log-series-plots constructed from the abundance data, the GD seems to be a depauperated area with significantly lower biomass (0.05 g ± 0,07) and species richness (45 sp.). No crustaceans were found in the center of the deep basin of the GD but parts of the interior gulf with adjacent mangrove areas seem to be important as nursery area for some commercially important penaeid shrimp species. The ST-estuary revealed the highest mean species number per station in the whole study area, but the GN had the highest total number of species. Biomass seems to be regularly distributed and not depth-depending within the GN, while species abundance varies clearly, confirming previous results. In contrast, abundance and biomass correlated well in the ST. Based on the results of the multivariate analysis, seven station groups of particular species assemblages can be distinguished in the study areas. Despite a high variability between stations in abundance and biomass, the following four areas of characteristic species assemblages can be identified which are also confirmed by an independent study on demersal fishes: (1) the interior part of the GN, characterized by juvenile shrimps (*Sicyonia disdorsalis, Trachypenaeus fuscina*), several patchily distributed anomurans, brachyurans and other predator species like portunids (especially *Portunus asper*) and pre-adult stomatopods (*Squilla* spp.); (2) the exterior part of the GN with high amounts of caridean (*Pantomus affinis, Plesionika* spp.) and penaeid shrimps (*Sicyonia picta, Solenocera mutator*), the highly abundant *Iliacantha hancocki* and some specimens of the stomatopod *Hemisquilla stylifera* and the deep water portunid *Portunus iridescens*; (3) a transition zone between 60 and 120 m water depth with a heterogeneous faunal composition, located in the ST and east of Isla Tortugas in the GN, and (4) the oxygen-depleted shelf edge area, dominated by the galatheid *Pleuroncodes monodon*. Mass occurrence of this species takes place off the GD and to a lesser extent off the ST-estuary, associated with high numbers of *Solenocera* spp. There seems to be a general trend of species groupings along abiotic gradients (depth, temperature, oxygen saturation) interrupted by small-scale variations in habitat type, current regime, food availability and other factors not identified in this study. Neither total abundance and biomass nor biotic summary parameters like diversity, dominance or species richness correlated well with the abiotic factors measured during this survey.

Key words: Costa Rica, crustacean assemblage, abundance and biomass distribution, diversity.

The study reported here represents the second part of the analysis of the demersal assemblages surveyed during the VH cruise 1993/94 in the Golfo de Nicoya (GN), the Golfo Dulce (GD) and in Coronado Bay in the Sierpe-Térraba estuary (ST). While the first part deals with the fish assemblages (Wolff 1996), this paper focuses on the part of the beamtrawl and ottertrawl collections corresponding to the decapod crustaceans. The decision to separately analyse the crustacean fauna was made at the end of the first cruise leg in december 1993 during the transition from the rainy to the dry season, when an unexpected species richness and biomass of crustaceans was found in the collections. This did not only hold for commercially important shrimp species but also for a great variety of brachyuran and anomuran species. This indicates that the crustacea play a significant role in the benthic food web on several trophic levels as detrivorous organisms and filter feeders as well as predators of the smaller epifauna and the infauna. While the crustaceans were analysed only qualitatively as by-catch during the first cruise leg, the collections of the second leg were analysed qualitatively and quantitatively. For that reason any comparison between the two cruise legs can only be done qualitatively.

The samples of the second part of the cruise were therefore analysed in order to investigate the quantitative (abundance and biomass) and qualitative (species richness, diversity, dominance) characteristics of the crustacean assemblages of the three study areas and to identify area or depth specific species assemblages. Similar stations in terms of species composition were related to abiotic parameters to see if and how certain faunal groups relate to environmental conditions.

Past studies on the structure of crustacean assemblages of the Pacific coast of Costa Rica are restricted to the Golfo de Nicoya and, except for the Skimmer expedition in 1979, dealed only with particular groups. In the Golfo de Nicoya area 54 crustacean species were found by Maurer *et al.* (1984). They reported the highest abundance and biomass values for shrimp species, whereas the brachyurans showed the highest species numbers among invertebrates. According to the authors, abundance varied greatly with the season, while biomass remained relatively constant. The commercially important shrimp species (especially *Penaeus* spp.) showed a high small-scale-variability but no significant difference in their occurrence between seasons. Some more investigations on larval distribution in the GN are done by Dittel & Epifanio (1991).

MATERIAL AND METHODS

Sampling and processing: Sampling was done in December 1993 and February 1994 once at 24 beamtrawl stations (mesh size 1 cm) for 15 minutes with an average towing speed of 1,5 knots, sweeping an area of 2084 m^2 per station. On those stations where the employment of an ottertrawl was possible, sampling was repeated and 10 ottertrawl hauls (mesh size 2,5 cm) for 30 minutes at a speed of 2 knots, sweeping an area of 81025 m^2 per station. (see fig. 1).

The samples were sorted into species, which were then counted and weighed to the nearest 0,5 g on board if total weight exceeded 200 g. Species with lower biomass per sample were preserved in 4 % formalin and weighed in the laboratory to the nearest 0,01 g to avoid the high measuring error when weighing on board. For each abundant species (> 50 ind./sample) length frequencies were recorded. In a few cases where the number of organisms was very high, a subsample was taken and numbers were estimated by extrapolating to the total weight. Species were identified in the laboratory by the author, and with assistance of Dr. Türkay from the Senckenberg Institute in Frankfurt, according to: Burukovsky 1981, Carvacho & Bonfil 1989, Chace 1937, Farfante 1971; 1985, Faxon 1895, Galil 1993, Garth 1940; 1958; 1973; 1986, Garth & Stephenson 1966, Guinot 1984, Hendrickx 1989; 1990, Hendrickx & Salgado-Baragán 1991, Kim & Abele 1988, Milne-Edwards & Bouvier 1983, Prahl & Sanchez 1986, Rathbun 1910; 1918; 1925; 1930; 1933; 1937 Schmitt 1938; Serène 1964, Wicksten 1978; 1982a; 1982b.

Data analysis: Data from the beamtrawl collections were analysed as described by Wolff (1996) for the fish data. The station G which is located outside the sill rigde was excluded from the Golfo Dulce data analysis. The ottertrawl collections were excluded from further analysis as the ottertrawl did not sample the small crustacean fauna adequately due to its large mesh size (2,5 cm). A comparison of the data between the two cruise legs was done only qualitatively due to missing quantitative data from the first part of the cruise. In order to compare the three study areas a rank order of species according to their corresponding number was established. As the data fell on a straight line using the logarithm of the abundances, the

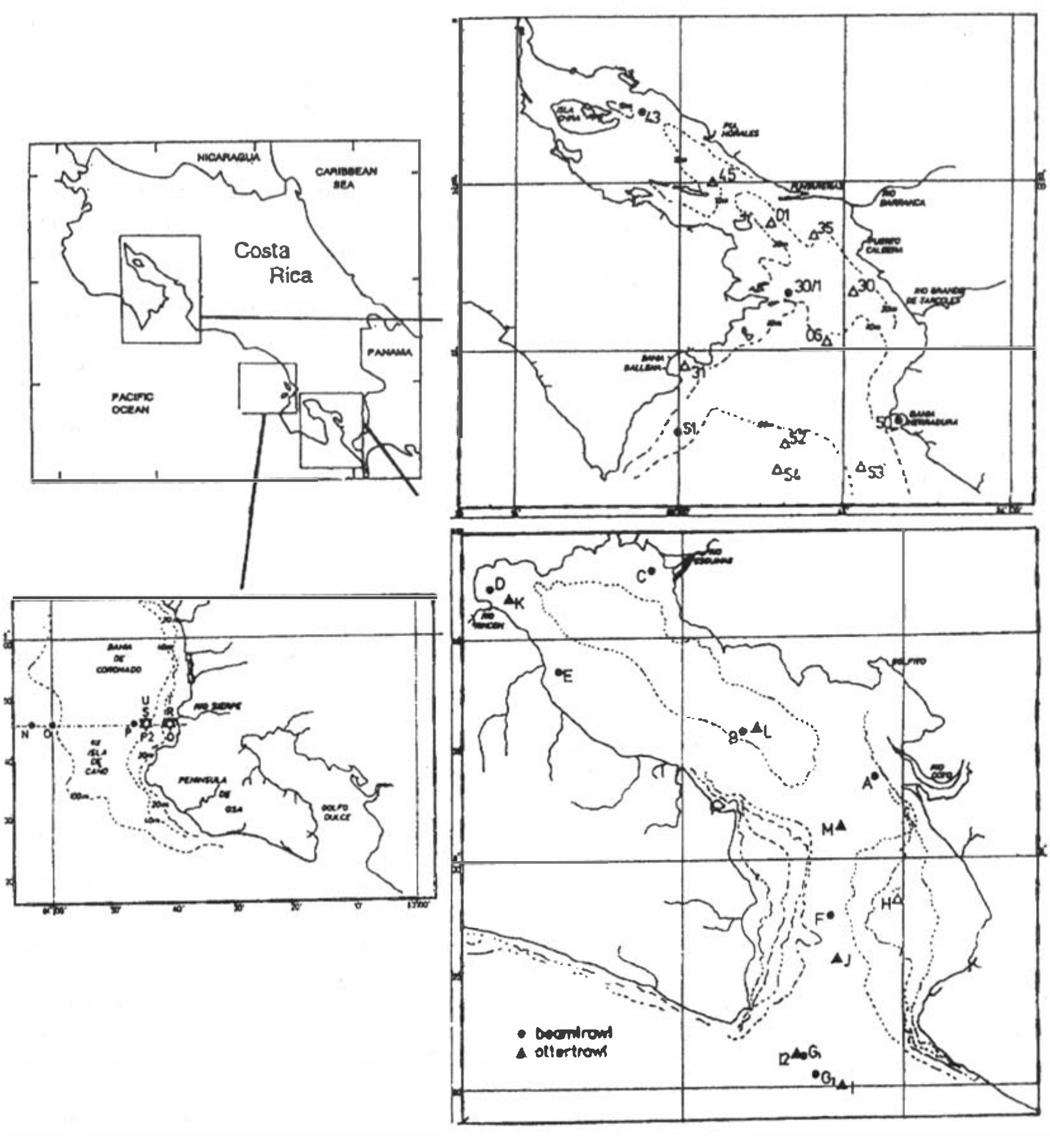


Fig. 1. Study areas with sampling sites (upper left: overview; upper right: Golfo de Nicoya; lower right: Golfo Dulce; lower left: Bahía Coronado/Sierpe-Térraba).

