

Comparative biomass spectra and species composition of the zooplankton communities in Golfo Dulce and Golfo de Nicoya, Pacific coast of Costa Rica

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Abstract: This study is based on a subset of plankton samples obtained during an expedition of the German RV Victor Hensen to the Pacific coast of Costa Rica in 1993/94. It aims at the identification of the main plankton taxa for a general description and comparison of the plankton communities of the gulf systems Golfo de Nicoya (GN) and Golfo Dulce (GD) and the analysis of biomass spectra at inshore and offshore stations at the end of the rainy season and during the dry season. Inshore plankton biomass was significantly higher in GN than GD and exceeded offshore biomass several times, while in the GD area the reverse was found. In the rainy season, inshore biomass spectra of GN and GD were discontinuous with biomass concentrations at small sizes (around 0.06mg) suggesting little developed communities, with highest production and energy use occurring in the small organisms. From the rainy to the dry season inshore species richness increased in both gulf systems and a shift was observed towards the larger size groups resulting in more continuous biomass spectra. In GN, bivalve larvae, foraminifers, ostracods, mysids and nauplii increase heavily in abundance and some gelatinous specimens occur. In GD, gelatinous zooplankton appears in enormous abundance and dominates the community biomass, followed by large chaetognaths and ostracods. In GD, inshore plankton has neritic and oceanic elements and differs less from the offshore plankton, whereas in GN, inshore plankton is largely neritic. The high abundance of fish eggs and invertebrate larvae suggest that this area is an important spawning ground. While in the rainy season inshore biomass was about 15 times higher in GN compared to GD, this difference was reduced to 3-4 times in the dry season due to the appearance of the large predators mentioned above. The changes from the rainy to the dry season at the offshore stations of both gulf systems are less pronounced in terms of total biomass, shape of the biomass spectra and taxonomic composition of the community. The differences - relatively continuous biomass spectra with an increasing slope and a high total biomass in GD versus flat and shorter spectra due to the absence of large chaetognaths and medusa in the GN - suggest that conditions in the former area allow for a better development of a trophodynamically tightly structured plankton community.

Key words: Zooplankton, biomass spectra, Costa Rica.

This study focused on the comparison of the zooplankton communities (>300µm) of the two gulf systems (GN, GD, Fig. 1), which differ in their topography. Golfo de Nicoya is a tectonic estuary extending about 100km from the Tempisque river to the 500m isobath of the Pacific coast. The inner gulf is shallow (<25m) and fringed by mangroves and mud flats. The outer gulf, delimited by the line San Lucas Island-Península de Puntarenas, deepens sharply towards the mouth and is surrounded

by rocky shores and sandy beaches. It is the nation's largest bay (1543 km²), with important semidiurnal tides (mean range 2.5m). The sharp contrast between dry season (December to April, < 50 mm precipitation/month) and rainy season (May to November, 100 to 500 mm/month; Herrera 1985) has a significant impact on riverine flow and water characteristics, as in many other river influenced tropical estuaries.

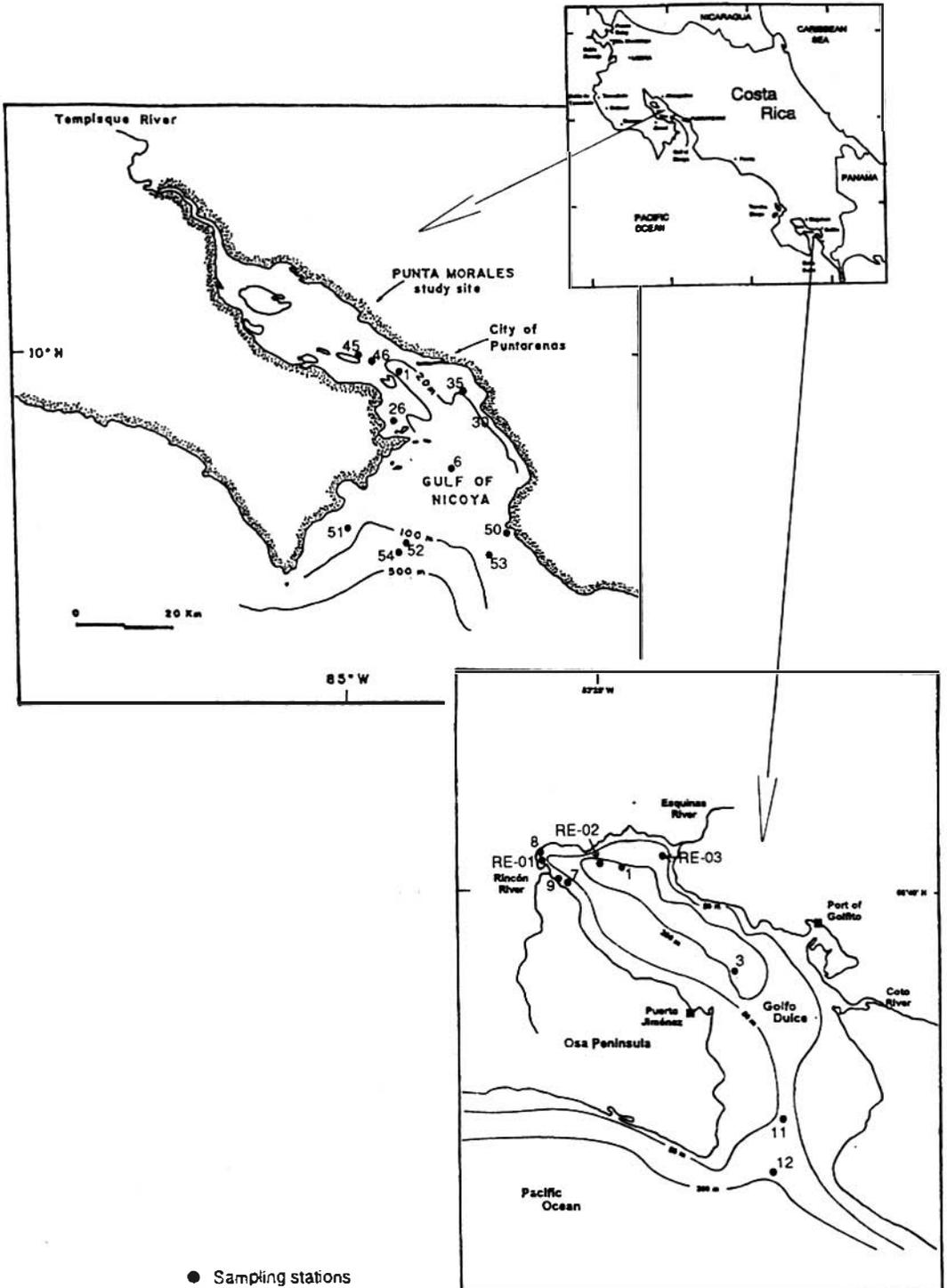


Fig. 1. Study areas: Golfo de Nicoya (GN, upper left) and Golfo Dulce (GD, lower right) with sampling stations.

