

Demersal fish 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 two cruise legs with the RV Victor Hensen (December 1993, February 1994), the demersal fish assemblages of the Golfo de Nicoya (GN), Bahía Coronado - Sierpe Terraba (ST) and Golfo Dulce (GD) areas were assessed from nearshore (~20 m) to shelf edge (~200 m) waters. 44 Beam- and 29 otter trawl collections were made on an area of 2 119 405 m², yielding a total of 242 species of fish. Despite the lower number of samples taken, more species were collected by the otter trawl (189 compared to 160), due to a wider area swept. As revealed by the species-area curve and a lognormal - curve constructed from the pooled (log) abundance data, the fish assemblage appeared as well sampled and a theoretical species richness (SR) of ~ 306 was estimated for the whole area. Mean species number per collection and mean biomass per area were much lower in the GD - area (9.3 species, 0.36 g /m²) compared to the ST (15.4, 0.81 g /m²) and GN (17.3, 0.74 g/m²) areas, indicating a depauperate fish assemblage in the former. Lowest species numbers and biomass were found in the central deep part of GD with increasing values towards the sill area at the opening of the gulf and towards the shallow stations above the thermocline. Average biomass was an order of magnitude higher in the interior part of GN compared to the other areas with values up to 18.1 g/m². Based on results of a multivariate analysis of the collections, the GN area can be divided into (1) an interior shallow area above the thermocline (<50 m) characterized by scianids, sea catfishes, stingrays, flatfishes, sea robins, (2) an outer part (>100 m) characterized by cods, scorpionfishes, gobies, cutlassfishes, serranids, anglerfishes and flatfishes and (3) a transition zone of the central and lateral parts with a mixed species assemblage with carangids, pufferfish, snappers, several flatfish species and the lizardfish as common elements. Characteristic for the deep basin of GD were small species of the genera *Cynoscion* and *Porichthys*. These occurred in low densities, suggesting a reduced carrying capacity of this deep basin for fish biomass in terms of food and oxygen. Species occurring at the shallow stations of GD are also found at a similar depth in the other areas, but many species are missing, namely ariids and many scianids found in the GN area. The species assemblage of the ST area resembles that of GN. Ariids, however, are missing here too. Biotic station parameters like species richness, biomass, abundance and production were not significantly correlated with abiotic parameters (temperature, oxygen, nutrients) suggesting that other habitat factors not evaluated in this study like habitat heterogeneity, distance to the open ocean, current regime and food availability probably are important factors for the structure of the fish assemblage.

Key words: Fish assemblage, fish diversity, biomass, Costa Rica, multivariate analysis.

The study reported here forms part of a research program between the Center for Tropical Marine Ecology (ZMT), Germany and the Center for Marine and Limnological studies (CIMAR), University of Costa Rica, Costa Rica. The program was initiated with the employment of the German RV Victor Hensen in Costa Rican shelf waters from December 1993 to February 1994 (Wolff & Vargas 1994).

In the study areas Golfo de Nicoya, Bahía Coronado -Sierpe Terraba and Golfo Dulce,

(see Fig. 1), beam trawl and otter trawl hauls were conducted from nearshore waters (about 20 m) to the shelf edge (about 200 m) in order to sample the demersal fish and macrofauna along this depth gradient and to investigate (1) if there were areas with commercially important concentrations of fish and invertebrate species, (2) if certain areas/stations could be characterized by assemblages of a particular set of species, (3) if and how the two gulf systems (Golfo de Nicoya and Golfo Dulce) and the

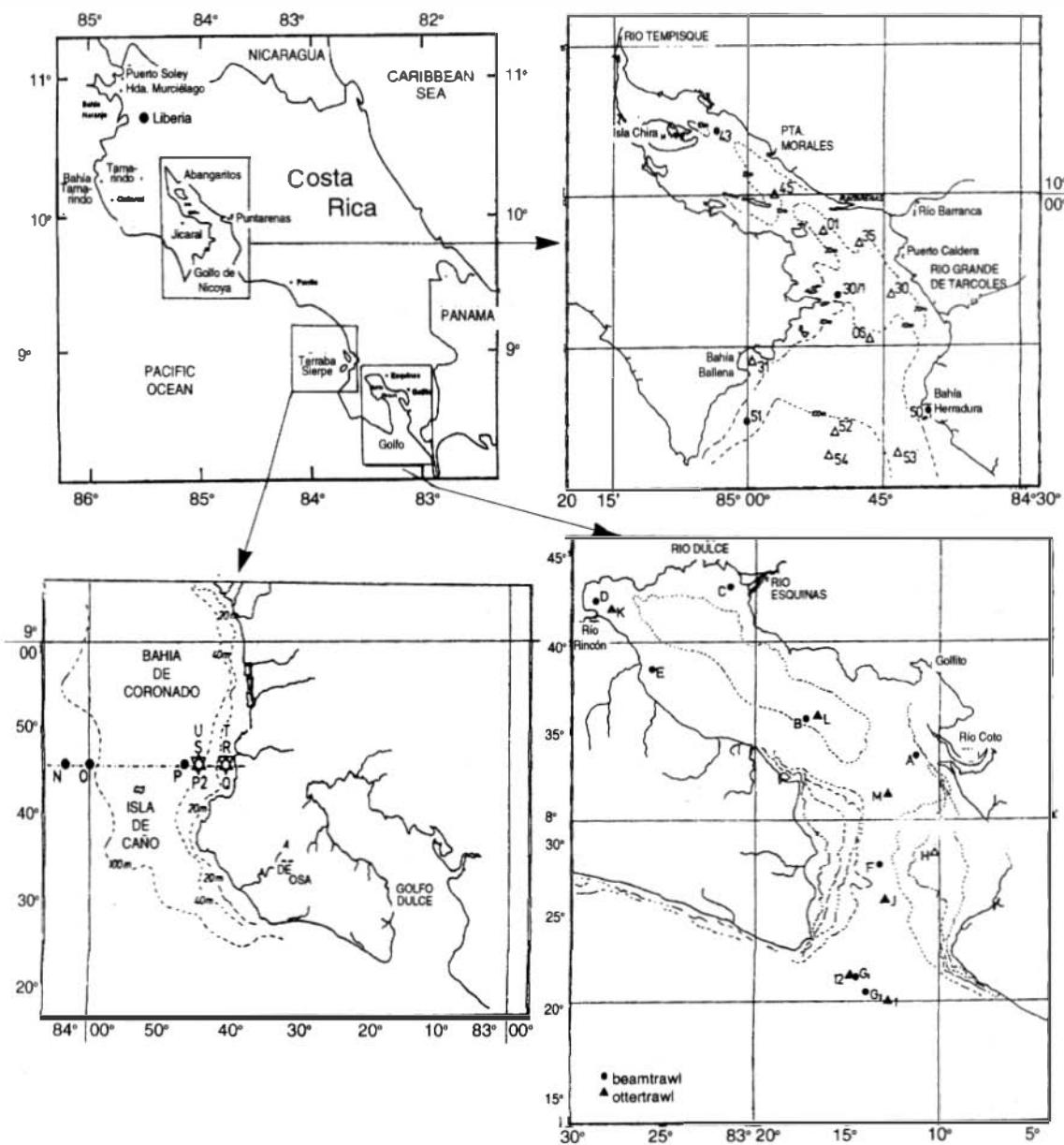


Fig. 1. Study areas with sampling sites (upper left: overview; upper right: Golfo de Nicoya; lower right: Golfo Dulce; lower left: Bahía Coronado-Sierpe-Téraba).

Bahía Coronado - Sierpe-Téraba estuary differ in their species composition, abundance and biomass and how differences relate to oceanographical conditions, water depths, coastal mangrove cover and season. As the Golfo de Nicoya area had been surveyed ten years before by the American RV Skimmer, our findings on fish assemblage structure in this gulf could be compared with these data. The other two areas,

however, had not been surveyed previously and our results represent the first quantitative assessment of the demersal fauna in these areas.

MATERIAL AND METHODS

Sampling: Beam trawls and otter trawls were employed to sample the smaller fish and macroinvertebrates as well as the bigger fish.

At the stations (Fig. 1), 15 min beam trawl hauls (mesh size 1cm) were conducted at an average towing speed of 1.5 knots. The catch was separated into fish and invertebrates, and the total weight of all specimens of each species was registered (in some rare occasions subsamples had to be taken). The length frequencies of the abundant species ($> 10/\text{sample}$) were recorded. Most taxonomic identification of the fish species was done on board by Prof's William Bussing and Myrna López (CIMAR) based on a fish guide published by Bussing & López (1993). A complete list is presented in Bussing and López (1996). Unidentified species (the majority represented by invertebrates) were numbered for later identification and preserved in 4% formalin.

On those sampling stations where coral pieces, tree trunks or stones appeared in the beam trawl, the otter trawl was not employed because of the danger of damage-otherwise the sampling stations of the beam trawl were repeated with the otter trawl (mesh size 2.5 cm), that was towed for 30 min at an average speed of 2.5 knots. The catch was then analysed as described for the beam trawl. The beam trawl (opening width: 3 m) swept an area of approx. 2084 m², while the otter trawl (opening width: 35 m, head rope: 27.5 m; foot rope: 34 m) swept an area of approx. 81 025 m² per tow. During the first leg, the otter trawl was heavily destroyed on a coral reef in the Golfo Dulce area (st. I, see Fig. 1), but sampling was continued using an identical spare trawl. At another occasion (st. 51, Fig. 1) the beam of the beam trawl broke and had to be repaired. The number of samples taken by the ottertrawl was lower during the second (11) than during the first leg (18).

Data processing: For the data analysis the following steps were done:

1. For each sample (station), a species list was elaborated containing biomass (Bm^{-2}), abundance (number) (Am^{-2}), and a descriptor (Pm^{-2}) which combines biomass and number. This descriptor is given by $P = (B/A) 0.73 * A$ (Warwick & Clarke 1993) and represents a measure for production.
2. For an overview on the number of species caught in the whole study area and their respective contributions to the total abundance and production, the species were ranked and a log-normal - plot was established with the pooled data of both legs, from which the theoretical species richness (SR) was calculated.
3. A species - area curve was established from the beam trawl and otter trawl catches and from all samples combined by plotting the cumulative species number against the number of samples taken.
4. The heterogeneity of the biomass distribution within the study area was shown by a histogram, in which the number of samples was plotted against their respective biomass values.
5. To visualize the bathymetrical distribution of biomass, the samples were grouped into the following depth ranges (10-59 m, 60-109 m, 110-159 m, 160-209 m, 210-259 m) to relate average biomass per station to water depth.
6. A station/species matrix was constructed for the beam trawl and otter trawl samples for both cruise legs separately and a similarity matrix using the Bray Curtis index was computed with the fourth-root transformed data by the use of the PRIMER software following Clarke & Warwick (1994). For this matrix the descriptor "P" (s. above) was used. Prior to the calculations, the original species matrix was reduced such that the remaining species accounted for about 95% of the sum of the total P-values, eliminating the very rare species and those having very low P-values.
7. The group average linkage algorithm was used to construct station and species clusters from the similarity matrix.
8. Species indicative for particular groups within the dendograms were identified using the SIMPER (Similarity percentage) - routine of the PRIMER - package.
9. A "station parameter table" was constructed for the abiotic data of all beam trawl and otter trawl samples taken during both legs. To do so, for each station, bottom temperature, oxygen, water depth, phosphate and nitrate were considered.

10. A correlation matrix was calculated to find out if and how our biotic summary parameters for each station (biomass, abundance, production, dominance) correlate with the above-mentioned abiotic station descriptors.