log-series-model (Taylor *et al.* 1976) was applied and the model parameter which represents a measure for diversity was calculated by maximum likelihood using the following equation (Southwood 1978):

$$ST = \alpha \times \log\left(1 + \frac{N}{\alpha}\right)$$

where ST is the total number of species and N is the total number of individuals sampled. Contrary to other numerical estimators of diversity like the Shannon-Weaver-index H' this model also allows for a graphical representation of the relative importance of the species of the assemblages (Wolff & Alarcon 1993). In order to compare species composition of the Golfo Dulce, the Sierpe-Térraba estuary/ Coronado Bay and Golfo de Nicoya the Sørensen's index (1948) was calculated after:

$$CC = \frac{2C}{A+B}$$

where C is the number of species shared in the two areas under comparison and A and B are the total numbers of species in area A and B, respectively.

In addition and for the purpose of comparison with published data, the Shannon-Weaver-index of diversity H' after Pielou (1969) and the dominance index d after Whitaker (1965) was calculated for each station:

$$H' = -\sum \frac{n_i}{N} \times \log \frac{n_i}{N}$$

$$d = \sum \left(\frac{n_i}{N} \right)^2$$

where N is the total number of individuals and n_i is the number of individuals of the i^{th} species in the sample.

The multivariate analysis was performed with the beamtrawl collections of the dry season (February 1994). A station/species matrix was constructed and a similarity matrix using the Bray-Curtis-index was computed using the fourth-root-transformed data by the use of the PRIMER software following Clarke & Warwick (1994). For this matrix the P-value was used. The descriptor P [g/m²] which represents a measure for the ecological importance of each species was modified by using a crustacean specific exponent and calculated after $P = (B/A)^{0.64} * A$ (Brey 1990). Prior to the calculations, the original species matrix was reduced such that the remaining species accounted for about 99 % of the sum of the total P-values, eliminating the very rare species. The group average linking algorithm was used to construct station- and species cluster dendrograms from the similarity matrix. Species indicative for particular groups within the station dendrogram were identified using the SIMPER (percentage of similarity)-routine of the PRIMER-software.

A "station parameter" table was constructed for the abiotic and biotic data of all stations in february 1994. Species composition at each station was correlated to the abiotic factors depth, temperature and oxygen saturation; additionally biotic station descriptors as total abundance and biomass per station, diversity, dominance and species richness were correlated with these parameters to see if patterns occurr not only at species level but on a lower (summary) level. For that a multidimensional scaling (MDS) based on the station similarity matrix mentioned above was undertaken using the PRIMER-package. The MDS-plot derived from this analysis was overlayed by sealed symbols for the abiotic and biotic variables measured for each station in order to see if spatial configuration of the stations is reflected in the different variables considered.

RESULTS

Species richness, spatial and bathymetric distribution of biomass and abundance: Table 1 contains all crustacean species collected during February 1994 (fourth leg of the cruise). Fig. 2 shows the species-per-area-curves for the beamtrawl collections for each study area. The log-series-plot derived from ranked, log-transformed abundance data along with their linear regressions is given in Fig. 3. Fig. 4 shows the biomass distribution along a depth range for the Pacific coast of Costa Rica and for each study area. High biomasses (0,2 - 0,4 g/m) were found in shallow waters above the thermocline. It was heavily reduced below the thermocline (< 0,1 g/m^2), but increased again with depth and reached another maximum in the region of the shelf edge. This pattern differs in the GD area, where no decapod crustaceans were found below 100 m depth. Table 2 summarizes species with more than 5 % relative biomass for each study area.

As seen in Fig. 5, abundance and biomass within each study area are heterogeniously distributed. Whereas station C and D in the interior part of the Golfo dulce are comparable with the interior GN stations 30/35, the other GD stations reveal much lower biomass compared to sampling sites in the other areas. The shelf-edge-station G shows the highest biomass of all. The fauna which is

TABLE I

Species list for crustacea from the fourth leg in Febuary 1994 of the VH cruise 1993/1994 along with their respective frequency of occurrence; GD(bt): Golfo Dulce beamtrawl, GD(ot): Golfo Dulce ottertrawl, ST(bt): Sierpe-Térraba beamtrawl, ***GN(bt): Golfo de Nicoya beamtrawl, GN(ot): Golfo de Nicoya ottertrawl; (*) = number of records per area and gear***

SPECIES	GD (bt)	GD (ot)	ST (bt)	GN (bt)	GN (ot)
Diogenidae					
Clibanarius sp.			*		
Dardanus sinistripes Stimpson 1858					*
Dardanus sp.1	*			****	*
Dardanus sp.2				*	
Paguristes sp.1	*			*	*
Paguristes sp.2	*		***	*	*
Paguristes sp.3				**	
Petrochirus californiensis Bouvier 1895	*				
Galatheidae					
Munida obesa Faxon 1893				*	
Munida sp. n.		*	*	*	
Pleuroncodes monodon Milne-Edwards 1837	*	*	*		*
Paguridae					
Eupagurus californiensis Benedict 1892				**	
Iridopagurus sp.	*		*		
Pagurus sp.1	*			***	**
Pagurus sp.2				*	
Pylopagurus sp.			*	**	
Xylopagurus sp.			*	***	
Porcellanidae					
Porcellana hancocki Glassell 1936				*	
Calappidae					
Acanthocarpus delsolari Garth 1973	*		*	*	
Acanthocarpus sp.			*		
Calappa convexa Saussure 1853				*	*
Calappa saussurei Rathbun 1898			*	*	*
Cycloes bairdii Stimpson 1860				*	
Hepatus lineatus Rathbun 1937				*	
Hepatus sp. n.				*	*
Platymera gaudichaudii Milne-Edwards 1837	*			**	**
Platymera sp.			*		
Cancridae					
Cancer johngarthi Rathbun 1900		*			
Dorippidae					
Ethusa ciliatifrons Faxon 1893			*	**	
Ethusa lata Rathbun 1893	*		**	**	
Ethusa panamensis Finnegan 1931				*	
Ethusa tenuipes Rathbun 1897	*			**	
Dromiidae					
Hypoconcha panamensis Smith 1869	**			***	
Goneplacidae					
Chasmocarcinus latipes Rathbun 1898				**	
Chasmocarcinus panamensis Serene 1964				**	
Glyptoplax pugnax Smith 1870			*	*	
Malacoplax cf californiensis Lockington 1877			box corer		
Oediplax granulata Rathbun 1893			box corer		
Speocarcinus granulimanus Rathbun 1893				*	
Trizocarcinus dentatus Rathbun 1893			**		
Leucosiidae					
Ebalia cristata Rathbun 1893	*		**		
Ebalia sp.			*		
Iliacantha hancocki Rathbun 1935	*		**	******	***
Iliacantha schmitti Rathbun 1935	**		**	**	
Lithadia cumingii Bell 1855	*			**	
Persephona townsendi Rathbun 1893	*		**	*****	**
Randallia agaricias Rathbun 1898				****	
Randallia minuta Rathbun 1935				*	
Majidae					
Collodes granosus Stimpson 1860			*	*	
Collodes tenuirostris Rathbun 1893	*		**	**	
Collodes sp.	***		*		
Herbstia tumida Stimpson 1871				****	
Maiopsis panamensis Faxon 1893					*
Majidae sp.			*	***	*
Notolepas lamellatus Stimpson 1871					*
Paradasygyius depressus Bell 1835	**				**
Podochela angulata Finnegan 1931				*	
Pyromaia tuberculata Lockington 1877	*			**	
Sphenocarcinus agassizii Rathbun 1893				***	
Stenocionops ovata Bell 1835		*			
Stenorhynchus debilis Smith 1871				***	
Palicidae					
Palicus tuberculatus Rathbun 1893	*		*	*	
Parthenopidae					
Heterocrypta colombiana Garth 1940				*	
Heterocrypta macrobrachia Stimpson 1871	*		*	***	*
Heterocrypta cf. macrobrachia				*	
Leiolambrus punctatissimus Owen 1839	***		**	*	*
Mesorhoea belli Milne-Edwards 1878			***	*	
Parthenope exilipes Rathbun 1893				**	
Parthenope hyponca Stimpson 1871			*		***
Solenolambrus arcuatus Stimpson 1871	**		*	***	
Pinnotheridae					
Pinnixa sp.			*	*	*
Pinnixa valerii Rathbun 1931			*		
Portunidae					
Arenaeus mexicanus Gerstaecker 1856				*	
Callinectes arcuatus Ordway 1863	*			****	*
Callinectes sapidus Rathbun 1896	*			*	
Callinectes toxotes Ordway 1863				***	
Euphylax robustus Milne-Edwards 1871				*	
Portunus acuminatus Stimpson 1871	**			***	**
Portunus asper Milne-Edwards 1871		*	**	*******	*
Portunus iridescens Rathbun 1893			*	**	****
Portunus panamensis Stimpson 1871				***	*
Portunus xantusii affinis Faxon 1893		*		*****	*
Raninidae					
Raninoides benedicti Rathbun 1930	**		*	***	
Xanthidae					
Edwardsium lobipes Rathbun 1898	*				
Pilumnus fernandezi Garth 1973			*	***	
Pilumnus xantusii Stimpson 1860				*	
Xanthidae sp.1	*		*	*	
Xanthidae sp.2	*		*	*	
Xanthidae sp.3				***	
Xanthidae sp.4	**		**	***	
Palinuridae					
Panulirus sp.				*	
Axiidae sp.					*
Alpheidae					
Alpheus exilis Kim & Abele 1988				****	
Alpheus floridanus Kingsley 1880			*		
Alpheus websteri Kingsley 1880			*	***	*
Hippolytidae					
Lysmata sp. n.			*	**	
Pandalidae					
Heterocarpus vicarius Faxon 1893		*	*		
Pandalidae sp.			*	*	
Pantomus affinis Chace 1937				**	**
Plesionika beebei Chace 1937					**
Plesionika mexicana Chace 1937			*	**	
Plesionika sp. n.			*		
Plesionika trispinus Squires & Barragan 1976		*	*	*	*
Processidae					
Processa sp.			*	**	
Penaeidae					
Metapenaeopsis beebei Burkenroad 1938				*	
Metapenaeopsis kishinouyei Rathbun 1902				*	
Parapenaeopsis balli Burkenroad 1934	*				
Penaeus brevirostris Kingsley 1878	*	*	*	***	**
Penaeus californiensis Holmes 1900			**	**	
Trachypenaeus byrdi Burkenroad 1934					*
Trachypenaeus faoe Lindner 1957				***	*
Trachypenaeus fuscina Lindner 1957	*	*	**	*****	**
Trachypenaeus pacificus Burkenroad 1934			*	****	
Trachypenaeus sp.1				**	*
Trachypenaeus sp.3				*	
Xiphopenaeus riveti Bouvier 1907				*	*
Sicyonidae					
Sicyonia disdorsalis Burkenroad 1934	*		***	*******	**
Sicyonia disedwardsi Burkenroad 1934	**	*			
Sicyonia picta Faxon 1893	**		***	*****	***
Solenoceridae					
Solenocera agassizii Faxon 1893	***	*	**		*
Solenocera mutator Burkenroad 1938	**		*	***	***
Solenocera florea Burkenroad 1938	*			*	*
Hemisquillidae					
Hemisquilla stylifera Milne-Edwards 1837				**	
Pseudosquillidae					
Pseudosquilla similis			*		
Pseudosquilla veleronis Schmitt 1940				*	
Squillidae					
Squilla aculeata				***	*
Squilla biformis Bigelow 1891	*		*		*
Squilla panamensis Bigelow 1891	*	**	*	*	***
Squilla parva Bigelow 1891				****	