Nitrogen enters the system year around from offshore subsurface water, similar to processes of partially mixed and saltwedge estuaries in temperate zones. The gulf is Costa Rica's main fishing ground, providing more than 50% of the national landings (Madrigal 1985). For a detailed review on the hydrographical conditions of Golfo de Nicoya see Voorhis (1983) and Vargas (1995).

Golfo Dulce, also of tectonic origin, is smaller (about 50 km long and 10-15 km wide, with a surface area of 750 km²) and of a fjord-like bathymetry (a steeply sloped deep inner basin with a flat bottom and maximum depth of about 215 m and a shallow outer basin with a maximum sill depth of 60 m). Shorelines are dominated by steep, forested rocky slopes to the north and northeast, and to the south. Gentle, largely deforested slopes with sandy beaches prevail to the west (Puerto Jiménez) and east (Coto Colorado river basin). Because most rivers entering are small, and basin slopes are steep, mangroves are less developed than in Golfo de Nicoya (about 200 ha, compared to 15000 ha around Golfo de Nicoya). The catchment basin receives more rain (4000-5000 mm/y, Herrera 1985) than Golfo de Nicoya, and seasonal variations in climate are less pronounced. Because of its topography, and its small catchment basin/volume ratio (catchment basin surface area = 2050 km² excluding the Gulf itself), its water circulation is restricted, resembling that of high-latitude fjords, and it is one of only three such embayments known in the tropics. For further descriptions of Golfo Dulce see Cortés (1990), Richards *et al.* (1971) and Nicols Driscoll (1976).

This paper is based on plankton samples obtained during two cruise legs of the German "Victor Hensen" expedition to the Pacific coast of Costa Rica at the end of the rainy season (2.12.-9.12. 1993) and during the dry season (2.2.-9.2. 1994). Besides the identification of the main taxa for a general description and comparison of the plankton communities of both gulf systems, the main emphasis was laid upon the analysis of the biomass spectra.

This approach is based on the fact that many species characteristics like general metabolism, respiration, specific production (P/B) are a function of the individual body weight and that when composite data for ecosystems are assembled in a way that biomass per unit of

area (B/A) is plotted against individual body weight, a so called "biomass spectrum" is obtained whose shape is a reflection of the structure and energy flow of the system (Boudreau & Dickie 1989, 1991). If the spectrum is flat, each size group contributes the same biomass to the system. If the spectrum has a positive slope, system biomass increases with the size of the organisms. As smaller organisms have a higher specific production rate (P/B) and energy use per unit of body weight, a flat spectrum (or one with a negative slope) would represent a situation in which more system energy is used by the smaller sized organisms and accordingly system production is increased towards the smaller organisms. If the spectrum has a positive slope of about 0.36 the specific production (P/B) remains about constant over the range of body sizes analysed. McNeill & Lawton (1970) and Boudreau & Dickie (1992) also showed that the energy use per unit of area (E/A) remains about constant over the analysed size range of organisms if the slope of the biomass spectrum is about 0.25. Ecological theory predicts that a more developed and trophodynamically tightly structured plankton community should have a continuous biomass spectrum (in which each size group has its functional niche) with a positive slope as a result of larger plankton organisms structuring the community by grazing pressure from above.

With this background and the differences in the topography and water dynamics of both bay systems in mind, the following working hypothesis were elaborated:

(1) The inshore plankton community of GN differs from the offshore community by higher plankton biomass and the dominance of neritic species typical for other tropical river dominated estuaries. Due to the highly dynamic and tidally driven water column, the community can be expected as little developed (loose trophic structure) reflected by a discontinuous biomass spectrum and a dominance of smaller over larger-sized zooplankton organisms. (2) In the GD ecosystem inshore - offshore community differences are less pronounced and more oceanic species predominate. Due to an (almost) year-around stable and strongly stratified water column, the euphotic zone contains a well developed community with a tight trophic structure reflected by a more continuous

biomass spectrum and the dominance of larger over smaller plankton organisms. (3) More pronounced seasonal differences in plankton biomass and composition are to be expected in the GN system due to higher seasonal differences in hydrographic conditions.

MATERIAL AND METHODS

Sampling: Plankton samples were obtained at the end of the rainy season (2.12-9.12. 93) and during the dry season (2.2-9.2. 94). Sample locations followed previous studies of Voorhis *et al.* (1983) for the Gulf of Nicoya, and Richards *et al.* (1971) for Golfo Dulce. The stations selected for the present study are seen in Fig. 1.

At each station, 2 bongo hauls (60 cm net opening, 250 cm net length) were performed with a pair of nets; one set was done with 200 μ m and 300 μ m nets (for the copepods and the plankton community, biomass spectrum and chaetognath analyses, respectively) and the other with 500 μ m and 1000 μ m nets for ichthyoplankton of different size ranges. A "Hydrobios" flowmeter was attached to the mouth of each net.

Oblique hauls were done from the surface to the ground at a towing speed of approx. 1.5 knots. Towing time varied between 5 and 10 min, depending on the water depth. The towing depth (and the required length of wire) was determined by a clinometer.

After each haul, the nets were washed with seawater to concentrate the plankton into the bucket at the cod end of the net. Thereafter, the plankton was washed out of the bucket with seawater into a strainer before it was transferred into a 1L kautex bottle. For fixation, 100 ml of commercial formaldehyde (40%), buffered with borax (2g at 98 ml formaldehyde), was added to the 3/4 filled kautex bottle, which was then filled to the top with sea water to arrive at a concentration of 4% formalin. After three months, the samples were transferred into a preservation solution described in Steedman (1976).

Sample processing: The wet volume of the plankton samples was determined in 1000 ml sedimentation funnels.

For further analysis, samples were divided depending on the total plankton biomass to a maximum of 1/80 of the original sample using a Wiborg divider. Subsamples were sorted into taxonomic groups, specimens were counted and abundance was expressed as individuals per m³ water filtered. For the further sorting procedure, a table with the numbers of each taxa for logarithmic size groups was constructed. Thus, specimens were measured in their longest dimension (using an ocular with a micrometer scale) and put into the corresponding size group of the table. This "length frequency table" was then transformed into a "body weight frequency table" (Tables 1-4) by the following steps: (1) calculation of the average body weight for 10 specimens of each taxon of a certain size group by assuming a geometric form and calculating the corresponding volume (Table 5). By doing so and assuming that the calculated volume (ml) equals wet weight (mg), the individual biomass of each taxon and size group was obtained; (2) calculating the biomass per size group pooled over all taxa for each sample; (3) transforming the data logarithmically for the construction of the biomass spectra; (4) for a better representation of the taxonomic composition of each body size group, the taxa were regrouped into the following broader categories: crustacea, gelatinous forms, annelids, chaetognaths, molluscs, rhizopods, fish, and others.