RESULTS AND DISCUSSION

Species richness, spatial and bathymetrical distribution of biomass: Table 1 contains the list of all species collected during the study

TABLE I

Complete list of species collected during the cruise along with their respective frequency of occurrence based on Bussing and López (1996)

species	f	species	f	species	f	species	f
<i>Achirus klunzingeri</i>	3	<i>Cynoscion squamipinnis</i>	1	<i>Microgobius erectus</i>	5	<i>Rhinobatos leucorhynchus</i>	3
<i>Achirus maculatus</i>	6	<i>Cynoscion stolzmanni</i>	1	<i>Monodactylus argenteus</i>	2	<i>Rhynchoconger nitens</i>	9
<i>Achirus scutum</i>	5	<i>Dasyatis langsdorffii</i>	8	<i>Monodelphis maculipinnis</i>	10	<i>Rypticus bicolor</i>	2
<i>Albulina nemoptera</i>	2	<i>Decodon melampus</i>	3	<i>Mullus dentatus</i>	2	<i>Rypticus nigrirostris</i>	1
<i>Alphestes multiguttatus</i>	1	<i>Diapterus aureolus</i>	3	<i>Muraena argus</i>	2	<i>Sciaenichthys troschelii</i>	1
<i>Aluterus monostigma</i>	1	<i>Diapterus peruvianus</i>	5	<i>Mustelus lunulatus</i>	6	<i>Scomber japonicus</i>	1
<i>Anchoa exigua</i>	1	<i>Diodon hispidus</i>	3	<i>Myrichthys uspiatichirius</i>	1	<i>Scorpaena histrio</i>	2
<i>Anchoa ischiarini</i>	4	<i>Diodon holocanthus</i>	1	<i>Myripristis nigricans</i>	1	<i>Scorpaena mystes</i>	1
<i>Anchoa lucida</i>	3	<i>Diplectrum eumelium</i>	7	<i>Narcine brasiliensis</i>	5	<i>Scorpaena russula</i>	13
<i>Anchoa nasus</i>	2	<i>Diplectrum euryptectum</i>	8	<i>Nebris occidentalis</i>	1	<i>Selar crumenophthalmus</i>	2
<i>Anchoa starksii</i>	1	<i>Diplectrum labarum</i>	6	<i>Neobithys stelliferoides</i>	6	<i>Selenaspis dowii</i>	3
<i>Anchoa walkeri</i>	1	<i>Diplectrum macropoma</i>	10	<i>Neopristipomus tropicus</i>	6	<i>Selene brevoortii</i>	1
<i>Anchovia macrolepidota</i>	1	<i>Diplectrum nucatum</i>	1	<i>Ophichthys ramiger</i>	1	<i>Selene nerstedi</i>	4
<i>Ancylorhynchus dendriticus</i>	1	<i>Diplectrum pacificum</i>	6	<i>Ophichthys sp. A</i>	4	<i>Selene peruviana</i>	8
<i>Anisostremus dovi</i>	3	<i>Diplectrum rostratum</i>	1	<i>Ophichthys sp. B</i>	2	<i>Serranus aequidens</i>	2
<i>Anisostremus pacifici</i>	1	<i>Diplodus omanensis</i>	4	<i>Ophichthys sp. C</i>	1	<i>Serranus psittacinus</i>	2
<i>Antennarius australis</i>	6	<i>Echiophis bruneus</i>	1	<i>Ophichthys sp. D</i>	1	<i>Sphaeroides annulatus</i>	10
<i>Argentinasilvestre</i>	5	<i>Euglyptophrys sanctilaurentii</i>	9	<i>Ophiascina sciara</i>	1	<i>Sphaeroides lobatus</i>	11
<i>Arius dasyccephalus</i>	1	<i>Epinephelus acanthistius</i>	1	<i>Ophioscion typicus</i>	2	<i>Sphaeroides trichocephalus</i>	3
<i>Arius kessleri</i>	2	<i>Epinephelus cifuentesi</i>	1	<i>Ophiothrix macrurum</i>	1	<i>Squatina californica</i>	1
<i>Arius osculus</i>	1	<i>Epinephelus exsiliens</i>	1	<i>Opisoma propterum</i>	5	<i>Stellifer chrysoleucus</i>	1
<i>Arius platyrhynchos</i>	2	<i>Epinephelus niphonides</i>	3	<i>Ophistognathus rhomaleus</i>	1	<i>Stellifer furthii</i>	1
<i>Arius sp. A</i>	1	<i>Etrypus crossinus</i>	2	<i>Opisthotropus acutirostris</i>	1	<i>Stellifer illecebrosus</i>	4
<i>Arius sp. B</i>	1	<i>Etrypus peruvianus</i>	2	<i>Opisthotropus dovi</i>	3	<i>Stellifer manciurensis</i>	1
<i>Artronotus hispidus</i>	1	<i>Eucinostomus argenteus</i>	7	<i>Paralabrax loralis</i>	2	<i>Stellifer macrurus</i>	2
<i>Auxis sp.</i>	1	<i>Eucinostomus currani</i>	1	<i>Paralichthys woolmani</i>	2	<i>Stellifer zosterinus</i>	1
<i>Bairdiella armata</i>	1	<i>Eucinostomus gracilis</i>	5	<i>Paralonchurus dumerilli</i>	4	<i>Syacium cf longidorsale</i>	4
<i>Balistes polylepis</i>	1	<i>Fistularia commersoni</i>	1	<i>Paralonchurus rufibarbis</i>	3	<i>Syacium latifrons</i>	11
<i>Batrachoides sp.</i>	1	<i>Gerres cinereus</i>	1	<i>Parauthis colonus</i>	1	<i>Syacium ovale</i>	9
<i>Bellator gymnostethus</i>	5	<i>Gobiesox milleri</i>	1	<i>Peripodus medius</i>	1	<i>Syphurus atrimentatus</i>	8
<i>Bellator loxias</i>	3	<i>Gobioides peruvianus</i>	1	<i>Peripodus snyderi</i>	7	<i>Syphurus callipterus</i>	16
<i>Bellator xenisma</i>	11	<i>Guentherus altivelis</i>	1	<i>Perissis taeniopterus</i>	1	<i>Syphurus chabaudii</i>	11
<i>Bolbunnia clamydes</i>	23	<i>Gymnotorax equatorialis</i>	7	<i>Peristedion barbiger</i>	11	<i>Syphurus elongatus</i>	10
<i>Bolbunnia sp. nov.</i>	2	<i>Gymnotorax sp. nov.</i>	7	<i>Peristedion crustosum</i>	6	<i>Syphurus gorgonae</i>	8
<i>Boilbunnia stigmatura</i>	11	<i>Haemulon scudderii</i>	1	<i>Physiculus nematus</i>	15	<i>Syphurus leei</i>	6
<i>Bregmaceras bathymaster</i>	5	<i>Haemulopsis elongatus</i>	1	<i>Physiculus rastrelliger</i>	1	<i>Syphurus melanurus</i>	2
<i>Brotula clarkei</i>	2	<i>Haemulopsis leuciscus</i>	2	<i>Pikops longilepis</i>	1	<i>Syphurus melastomithera</i>	1
<i>Calamus brachysomus</i>	2	<i>Haemulopsis nitidus</i>	2	<i>Platycephalum latipinnis</i>	1	<i>Syphurus oligomerus</i>	7
<i>Caranx caballus</i>	2	<i>Hemimulius peruvianus</i>	5	<i>Polydactylus approximans</i>	6	<i>Syphurus undecimpunctatus</i>	3
<i>Caranx caninus</i>	3	<i>Hemimimus signifer</i>	10	<i>Polydactylus cruentum</i>	1	<i>Syphurus williamsi</i>	8
<i>Caranx ignobilis</i>	3	<i>Hemicarctus leucorus</i>	1	<i>Pomadasys hancockii</i>	3	<i>Synchiropus atrilobatus</i>	15
<i>Caranx speciosus</i>	3	<i>Himantura atra</i>	1	<i>Pomadasys macracanthus</i>	1	<i>Synodus eversmanni</i>	18
<i>Caranx vinctus</i>	4	<i>Hippoglossina holmani</i>	1	<i>Pominus surcirhinus</i>	3	<i>Synodus scituliceps</i>	21
<i>Cathorops furtii</i>	1	<i>Hippoglossina tetraphthalmus</i>	5	<i>Pontinus sierra</i>	17	<i>Synodus securae</i>	10
<i>Cathorops steindachneri</i>	1	<i>Hoplopagrus guntheri</i>	1	<i>Pontinus sp. nov.</i>	1	<i>Torpedo tremens</i>	2
<i>Cathorops tayra</i>	1	<i>Ilisha furtii</i>	1	<i>Porichthys greeni</i>	16	<i>Trachinotus paientensis</i>	4
<i>Caulorhynchus affinis</i>	3	<i>Isophisus altipinnis</i>	6	<i>Porichthys marginatus</i>	24	<i>Trichiurus nitens</i>	10
<i>Cetengraulis mysticetus</i>	2	<i>Kuhliostoma averruncus</i>	6	<i>Prionotus ariirostris</i>	2	<i>Trinectes fonscensis</i>	2
<i>Chaetodipterus zonatus</i>	1	<i>Larimus acclivis</i>	1	<i>Prionotus horrens</i>	8	<i>Trinectes sp. nov.</i>	1
<i>Chiloconger tubianus</i>	3	<i>Larimus pacificus</i>	1	<i>Prionotus ruscarius</i>	7	<i>Umbrina huusangi</i>	5
<i>Chloruraphthalus mento</i>	4	<i>Lepophidium microlepis</i>	1	<i>Psihamnus stephanophrys</i>	2	<i>Umbrina xanti</i>	1
<i>Citharichthys gibberti</i>	6	<i>Lepophidium negropinna</i>	2	<i>Prionotus teuguei</i>	3	<i>Urolophus concentricus</i>	1
<i>Citharichthys platophrys</i>	14	<i>Lepophidium prorates</i>	5	<i>Pristigenys securula</i>	1	<i>Urotrygon aspirata</i>	1
<i>Coelorhynchus scaphopsis</i>	1	<i>Lophiodes caulinurus</i>	14	<i>Pronotogrammus eos</i>	11	<i>Urotrygon chilensis</i>	6
<i>Coryphaenoides leucophaeus</i>	1	<i>Lophiodes spluritus</i>	5	<i>Pronotogrammus multifasciatus</i>	1	<i>Urotrygon munda</i>	1
<i>Cyclopterus panamensis</i>	11	<i>Lutjanus argenteus</i>	1	<i>Pseudomyrophis micropinna</i>	4	<i>Urotrygon vittata</i>	2
<i>Cyclopterus querna</i>	10	<i>Lutjanus guttatus</i>	10	<i>Pseudohaliotis naufragium</i>	1	<i>Urotrygon rogersi</i>	1
<i>Cynoglossus albus</i>	1	<i>Lutjanus peru</i>	2	<i>Pseudupeneus grandisquamis</i>	2	<i>Zaliosus elater</i>	16
<i>Cynoscion nanus</i>	4	<i>Menticirrhus panamensis</i>	1	<i>Pycnopterus aureolus</i>	1	<i>Zapteryx exasperata</i>	5
<i>Cynoscion phaeocephalus</i>	6	<i>Menticirrhus nasus</i>	5	<i>Raja equatorialis</i>	3		
<i>Cynoscion reticulatus</i>	2	<i>Merluccius angustifrons</i>	1	<i>Raja velezi</i>	8		
							sum: 242 species

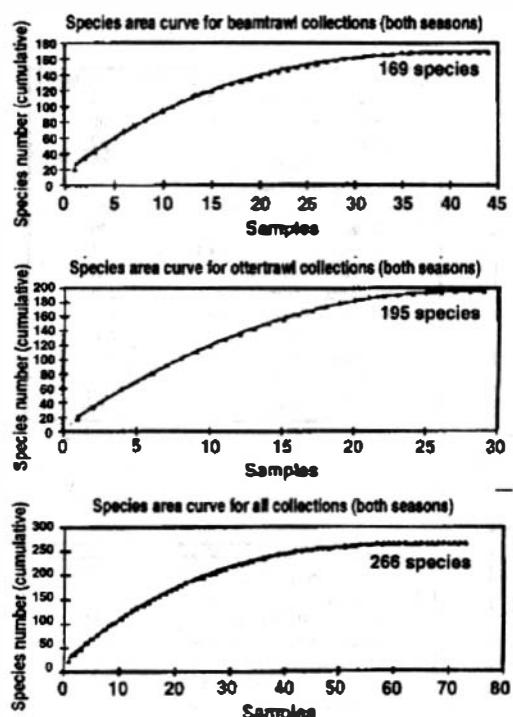


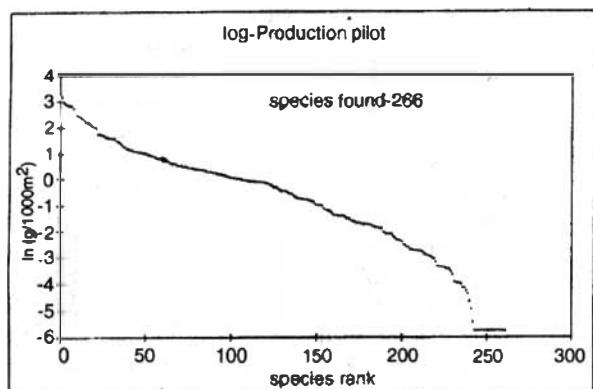
Fig. 2. Species-area curves for the beamtrawl-, ottertrawl- and the combined collections of both sampling dates.

with their respective frequencies of occurrence. Fig. 2 shows the species area curves constructed from the beam trawl - and otter trawl collections and for all collections pooled. The number of fish species collected (242) exceeds that reported by Bartels *et al.* (1983), who found 214 species during a 17 day and 3 night sampling programme with the RV Skimmer in 1979/1980. This difference can be explained through the wider area covered by our cruise ($2\ 119\ 405\ m^2$ compared to about $750\ 000\ m^2$), the wider depth range (10-261 m compared to 8-60 m) but also through the different gears used. As seen in Fig. 2, more species (195) were collected by the otter trawl than by the beam trawl (169), which was to be expected as the total area swept was about 25 times larger. The difference in cumulative species number between the two gears is not large, however, reflecting a higher species density of smaller fish that dominated the beam trawl catches. Fig. 3 shows the ranking of all species collected during both seasons according to the logarithm of their abundance and production values and the normalized log-normal - plot

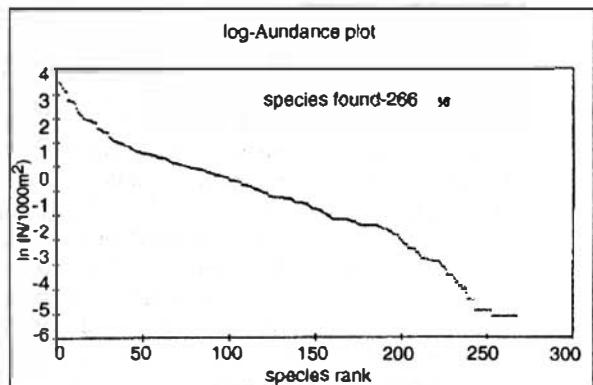
derived from these data with the estimate of the theoretical species richness in the total area. The names of the most dominant species in rank order are also given. Judging from the fit of the lognormal - curve and the species-area curve discussed above, the demersal fish species assemblage can be regarded as well sampled. The theoretical estimate of total species richness (SR~306) for the whole area therefore seems reasonable. It must be emphasized, that this number concerns the demersal fish assemblage, as although some pelagic fish were caught during the lowering and lifting of the fishing gear, most fast swimming pelagics are missing in the catches. This was apparent in the GD area, where large shoals of medium-sized tunalike fish were frequently seen in the surface waters, but not a single specimen was caught by the net.