TABLE 2

Species with more than 5 % relative biomass of the beamtrawl catches of Febuary 1994 in four depth ranges: shallow waters (10-60 m), within the thermocline (61-100 m), warmer deep waters (101-160 m); shelf edge (161-210 m)

species 10-60 m	B [%]	species 61-100 m	B [%]	species 101-160 m	B [%]	species 161-210 m	B [%]
Sicyonia disdorsalis	19,91	*Hemisquilla stylifera*	35,91	*Sicyonia picta*	42,02	*Pleuroncodes monodon*	43,30
Solenocera agassizii	7,02	*Pagururs sp.1*	12,31	*Solenocera agassizii*	24,10	*Solenocera agassizii*	28,49
Callinectes toxotes	6,81	*Sicyonia picta*	7,66	*Portunus iridescens*	15,55	*Solenocera mutator*	9,43
Trachypenaeus fuscina	6,80	*Xylopagurus sp.*	7,56	*Plesionika mexicana*	4,90	*Pandalidae sp.*	4,57
Squilla panamensis	5,19	*Iliacantha hancocki*	6,47				
Portunus asper	4,80	*Plesionika mexicana*	4,74				
		Collodes tenuirostris	4,63				

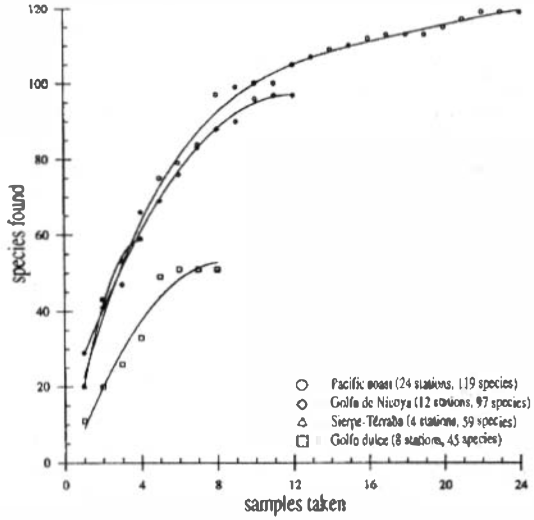


Fig. 2. Number of samples taken versus cummulative species number per sample for Golfo de Nicoya (GN), Sierpe-Térraba estuary (ST), Golfo Dulce (GD) and the whole study area for Febuary 1994.

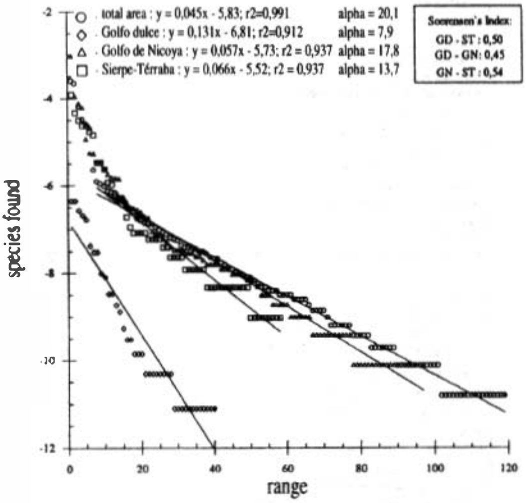


Fig. 3. Rank order of species found in the beamtrawl catches of Febuary 1994 (log-series-model) for abundance data along with their linear regressions and estimates for the model-parameter for species diversity and the Sørensen index for Golfo de Nicoya (GN), Sierpe-Térraba estuary (ST), Golfo Dulce (GD).

the inner part of the gulf where fine sediments were dominanting (95-100 % clay), living on the rich infauna throughout the year (Maurer *et al.* 1987). They seem to be an important prey for the high numbers of demersal fish in the same area (Wolff, pers. com.). At the shelf edge the galatheid *Pleuroncodes monodon* was dominating all study areas. His occurrence was closely related to that of *Solenocera* spp. (*S. agassizii* off GD ST, *S. mutator* in the outer part of the GN).

Mean biomass in GN and ST represent 50 % of the demersal fishes. In the latter area the galatheid-associated species assemblage located at the shelf edge showed significantly lower biomass values, may be due to low primary productivity as a result of interruption of upwelling processes. The nearshore species assemblages in the ST to the contrary had the highest biomass of all areas, probably as a result of high input of organic material from the large mangrove areas in this region. In both areas the benthic fauna seems to play an important role in the benthic food web, especially as a ressource for the commercially important demersal fishes. Beyond this, the fauna in the GN may be privileged through a heterogenious bottom structure which offers different habitat types and could explain the high species richness there. The great differences in the faunal structure and diversity as pointed out by the

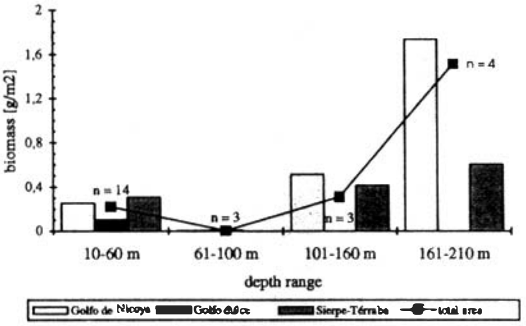


Fig. 4. Bathymetric biomass distribution (average over all stations in each area) for the beamtrawl stations in febuary 1994 for the hole study area and separated for each area (Golfo Dulce without station G): shallow waters (10-60 m), within the thermocline (61-100 m), warmer deep waters (101-160 m); shelf edge (161-210 m); n = number of stations.

located above the thermocline in the ST has a very low biomass which suddenly reaches high values below the thermocline and seems to be independant from depth. The biomass distribution in the Golfo de Nicoya confirms the results from Maurer *et al.* (1984) who found a regular biomass pattern with high variations in abundance data. Station 54 near the shelf edge exceeds all other stations in GN.

During the first leg in December 1993, 75 species belonging to 23 families were collected. The fourth leg yielded 127 species, 5 of which seem to be new species (see table 1). 16 species could be identified only to genus level due to damage of the organisms in the net. Total species number in both legs was 156. Whereas brachyurans, anomurans and caridean shrimps show twofold species numbers in the dry season, penaeid shrimps and stomatopods remained relatively constant throughout the year (Fig. 6).