RESULTS

Table 6 shows seven to tenfold higher inshore biomass of GN compared to the offshore biomass in both seasons. In GD, the reverse holds true in the rainy season, while inshore-offshore biomass differences were small in the dry season. Offshore plankton volumes are higher in the GD than the GN area. For the inshore plankton the reverse is true for both seasons with a four to tenfold higher values in GN.

TABLE 1
Zooplankton biomass distribution over body size groups and main taxa for both seasons at the inshore stations of Golfo Dulce

Station GD-1, 1993	Individual bodyweight (mg)												
	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³
taxonomical groups	0.006	0.02	0.06	0.2	0.6	2	6	20	60	200	600	insg.	Biom./m ³
Others	0.00	0.00	0.00	0.73	0.00	0.73	0.00						
Cladocera	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Brachyura Zoeca	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Euphausiacea	0.00	0.00	0.00	0.04	0.10	0.20	0.00	0.00	0.00	0.00	0.00	0.34	0.00
Cycl. Copepoda	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Ostracoda	0.00	0.02	0.00	0.07	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.35	0.00
Cal. Copepoda	0.00	0.15	4.56	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.80	0.00
Crustacea	0.00	0.18	4.57	0.21	0.10	0.45	0.00	0.00	0.00	0.00	0.00	5.52	0.00
Gelatininos formes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pteropoda	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00
Mollusca	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00
Fish eggs	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
Fish	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
Polychaeta	0.00	0.00	0.12	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.00
Annelida	0.00	0.00	0.12	0.21	0.00	0.34	0.00						
Rhizopoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chaetognatha	0.00	0.00	0.00	0.46	0.00	1.53	1.21	0.00	0.00	0.00	0.00	3.19	0.00
Chaetognatha	0.00	0.00	0.00	0.46	0.00	1.53	1.21	0.00	0.00	0.00	0.00	3.19	0.00
Sum	0.00	0.19	4.70	1.63	0.13	1.98	1.21	0.00	0.00	0.00	0.00	9.83	0.00

continued table 1

Station RE-002, 1994	Individual bodyweight (mg)												
	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³
taxonomical groups	0,006	0,012	0,06	0,2	0,6	2	6	20	60	200	600	insg.	
Others	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Brachiuren Zoen	0,00	0,00	0,00	0,00	0,00	0,31	0,00	0,00	0,00	0,00	0,00	0,31	
Ostracoden	0,07	0,85	0,00	11,40	0,00	0,00	0,00	0,00	0,00	0,00	0,00	12,32	
Calanoide Copepoden	0,00	0,75	1,31	1,59	0,00	0,00	0,00	0,00	0,00	0,00	0,00	3,65	
Euphausiaceen	0,00	0,00	0,00	0,00	0,01	0,36	0,00	0,00	0,00	0,00	0,00	0,37	
Cyclopoide Copepoden	0,00	0,00	0,20	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,20	
Dekapoden	0,00	0,00	0,01	0,01	0,05	0,00	0,00	0,00	0,00	0,00	0,00	0,08	
Crustacea	0,07	1,59	1,52	13,01	0,06	0,67	0,00	0,00	0,00	0,00	0,00	16,92	
Medusa	0,00	0,00	0,00	0,00	0,00	0,03	0,11	0,00	0,00	38,38	53,30	91,82	
Siphonophora	0,00	0,00	0,00	0,00	0,00	0,00	0,20	0,00	0,00	0,00	0,00	0,20	
Hemichordata	0,00	0,00	0,00	0,01	0,03	0,03	0,32	0,00	0,00	0,00	0,00	0,05	
Salps	0,00	0,00	0,00	0,03	0,32	0,00	0,00	0,00	0,00	0,00	0,00	0,35	
Gelatinuos formes	0,00	0,00	0,00	0,04	0,35	0,06	0,62	0,00	0,00	38,38	53,30	92,42	
Cephalopoda	0,00	0,00	0,00	0,00	0,02	0,00	0,00	0,59	0,00	0,00	0,00	0,61	
Pteropoda	0,00	0,01	0,05	0,45	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,51	
other Gastropods	0,00	0,00	0,03	0,00	0,23	0,00	0,00	0,00	0,00	0,00	0,00	0,26	
Mollusca	0,00	0,01	0,08	0,45	0,25	0,00	0,00	0,59	0,00	0,00	0,00	1,37	
Fish larvae	0,00	0,00	0,00	0,00	0,02	0,15	0,00	0,85	0,00	0,00	0,00	1,02	
Fish	0,00	0,00	0,00	0,00	0,02	0,15	0,00	0,85	0,00	0,00	0,00	1,02	
Annelida	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	
Foraminifera	0,00	0,01	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,01	
Rhizopoda	0,00	0,01	0,00	0,01									
Chaetognatha	0,00	0,00	0,00	0,00	0,00	1,07	2,86	5,66	0,00	0,00	0,00	9,60	
Sum	0,07	1,62	1,60	13,47	0,37	1,96	3,48	7,10	0,00	38,38	53,30	121,34	

TABLE 2

Zooplankton biomass distribution over body size groups and main taxa for both seasons at the offshore stations of Golfo Dulce

Statione GD-12,1993 taxonomical groups	Individual bodyweight (mg)											
	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³
	0.006	0.02	0.06	0.2	0.6	2	6	20	60	200	600	insg.
Others	0,00	0,00	0,05	0,07	0,00	0,84	0,00	0,00	0,00	0,00	0,00	0,95
Nauplien	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Cladocera	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Amphipoda	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
Brachiura Zoea	0.00	0.00	0.00	0.15	0.12	0.43	0.00	0.00	0.00	0.00	0.00	0.70
Dekapoda	0.00	0.00	0.02	0.06	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.32
Euphausiacea	0.00	0.03	0.03	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13
Cycl. Copepoda	0.00	0.00	0.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.45
Ostracoda	0.12	0.10	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.48
Cal. Copepoda	0.00	1.57	0.59	0.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.02
Crustacea	0,12	1,70	1,15	1,52	0,35	0,43	0,00	0,00	0,00	0,00	0,00	5,28
Siphonophora	0.00	0.00	0.00	0.00	0.27	0.70	0.00	0.00	0.00	0.00	0.00	0.97
Appendicularia	0.00	0.11	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22
Salps	0.00	0.00	0.00	0.03	0.26	0.23	0.74	0.00	0.00	0.00	0.00	1.26
Celantinos formes	0,00	0,11	0,11	0,03	0,53	0,93	0,74	0,00	0,00	0,00	0,00	2,45
Pteropoda	0.00	0.00	0.07	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16
other Gastropods	0.00	0.00	0.04	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.28
Bivalvia	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Mollusca	0.00	0.02	0.10	0.09	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.46
Fish eggs	0.00	0.00	0.00	0.05	2.43	0.00	0.00	0.00	0.00	0.00	0.00	2.48
Fish larvae	0.00	0.00	0.05	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
Fish	0,00	0,00	0,05	0,11	2,43	0,00	0,00	0,00	0,00	0,00	0,00	2,59
Polychaeta	0.00	0.00	0.05	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12
Annelida	0,00	0,00	0,05	0,07	0,00	0,12						
Radiolaria	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.19
Foraminifera	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Rhizopoda	0,00	0,05	0,00	0,00	0,19	0,00	0,00	0,00	0,00	0,00	0,00	0,24
Chaetognatha	0,00	0,00	0,00	0,88	0,00	5,91	23,53	9,97	0,00	0,00	0,00	40,29
Sum	0.13	1.88	1.50	2.77	3.75	8.10	24.27	9.97	0.00	0.00	0.00	52.38