It is difficult to compare species richness between the study areas because of the different numbers of collections made in each. However, if we calculate the mean species number per collection in each area from the data of table 4 (GD: 9.3, ST: 15.4 and GN: 17.3), GD appears as significantly poorer in species than the other two areas. As to be expected, the lowest species numbers were found in the central deep (and at least in part anoxic) part of GD, while numbers increased towards the sill area at the gulf's opening and towards the shallow stations above the thermocline. Highest numbers were found at the shelf edge outside the gulf. This pattern is not repeated in the other study areas, where both shallow stations and deep shelf edge stations had (at an average) comparatively higher species numbers (Table 2).

The bathymetrical and spatial distribution of biomass (Table 2, Fig. 4) reveals a general concentration of fish biomass in two depth ranges: a shallower water (10 - 60 m), above or around the thermocline and a deep-water (160 - 210 m) area around the shelf edge, with relatively little biomass found in between (60 - 160 m). This is interesting as Bartels *et al.* (1984) found a general decrease in fish biomass from the shallow upper gulf to the deeper stations in the center of the gulf. They, however, did not sample the shelf edge stations considered in the present study. Apparently, the shelf edge region contains a different faunal group (see also "description of faunal assemblages" further below) adapted to cool and little oxygenated waters.



rank	species	g/1000ml	% of total production
1	<i>Synodus aculeiceps</i>	24.32	4.44
2	<i>Pontinus sierra</i>	20.05	3.66
3	<i>Himantura pacifica</i>	18.75	3.42
4	<i>Pontinus fuscithinus</i>	17.89	3.27
5	<i>Porichthys marginatus</i>	17.49	3.19
6	<i>Syacium ovale</i>	17.14	3.13
7	<i>Symphurus callotropis</i>	16.92	3.09
8	<i>Arius ocellatus</i>	15.60	2.85
9	<i>Physiculus nematopus</i>	12.15	2.22
10	<i>Hemianthus signifer</i>	12.11	2.21
11	<i>Anisostremus dovi</i>	11.97	2.19
12	<i>Syacium latifrons</i>	10.97	2.00
13	<i>Porichthys greeni</i>	10.92	1.99
14	<i>Citharichthys planiphrys</i>	10.14	1.85
15	<i>Diplodus peruvianus</i>	9.27	1.69



rank	species	g/1000ml	% of total production
1	<i>Porichthys marginatus</i>	6.39	7.11
2	<i>Pontinus sienna</i>	4.64	5.16
3	<i>Synchiropus atrabilabistus</i>	4.27	4.75
4	<i>Syacium ovale</i>	3.68	4.09
5	<i>Bolinichthys chalybeus</i>	3.21	3.57
6	<i>Symphurus callopterus</i>	3.17	3.53
7	<i>Synodus aculeiceps</i>	2.19	2.43
8	<i>Physiculus nematopus</i>	2.15	2.39
9	<i>Syacium latifrons</i>	2.19	2.33
10	<i>Neophistopterus tropicus</i>	2.08	2.31
11	<i>Synodus evermanni</i>	1.91	2.13
12	<i>Symphurus oligomerus</i>	1.59	1.77
13	<i>Syacium sp.</i>	1.35	1.50
14	<i>Monolene maculipinnis</i>	1.21	1.35
15	<i>Sympodus stramentatus</i>	1.16	1.29

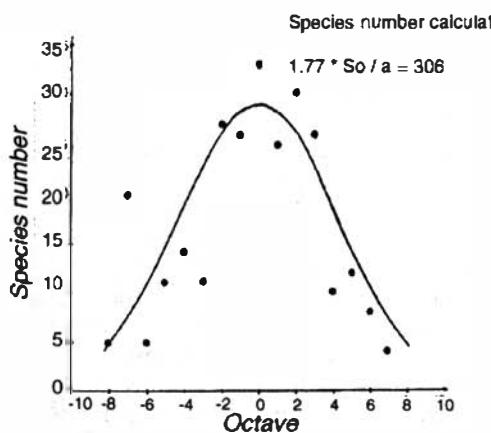


Fig. 3. Species rank plots (top: log production vs. species rank; center: log abundance vs. species rank; lower graph: calculated lognormal curve for estimation of theoretical species richness).

TABLE 2

Station parameter table containing biotic (species richness, biomass, abundance, production and dominance) and abiotic (depth, temperature, oxygen, nitrate and phosphate) station descriptors

Beamtrawl

Station	water depth [m]	temperature [°C]	oxygen [%]	species richness	Biomass [g/m²]	Abundance [n/m²]	Production [g/m²]	dominance	NO3	PO4
A1	107	17	2	3	0.1368	0.0466	0.0943	0.3923	15.70	2.60
B1	191.4	16	0	6	0.3053	0.4843	0.3366	0.9823	3.30	7.90
B2	192	16	0	2	0.0872	0.0010	0.0222	0.4992	17.93	2.22
C1	42	20	22	6	0.6811	0.0965	0.2735	0.5548	24.80	0.15
C2	48	20	22	2	0.0254	0.0024	0.0133	0.5199	11.40	2.30
D1	32.5	23	15	10	0.4632	0.0250	0.1741	0.3107	8.76	1.14
D2	25	24	15	11	1.0052	0.0240	0.3132	0.1144	9.81	1.03
E1	50	19	12	11	0.1869	0.0158	0.0778	0.1901	17.20	3.10
E2	40	20	12	2	0.0468	0.0010	0.0148	0.4999	13.70	1.77
F1	73	15	10	13	1.1322	0.0293	0.2258	0.2771	20.80	2.00
F2	75	15.5	10	2	0.0240	0.0024	0.0124	0.5199	16.83	0.74
G1	200	16	2	21	3.1990	0.3715	1.3577	0.3534	2.47	2.21
G2	200	13	2	22	1.9940	0.1550	0.9786	0.1433	21.26	1.46
H2	15	27	100	7	1.4620	0.0198	0.2266	0.5551	0.20	0.16
N1	164	14	8	23	1.2921	0.0802	0.5211	0.1189	23.76	1.98
N2	186.5	13	10	20	2.4324	0.0945	0.9240	0.1424	28.90	2.13
O1	109.9	14	10	8	0.2381	0.0182	0.0765	0.1828	23.19	1.83
O2	103.3	18.2	40	20	0.8051	0.0811	0.3742	0.1718	19.60	1.53
P(2)1	50.2	18.2	40	15	0.9880	0.0931	0.4110	0.2090	12.70	1.21
P2	48	26	75	12	1.1135	0.1275	0.5559	0.2612	17.21	1.61
Q1	21.1	26	75	10	0.3857	0.0341	0.1439	0.3152	0.86	0.27
Q2	21	26	75	12	0.5611	0.0725	0.2116	0.2971	0.15	0.16
T1	19.7	26	75	2	\	0.0019	\	0.6295	0.86	0.27
U1	50.1	26	75	6	0.0163	0.0038	0.0108	0.1875	12.70	1.21
bk01/1	36.3	26	50	13	1.2346	0.0212	0.2937	0.1271	4.51	0.51
bk01/2	33	26	50	19	0.3910	0.0293	0.1445	0.1432	\	\
bk06/1	43	19.5	50	3	0.0053	0.0034	0.0038	0.5509	8.83	0.74
bk06/2	43	19.5	50	16	0.8671	0.1200	0.4269	0.2875	\	\
bk30/1	28.9	22	50	11	0.1483	0.0182	0.0711	0.2908	10.32	1.29
bk30/2	31	22	50	4	0.1013	0.0182	0.0603	0.5396	\	\
bk31/1	21.7	25	80	12	1.1470	0.0456	0.3856	0.4854	1.88	0.40
bk31/2	22	25	80	11	0.4348	0.0240	0.1800	0.3768	4.40	0.65
bk35/1	14.8	26	70	18	1.0869	0.0667	0.4735	0.1207	3.41	0.65
bk35/2	19	26	70	14	1.0874	0.0653	0.4553	0.1940	\	\
bk43/2	10	27	60	25	11.4650	0.1044	2.3031	0.1035	\	\
bk45/1	13.2	29	75	7	3.0391	0.0062	0.4219	0.1716	5.79	0.66
bk45/2	15	27	50	9	0.1544	0.0120	0.0732	0.2544	\	\
bk50/2	32	24	55	18	0.5068	0.1512	0.3394	0.1837	\	\
bk51/1	58.5	16	25	11	0.0866	0.0211	0.0469	0.2293	3.49	0.56
bk51/2	64	16	25	20	0.6345	0.1497	0.3581	0.4651	12.23	1.12
bk52/1	117.6	15	10	3	0.0022	0.0014	0.0018	0.3333	8.52	0.72
bk52/2	118	15	10	15	0.6100	0.0014	0.0029	0.2769	0.00	1.96
bk53/1	85	14	10	6	0.0130	0.0048	0.0084	0.2400	22.53	1.75
bk53/2	83	14	10	9	0.0893	0.0187	0.0513	0.2715	11.36	0.81
bk54/1	228	12	2	9	0.0910	0.0005	\	0.1712	27.18	2.24
bk54/2	228	12	2	15	0.9721	0.0994	0.4897	0.2935	\	\

Continued

Continued Table 2

Ottertrawl

Station	water depth [m]	temperature [°C]	oxygen [%]	species richness	Biomass [g/m²]	Abundance [n/m²]	Production [g/m²]	dominance	NO3	PO4
H1	12.3	27	75	17	0.257	0.0011	0.0485	0.1625	2.51	0.24
H2	23	14	5	20	0.6692	0.0019	0.1088	0.1472	\	\
J1	261.5	14	5	16	0.0791	0.0018	0.0232	0.1195	2.47	2.21
I(2)1	235	14	5	9	0.8518	0.0244	0.3031	0.2816	2.47	2.21
I(2)2	210	16	10	21	0.036	0.0006	0.0098	0.3313	21.26	1.46
J1	52.5	20	15	21	0.7552	0.002	0.1069	0.1562	2.47	2.21
K1	53.8	16	0	8	0.2031	0.0161	0.0889	0.7416	8.76	1.14
L1	194	16	0	6	0.0575	0.0072	0.0249	0.3059	2.5	4.44
M1	122.8	16	5	13	0.2961	0.0127	0.1199	0.3356	14.7	2.1
M2	82	14	8	15	0.1781	0.0004	0.0294	0.1105	16.83	0.74
R1	20.1	26	75	15	0.0364	0.0003	0.0077	0.0865	0.86	0.27
S1	21.3	26	75	19	0.2373	0.0009	0.0464	0.0852	12.7	1.21
ga01/1	47	26	50	21	0.826	0.0044	0.1747	0.1637	4.51	0.51
gn06/1	43.7	19.5	50	20	2.8793	0.0136	0.4996	0.1611	8.83	0.74
gn06/2	44	19.5	50	22	0.9941	0.0053	0.1425	0.147	\	\
gn30/1	31.5	22	50	23	1.8418	0.0117	0.2642	0.1291	10.3	1.28
gn31/1	22.7	25	80	34	0.3418	0.0071	0.0882	0.2292	1.88	0.4
gn31/2	22	25	80	39	2.1915	0.0126	0.3635	0.3172	\	\
gn35/1	14.5	26	70	19	1.6863	0.0128	0.3905	0.1608	3.41	0.65
gn45/1	13.2	29	75	33	18.0702	0.1185	2.2856	0.2457	5.79	0.66
gn45/2	18	7	50	29	0.6006	0.0277	0.148	0.6423	\	\
gn52/1	97.7	15	10	27	0.6569	0.21	0.2067	0.2967	8.52	0.72
gn52/2	109	15	10	19	0.1178	0.0045	0.0438	0.2153		1.96
gn53/1	80	14	10	27	0.3091	0.0369	0.0662	0.2111	22.53	1.75
gn53/2	80	14	10	30	0.2698	0.0049	0.0637	0.2462	11.36	0.81
gn54/1	199	12	2	8	0.1505	0.0088	0.0645	0.8449	27.18	2.24
gn54/2	239	12	2	25	0.5086	0.004	0.1187	0.1946	\	\