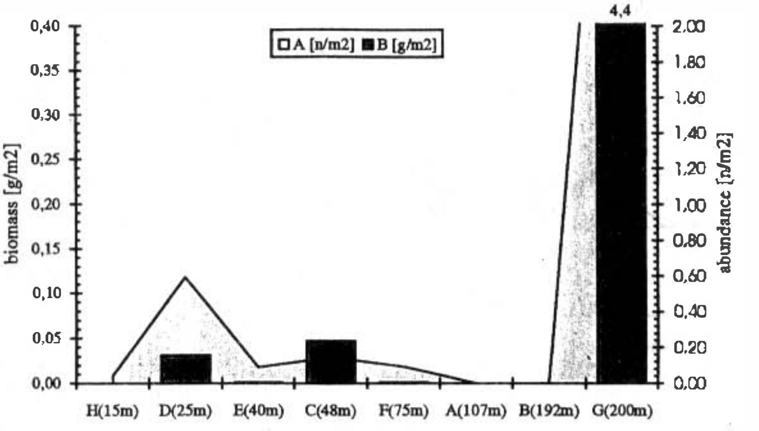
Description of faunal assemblages: Table 3 contains the reduced station-species-matrix (70 from 119 species which account for 99 % of total P-value) used for the multivariate analysis. Species were ranked according to their P-value. Table 4 gives the abiotic and biotic summary and descriptive parameters for each sampling station. Fig. 7 shows the station dendrogram for the beamtrawl samples of the dry season based on the data of table 3. Species accounting for the similarity of stations within the cluster groupings are included in the figure. The MDS-plots based on the same data and overlayed with scaled symbols for abiotic and biotic variables for each station are given in fig. 8. MDS-plots and cluster dendrogram for stations reveal the same pattern and fit quite well. Seven groups of stations can be identified with similarities between 10 to 50 %. There seems to be a trend in faunal composition along the abiotic environmental parameters, whereas the univariate biotic station descriptors such as total abundance and biomass, species richness, species diversity and species dominance did not correlate well with species composition or environmental conditions.

Fig. 9 shows the species dendrogram including the station names for each species. There was no MDS-plot implemented for species. Due to the low frequency of occurence of many species no pattern appeared in the MDS-plots for species which was therefore omitted from further discussion.

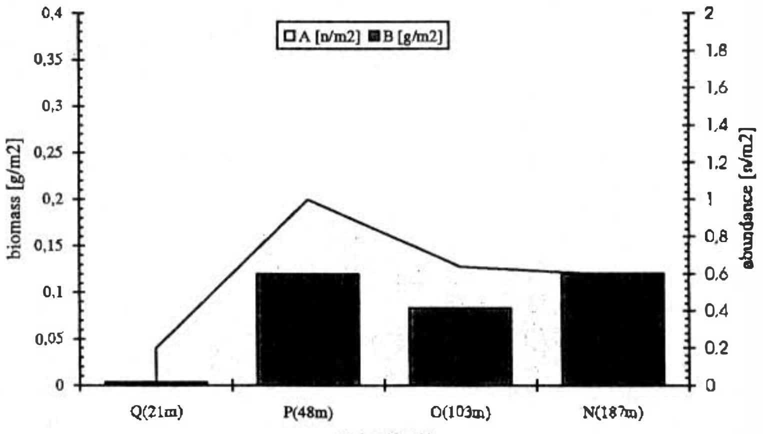
DISCUSSION

Species richness, spatial and bathymetric distribution of biomass and abundance: The number of crustacean species found in the Golfo de Nicoya (n = 97) was twice as high as that of the Skimmer - Expedition 1979 (n = 54) (Maurer *et al.*, 1984). By judging from the species-per-area-curve (Fig. 2) the total number of species collected during the cruise (119) can be regarded as representative for the study area and bathymetric range, respectively. The high number of brachyuran and anomuran species with low abundance was probably due to the wide area sampled (50.000 m^2) which allowed to cover many different habitat types. Compared to the ottertrawl catches, the beamtrawl catches showed in spite of the smaller sampling area much higher species numbers: in GN 97 sp. instead of 49 sp., but only 7 newly reported sp., in Golfo dulce (GD) 45 sp. instead of 14 sp., but only 9 newly reported sp.) For that reason it seemed reasonable to exclude the results from the ottertrawl catches from further analysis.

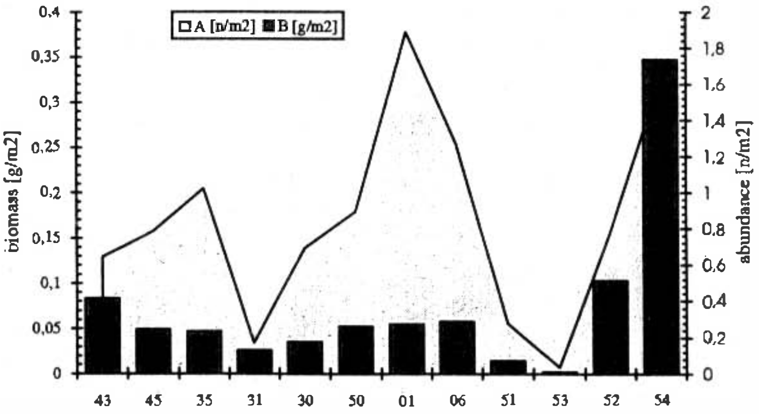
Due to a reduction in species number (5,6 sp./station compared to 8 in GN and 14,7 in



a) Golfo dulce



b) Sierpe-Térraba



c) Golfo de Nicoya

Fig. 5. Abundance and biomass distribution along a depth gradient for February 1994 in a) Golfo Dulce (GD), b) Sierpe-Térraba estuary/Bahía Coronado (ST), c) Golfo de Nicoya (GN).

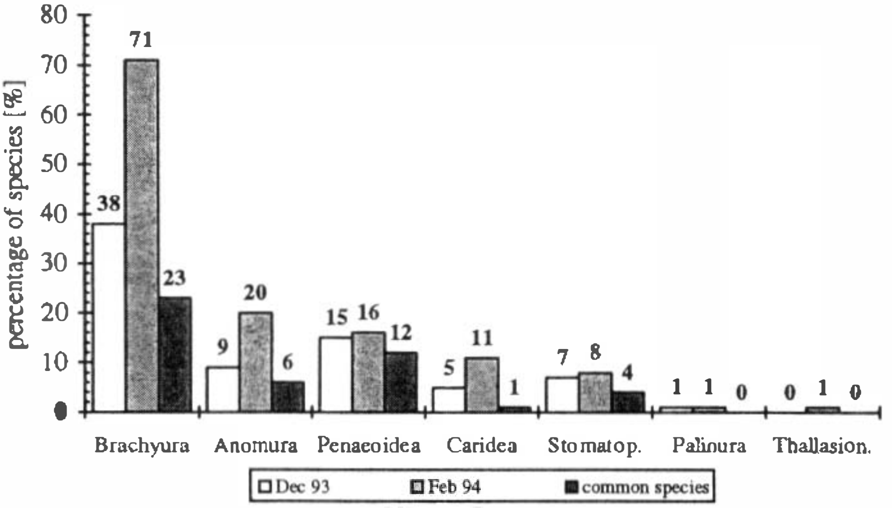


Fig. 6. Percentage of species of the total catch of the three study areas (summarized in subclasses) during the transition from the rainy to the dry season (December 1993) and in the dry season (February 1994) and percentage of common species in both seasons; numbers above the columns are numbers of species per group.

Sierpe-Térraba estuary (ST), a low mean biomass (0,05 g/m² compared to 0,36 in GN and 0,41 in ST) and the dominance of small-sized species, the GD seems to be a depauperated area at the Pacific coast of Costa Rica. Characteristic dominating shrimp species were lacking as were high numbers of predators like portunids. One reason may be the topographic relief of the gulf with steep coasts not being suitable as habitat for shallow water species. Due to the sill in the mouth of the gulf the center of the deep basin seems not to be attainable for the rich shelf edge fauna outside. The main biomass comes from juvenile penaeids near the mouth of the Río Esquinas (station C) which entered the gulf with the ocean surface water. A comparison of the two stations located in front of a river mouth in the extreme interior of the GD shows nearly the same biomass but much higher numbers of individuals off the east coast (station C, Fig. 5) where adjacent mangrove areas are located, confirming the importance of mangroves as support for nursery areas extended in front of them.

A comparison of the beamtrawl and ottertrawl catches for biomass points to much greater differences between the two gulfs indicating a lack of bigger-sized species in the GD. The low abundances of the occuring species point to small populations adapted to extreme environmental conditions (lower oxygen concentrations above the thermocline compared with the other study areas). Below 100 m water depth the oxygen saturation declines even to 1-0 % but temperature remains fairly high (17 °C instead of < 12 °C in the GD and ST) (Wolff & Vargas 1994). The benthic fauna seems to depend on the small mangrove area (only 2300-4100 g C $m^{-2}y^{-1}$) as primary producers due to a self-contained pelagic food chain based on the permanent thermocline (Hartmann, pers. com.).