continued table 3

Station GN-46, 1994	Individual bodyweight (mg)												
	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³
taxonomical groups	0.006	0.02	0.06	0.2	0.6	2	6	20	60	200	600	Biom./m ³	Biom./m ³
Others	0.00	0.00	0.30	2.65	0.00	6.62	0.00	0.00	0.00	0.00	0.00	0.00	9.57
Nauplien	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Stomatopoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28.69	0.00	0.00	0.00	28.69
Cladocera	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07
Cirripedia	0.14	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.47
Brachiura Zoea	0.00	0.18	0.00	3.58	25.20	38.02	0.00	0.00	0.00	0.00	0.00	0.00	66.97
Dekapoda	0.00	0.00	0.88	0.76	4.63	5.74	0.00	0.00	0.00	0.00	0.00	0.00	12.02
Euphausiacea	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Cycl. Copepoda	0.00	0.01	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
Ostracoda	0.00	0.03	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16
Cal. Copepoda	0.00	2.73	70.76	2.99	1.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	78.32
Crustacea	0.16	3.03	72.06	7.46	31.67	43.76	0.00	0.00	28.69	0.00	0.00	0.00	186.83
Ctenophora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.07	0.00	0.00	0.00	0.00	8.07
Medusa	0.00	0.00	0.13	1.39	0.00	0.55	0.00	0.00	0.00	0.00	0.00	0.00	2.07
Gelatinuos formes	0.00	0.00	0.13	1.39	0.00	0.55	0.00	8.07	0.00	0.00	0.00	0.00	10.14
other Gastropods	0.00	0.05	0.64	0.00	1.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.21
Bivalvia	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07
Mollusca	0.00	0.12	0.64	0.00	1.52	0.00	2.29						
Fish eggs	0.00	0.02	0.00	2.65	31.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	33.66
Fish larvae	0.00	0.00	0.41	0.84	1.31	5.20	0.00	0.00	0.00	0.00	0.00	0.00	7.77
Fish	0.00	0.02	0.41	3.48	32.31	5.20	0.00	0.00	0.00	0.00	0.00	0.00	41.43
Polychaeta	0.00	0.03	1.06	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.34
Annelida	0.00	0.03	1.06	0.25	0.00	1.34							
Radiolaria	0.00	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23
Rhizopoda	0.00	0.00	0.00	0.00	0.23	0.00	0.23						
Chaetognatha	0.00	0.00	0.00	12.98	0.00	88.15	0.00	0.00	0.00	0.00	0.00	0.00	183.10
Sum	0.17	3.20	74.60	28.20	65.73	144.28	81.98	8.07	28.69	0.00	0.00	0.00	434.92

Station GN-54, 1994	Individual bodyweight (mg)											
	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³	Biom./m ³
taxonomical groups	0.006	0.02	0.06	0.2	0.6	2	6	20	60	200	600	insg.
Others	0,00	0,00	0,07	0,91	0,00	3,12	0,00	0,00	0,00	0,00	0,00	4,10
Harp. Copepoda	0.00	0.00	0.02	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07
Isopoda	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Nauplien	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Cladocera	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Cirripedia	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
Brachiura Zoea	0.00	0.00	0.00	0.14	0.52	0.00	0.00	0.00	0.00	0.00	0.00	0.66
Dekapoda	0.00	0.00	0.04	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.45
E phasiacea	0.00	0.02	0.22	0.06	0.00	0.84	0.00	0.00	0.00	0.00	0.00	1.14
Cycl. Copepoda	0.00	0.02	0.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
Ostracoda	0.01	0.06	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Cal. Copepoda	0.00	0.56	7.74	7.23	5.61	2.13	9.15	0.00	0.00	0.00	0.00	32.42
Crustacea	0.12	0.67	8.68	7.97	6.12	0.00	9.15	0.00	0.00	0.00	0.00	32.72
Medusa	0.00	0.00	0.00	0.00	0.00	0.34	2.28	0.00	0.00	0.00	0.00	2.61
Appendicularia	0.00	0.06	0.12	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41
Salps	0.00	0.00	0.00	0.10	0.13	0.34	0.00	0.00	0.00	0.00	0.00	0.57
Gelatinous formes	0.00	0.06	0.12	0.33	0.13	0.00	2.28	0.00	0.00	0.00	0.00	2.92
Pteropoda	0.00	0.00	0.02	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16
other Gastropods	0.00	0.01	0.21	0.00	0.74	0.00	0.00	0.00	0.00	0.00	0.00	0.96
Mollusca	0.00	0.01	0.23	0.14	0.74	0.00	0.00	0.00	0.00	0.00	0.00	1.13
Fish larvae	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Fish	0.00	0.00	0.00	0.05	0.00	0.05						
Polychaeta	0.00	0.00	0.05	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.16
Annelida	0.00	0.00	0.05	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.16
Radiolaria	0.00	0.00	0.00	0.11	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.26
Foraminifera	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Rhizopoda	0.00	0.03	0.00	0.11	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.29
Chaetognatha	0.00	0.00	0.00	0.95	0.00	4.23	8.35	7.43	0.00	0.00	0.00	20.97
Sum	0.12	0.77	9.15	10.46	7.26	10.99	19.79	7.43	0.00	0.00	0.00	66.50

TABLE 5
Biomass estimates for each taxon and size group (geometrical formulas and calculation are given in the lower part of the table)