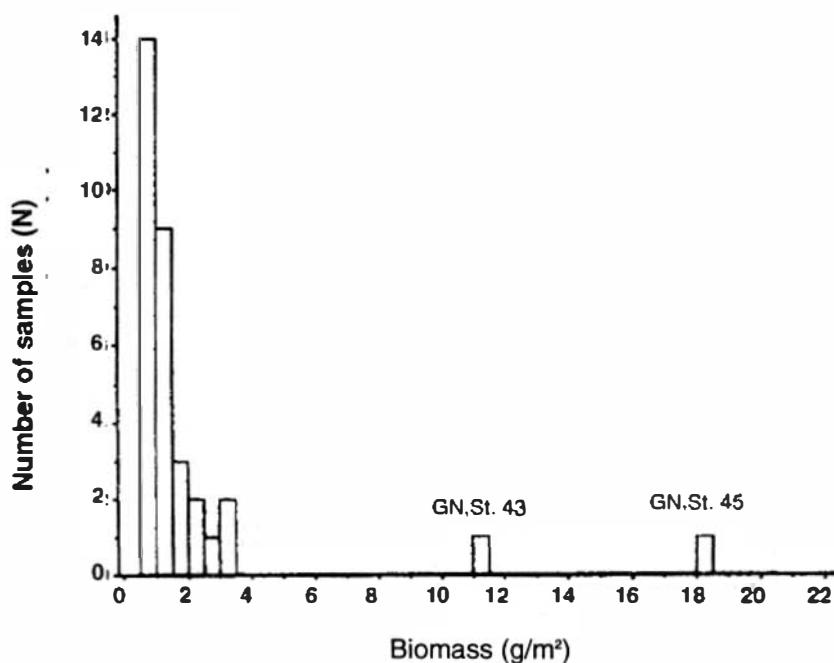
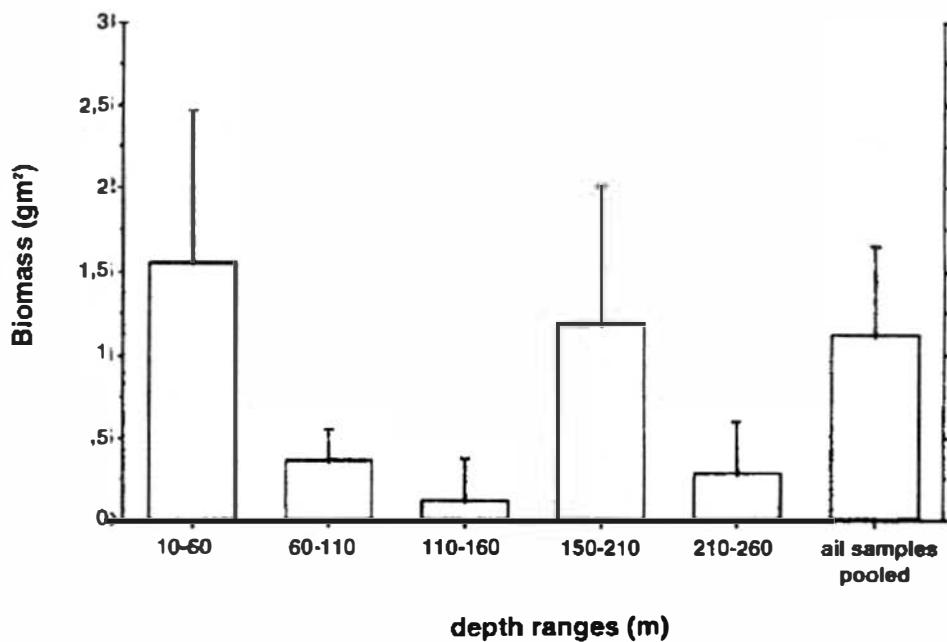


Fig. 4. Bathymetrical distribution of fish biomass (upper graph) and frequency of samples vs. biomass (lower graph) in the study area.

TABLE 3

Correlation matrix established from the station parameters of Table 2

	Correlation matrix							
	waterdepth	temperat...	oxygen	speciesr...	biomass	abundance	production	dominance
waterdepth	1							
temperat...	-.72	1						
oxygen	-.732	.872	1					
speciesr...	-.034	.07	.231	1				
biomass	-.151	.293	.225	.387	1			
abundance	.139	-.125	-.191	.113	.215	1		
production	-.018	.192	.11	.388	.898	.465	1	
dominance	.015	-.205	-.149	-.42	-.16	.283	-.167	1

Biomass is very heterogeneously distributed in the study area, with most samples comprised of low values ($0.5 - 1.5 \text{ g/m}^2$). The general biomass distribution among the 73 samples taken underlines the above-mentioned pattern of species richness: average station biomass of GD was less than half (0.36 g/m^2) of what was found in the GN and ST areas (1.5 and 0.81 g/m^2 respectively). The biomass (and species richness) values of stations 43 and 45 of the interior part of GN are an order of magnitude higher, however, (18.1 and 11.5 g/m^2 respectively) indicative for a much richer fish assemblage in this shallow nutrient loaded more estuarine part of the gulf, which confirms the findings of Bartels *et al.* (1984). Species characteristic for estuarine environments, like ariids, scianids, stingrays, several flatfishes as well as small engraulids contribute to the fish diversity and biomass at these stations.

Our biomass/area estimates are rather low when compared with the literature for other tropical shelf areas: Browder (1993) reported about 4.3 g/m^2 as an average for the demersal fish biomass of the shelf of the Gulf of Mexico. For the Southwestern gulf of Mexico Areaguin-Sanchez *et al.* (1993) reported values of about 7.6 g/m^2 , while Mendoza *et al.* (1993) give values of about 3 g/m^2 for the Northeastern shelf of Venezuela excluding carangids. DePaula *et al.* (1993) report values around 8 g/m^2 for the Mozambique coast. These are higher than our averages but in the order of magnitude of our values for the interior and central part of GN.

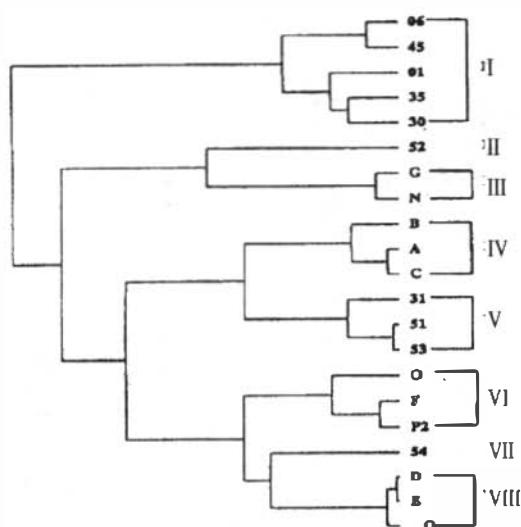
The correlation matrix established from the biotic and abiotic summary parameters of all 73

stations is given in Table 3. It shows that biomass, abundance, production, species richness and dominance is not strongly correlated with any one of the abiotic variables measured, which has also been found by Rojas *et al.* (1994) who studied fish assemblages at three shallow water stations adjacent to mangrove areas within the GN. This indicates that other habitat factors not evaluated in this study like habitat heterogeneity, distance to the open ocean, current regime and food availability are likely important factors for the structure of the fish assemblage.

Description of faunal assemblages: Contrary to Bartels *et al.* (1983) who first subdivided their study area (GD) by clustering the abiotic factors and then related species occurrence with environmental parameters, we started the procedure by "letting the species tell their story" first (Clarke & Warwick 1994), in order to find areas of common faunal structures. By doing so we did not start with the pre-conception that our environmental variables measured determine the faunal structure.

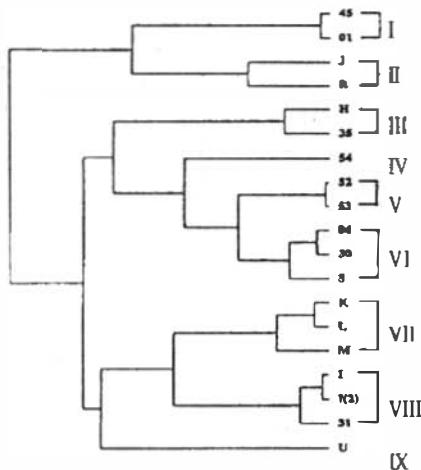
Figs. 5 a, b and 6 a, b show the station dendograms and MDS-plots derived from the beam trawl and otter trawl catches in December 1993 and February 1994 based on the data of Table 4, which gives the reduced (95%) station - species matrix from the beam trawl and otter trawl collections used for the multivariate analysis. By using the SIMPER algorithm of the PRIMER software, the species accounting for the groupings within the dendograms were determined and are included in the figures. In

Beamtrawl, December'93 (59 species represents 95% of total production)

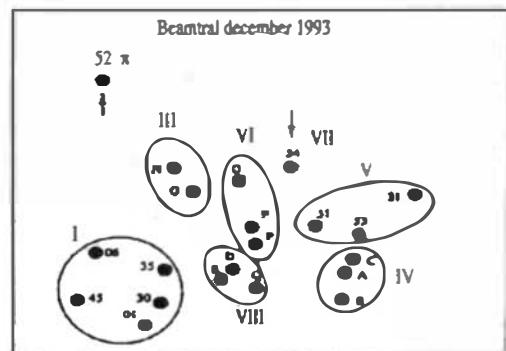


BRAY-CURTIS SIMILARITY (RANKED)

Ottertrawl, December'93 (79 species representing 95% of total production)

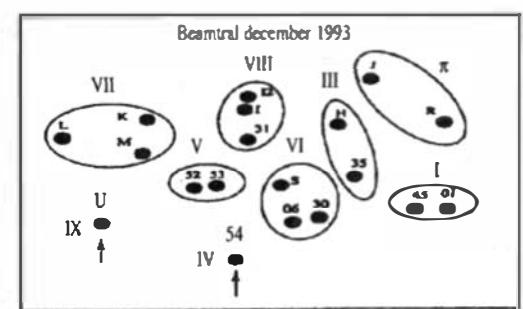


BRAY-CURTIS SIMILARITY (RANKED)



Species accounting for similarity of groups:
Beamtrawl Dec'93

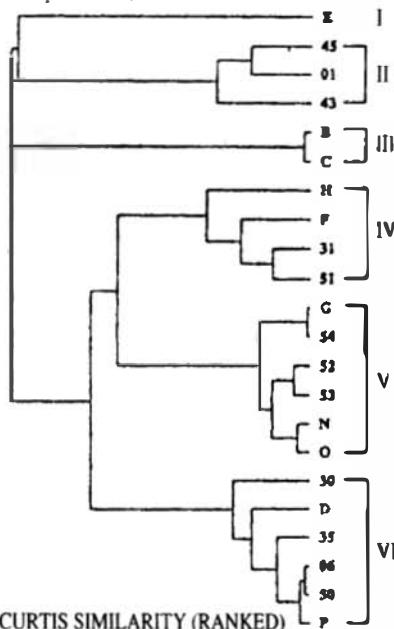
- | | | | |
|------|---|-------|---|
| I: | Symphurus elongatus
Ophioscion typicus
Sycium ovale
Menticirrhus nasus | V: | Syacium latifrons
Porichthys marginatus |
| II: | Physiculus nemanopterus | VI: | Citharichthys platophrys
Synodus scituliceps
Synodus evermanni |
| III: | Lophiodes caulinares
Pontinus sierra
Monolepis maculipinna
Physiculus nemanopterus | VII: | Prionotus albirostris |
| IV: | Porichthys marginatus
symphurus atramentatus | VIII: | Achirus mazatlanus
Sphoeroides annulatus
Synodus scituliceps
Synodus evermanni
Cyclopsetta panamensis |



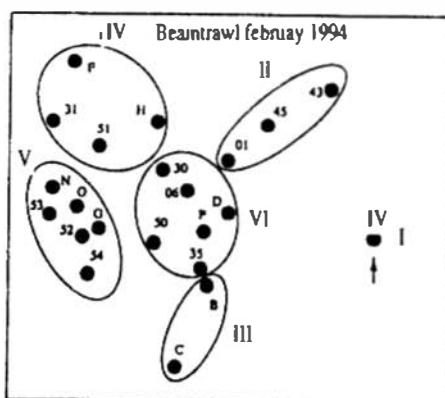
- | | | | |
|------|--|-------|---|
| I: | Cynoscion albus
Dasyatis longus
Isopisthus alutinus
Paralonchurus dumerili
Polydactylus approximans
Prionotus horrens
Rhinobatos leucorhynchus
Anchoa sp
Arius doovi
Arius troschelli | II: | Hippoglossina ertaophthalmus
Mustelus lunulatus
Pomadasys branickii
Synodus scituliceps |
| III: | Cynoscion nannus (L,M)
Diplectrum labarum (K,M)
Eucinostomus gracilis (K,L) | VI: | Lutjanus guttatus
Synodus aculeatus
Trichiurus nitens (6,30)
Seleni peruviana (6,30)
Leiophidium prorates (6,30)
Isopisthus altipinnis (6,30)
Cyclopaetta quema (6,5) |
| IV: | Eucinostomus argenteus
Pseudopeneus vancouverensis | VII: | Argentina alicea
Bolimannia stigmatura
Pontinus sierra
Physiculus namaquopterus |
| V: | Trichiurus nitens
Raja velezi
Hemarhias peruvanus
Diplectrum Eumelum
Citharichthys platophrys
Caulolatilus affinis | IX: | Leiophidium prorates
Ophichthidae
Porichthys marginatus |
| VI: | | VIII: | |

Fig. 5. Station dendograms and MDS-plots for beamtrawl (a) and ottertrawl (b) collections during December (species responsible for groups are given in the lower right of the figure).