In contrast to the Golfo dulce, the Golfo de Nicoya and the ST-estuary show a rich crustacean fauna typical for the east coast of the tropical Pacific. The latter revealed the highest species number per station but the GN exhibited the highest total species richness which might be convincing due to the shape of the species-per-area-curve. Penaeids of the genus *Sicyonia* and *Trachypenaeus* were dominating the shallow water assemblages which are replaced by *Solenocera* spp. and caridean species in the mean water depth (40-100 m). Biomass was comparable in both areas but abundances were significantly higher in the GN tereading it as a nursery area for many species. Especially juvenile portunids were abundant in

TABLE 3

***P*-value for the 70 most important species of the beamtrawl catches of February 1994 from Golfo dulce, Golfo de Nicoya and Sierpe-Térraba-estuary Bahía Coronado**

	Golfo dulce						Sierpe-Térraba				Golfo de Nicoya											
70 species (95% P-value)	C	D	E	F	G	H	N	O	P	Q	1	6	30	31	35	43	45	50	51	52	53	54
Acanthocarpus delsolari	0	0	0	0	0,0020	0	0,0148	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0006
Acanthocarpus sp.	0	0	0	0	0	0	0,0030	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calappa convexa	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0147	0	0	0	0	0	0	0	0
Calappa saussurei	0	0	0	0	0	0	0	0,0081	0	0	0	0	0	0	0	0	0	0,0081	0	0	0	0
Callinectes arcuatus	0	0,0031	0	0	0	0	0	0	0	0	0,0094	0	0	0	0,0058	0,0026	0,0024	0	0	0	0	0
Callinectes sapidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0089	0	0	0	0	0	0
Callinectes toxotes	0	0,0037	0	0	0	0	0	0	0	0	0,0059	0	0	0	0	0,0310	0,0041	0	0	0	0	0
Collodes granosus	0	0	0	0	0	0	0	0,0016	0	0	0,0045	0	0	0	0	0	0	0	0	0	0	0
Collodes sp.	0	0,0013	0,0009	0,0010	0	0	0	0,0032	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collodes tenuirostris	0	0,0001	0	0	0	0	0	0,0032	0,0330	0	0	0	0	0	0	0	0	0	0,0036	0,0013	0	0
Ethusa ciliatifrons	0	0	0	0	0	0	0	0,0002	0	0	0	0	0	0	0	0	0	0	0	0,0003	0	0,0442
Ethusa tenuipes	0	0,0012	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0006	0	0	0	0,0417
Euphylax robustus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0218	0	0	0	0
Hemisquilla stylifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0070	0,0025	0	0
Herbstia tumida	0	0	0	0	0	0	0	0	0	0	0,0128	0,0005	0	0,0005	0,0009	0	0	0	0	0	0	0
Heterocarpus vicarius	0	0	0	0	0	0	0,0157	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterocrypta macrobrachia	0	0	0	0	0	0,0006	0	0	0	0,0002	0,0003	0	0	0,0005	0	0,0077	0	0	0	0	0	0
Hypoconcha panamensis	0	0	0	0	0	0,0006	0	0	0	0	0	0	0	0,0017	0	0,0042	0	0	0,0004	0	0	0
Iliacantha hancocki	0	0	0	0	0	0	0	0,0099	0,0015	0	0	0,0004	0	0	0,0004	0	0,0112	0	0,0057	0,0009	0	0,0002
Iliacantha schmitti	0	0,0002	0,0008	0	0	0	0,0039	0,0023	0	0	0,0003	0	0,0005	0	0	0	0	0	0	0	0	0
Leiolambrus punctatissimus	0	0	0,0002	0,0002	0	0,0001	0	0,0019	0,0136	0	0	0,0061	0	0	0	0	0	0	0	0	0	0
Lysmata sp.	0	0	0	0	0	0	0	0	0	0,0013	0,0013	0	0	0	0	0	0,0006	0	0	0	0	0
Majidae sp.	0	0	0	0	0	0	0	0	0	0,0012	0	0	0	0	0	0,0020	0,0540	0	0	0	0,0009	0
Mesorhoea belli	0	0	0	0	0	0	0	0,0020	0,0016	0,0003	0	0	0	0	0	0	0	0	0,0012	0	0	0
Munida obesa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0208
Munida sp.	0	0	0	0	0	0	0,0763	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0016
Mursia gaudichaudii	0	0	0	0	0	0	0	0	0	0	0,0078	0	0	0	0	0	0	0	0	0	0	0,0153
Mursia sp.	0	0	0	0	0	0	0,0028	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paguristes sp.1	0	0	0	0,0004	0,0061	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0010	0	0	0
Paguristes sp.2	0	0	0	0,0029	0	0	0,0031	0,0015	0,0004	0	0	0,0004	0	0	0	0	0	0	0	0	0	0
Paguristes sp.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0002	0	0	0	0,0063	0	0	0	0
Pagurus sp.1	0	0	0	0,0035	0	0	0	0	0	0	0	0	0	0,0007	0	0	0	0	0,0063	0,0061	0	0
Palicus tuberculatus	0	0	0	0	0,0010	0	0,0024	0	0	0	0	0	0	0	0	0	0	0	0	0,0017	0	0
Pandalidae sp.	0	0	0	0	0	0	0,0157	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,1466

continuation TABLE 3

Pantomus affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0004	0,1466
Paradasygius depressus	0	0,0027	0,0047	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Penaeus brevirostris	0	0,0185	0	0	0	0	0	0	0,0341	0	0	0	0,0016	0	0,0008	0	0	0	0,0009	0	0	0
Penaeus californiensis	0	0	0	0	0	0	0	0	0,0165	0,0036	0	0	0,0008	0	0	0	0	0,0013	0	0	0	0
Persephona townsendi	0	0,0021	0	0	0	0	0	0,0029	0,0103	0	0,0014	0	0	0,0013	0,0004	0	0,0009	0	0	0,0003	0	0
Petrochirus californiensis	0,0037	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pilumnus fernandezi	0	0	0	0	0	0	0	0,0017	0	0	0,0003	0	0	0,0003	0	0	0	0	0	0,0004	0	0
Plesionika mexicana	0	0	0	0	0	0	0	0,0011	0	0	0	0	0	0	0	0	0	0	0,0036	0,0426	0	0
Plesionika trispina	0	0	0	0	0	0	0,0071	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0403
Pleuroncodes monodon	0	0	0	0	1,4808	0	0,0658	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Portunus acuminatus	0	0,0064	0	0	0	0,0004	0	0	0	0	0,0043	0	0	0	0	0,0073	0	0,0436	0	0	0	0
Portunus asper	0	0	0	0	0	0	0	0,0022	0	0,0015	0,0202	0,0020	0,0036	0,0034	0,0104	0,0293	0,0246	0	0	0	0	0
Portunus iridescens	0	0	0	0	0	0	0	0,0175	0	0	0	0	0	0	0	0	0	0	0,0002	0,0419	0	0
Portunus panamensis	0	0	0	0	0	0	0	0	0	0	0	0,0004	0	0	0	0,0030	0,0018	0	0	0	0	0
Portunus xanthusii	0	0	0	0	0	0	0	0	0	0	0	0,0021	0	0,0022	0,0033	0,0042	0,0000	0,0015	0	0	0	0
Processa sp.	0	0	0	0	0	0	0	0,0074	0	0	0,0051	0	0,0004	0	0	0	0	0	0	0	0	0
Pseudosquilla similis	0	0	0	0	0	0	0,0181	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyromaja tuberculata	0	0,0093	0	0	0	0	0	0	0	0	0,0014	0	0	0	0	0	0	0,0308	0	0	0	0
Raninoides benedicti	0	0,0012	0,0010	0	0	0	0	0	0,0097	0	0	0,0003	0	0,0018	0	0	0	0,0005	0	0	0	0
Sicyonia disdorsalis	0	0	0	0	0	0,0002	0	0,0017	0,1209	0,0114	0,1290	0,0003	0,0771	0,0002	0,1013	0	0,0033	0,0322	0	0	0	0
Sicyonis disewardsii	0	0,0139	0,0004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sicyonia picta	0	0,0008	0	0	0,0068	0	0,0062	0,0456	0,0003	0	0	0,0003	0	0	0	0	0	0	0,0073	0,1858	0,0009	0,1558
Solenocera agassizii	0,1021	0,0022	0	0	0,8833	0	0,0254	0,1250	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solenocera mutator	0	0,0012	0	0	0,0717	0	0	0	0,0015	0	0	0,1261	0	0	0	0	0	0	0	0,0157	0	0,2480
Solenolambrus arcuatus	0	0	0	0,0002	0	0,0001	0	0	0	0,0004	0	0	0	0,0054	0,0003	0	0	0,0073	0	0	0	0
Squilla aculeata	0	0	0	0	0	0	0	0	0	0	0,0187	0	0	0	0	0,0169	0,0134	0	0	0	0	0
Squilla biformis	0	0,0163	0	0	0	0	0,0175	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Squilla panamensis	0	0	0	0	0,0151	0	0	0	0,0540	0	0	0,0249	0	0	0	0	0	0	0	0	0	0
Squilla parva	0	0	0	0	0	0	0	0	0	0	0,0073	0	0,0115	0,0003	0,0050	0	0	0	0	0	0	0
Trachypenaeus faoe	0	0	0	0	0	0,0003	0	0	0	0	0,0156	0,0037	0	0,0007	0	0	0	0	0	0	0	0
Trachypenaeus fuscina	0	0,0050	0	0	0	0	0	0	0,0285	0,0022	0	0,0040	0,0156	0	0,0803	0	0,0819	0,0011	0	0	0	0
Trachypenaeus pacificus	0	0	0	0	0	0	0	0	0,0368	0	0,0004	0	0,0003	0	0,0036	0	0	0,0224	0	0	0	0
Trachypenaeus sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0,0056	0	0	0,0697	0	0	0	0	0	0
Trachypenaeus sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0,0363	0	0	0	0	0	0	0	0	0
Xanthidae sp.4	0	0	0,0003	0	0	0,0000	0	0,0013	0,0013	0	0,0026	0	0	0	0	0	0	0	0	0,0007	0	0,0004
Xylopagurus sp.	0	0	0	0	0	0	0	0,0013	0,0014	0	0	0	0	0	0	0	0	0	0,0010	0,0013	0,0046	0