taxonomical groups	geometrical forms	1	2	3	4	5	6	7	8	9	10
Others	ball	<400(µm)	<630(µm)	<1000(µm)	<1600(µm)	<2500(µm)	<4000(µm)	<6300(µm)	<10000(µm)	<16000(µm)	<25000(µm)
harp. Copepoda	spherical segment	0.0715	0.1966	0.6058	1.915	6.654	21.089	66.607	203.4	630.1	1966.0
Isopoda	rotation ellipsoid / 2	0.0018	0.0018	0.0018	0.0018	0.0018	0.0018	0.0018	0.0018	0.0018	0.0018
Ctenophora	spherical segment		0.405	0.405	0.405	0.405	0.405	0.405	0.405	0.405	0.405
Cephalopoda	2*rotation ellipsoid / 2		0.0433	0.0433	0.0433	0.0433	0.0433	0.0433	0.0433	0.0433	0.0433
Nauplien	spherical segment										
Stomatopoda	ashlar (head)+circle cylinder (Thorax)+ashlar (tail)										
Myxidacea	cone (top)+triangle*height (tail)										
Fish eggs	ball or stretch rotation ellipsoid	0.018	0.0715	0.284	0.0763	0.0738	0.0738	0.615	3.2044	11.250	34.11
Cladocera	rotation ellipsoid		0.0158	0.0498	0.258	1700=0.32					
Amphipoda	spherical segment			0.0156	0.528	1.426					
Polychaeta	circle cylinder	0.003	0.0157	0.0327	0.087	0.1001	0.2297				
Siponophora	tetraheder or cone		0.0064	0.0259	1.015	4.046					
Cirripedia	ball section	0.005	0.0373	0.0597	0.0328	0.0906	0.3902	1.1404	1.953	8.6605	
Fish larvae	pyramid (top)+triangle (tail)		0.0464	0.1183	0.238	0.615					
Hemichordata	ashlar		0.0516	0.1831	0.6538	2.2152	112.03	544.54			
Mollusca	ball sector		0.111	0.277	0.696	1.434					
Radiolaria	ball		0.0325	0.0526	0.1301	1.434					
Pteropoda	cone		0.0173	0.0185	0.0257	0.1484					
Appendicularia	stretch rotation ellipsoid (top)+ashlar (tail)			0.096	0.251	0.666	2.149	13.138	63.805		
Salpa	circle cylinder			0.00339							
Foraminifera	flat rotation ellipsoid	0.013	0.0138	0.00339							
Brachyura Zoae	barrel (top)+circle cylinder (tail)	0.016	0.0886	0.3367	1.2556	4.676					
Other Gastropoda	flat rotation ellipsoid	0.012	0.0509	0.2145	0.5088	4.676					
Delapoda	cone (top)+triangle*height (tail)	0.003	0.014	0.0314	0.0383	0.0905	0.2399	0.4482	1.366		
Euphausiacea	cone		0.008	0.0255	0.0532	1.098	0.2574	0.8174			
Cycl. Copepoda	2* truncated cone (top)+circle cylinder (tail)	0.008	0.0221	0.0594							
Bivalvia	ball sector*2	0.003	0.0072								
Chaetognatha	rotation ellipsoid (head)+barrel (Thorax)+cone (end of the Thorax)		0.0036	0.0146	0.0747	0.157	0.157	0.685	3.249	14.456	
Ostracoda	ball sector*2		0.0035	0.018	0.151	0.677					
Cal. Copepoda	rotation ellipsoid (top)+ circle cylinder (tail)		0.0126	0.0519	0.178	0.436	0.828	4.45			

formulas for the volume of the geometrical forms:
cone: $\pi r^2 h / 3$
ball: $4/3 \pi r^3$
flat rotation ellipsoid: $4/3 \pi a^2 b$
circle cylinder: $\pi r^2 h$
ball sector: $\pi b/6 (3 R^2 + h^2)$
stretch rotation ellipsoid: $4/3 \pi a^2 b^2$
tetraheder: $1/3 G * h$
barrel: $\pi h / 15 (2D^2 + Dd + d^2)$
truncated cone: $\pi h / 3 (R^2 + Rr + r^2)$

TABLE 6

Inshore and offshore plankton biomass in GD and GN for both seasons (mg/m³)

seasons	Golfo de Nicoya		Golfo Dulce	
	interior part	exterior part	interior part	exterior part
rainy season	156,1	14,1	9,8	52,8
dry season	425,4	62,3	121,3	101,9
average	290,7	38,2	65,6	77,2

Fig. 2 (a,b) show the biomass spectra of the pooled samples of GD and GN respectively during the rainy season (December 1993). It is clearly shown that (1) the biomass spectrum is more continuous in the GD area and (2) larger organisms dominate in the former and smaller in the latter gulf. Fig. 2 (c,d) give the corresponding inshore and offshore spectra of both gulf systems during the same period. In both systems the offshore biomass spectra are more continuous and smaller and larger organisms tend to dominate the inshore and offshore spectra respectively. This is also confirmed by Fig. 3 (a-d) showing the taxonomic composition of the body size groups: inshore, the largest size groups are those of 6 mg and 2 mg for GD and GN respectively, while offshore those of 20mg and 6mg respectively. Taxonomic groups corresponding to the different size groups also differ between the two gulf systems which is pronounced for the groups >0.06mg (see also Table 1-4).

While below this size copepods dominate in both gulf systems, the larger groups of the GN are dominated by meroplanktonic molluscs and fish larvae, whereas in the GD these are of little contribution to the overall biomass. Offshore, the taxonomic composition seems more similar between the two areas with chaetognaths and fish larvae dominating the larger, and an increasing proportion of smaller copepods the smaller size classes (Table 1-4).

If the situation for the rainy season is compared to that of the dry season (Fig. 4(a-d) and 5(a-d), Table 1-4), the following can be stated: (1) the general shapes of the biomass spectra for the pooled samples and for the inshore and offshore samples are similar between both gulf systems in both seasons, but the spectra are elevated in the dry season, reflecting a general higher biomass in most of the size groups in February; (2) all biomass spectra in the dry season contain additional size groups of larger organisms; (3) the prevalence of biomass in the small size groups in the GN samples of the rainy season is attenuated in the dry season, when the spectra are more continuous; (4) taxonomic composition differs between both seasons in both systems, the most pronounced differences being: at the inshore and offshore stations of GD high amounts of gelatinous groups (siphonophores and salps) dominate the largest size groups (200mg, 600mg), while these are absent in the GN area; ostracods and brachyuran zoea appear as major components of the crustacea inshore of GD in the dry season (Table 1-4); mollusc larvae, almost absent in the rainy season, also appear here during the dry season; offshore, stomatopod larvae, ostracods and siphonophores also increased their biomass significantly from the rainy to the dry season in GD; cirripeds, brachyuran zoea and bivalve larvae increased their biomass manifold inshore of GN from the rainy to the dry season;