Beamtrawl, February '94 (75 species representing 95% of total production)



BRAY-CURTIS SIMILARITY (RANKED)



Beamtrawl Feb '94

I: *Diplectrum macropoma*

II: *Cynoscion phoxocephalus*
Arius kessleri (45,43)
Prionotus horrens (01,43)
Stellifer sp. (45,43)

III: *Cynoscion nannus*

IV: *Syacium latifrons*
Pontinus sierra (31,51)
Synchiropus atrilabiatus (H,51)
Zalictes elater (31,51)

V: *Syphurus callopterus*

Physiculus nemaopterus
Pontinus sierra (G,53-54)

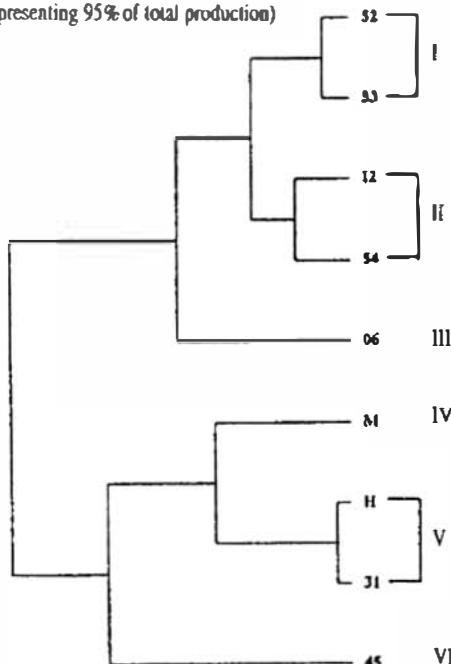
Monolepis maculipinna
(G,H,O,52)
Synchiropus atrilabiatus
(G,53,54,O)
Zalictes elater (52,53,N,O)

VI: *Ponchthys greeni*

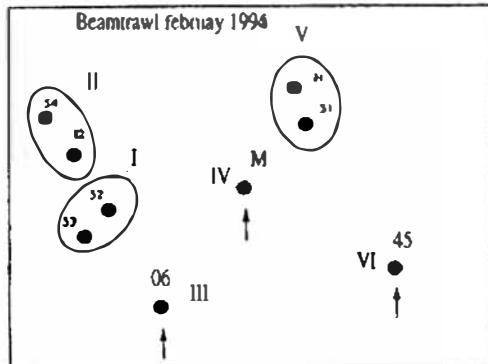
Porichthys marginatus
Bombyllaria chlamydes
(D,6,30,50,P)

Synodus evermanni (B,6,50,P)
Gymnophara equatorialis (D,6)
Sphoeroides annulatus (30,P)

Ottertrawl, February '94 (64 species representing 95% of total production)



BRAY-CURTIS SIMILARITY (RANKED)



Ottertrawl Feb '94

I: *Citharichthys platyphrys*
Synodus evermanni
Peristedion barbiger
Lophiodes caulinaris
Hemanthias signifer
Bombyllaria stagnatura

II: *Lophiodes caulinaris*
Peristedion barbiger
Pontinus sierra
Umbrina bussingii

III: 14 species, first 5:
Selene peruviana
Peprilus synderi
Cyclopsetta quema
Prionotus sp.
Syacium ovale

IV: 9 species, first 5:
Mustelus lunulatus
Dasyatis longus
Epinephelus niphobles
Raja velezi
Peprilus snyderi

V: 9 species, first 5:
Caranx otrymer
Cavax speciosus
Lutjanus guttatus
Narcine brasiliensis
Sphoeroides annulatus

VI: 17 species, first 5:
Neopristipopterus tropicus
Paralouichirus dumetilli
Dasyatis longus
Arius dovi
Acheinus scutum

Fig. 6. Station dendograms and MDS-plots for beamtrawl (a) and ottertrawl (b) collections during February (species responsible for groups are given in the lower right of the figure).

TABLE 4

Species-station matrices of the beamtrawl and ottertrawl collections of both sampling dates used for the multivariate analysis (a,b: beamtrawl and ottertrawl collections in December respectively; c,d: beamtrawl and ottertrawl collections in February respectively)

Beamtrawl December 1993

Continued Table 4

<i>Monalene maculipinna</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Monolene</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Narcine brasiliensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Neothlypterus stelliferoides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ophiocion typicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ophiosoma parigena</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Piratlonchirus dumetillii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Physiculus nematopterus</i>	0	0	0	0	0	0	0	0.0127	0	0	0	0	0	0	0	0	0	0.0615	0	0	0
<i>Pomadasys nitidus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0019	0.0358	0	0	0	0
<i>Poecilines fuscatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4394	0	0	0
<i>Pomitus sierra</i>	0	0	0	0	0	0	0	0.3024	0	0	0	0	0	0	0	0	0	0.0134	0	0	0
<i>Pomachilus greeni</i>	0	0	0	0	0	0	0	0.0039	0	0	0	0	0	0	0.0017	0.3499	0.00035	0.0013	0	0	0
<i>Pomachilus marginatus</i>	0.0361	0.0051	0.0111	0	0	0	0.0000	0	0.0019	0	0.0022	0	0	0	0	0	0	0	0.0682	0.0206	0
<i>Prionotus albostriatus</i>	0	0	0	0	0	0.0044	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0448	0
<i>Prionotus stephanophrys</i>	0	0	0.0521	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Protogonammus eos</i>	0	0	0	0	0	0	0.0072	0	0	0	0	0	0	0	0	0	0	0.0935	0	0	0
<i>Protogonogrammus multifasciatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0252	0	0	0
<i>Scorpis russula</i>	0	0	0	0.00107	0	0.00042	0	0	0.0016	0	0.0016	0	0	0	0	0	0	0	0.0028	0.0019	0
<i>Sphaeroides annulatus</i>	0	0	0.00312	0.0050	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0281	0
<i>Sphaeroides lobatus</i>	0	0	0	0.00030	0.0024	0	0	0	0	0	0	0	0	0	0	0	0.0013	0	0	0	0.0216
<i>Sphaerum laufonis</i>	0	0	0.0065	0	0	0	0.1276	0.0297	0	0.0024	0	0	0	0	0	0	0	0	0	0	0
<i>Syacium ovale</i>	0	0	0	0	0	0.0048	0	0	0	0	0	0	0	0	0	0.0022	0	0	0.1077	0	0
<i>Syphurus oligomerus</i>	0	0	0	0	0	0	0.0021	0	0	0	0	0	0	0	0	0	0	0.0371	0	0	
<i>Syphurus atramentatus</i>	0.0999	0.0033	0.0832	0	0	0.0116	0.0000	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Syphurus callipterus</i>	0	0	0	0	0	0	0.0719	0	0	0	0	0	0	0.0014	0	0	0	0	0	0	0
<i>Syphurus chabanaudi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0153	0.0294	0.0239	0.0053	0	0	0	0
<i>Syphurus elongatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0078	0.0043	0.0224	0	0	0.0228	0.0058	0
<i>Syphurus leei</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0147	0	0
<i>Syphurus melanurus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0031	0	0	0	0	0
<i>Synodus evermanni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0020	0.0050	0.0250	0.0040	0.0021	0
<i>Synodus sciuliiceps</i>	0	0	0	0	0.0025	0.0219	0.0115	0	0	0	0	0	0	0	0.1107	0	0	0	0.0112	0	0
<i>Synodus sechurae</i>	0	0	0	0	0.0045	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0061	0	0
<i>Urotrygon chilensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0637	0	0	0	0	0
<i>Urotrygon mundaus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0290	0	0	0	0	0	0

Production (95%, 82 species)	H	I	(2)	3	K	L	M	E0131	E0132	E0133	E0134	E0105	E0115	E0101	E0102	E0150	E0151	R	3	U	
<i>Achirus acutum</i>	0.0001	0	0	0	0	0	0	0	0	0	0	0.0153	0	0	0	0	0	0	0	0	0
<i>Anchoa lucida</i>	0	0	0	0	0	0	0	0	0	0	0	0.0087	0	0	0.0092	0	0	0	0	0	0
<i>Anchos sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0.0145	0.0010	0.0003	0.0011	0	0	0	0	0	0
<i>Anisostomus pacifici</i>	0	0	0	0	0	0	0	0	0	0	0	0.0069	0	0	0	0	0	0	0	0	0
<i>Argentina alliceae</i>	0	0.0017	0.0102	0	0	0	0	0.0012	0.0009	0	0	0	0	0	0	0	0	0	0	0	0
<i>Arius dasyccephalus</i>	0	0	0	0	0	0	0	0	0	0	0	0.1937	0	0	0	0	0	0	0	0	0
<i>Arius doovi</i>	0	0	0	0	0	0	0	0	0	0	0	0.0415	0.0021	0	0	0	0	0	0	0	0
<i>Arius trocheili</i>	0	0	0	0	0	0	0	0	0	0	0	0.0014	0.0013	0	0	0	0	0	0	0	0
<i>Arotrolepis hispida</i>	0	0	0	0	0	0	0	0.0063	0	0	0	0	0	0	0.0014	0	0.0018	0	0	0	
<i>Bolitoglossa signifera</i>	0	0.0001	0.0001	0	0	0	0	0.0003	0.0003	0	0	0.0054	0	0	0	0	0	0	0	0	0
<i>Calamus brachysomus</i>	0	0	0	0	0	0	0	0.0136	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Caranx oblongoides</i>	0.0016	0.0005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Caranx speciosus</i>	0	0	0	0	0	0	0	0.0110	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Caranx vinctus</i>	0.0163	0.0113	0.0011	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Caulophryne affinis</i>	0	0	0	0	0	0	0	0	0	0	0	0.0054	0.0011	0	0	0	0	0	0	0	0
<i>Cetengrammus mysicetus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chaetostomus sonatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0251	0	0	0	0	0
<i>Chlorophthalmus mento</i>	0	0.0001	0.0231	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Citharichthys plastocephalus</i>	0	0	0	0	0	0	0	0	0	0	0	0.0047	0.0024	0	0	0	0	0	0	0	0
<i>Cyclopetetta querna</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0222	0	0	0	0
<i>Cynocosticeps coniceps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0005	0.0141	0	0.0081	0
<i>Cynoscion albus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0003	0.0141	0	0.0081	0
<i>Cynoscion namus</i>	0	0.0006	0.0006	0	0	0	0	0.0048	0.0743	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cynoscion phoxocephalus</i>	0	0	0	0	0	0	0	0	0	0	0	0.1040	0	0	0	0	0	0	0	0	0
<i>Cynoscion stolzmanni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0099	0	0	0	0	0
<i>Cynostium reticulatum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0173	0	0	0	0	0
<i>Dasyatis longissima</i>	0	0	0	0.0158	0	0	0	0	0	0	0	0	0	0	0	0.0079	0.0019	0	0	0	0
<i>Diapterus auratus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0162	0.0000	0.1372	0.0073	0	0
<i>Diapterus peruvianus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Diodon histrio</i>	0	0	0	0	0	0	0	0	0	0	0	0.0014	0	0	0	0	0	0	0	0	0
<i>Diplectrum eumelium</i>	0	0	0	0	0	0	0	0	0	0	0	0.0121	0.0003	0	0	0	0	0	0	0	0
<i>Diplectrum styroplectrum</i>	0	0.0042	0	0	0	0	0	0	0	0	0	0.0002	0	0.0039	0	0	0	0	0	0	0
<i>Diplectrum labarum</i>	0	0	0	0	0.0045	0	0	0	0.0335	0	0	0	0.0004	0	0	0	0	0	0	0	0
<i>Eucinostomus argenteus</i>	0.0046	0.0009	0	0	0	0	0	0	0.0006	0	0	0	0	0	0	0.0154	0	0	0	0	0
<i>Bucinostomus aureolus</i>	0	0	0	0	0	0	0	0	0	0	0	0.0000	0	0	0	0.0065	0	0	0	0	0
<i>Bucinostomus gracilis</i>	0	0	0	0	0	0	0	0.0778	0.0069	0.0155	0	0	0	0	0	0	0	0	0	0	0
<i>Gymnothorax equatorialis</i>	0	0	0	0	0	0	0	0	0	0	0	0.0010	0	0	0	0.0077	0	0	0	0	0