TABLE 4

Station parameter table containing station location, abiotic (depth, temperature, relative oxygen saturation) and biotic (total biomass, total abundance, P-value, diversity, dominance, species richness) station descriptors for beamtrawl and ottertrawl stations for February 1994

station	longitude	latitude	depth [m]	temp. [°C]	●2 [%]	A [n/m2]	B [g/m2]	P [g/m2]	SR	H'	d
A	08°33,3"	83°11,3"	107	17	2	0	0	0	0	0	0
B	08°35,7"	83°17,2"	192	16	0	0	0	0	0	0	0
C	08°43"	83°21,4"	48	20	22	0,0292	0,237	0,1100	3	0,23	0,91
D	08°42,3"	83°28,8"	25	24	35	0,1181	0,1593	0,0981	21	2,29	0,14
E	08°38,4"	83°25,6"	40	20	12	0,0183	0,0075	0,0098	9	1,64	0,30
F	08°27,5"	83°13,3"	75	15,5	15	0,0187	0,0077	0,0103	9	1,76	0,22
G	08°21,2"	83°14,6"	200	13	2	0,9243	4,4032	2,4672	9	0,96	0,47
H	08°38,4	83°10,2"	15	27	100	0,0082	0,0021	0,0033	11	2,28	0,14
H(gsn)	08°28,2	83°10,3"	23	27	100	0,0001	0,0014	0,0003	3	1,03	0,38
I2(gsn)	08°21"	83°15,7"	210	13	2	0,0014	0,0609	0,0126	7	1,48	0,26
K(gsn)	08°41,8	83°27,8"	53	20	28	0	0	0	0	0	0
L(gsn)	08°36"	83°16,5"	194	16	0	0	0	0	0	0	0
M(gsn)	08°31,3"	83°12,9"	82	16	8	0,0002	0.0025	0,0010	5	0,95	0,55
N	08°47"	84°03.5"	187	13	2	0,1186	0,603	0,2804	20	2,02	0,23
O	08°47"	84°00,5"	103	14,5	8	0,1275	0,4138	0,2452	28	2,13	0,22
P	08°47"	83°44,6"	48	15,5	10	0,1997	0,5992	0,3661	20	2,19	0,15
Q	08°47,1"	83°41,5"	21	26	75	0,0394	0,0162	0,0216	12	1,52	0,39
1	09°56,3"	84°51,2"	33	27	65	0,3781	0,2753	0,2513	29	1,03	0,66
6	09°45,3"	84°46,6"	43	19,5	50	0,2543	0,2902	0,2622	17	1,28	0,40
30	09°50,7"	84°44,9"	31	22	50	0,1389	0,1759	0,1605	14	1,56	0,31
31	09°42,7"	84°59,4"	22	26	80	0,034	0,1297	0,0430	28	3,00	0,07
35	09°55,1"	84°47,5"	19	25	55	0,2046	0,2347	0,2158	17	1,36	0,36
43	10°06,7"	85°03,6"	10	27	60	0,1288	0,4163	0,1887	15	1,50	0,40
45	10°02,2"	84°57,5"	15	27	50	0,1572	0,2483	0,1998	13	1,46	0,37
50	09°38,5"	84°40,8"	32	24	55	0,1784	0,2617	0,1833	22	2,14	0,16
51	09°37"	85°00,1"	64	16	40	0,0555	0,0713	0,0500	21	2,53	0,10
52	09°36"	84°50,6"	118	15	10	0,1548	0,5143	0,3022	17	1,62	0,27
53	09°34,4"	84°42,9"	83	15	18	0,0073	0,0097	0,0079	5	1,37	0,29
54	09°34,5"	84°51,9"	228	12	2	0,3257	1,7385	0,8637	15	1,71	0,22
6(gsn)	09°45,3"	84°47,1"	44	19,5	50	0,0026	0,0127	0,0777	16	2,02	0,19
31(gsn)	09°42,9"	84°52,4"	22	26	80	0,0002	0,0042	0,0989	3	0,48	0,77
45(gsn)	10°01,5"	84°56,9"	18	27	50	0,0054	0,0259	0,0769	17	1,45	0,45
52(gsn)	09°36,9"	84°50,7"	109	14,5	10	0.0027	0,0114	0,0388	9	1.22	0,37
53(gsn)	09°34,9"	84°43,2"	80	14,5	18	0,0027	0,0194	0,0879	9	1,23	0,48
54(gsn)	09°35"	84°53,3"	239	12	2	0,0188	0.0506	0,1576	13	1,33	0,39

log-series-model and the low value for the Sørensen's index (Fig. 3) underlines the qualitative differences in species richness and species composition of the three study areas which differ in topography and hydrographic regime.

Abundance and biomass seem to be positively correlated with depth in the ST so a continuous biomass-size-spectrum can be assumed. In the GN, abundance varies a lot along a depth gradient throughout the gulf (Fig. 4), indicative for local, small-scale influences like substrate composition, shelter quality or food availability. Abundance was highest between Isla Chira and the mangrove area around Puntarenas (station 45, 35, 01) where high numbers of juvenile crab and shrimp species were found. The difference between the two embayments in the exterior part of the gulf (Bahía Ballena 31, Bahía Herradura 50) is manifested in the proportion

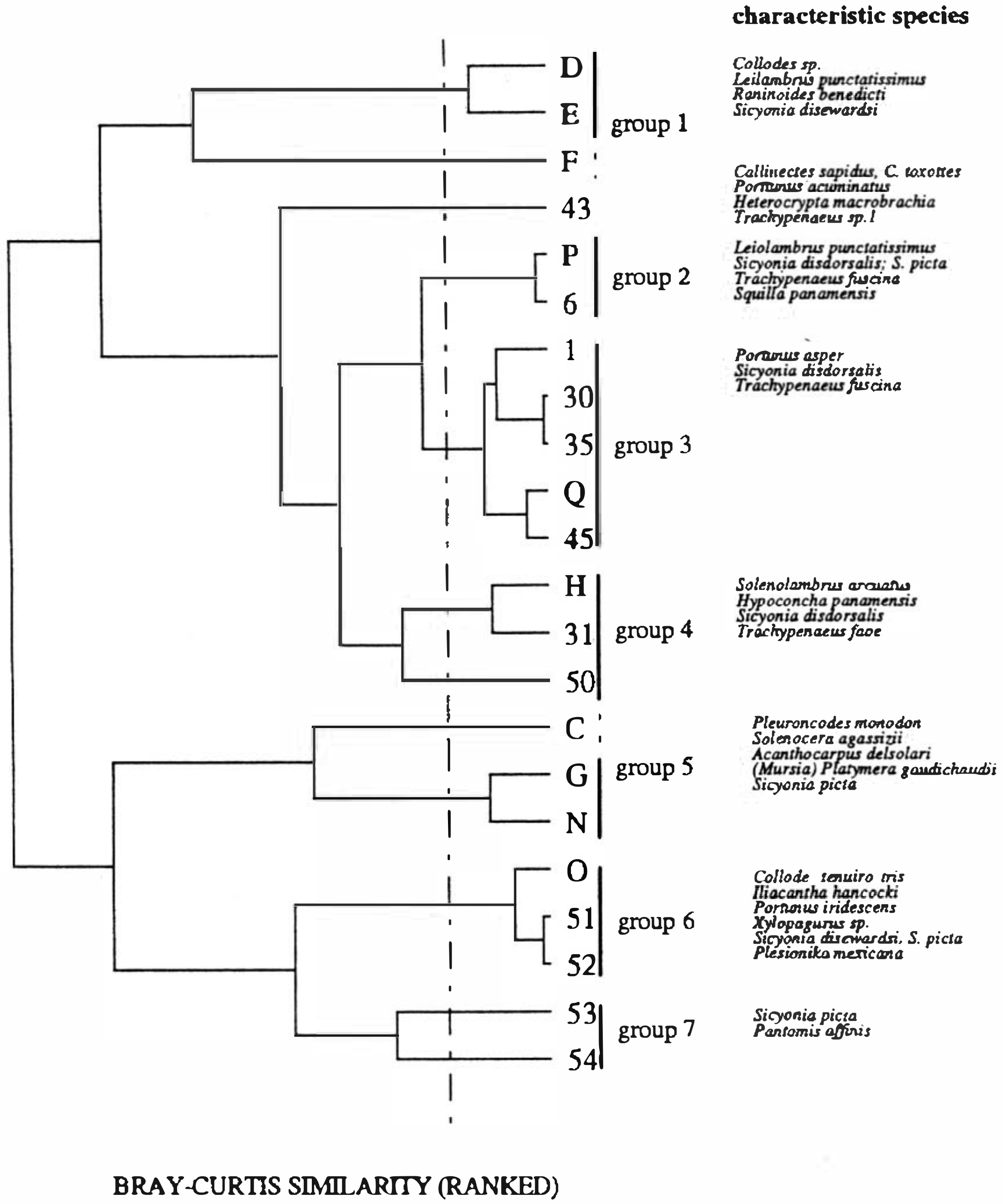


Fig. 7. Cluster analysis for beamtrawl stations in February 1994 (70 species, P-value), applying the Bray-Curtis-similarity-coefficient (ranked) and group-average-linking; characteristic species for station groupings are included.