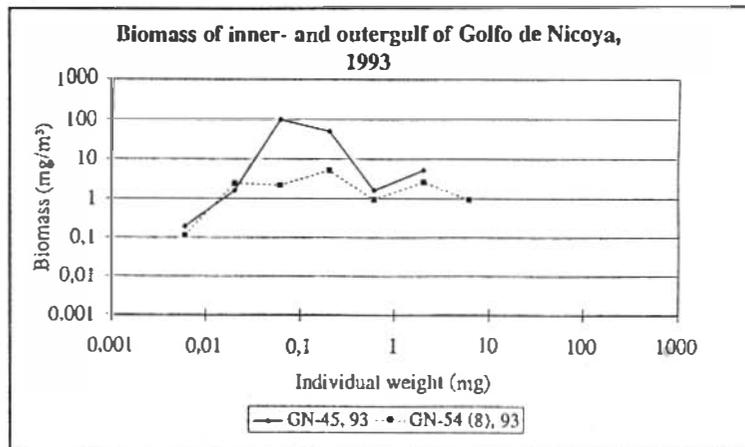
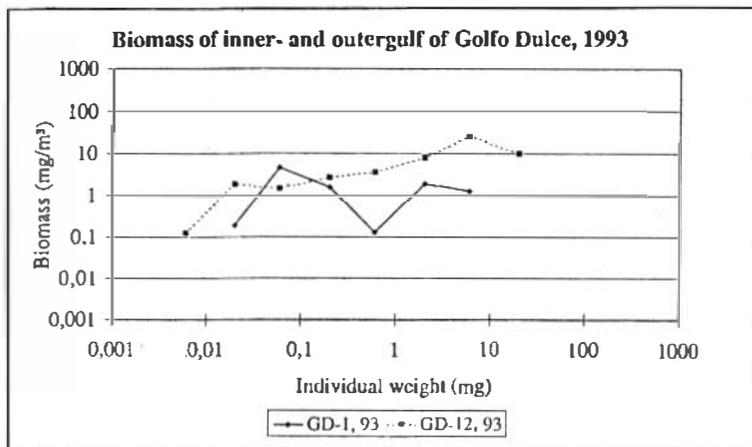
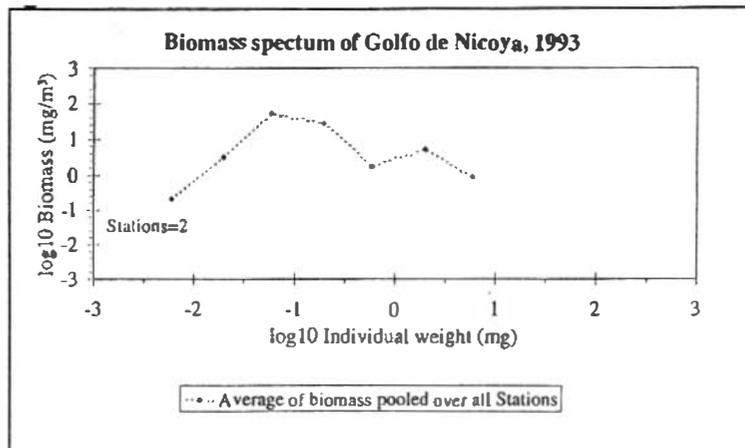
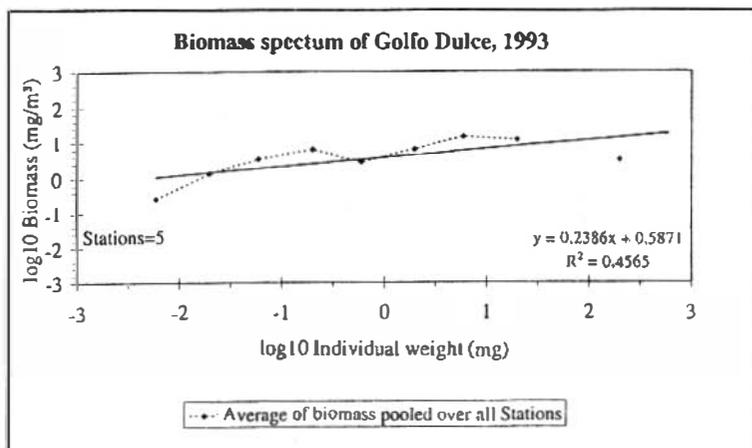


Fig. 2. Biomass spectra of GD and GN in the rainy season (Dec. 1993). a,b. biomass spectra pooled over all stations; c,d. biomass spectra separated for inshore and offshore samples.

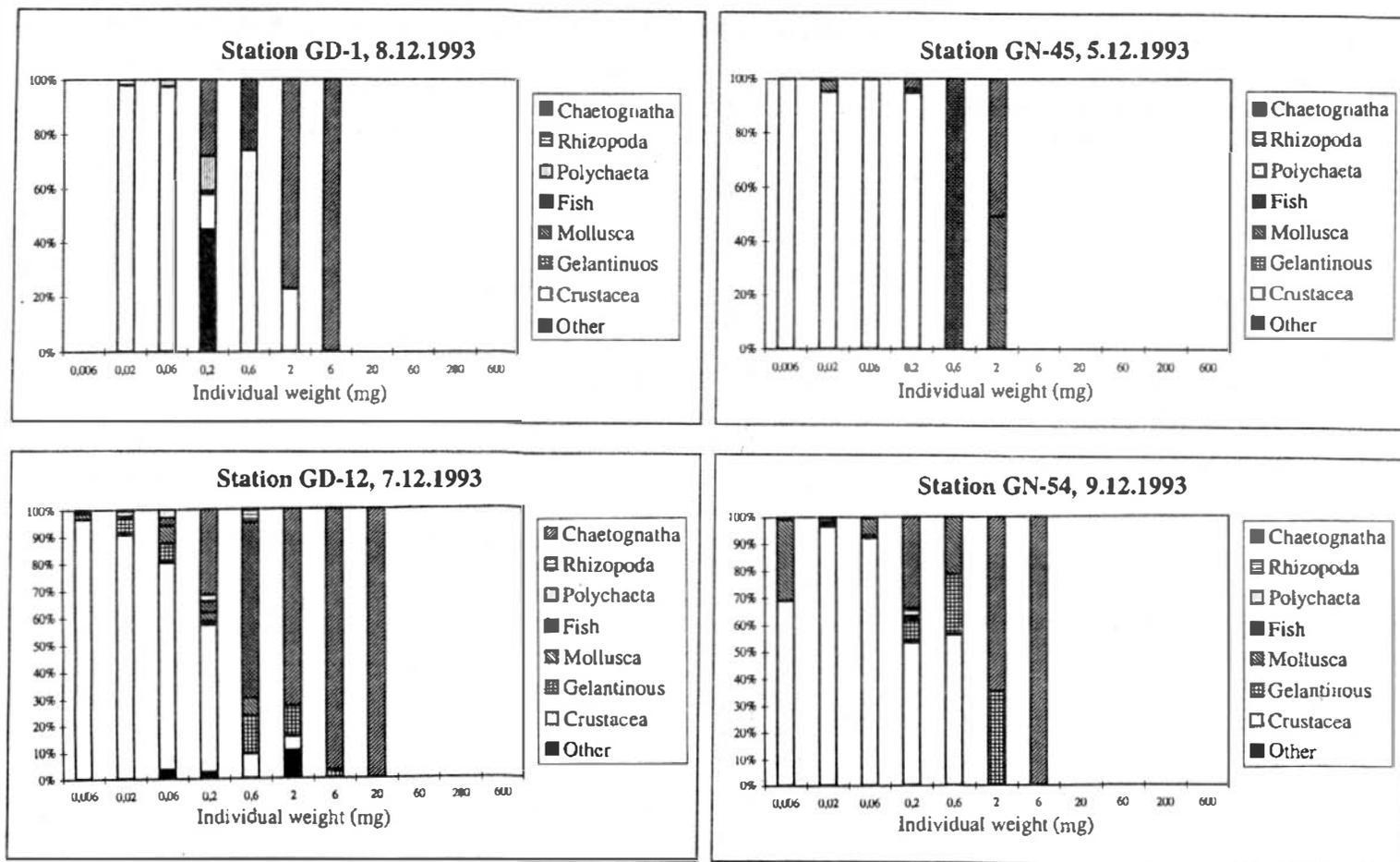


Fig. 3. Taxonomic composition of biomass size groups in the rainy season (Dec. 1993) of GD and GN. a,b for the inshore stations c,d offshore stations.