Continued *Ottertrawl December 1993*

Production (95%, 68 species)			B	C	D	E	F	G	H(B)	1841	1842	1843	1844	1845	1846	1847	1848	1849	1850	N	O	P	
<i>Achirus kuhzingeri</i>			0	0	0	0	0	0	0,0172	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Achirus scutum</i>			0	0	0	0	0	0	0,0024	0	0	0	0	0	0	0,0173	0	0	0	0	0	0	
<i>Acanthozenus dovi</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,3269	0	0	0	0	
<i>Acanthozenus avalonis</i>			0	0	0	0	0	0	0,0018	0,0041	0	0	0	0	0	0	0	0	0	0	0,0448	0	
<i>Arius keskeri</i>			0	0	0	0	0	0	0	0	0	0	0	0	0,0077	0	0	0	0	0	0	0	
<i>Arius osculus</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,4837	0	0	0	0	
<i>Arius sp. a</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,25	0	0	0	0	
<i>Arius sp. b</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0281	0	0	0	0	
<i>Bellator gymnocephalus</i>			0	0	0	0	0	0	0	0,0028	0	0	0	0	0	0	0	0	0	0	0,0139	0	
<i>Bolmannia chlamydes</i>			0	0	0,0026	0	0	0,0165	0	0	0	0,6716	0	0,006	0,0246	0	0	0	0,0029	0	0,0013	0	0,0682
<i>Bolmannia stigmatura</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cathetorops tuyra</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,2573	0	0	0	
<i>Chlorophthalmus mento</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Citharichthys platophrys</i>			0	0	0	0	0	0	0	0	0	0	0,0092	0	0	0,0013	0	0,0007	0	0	0	0	
<i>Cyclopsetta panamensis</i>			0	0	0	0	0	0	0,1451	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cyclopsetta querina</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0001	0	0	0	0	
<i>Cynoscia namus</i>			0,0212	0,0067	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cynoscia phoxocephalus</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0,0024	0,0217	0	0	0,2366	0	0	
<i>Diapterus auriculus</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0008	0	0	0	0	
<i>Diplectrum macropona</i>			0	0	0,0151	0,0129	0	0	0	0	0	0	0	0	0	0	0	0,0002	0	0	0	0,0074	
<i>Diplectrum sp.</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Engraulis sanctaurentii</i>			0	0	0	0	0	0	0	0,017	0	0	0	0	0	0	0	0	0,2127	0	0	0	
<i>Etropus crossotus</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0008	0	0	0	0	
<i>Etropus sp.</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0002	0	0	0	0	
<i>Euclitostomus argenteus</i>			0	0	0,0219	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Gymnothorax equatorialis</i>			0	0	0,0533	0	0	0	0	0	0	0	0	0	0,0056	0	0	0	0	0	0,0165	0	
<i>Gymnothorax sp.</i>			0	0	0	0	0	0	0,0163	0	0	0,02	0	0	0	0	0	0	0	0	0	0	
<i>Haemulon aculeatum</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,0226	0	0	0	0	
<i>Haemulopsis leuciscus</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Hemianthias signifer</i>			0	0	0	0	0	0	0	0,0057	0	0	0	0	0	0	0	0	0	0	0,0104	0,3331	
<i>Himantura pacifica</i>			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,5734	0	0	0	0	
<i>Hippoglossina tetraphthalmus</i>			0	0	0	0	0	0	0	0,021	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Katetostoma averuncus</i>			0	0	0	0	0	0	0,0096	0	0	0	0,0113	0	0	0	0	0	0	0	0	0	
<i>Lophiodes spinifilus</i>			0	0	0	0	0	0	0,0066	0	0	0	0	0	0,0377	0	0	0	0	0	0	0	
<i>Monodelphus assatus</i>			0	0	0	0	0	0	0,0123	0	0	0	0	0	0	0	0	0	0	0,0072	0	0	
<i>Monodelphus maculipinnis</i>			0	0	0	0	0	0	0,0759	0	0	0	0,002	0	0	0	0	0	0	0,0815	0,0245	0	

Continued Beamtrawl February 1994

Production (95%, 64 species)									
	II(gsn)	I2	M	gsn31	gsn52	gsn53	gsn54	gsn06	gsn45
<i>Achirus mazatlanus</i>	0	0	0	0,0008	0	0	0	0	0,0049
<i>Achirus scutum</i>	0	0	0	0	0	0	0	0	0,0064
<i>Albula nemoptera</i>	0,0066	0	0	0,021665	0	0	0	0	0
<i>Ancylopsetta dendrica</i>	0	0	0	0,0047	0	0	0	0	0
<i>A isostremus dovii</i>	0	0	0	0,0418	0	0	0	0	0,0016
<i>Arius dovii</i>	0	0	0	0	0	0	0	0	0,0062
<i>Arius platypogon</i>	0,0015	0	0	0,0262	0	0	0,028	0	0
<i>Arius trochelii</i>	0	0	0	0	0	0	0	0	0,0043
<i>Bolmannia stigmatura</i>	0	0	0	0	0,0024	0,0002	0	0,0002	0
<i>Calamus brachysomus</i>	0	0	0	0,0519	0	0	0	0	0
<i>Caranx otrynter</i>	0,0225	0	0	0,0075	0	0	0	0	0
<i>Caranx speciosus</i>	0,0104	0	0	0,008	0	0	0	0	0
<i>Caranx vinctus</i>	0	0	0	0,0086	0	0	0	0	0
<i>Citharichthys platophrys</i>	0	0	0	0	0,0031	0,0108	0	0,0007	0
<i>Cyclopsetta panamensis</i>	0,0019	0	0,0007	0,0111	0	0	0	0	0
<i>Cyclopsetta querna</i>	0	0	0	0	0	0	0	0,013	0,0017
<i>Cynoscion albus</i>	0	0	0	0,0047	0	0	0	0	0
<i>Cynoscion phoxocephalus</i>	0	0	0	0	0	0	0	0	0,003
<i>Dasyatis longus</i>	0,0078	0	0,0049	0,0312	0	0	0	0	0,0156
<i>Diapterus peruvianus</i>	0	0	0	0	0	0	0	0	0,005
<i>Diplectrum euryplectrum</i>	0	0	0	0	0	0,0026	0,0009	0	0
<i>Diplectrum macropoma</i>	0	0	0	0	0	0	0	0,004	0
<i>Epinephelus niphobles</i>	0	0	0,0035	0	0	0	0	0	0
<i>Eucinostomus gracilis</i>	0	0	0	0,0091	0	0	0	0	0
<i>Genes cinereus</i>	0	0	0	0,0096	0	0	0	0	0
<i>Gymnothorax equatorialis</i>	0	0	0	0	0	0,0028	0	0,0049	0
<i>Hemianthias peruanus</i>	0	0	0	0	0,0022	0,001	0	0	0
<i>Hemianthias signifer</i>	0	0	0	0	0,0011	0	0,0018	0	0
<i>Hoplopagrus guntheri</i>	0	0	0	0,0038	0	0	0	0	0
<i>Lophiodes caulinaris</i>	0	0,0014	0	0	0,0003	0,0019	0,0006	0,0005	0
<i>Lutjanus argentiventris</i>	0	0	0	0,0033	0	0	0	0	0

<i>Lutjanus guttatus</i>	0,0103	0	0	0,007708	0	0	0	0	0
<i>Lutjanus peru</i>	0	0	0	0,0045	0	0	0	0	0
<i>Mustelus lunulatus</i>	0	0	0,023603	0	0	0,001	0	0	0
<i>Narcine brasiliensis</i>	0,0122	0	0,0006	0,017	0	0	0	0	0
<i>Neopisthopterus tropicus</i>	0	0	0	0	0	0	0	0	0,0471
<i>Paralichthys woolmami</i>	0	0	0	0,0005	0	0,002	0	0	0
<i>Paralonchurus dumetalli</i>	0	0	0	0	0	0	0	0	0,0229
<i>Pepnites snyderi</i>	0	0	0,0016	0	0,0298	0	0,0002	0,0275	0
<i>Peristedion bartiger</i>	0	0,0024	0	0	0,0002	0,0001	0,0003	0	0
<i>Polydactylus approximans</i>	0	0	0	0	0	0	0	0	0,0032
<i>Pomadasys branickii</i>	0,0066	0	0	0	0	0	0	0	0
<i>Pontinus sierra</i>	0	0,0002	0	0	0,0003	0	0,0036	0	0
<i>Porichthys margaritatus</i>	0	0	0	0	0,0007	0	0	0,0056	0
<i>Prionotus albirostris</i>	0	0	0	0	0	0,0036	0	0	0
<i>Prionotus horrens</i>	0	0	0	0,0087	0	0	0	0	0,0036
<i>Prionotus sp.</i>	0	0	0	0	0	0	0	0,0114	0
<i>Raja velezi</i>	0	0,0048	0,0076	0	0	0,0223	0	0,0028	0
<i>Rhinobatos leucorrhyncus</i>	0	0	0	0,0203	0	0	0	0	0
<i>Selene brevortii</i>	0	0	0	0,0059	0	0	0	0	0
<i>Selene oerstedi</i>	0	0	0	0,0311	0	0	0	0	0
<i>Selene peruviana</i>	0	0	0	0	0	0	0	0,0501	0,0004
<i>Sphaeroides annulatus</i>	0,0031	0	0	0,0119	0	0	0	0	0
<i>Sphaeroides lobatus</i>	0,0151	0	0	0,0133	0	0	0	0	0
<i>Stellifer illecebrosus</i>	0	0	0	0	0	0	0	0	0,0005
<i>Syacium latifrons</i>	0	0	0	0,0017	0	0	0	0,004	0
<i>Syacium ovale</i>	0	0	0	0,0013	0	0	0	0,0076	0
<i>Synodus evermanni</i>	0	0	0,0002	0,0002	0,0015	0,0034	0	0	0
<i>Synodus scituliceps</i>	0	0	0	0,0002	0	0	0	0,0074	0
<i>Trichiurus nitens</i>	0	0	0	0	0	0	0,0735	0	0
<i>Trinectes sp.</i>	0	0	0	0	0	0	0	0	0,0006
<i>Umbrina bussingii</i>	0	0,000	0	0	0	0,0008	0,0028	0	0
<i>Urotrygon nana</i>	0	0	0	0	0	0	0	0	0,007
<i>Zapteryx exasperata</i>	0	0	0,0006	0,0072	0	0,0017	0	0	0

all cases the MDS-plots match the cluster dendograms well as seen by the coincidence of the group numbers between the clusters and MDS-plots. The following general pattern emerges:

(1) Groups are formed by stations of a certain depth range and/ or geographical location. Thus in the December beam trawl cluster and MDS plot for example, the stations of the interior and central part of GN (group I), those of the outer lateral part of GN (group V) and the shallow stations of GD and ST (group VIII) are grouped together. A similar pattern is repeated in the other cluster.

(2) The deepest station 54 (228 m) at the outer slope of GN is separated from other stations in December, both in the otter trawl and beam trawl catches.

(3) Flatfish species (generally small sized) are the main components in the beam trawl catches and important for the similarity within station groups whereas in the otter trawl catches, roundfish and rays are more important. Sharks and some pelagic fish like *Anchoa* sp., *Selene* spp. almost exclusively occur in the otter trawl catches;

(4) More species account for the similarity within groups in the otter trawl catches, reflecting a general higher species richness in the otter trawl catches. This is confirmed by the comparison of the species area curves of the beam trawl and otter trawl collections (Fig. 2).