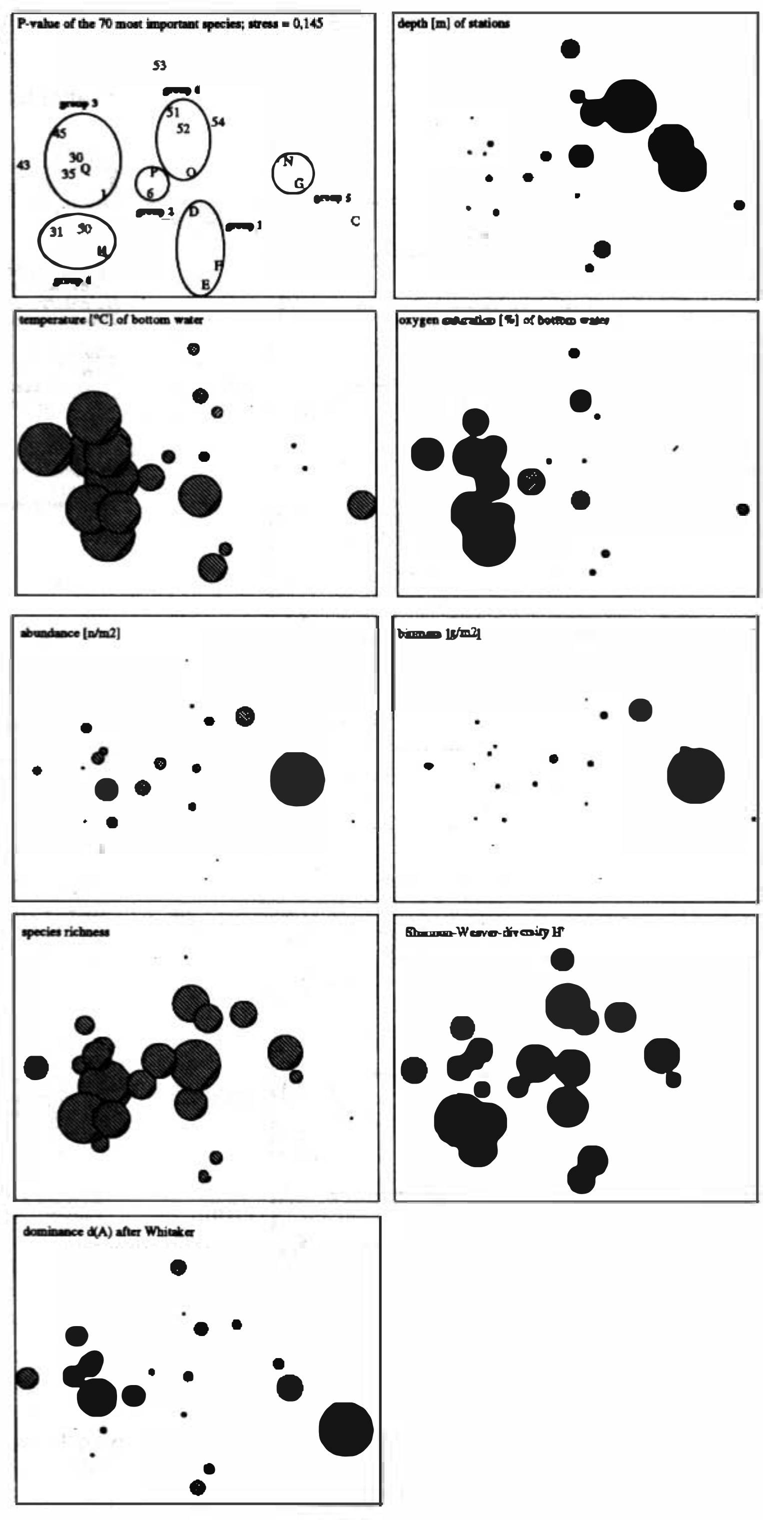


Fig. 8. MDS-plot for the 70 most important species (P-value) of the beamtrawl catches in February 1994 and overlay of scaled symbols for abiotic and biotic parameters (circle diameter corresponds to the numerical value of each parameter).

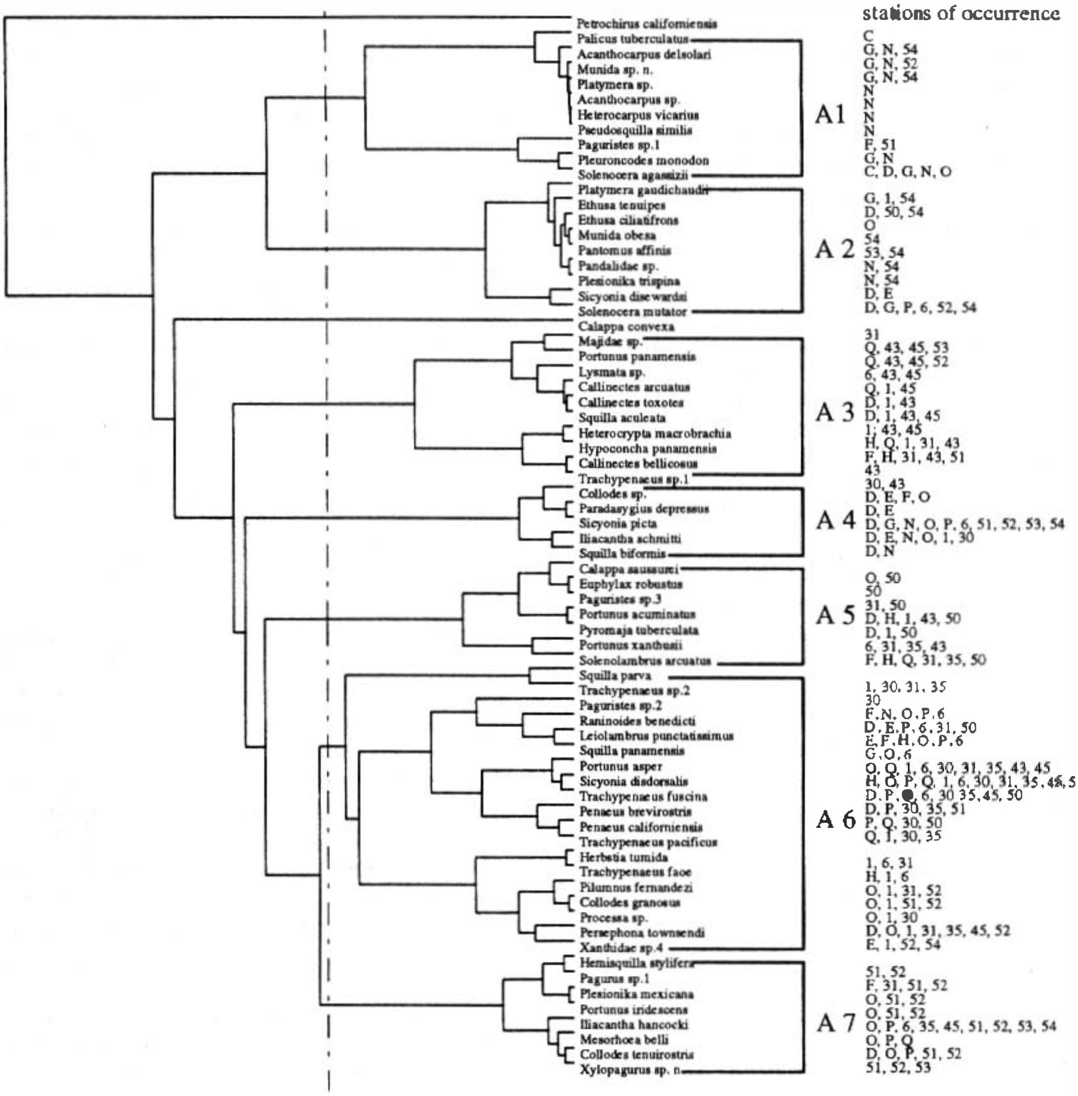


Fig. 9. Cluster analysis for beamtrawl stations in February 1994 for species (70 species, P-value), applying the Bray-Curtis-similarity-coefficient (ranked) and group-average-linking; stations on which the species occur are included.

of abundance and biomass as well. The more oceanic Bahía Ballena can be separated from the other shallow water stations due to the small number of individuals. The lack of high of juveniles may be due to higher predation pressure (some big individuals of portunids and stomatopods were found there).

The distribution of species in superorders was nearly the same in both seasons, whereas a significantly higher species richness (according to higher number of brachyuran and anomuran species) was found in all study areas during February. This contrasts the results of Maurer *et al.* (1984) and is difficult to explain. The patchy distribution of most of the brachyuran and anomuran species which may depend mainly on bottom structure renders a representative catch more difficult whereas shrimp species which are living in swarms over a wider area and might be catched with a higher probability.

Description of faunal assemblages: The interior shelf (0-20 m) is characterized through high energy flows, tidal cycles and current patterns which cause a dynamic water column (Darnell 1990). Temperature and oxygen saturation is high and a heterogeneous fauna composition is found. Species are adapted to strong environmental gradients and their occurrence is rather more dependant on substrate composition than on oceanographic conditions. This habitat has a characteristic fauna (A3, see Fig. 9) which occur at the flat east coast of GD, near the Isla Chira in GN and along the coast line of the ST-estuary. Filtrating species occurr as well as predators like juvenile portunids (*Callinectes arcuatus*, *C. bellicosus*, *Portunus panamensis*) and stomatopods (*Squilla aculeata*). The high nutrient input of the rivers into the upper GN and the inflow of nutrient rich waters from upwelling areas into the gulf from the ocean together with the year-around tide-driven mixing of the water column leads to a high primary productivity which can be used as ressource by the benthic organisms especially in shallow waters through an intensive bentho-pelagic-coupling.

Although the upper GN is known as the main fishing area for shrimps, only little shrimp biomass was found here. Trawling north from Isla Chira is forbidden so one might expect big populations there. The small percentage of commercially used species ("camarones blancos") in the catches, however, rather directs to an overexploitation of the commercially important species (*Penaeus* spp.) as described for the Panama coast (D'Croz *et al.* 1979).

The middle shelf area (20-80 m) reveals lower hydrodynamics with high sedimentation rates and lower variations in environmental conditions (Darnell 1990). Due to the different topography the three study areas show a high small-scale variation in habitat structure, so that one cannot ascribe the associated species of this depth range (A4-6, see Fig. 9) to a certain area. A small, soft-bottom prefering assemblage of detrivorous brachyuran species (*Paradasygius depressus*, *Iliacantha schmitti*, *Collodes* sp.) (Hendrickx 1990) seems to be characteristic for the interior GD, where high amounts of mangrove leaves occurred in the samples. These species generally stay in deeper waters up to 100 m (von Prahl & Guhl 1979, Garth 1958). Penaeids were represented here only by juveniles (*Sicyonia picta* in front of the mouth of Río Rincon and *Solenocera agassizii* in front of Río Esquinas) indicating the interior GD as an important nursery area for some shrimp species. The closed nature of the gulf and the adverse living conditions in its central part creates a protected area against oceanic demersal predators in the inner part of the gulf. The only predating crustacea was the stomatopod *Squilla biformis* which is a deep water species and was never found in Costa Rica above 100 m (Brusca 1980).