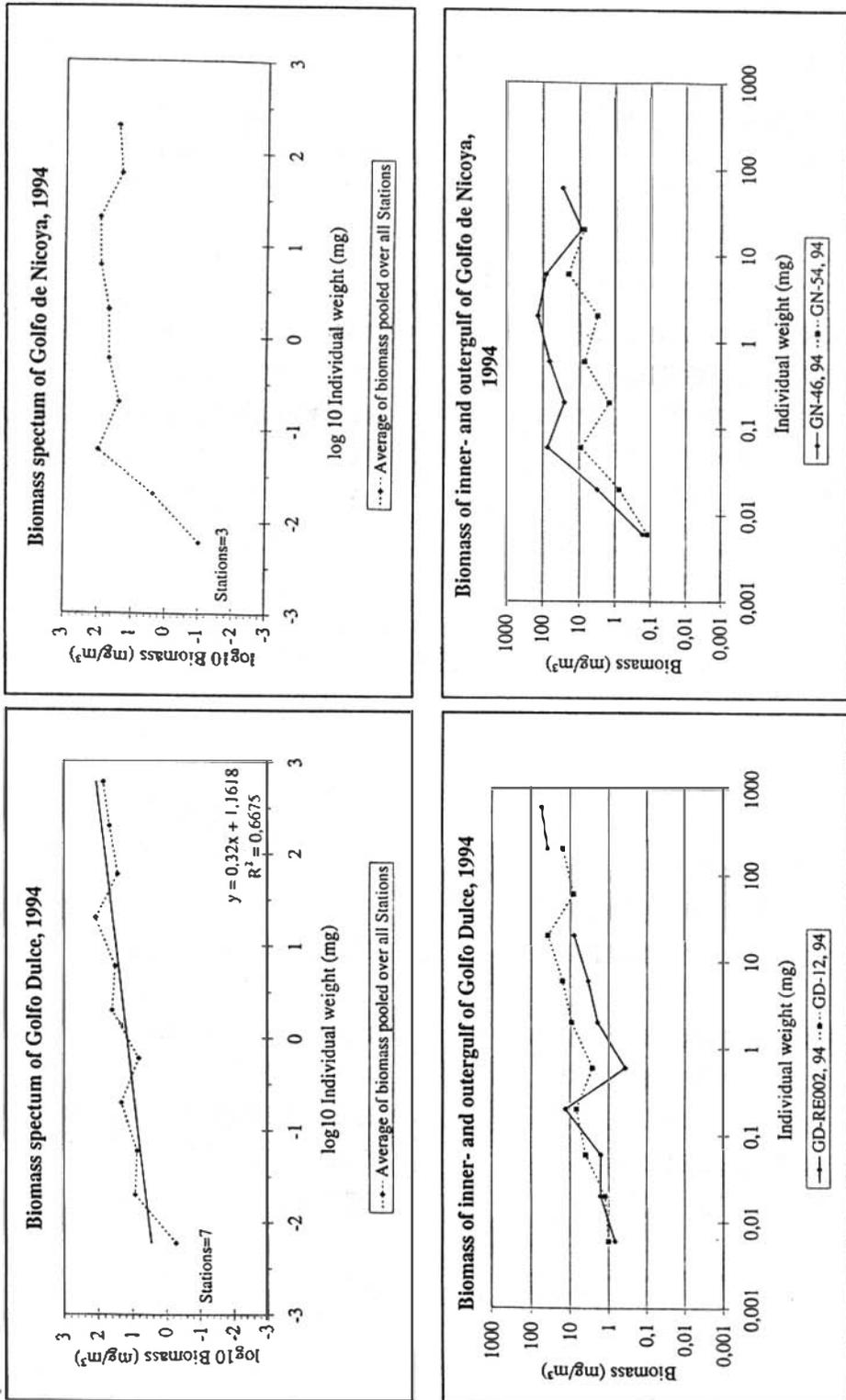


Fig. 4. Biomass spectra of GD and GN in the dry season (Feb. 1994). a,b. biomass spectra pooled over all stations ; c,d. biomass spectra separated for inshore and offshore stations.