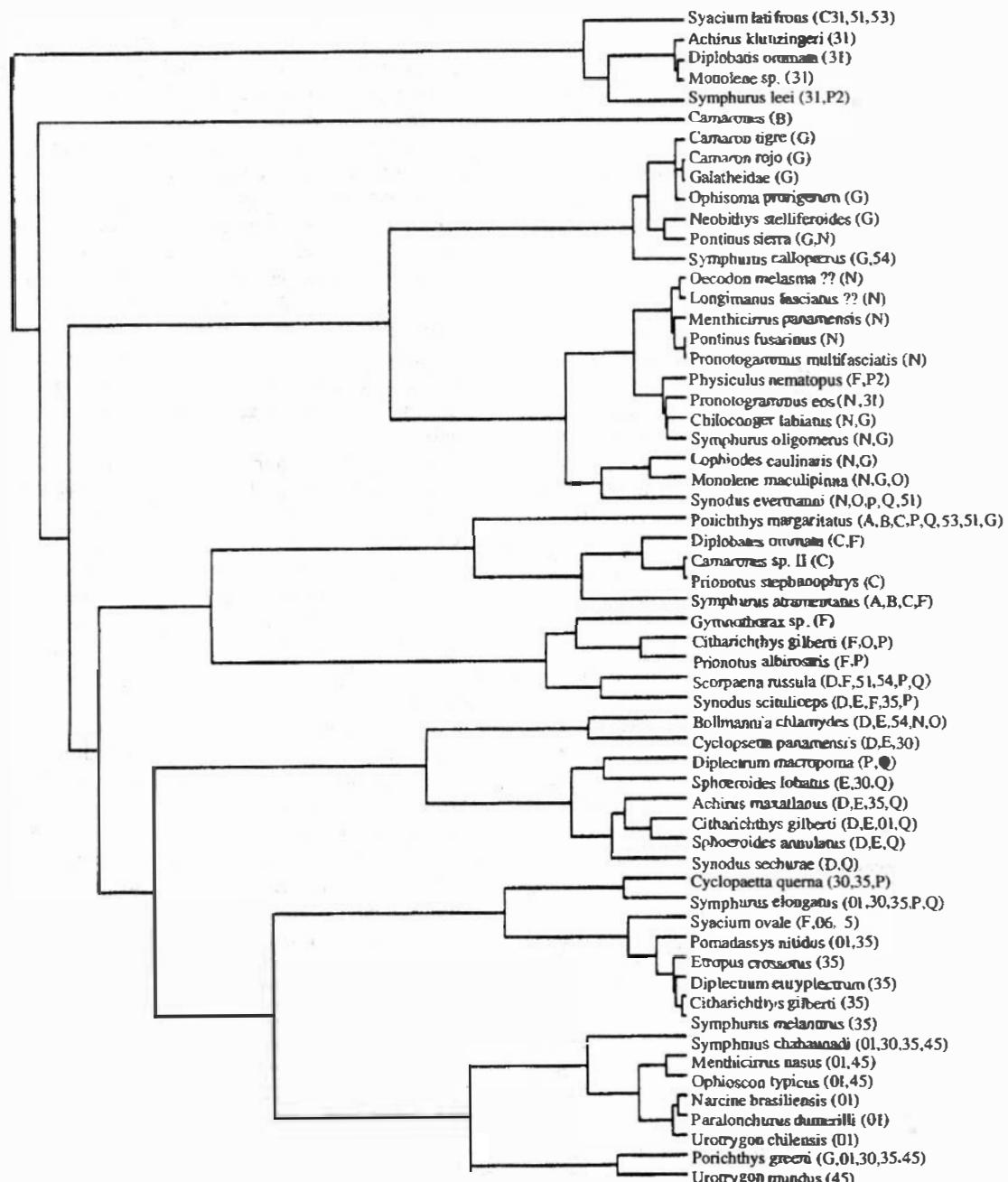
By observing the species cluster (Fig. 7a,b and 8a,b) it is seen that some species occurred only on a few, others on many stations. In the otter trawl catches the following were only found on the central and interior stations of Golfo de Nicoya (45,01,06,30) and might thus well characterize this area: *Cyclopsetta quernea*, *Achiurus mazatlana*, *Prionotus* sp., *Prionotus horrens*, *Arius troschelli*, *Arius dovii*, *Paralonchurus dumerillii*, *Polydactylus approximans*, *Trinectes* sp., *Diapterus peruvianus*, *Cynoscion phoxocephalus*, *Anisotremus dovii*, *Rhinobates leucorhynchus*. Other species were common on these stations, but also occurred in other areas, like *Selene peruviana* and *Achiurus scutum* (H), *Gymnothorax equatorialis* (53), *Peprilus snyderi* (52,54,M) or *Dasyatis longus* (M,H,J, R). The following species occurred only on the deeper stations during both seasons: *Mustelus lunatus* (I,52,53,M), *Hemanthias peruanus* (52,53),

Hemanthias signifer (52,54, I2), *Diplectrum euryplectrum* (52,53), *Umbrina bussingii* (52,53,54,M,I2). Some predominated at the deeper stations but also occurred further inshore like *Trichiurus nitens* (54,53,52,M,I, 06,30), *Pontinus sierra* (54,52,I2,I,M, 31), *Bollmannia stigmatura* (53,53,I, 06, I,I2,31), *Synodus evermanni* (53,52,M,3I).

In addition to the species mentioned above, there were many that occurred during one of both sampling dates only. Among those are several shoaling carangid species caught on station 31 (Bahía Ballena) during February: *Caranx vinctus*, *Selene brevortii*, *Selene oerstedi*, *Caranx otrynter*, *Caranx speciosus*. The latter was also found at this station during December, while *C. vinctus* and *S. oerstedi* (H,35,S) were also found in the Golfo Dulce area during December. *Cynoscion nannus*, a small scianid was the only species occurring exclusively in the otter trawl catches of the GD - area in both seasons (I,L,M,B,C). *Sphoeroides lobatus* (J) and *S. anulatus* (H,J,K) were restricted to the GD catches in the rainy season, as were *Caranx vinctus* (H,I,12), *Chlorophthalmus mentis* (I,12), *Neobythes stelliferoides* (I2), *Himantura pacifica* (H) and *Diplectrum labarum* (K,H). *Epinephelus niphobles* only occurred on station M during the dry season.

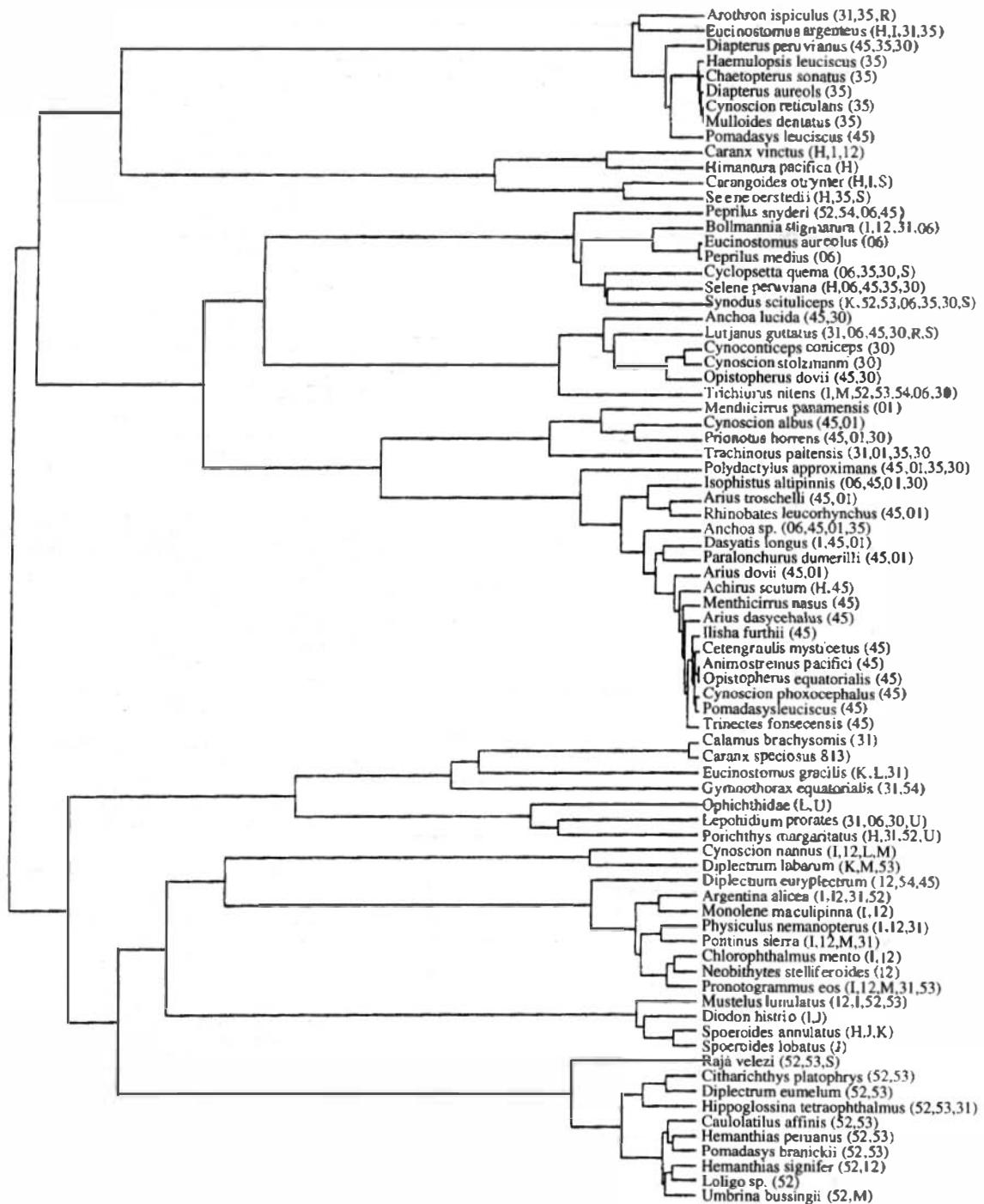
The following species were those most frequently captured by the ottertrawl (both seasons): *Synodus evermanni/scituliceps* (10), *Dasyatis longus* (8), *Bollmannia stigmatura* (8), *Lutjanus guttatus* (8), *Trichiurus nitens* (8), *Selene peruviana* (7) and *Raya velezi* (7).

The general pattern of species groups of the ottertrawl cluster are repeated in the beam trawl catches, although many species differ. The following were found on the stations of the central and interior parts of GN on both sampling dates (some of those were also found in the other study areas): flatfish: *Achiurus klunzingeri* (31), *Syacium latifrons* (31,C, 51, 53, F, H, N), *Cyclopsetta quernea* (30,35,P), *Syphurus elongatus* (30, 35, 01, P, Q, 06, 43), *Syacium ovale* (06,35,F,50,P), *Etropus crassotus* (35), *Syphurus chabaudi* (30,35,01,45,43); round fish: *Synodus scituliceps* (35,P,D,F,E, H,06,01,50), *Sphoeroides lobatus* (30, E, Q, H, 06,01,50,P), *Porichthys greeni* (01, 45, 30, 35, G,52, 06,50,P). During December, the following additional species were caught at these sta-



BRAY-CURTIS SIMILARITY (RANKED)

Fig. 7. Species dendograms for the beamtrawl (this page 59 species) and ottertrawl (next page 79 species) collections during December (stations of species occurrence are given in parenthesis).