The central GD did not reveal any crustacean fauna, may be due to low oxygen concentrations and bad food conditions. The small amount of organic carbon (Hebbeln & Cortés 1994) point to little or "not the bottom reaching" primary productivity in the surface waters. Furthermore, the organic material from river input and mangroves which supports the shallow water fauna ddoes not seem to reach the deep basin.

In the GN and ST to the contraty, the fauna is much richer in the corresponding depth range. Shrimp species seem to be pronounced generalists, especially *Sicyonia disdorsalis* and *S. picta* ("camarones de roca") are widely distributed. The former distributes to 100 m water depth, whereas the latter occurrs up to the shelf edge in higher numbers. Most of the specimens found in the GN were juveniles and pre adults with a total length of 15-60 mm which confirms the upper and central gulf as nursery area, likely due to the adjacent mangrove areas. Other penaeids like *Trachypenaeus* spp. occurr in higher numbers in the upper and central GN and in the corresponding depth range in the ST-estuary, particularly *T. fuscina* seem to be the equivalent to Golfo de Tehuantepec and Golfo de Chiapas (México) dominating species *T. pacificus* (Pérez-Farfante, 1988). The commercial importance of these species is subordinate in Costa Rica although specimens obtain a total length of 150 mm (Pérez-Farfante 1971).

The lower part of the GN is separated from the interior one by an oceanically influenced species assemblage which enters the gulf due to the current regime and which is favoured through the permanent thermocline which avoids disturbances (Voorhis *et al.* 1983). *Iliacantha hancocki*, *Leiolambrus punctatissimus* (Brachyura) and the stomatopod *Squilla panamensis* are characteristic for this area. They prefer sand and clay bottoms and show a wide bathymetrical distribution (Hendrickx 1990). *Sicyonia disdorsalis* is likewise fairly abundant.

Juvenile and adult portunids are characteristic for the ocean water-influenced bays Bahía Ballena and Bahía Herradura. These areas seem to have a very heterogeneous bottom structure with rocky areas as well as sandy to muddy bottoms. The fauna has a low biomass but high species richness with shallow water and oceanic species side by side. The very abundant *Heterocrypta macrobrachya* stays in 8-20 m water depth whereas *Hypoconcha panamensis* occurrs down to 100 m (Garth 1948, 1960). *Portunus acuminatus* is distributed from 4 to 100 m over sand and mud with mangrove leaves and crushed shells as well as hard substrate (Garth & Stephenson 1967). Some oceanic species appear to use this area for spawning, so some gravid females of the pelagic *Portunus xanthusii* were collected in Bahía Ballena.

The outer shelf area is characterized by reduced light conditions and fine sediments due to low current speed. Salinity is fairly constant but temperature and oxygen saturation can vary according to the origin of the watermasses (Darnell 1990). The species assemblage of the deeper shelf and the slope show three distinct groups (A1 and A7, see Fig. 9). The separation of the deeper GN-stations from the ST-station N and the station G off GD as seen in the MDS-plot might be caused by higher temperatures in the former.

The separation of the deep water fauna of off GD and ST-estuary may correspond to a separation of well oxygenated waters from those with extremely low concentrations found on the shelf edge where the east Pacific oxygen minimum layer meets the continental shelf (Brandhorst 1958, Bianchi 1992).

The galatheid *Pleuroncodes monodon* ("squat lobster") largely dominates in biomass and numbers the faunal group which is adapted to oxygen-depleted shelf edge water masses. Mass occurrence of this species may be explained in the light of lack of predation and the fact that the species is a detritus feeder (Bianchi 1992). This phenomenon is well known from soft bottoms with a high organic content resulting from sinking diatom blooms in upwelling areas (Longhurst 1968). The association of galatheid and penaeid species as found off GD and ST-estuary (*Solenocera agassizii*) is well known from the continental slope off Sinaloa and Sonora, Baja California (Pérez-Farfante 1971, Bianchi 1991). This assemblage dominates the biomass off GD and and is well represented off the ST-estuary whereas it is almost absent in the outer GN. The topographic profiles of the GN and the ST are not as steep as the GD's one and might not allow for a year around upwelling that provides enough food for large populations.

In the ST area some patchily distributed calapid crustaceans (*Acanthocarpus* sp., *Platymera* spp.) were abundant as well as some stomatopods (*Squilla biformis*). The co-occurrence of species with a high assimilation rate and low oxygen requirements in this area suggests often changing conditions in the water column.

The fauna in the outer GN seems to be specific in the whole area. Among the brachyuran species the deep water portunid *P. iridescens* is frequent. The shrimps are dominated by the penaeid *Sicyonia picta* which confirms the dominance of the genus *Sicyonia* in the whole gulf. Some necto-benthonic caridean shrimps (*Plesionika* spp., *Pantomus affinis*) found are known from the Mediterranean as steady member of shelf edge communities.

Areas with similar faunal structure in total abundance, biomass nor in diversity, dominance or species richness as pointed out in the MDS-plots. These biotic summary descriptors this do not correlat with environmental conditions in the study areas indicating other structuring factors for the assemblaze such as habitat heterogenity, distance to the open ocean or to river mouth, current regime or food availability. The tide- and wind-driven dynamics of the watermasses provide suitable nutrient- and oxygen supply in several areas and allow larval settling (Epifanio & Dittel 1982). A highly specialized fauna may not endure due to permanent changes in environmental conditions. The sedimentation of organic material from river inflow and phytoplankton blooms depend on small-scale current patterns and supports a patchy distribution of the benthic fauna. The food supply in deeper waters due to upwelling processes varies due to different topographic conditions and determines species distribution.

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RESUMEN

En la primera parte del viaje del buque V. Hensen al Pacífico de Costa Rica (Diciembre de 1993, fin de la estación lluviosa) se halló una inesperada riqueza de crustáceos (biodiversidad y biomasa). Se hizo análisis cuantitativos en la cuarta parte del viaje (febrero de 1993, estación seca) en las tres áreas de estudio, Golfo Dulce (GD), Bahía Coronado en el estuario Sierpe-Térraba (ST) y Golfo de Nicoya (GN). Se pudo hacer comparaciones cualitativas con el primer viaje. Se hizo un total de 24 recolecciones de muestras por "beamtrawl" y 10 por "ottertrawl" en un área de 860.000 m^2, obteniéndose 119 especies con una biomasa de 37.8 kg (10 275 especímenes). Aunque se cubrió menos área con el beamtrawl, se recolectó más especies y biomasa con el ottertrawl debido a su menor tamaño de trama (0.8 cm). Juzgando por la forma de las curvas de especies por área, los crustáceos fueron muestreados representativamente. En comparación con el GN (biomass 0.36±0.26, SR=97) y el ST (0.41g±0.27, SR=59) y según los resultados de las curvas de series logarítmicas de la abundancia, el GD es un área pobre,con significativamente menor biomasa (0.05 g ± 0.07) y biodiversidad (45 spp.). No se halló crustáceos en el centro de la fosa profunda del GD pero algunas partes del golfo interior, que tienen manglares adyacentes, parecen tener importancia como áreas de cría de especies comercialmente importantes de camarones peneidos.

Es estuario ST tuvo mayor promedio de especies por estación para toda el área estudiada, pero el GN tuvo el mayor número de especies. La biomasa aparece distribuida de forma regular y no varía con la profundidad en el GN, mientras que la abundancia de especies varía de manera clara. En cambio, la abundancia y la biomasa se correlacionan bien en el ST. El análisis multivariable indica siete grupos de estaciones de conjuntos particulares de especies. A pesar de la gran variación de abundancia y biomasa entre estaciones, se pueden identificar cuatro áreas de asociaciones características de especies, que coinciden con las de la ictiofauna: (1) parte interior del GN, caracterizada por camarones juveniles (*Sicyonia disdorsalis, Trachypenaeus fuscina*) varios anomuros de distribución agrupada, braquiuros y otros depredadores como portúnidos (especialmente *Portunus asper*) y estomatópodos subadultos (*Squilla* spp.). (2) la parte exterior del GN con abundancia de camarones carídeos (*Pantomus affinis, Plesionka* spp.) y peneidos (*Sicyonia picta, Solenocera mutator*), el muy abundante *Iliacantha hancocki* y algunos especímenes del estomatópodo *Hemisquilla stylifera* y el portúnido de profundidad *Portunus iridescens*. (3) una zona de transición de 60-120 m con una composición faunística heterogéneoa que se localiza en el ST y al este de Isla Tortuga en el GN (4) el área del borde de la plataforma, pobre en oxígeno que es dominada por el galateido *Pleuroncodes monodon*. Hay presencia masiva de esta especie en el GD y en menor grado frente al estuario ST, asociado con grandes cantidades de Solenocera spp. Parece haber una tendencia general de especies agrupadas a lo largo de gradientes abióticos (profundidad, temperatura, saturación de oxígeno) interrumpidas por variaones pequeñas en el hábitat, régimen de corrientes, disponibilidad de alimento y otros factores que no fueron identificados en el presente estudio. La abundancia total, las biomasa y los parámetros resumen de las características bióticas como diversidad, dominancia o riqueza de especies se correlacionaron bien con los factores abióticos medios.

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