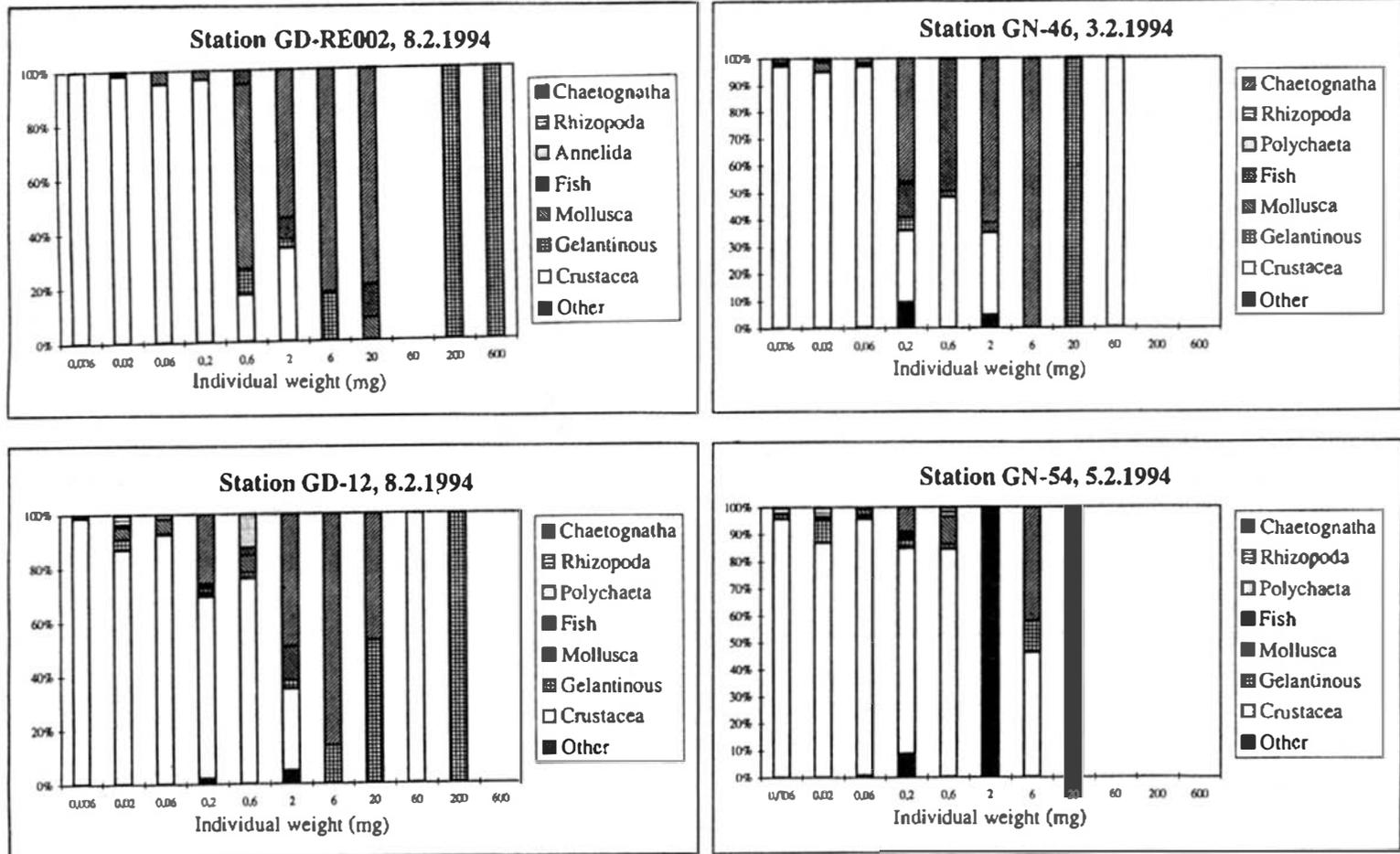


Fig. 5. Taxonomic composition of biomass size groups in the dry season (Feb. 1994) of GD and GN. a,b inshore stations; c,d offshore stations.

DISCUSSION

The results of our study confirm our working hypothesis for most parts. As expected, inshore plankton biomass of GN was several times higher than offshore. The discontinuous biomass spectrum of the December samples with most biomass distributed over the small sizes (around 0.06mg) reflects a little developed community, with highest production and energy use occurring in the small organisms. The dominance of small calanoid copepods as well as the high abundance of fish eggs, molluscs and zoea larvae point to this neritic area as an important spawning ground for fish and invertebrates.

In December, inshore plankton of GD shows neritic and oceanic characteristics. Small calanoid copepods and some polychaete larvae (0.06mg) dominate the spectrum, similar to the situation in GN. Another biomass concentration at 2mg and 6mg corresponds mostly to small chaetognaths and some ostracods, possibly the main predators of the first group. This also seems similar to the situation in GN. The general low inshore biomass, however, and the occurrence of oceanic euphausiids indicates the oceanic influence in this part of the gulf.

The inshore situation changes from December to February in both gulf systems: total biomass increases significantly, the biomass spectra get wider and more continuous, larger organisms tend to dominate, and species richness increases remarkably in both areas. In GN, bivalve larvae, foraminifers, ostracods, mysids and nauplii increase heavily in abundance and some gelatinous specimens occur. In GD, medusa appear in enormous abundances and dominate the community biomass, followed by large chaetognaths and ostracods. While total biomass was about 15 times higher in GN compared to GD in December, this difference was reduced to 3-4 times in February due to the appearance of the large predators mentioned above. Thus the more continuous and wider inshore biomass spectrum and its similarity with the offshore spectrum (Fig.4c) points to a more developed and more uniform zooplankton community in GD compared to GN in February, which is nicely shown by the combined biomass spectra of the samples (Fig.4a). The slope of the regression line (0.32) suggests that all size groups of the spectrum

contribute about equally to the production of the community, while energy use increases with the size of the organisms, reflecting a more predator controlled community.

The changes from December to February in the offshore plankton of both gulf systems are less pronounced in terms of total biomass (Table 6), shape of the biomass spectra and taxonomic composition. The differences between the offshore stations of both gulf systems—a relatively continuous biomass spectrum with an increasing slope and a high total biomass in GD, and flat and shorter spectra due to the absence of large chaetognaths and medusa in the GN—suggest that conditions in the former area allow for a better development of a trophodynamically tightly structured plankton community. It is interesting that demersal biomass was also found to be higher in this area (Wolff & Vargas, 1994) and that squat lobsters (*Pleuroncodes monodon*) dominated the invertebrate biomass (Jesse 1996). These detritus feeders are known for Pacific shelf edge communities over soft bottoms of high organic content influenced by upwelling processes (Longhurst, 1968, Wolff & Aroca, 1995). One might thus speculate, that upwelling processes in this area favour (at least in certain times of the year) the pelagic and benthic subsystems in the offshore area of GD.

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RESUMEN

Se estudió submuestras del plancton recolectado durante la expedición del barco Victor Hensen al Pacífico costarricense en 1993/94 para comparar las comunidades planctónicas del Golfo de Nicoya (GN) y el Golfo Dulce (GD). Se analizó espectros biomásicos en estaciones costeras y de mar adentro al final de la estación lluviosa y durante la seca. La biomasa de plancton costero fue significativa-

mente mayor en el GN que en el GD y superó en mucho a la biomasa de mar adentro; en el GD ocurrió lo contrario. En la estación lluviosa los espectros biomásicos costeros de ambos golfos mostraron discontinuidad con las concentraciones de biomasa en los tamaños pequeños (aproximadamente 0.06 mg) lo que sugiere que las comunidades están poco desarrolladas y que la mayor producción y uso de energía se dan en los organismos pequeños. De la estación lluviosa a la seca la riqueza de especies costeras aumentó en ambos golfos y hubo un cambio hacia los grupos más grandes, produciéndose un espectro biomásico más continuo. En el GN las larvas de bivalvo, foraminíferos, ostrácodos, mísidos y nauplios aumentan mucho en abundancia y aparecen algunos especímenes gelatinosos. En el GD el zooplankton gelatinoso es muy abundante y domina la biomasa comunitaria, seguido por quetognatos grandes y ostrácodos. En el GD el zooplankton costero tiene elementos neríticos y oceánicos y difiere menos del plancton de mar adentro, mientras que en el GN el plancton costero es fundamentalmente nerítico. La gran abundancia de huevos de pez e invertebrados larvales sugiere que el área tiene importancia reproductiva. Mientras que en la estación lluviosa la biomasa costera fue unas 15 veces mayor en el GN que en el GD, esta diferencia se redujo a 3-4 veces en la seca debido a la aparición de los grandes depredadores mencionados. Los cambios de la estación lluviosa a la seca en las estaciones de mar adentro en ambos golfos es menos pronunciada en biomasa total, forma de los espectros biomásicos y composición taxonómica de la comunidad. Las diferencias (espectros biomásicos relativamente continuos con una pendiente creciente y una alta biomasa total en el GD, contra espectros más aplanados y cortos debidos a la ausencia de grandes quetognatos y medusas en el GN) sugiere que las condiciones en el primero permiten un desarrollo mejor de una comunidad planctónica que es trofodinámicamente compacta.

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