BRAY-CURTIS SIMILARITY (RANKED)

Fig. 7 (continued)

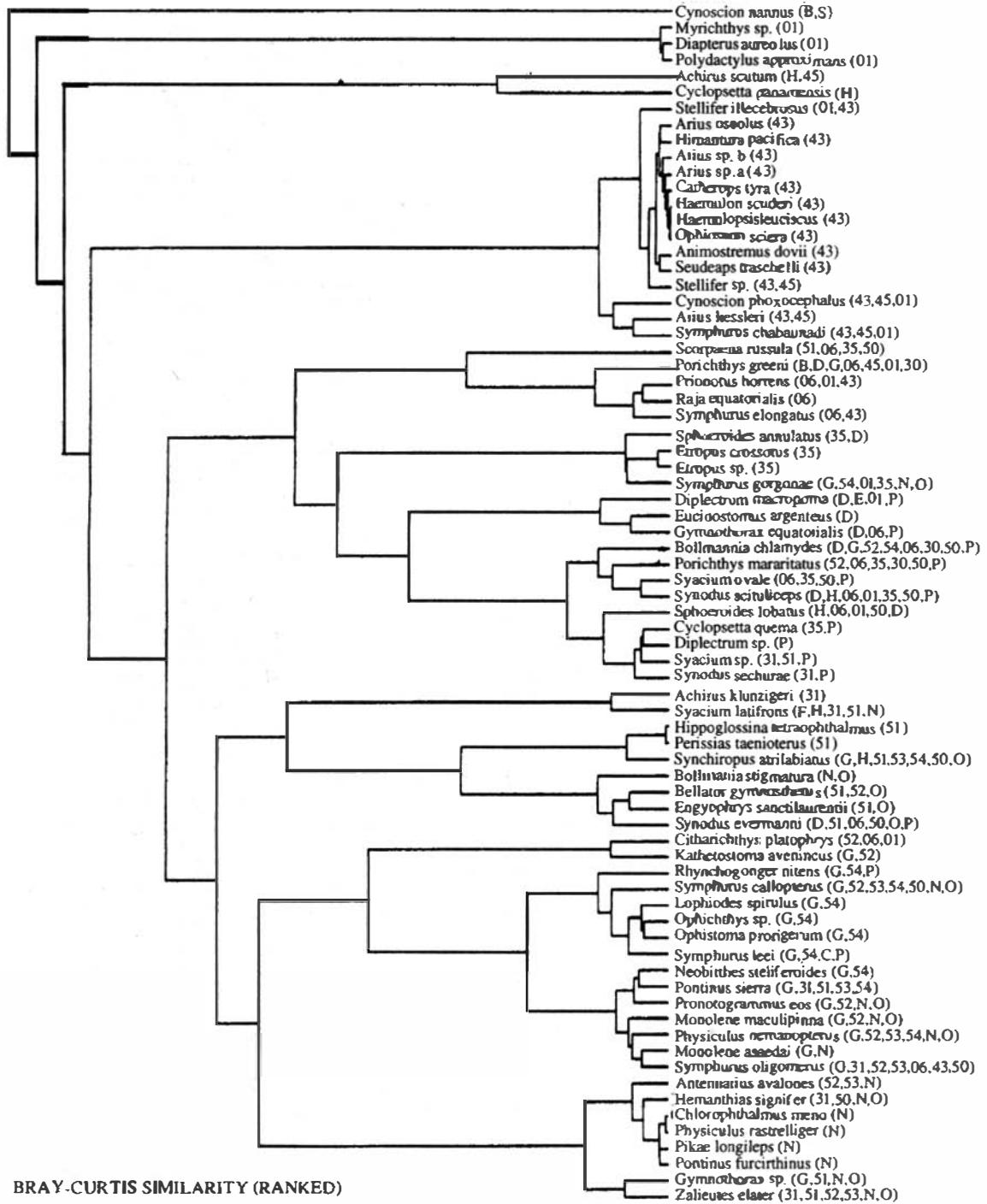
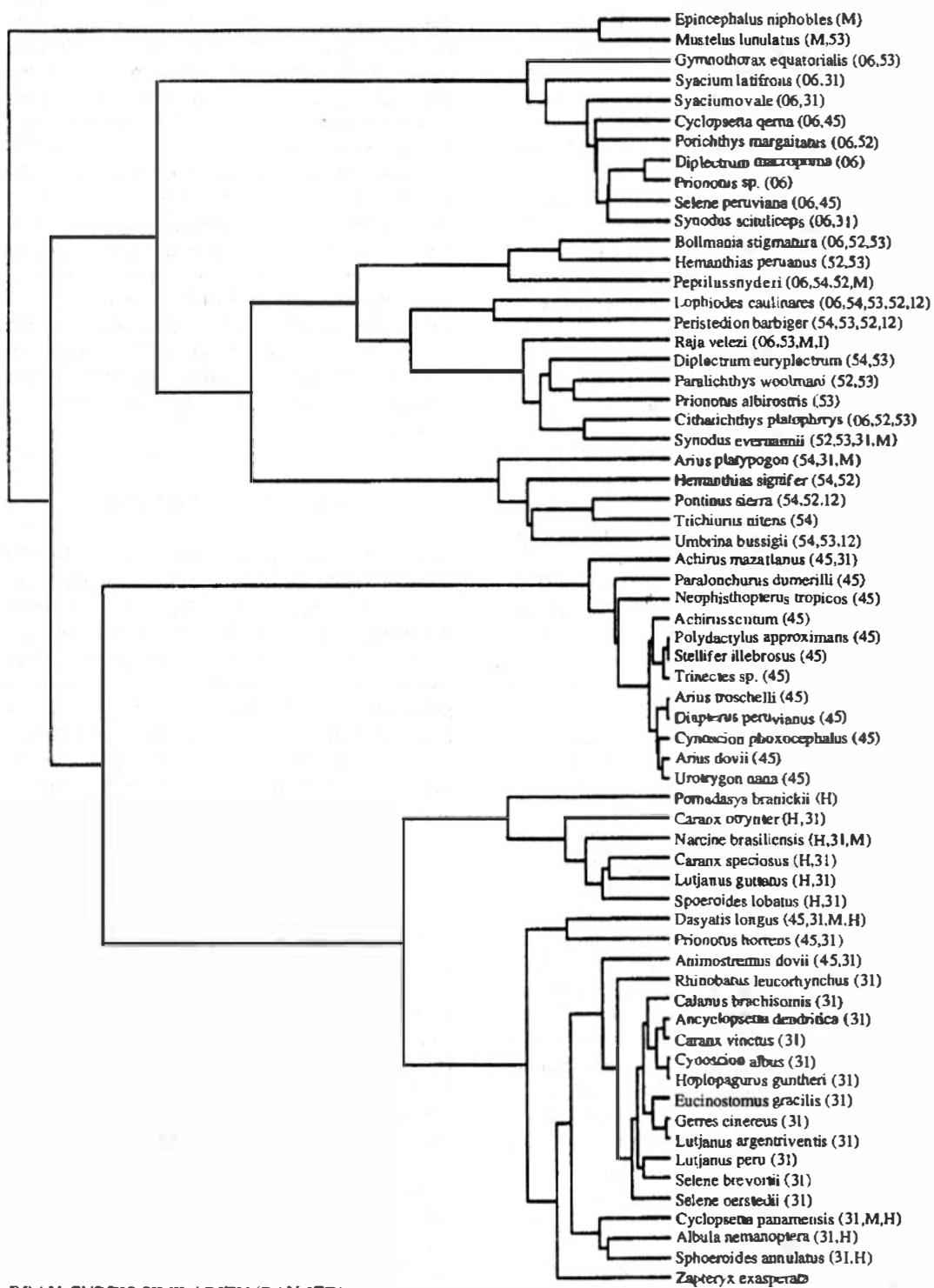


Fig. 8. Species dendograms for the beamtrawl (this page 68 species) and ottertrawl (next page 64 species) collections during February (stations of species occurrence are given in parenthesis).



BRAY-CURTIS SIMILARITY (RANKED)

Fig. 8 (continued)

tions: *Diplobatis ommata* (31), *Monolene* sp. (31), *Sympodus lei* (31,P), *Promatogrammos eos* (31,N), *Achiurus mazatlanus* (35,E,D,Q), *Citharychthys gilberti* (01, D, E, Q), *Pomadasys nitidus* (35,01), *Diplectrum euryplectrum* (35), *Sympodus melanodus* (35), *Menticirrhus nasus*, *Ophioscion typicus* (10,45), *Narcine brasiliensis*, *Paralonchurus dumerillii*, *Urotrygon chilensis* (01) and *Urotrygon mundus* (45). The shallow water station 43 (10 m) was only sampled during February and provided three new ariid species and several further species only found here.

Few species were restricted to deep water stations in both seasons: *Ophisoma pangina* (G,54), *Neobythites stelliferoides* (G,54), *Pontinus fusarius* (N), *Pronotogrammus multifasciatus* (N,G,52,O). The genera *Porichthys*, *Sympodus*, *Synodus*, *Bollmannia* and *Syacium* contributed with several species to the catches on several stations during both seasons.

An in detail comparison of our collections with those of Bartels *et al.* (1984), Leon (1973), Phillips (1983) or Rojas *et al.* (1994) is difficult as most sampling stations, time of the collections as well as sampling gears used were different. In addition, they did not give biomass per swept area estimates for direct comparison with our data. The latter three authors concentrated their sampling to the shallow upper region of GN, while the first also included the central part of the gulf, but their sampling did not exceed 60 m water depth. Consequently, many of the deeper water species found in this study, namely those mentioned in the above paragraph (and others), were absent in their collections. In addition, our large otter trawl had a higher capturability for larger sized fish which resulted in comparatively higher proportions in the catches of rays, sharks, large congrid and carangids. However, the general findings of the above authors regarding the dominant groups of the upper GN (sciaenids, sea catfishes and flatfishes) and the lower GN (flounders, gobies, morays and congers among others) are confirmed by the present study. In addition, the subdivision of Bartels *et al.* (1983) of the GN based on abiotic factors (dissolved oxygen, temperature, salinity, depth, distance to the ocean), coincides quite well with our subdivision based on the stations similarity based on the station - species matrix. All species that were shared between the first twenty-

ty (in terms of percentage of occurrence) of the three cruises reported by Bartels *et al.* (1983), were also among the first 20 (in terms of production) in our beamtrawl and/or ottertrawl catches. These were: *Synodus scituliceps*, *Prionotus horrens*, *Porichthys* sp., *Cyclopsetta querna*, *Syacium ovale*, *Diplectrum pacificum*, *Sphoeroides furthii*, *Sympodus* sp., *Bollmannia chlamydes*.

Although some species only occurred in the December and February samples and others more frequently at one sampling date, the station groupings derived from the station species-matrix were similar in both seasons. This confirms the statement of Bartels *et al.* (1983), that the position of the "assemblage zones" (station groups in the present study) did not change significantly between seasons indicating stable estuarine configurations from a biological perspective.

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I thank the captain and crew of the RV Victor Hensen for the excellent work done during the two cruise legs of this study. Without the taxonomic knowledge and tireless identification work of William Bussing, Myrna López and Raul Rojas this work would not have been possible. My thanks also to Angelika Dummernuth for her help with the elaboration of the data and preparation of the figures and to three anonymous reviewers whose constructive suggestions helped to improve the manuscript.

RESUMEN

Durante un crucero con el BC Victor Hensen en diciembre 1993 y febrero 1994 la comunidad de peces demersales fue evaluada en las áreas de Golfo de Nicoya (GN), Bahía Coronado - Sierpe-Térraba (ST) y Golfo Dulce (GD) a lo largo de transectos desde aguas sombras (20 m) hasta aguas del borde de la plataforma (200 m). Se tomó 44 muestras con una draga y 29 muestras con una red de arrastre de un área total de 2 119 405 m², recolectando un total de 242 especies de peces. Aunque el número de muestras fue menor para la red de arrastre, se recolectó más especies (195 comparado con 169 de la draga). Las curvas de

especies vs. área muestreada y logarítmica-normal indican que la comunidad de peces fue muestreada y se calculó la riqueza específica teórica (SR) para el área total (306). Los promedios del número de especies y biomasa por muestra fueron muy inferiores para el GD (9.3 especies, 0.36 g/m²) al los de ST (15.4, 0.81) y GN (17.3, 0.74), indicando una comunidad de peces demersales muy empobrecida en el área de GD. Los valores mas bajos del número de especies como también de la biomasa fueron los de la parte central profunda (200 m) del GD, incrementando hacia el área de la entrada ("sill area") y hacia las estaciones someras sobre la termoclina. La biomasa promedio fue un orden de magnitud superior en la parte interior del GN comparado con las otras áreas con valores máximos de 18.1g/m². Con base en los resultados del análisis multivariado de las colecciones, se puede dividir el GN en las siguientes zonas: (1) una zona somera interior (<50 m) caracterizada por esciánidos, bagres, rayas látigo, lenguados, cabros, (2) una zona exterior (>100 m) caracterizada por moras, lapones, gobios, cintas, cabrillas, bocones y lenguados y una zona de transición de las partes centrales y laterales del golfo con una comunidad mezclada de peces con carángidos, chayotes, pargos, algunos lenguados y garrobos como elementos comunes. Muy característico para la parte profunda del GD son las especies pequeñas de *Cynoscion* y *Porichthys*, de los cuales el primero solo apareció aquí. Estas especies aparecieron en densidades muy bajas, indicando una capacidad de carga muy reducida de esta zona para biomasa de peces en cuanto al alimento y oxígeno. Muchas especies características de esta profundidad para otras áreas estuvieron ausentes aquí. Las especies que aparecieron en las estaciones someras del GD también se encontraron en las otras áreas, pero faltan muchas especies, como los bagres y muchas de las corvinas del área de GN. La comunidad de especies en el área de ST se asemeja la del GN, pero los bagres también faltan. Descriptores bióticos para las estaciones tales como biomasa, abundancia, producción y dominancia no se correlacionaron en forma significativa con factores abióticos (temperatura, oxígeno, profundidad) indicando que otros factores del hábitat, que no medidos, tales como heterogeneidad ambiental,

distancia al océano abierto, corrientes y disponibilidad de alimento pueden ser de gran importancia para la estructuración de las comunidades de peces.

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