Rev. Biol. Trop., 44, Suppl. 3: 157-172, 1996

Distribution and biomass of arrow worms (Chaetognatha) in Golfo de Nicoya and Golfo Dulce, Costa Rica

Britta Hossfeld
Center for Tropical Marine Ecology (ZMT), Fahrenheitstrasse 1, 28359 Bremen, Germany.

(Rec. 22-VIII-1995 - Rev. 2-I-1996 - Acep. 22-IV-1996)

Abstract: The chaetognath species guild was analyzed from samples collected during the cruise of the German RV Victor Hensen to the Pacific coast of Costa Rica in December 1993 and February 1994, finding the following ten species of the genera *Sagitta* and *Krohnitta: S.enflata, S. hexaptera, S. pacifica, S. neglecta, S. regularis, S. bedoti, S. friderici, S. popovicii, S. pulchra* and *K. pacifica*. Because of their distributional patterns in the study area these species were ascribed to the following ecological groups: neritic, semi-neritic and oceanic. A strong gradient in species richness from offshore to inshore waters (8 to one respectively) was found in both gulf systems. Inshore chaetognaths were dominated by juveniles and adults of *S. friderici* in Golfo de Nicoya and by *S. popovicii* in Golfo Dulce. Biomass spectra were more continuous and of wider range in the Golfo Dulce area showing a dominance of larger chaetognaths, suggesting a more general developed pelagic system in Golfo Dulce, where larger chaetognaths might structure the plankton community by strong grazing pressure from above.

Key words: Pacific, Arrow worms, Chaetognatha, *Sagitta, Krohnitta*, distribution, biomass, gulf system, Costa Rica.

In the last decades several authors have pointed out the importance of chaetognaths in the zooplankton community. Reeve (1970) suggested, that they "must form a very significant intermediate link in the food chain, whereby the majority of energy converted into animal material by copepods must be distributed to higher trophic levels via chaetognaths". Chaetognaths are considered to represent 5-15% of the zooplankton and 10-30% of the copepods in the world oceans (Bone *et al.* 1991). Because of their occurrence in every marine habitat and their potential predation pressure on copepods, chaetognaths are probably an important factor in the structuring of most plankton communities (Pearre 1980).

In the Eastern Tropical Pacific Ocean, chaetognaths have been studied by Sund and Renner (1959), Sund (1961a), Alvariño (1972) and Segura *et al.* (1992), but little attention has been given to their role within zooplankton communities in estuarine environments. Estuaries, characterized by low salinity and tidally mixed water masses belong to the most productive marine ecosystems. They play an important role as nursery areas and spawning grounds for coastal fish and invertebrates, whose eggs and larval stages are found in the meroplankton. The meroplankton density in these waters can be considerable, but generally, holoplanktonic organisms, especially copepods still dominate these waters.

In this study, the chaetognath species guilds of the two gulf systems, Golfo de Nicoya and Golfo Dulce, are compared. Whereas the former is a relatively shallow, tidally driven system with estuarine character and a high water exchange rate, the latter is a deep fjord-like basin with partially anoxic conditions near the bottom and a low water exchange rate (for further description of the two gulf systems see Wolff and Vargas 1994). Because of these differences, it was expected that the plankton communities as a whole, and the chaetognath species guild as a top predatory component, would differ significantly between the two gulf systems. The present study aims at (1) the analysis of the species composition of chaetognaths in both gulf systems, with regard to their distribution, abundance and biomass at inshore and offshore stations and at two seasons (December 1993/February 1994) and (2) an analysis of the chaetognath biomass spectra, to see if their ranges and shapes (i.e. the relative contribution of different size groups of chaetognaths) differ between the two gulf systems and seasons. It is hypothesized that Golfo Dulce due to its great depth and stable euphotic layer, has a more developed and trophodynamically more tightly structured zooplankton community than the highly dynamic Golfo de Nicoya, which should be reflected in a more continuous biomass spectrum and the dominance of larger sized over smaller sized plankton organisms. This general pattern is expected also to hold for the chaetognath species guild.

MATERIAL AND METHODS

Sampling strategy: During a research cruise with the RV Victor Hensen to the Pacific coast of Costa Rica in 1993/1994, zooplankton surveys were conducted during two weekly periods in Golfo de Nicoya and Golfo Dulce. The first period took place at the end of the rainy season in December, 2-9 (1993) and the second during the dry season in February, 2-9 (1994). The station locations followed previous studies of Voorhis *et al.* (1983) for the Golfo de Nicoya, and Richards *et al.* (1971) for Golfo Dulce.

A total of 43 zooplankton samples was collected with a Bongo net (60 cm net diameter, 250 cm net length) of 300µm mesh size. For this study, eleven samples were selected in representation for the inshore, central and offshore areas of the two gulf systems in both seasons. The station locations are shown in Fig. 1. Oceanographical data were recorded by a conductivity-temperature-density sensor (CTD). (Table 1)

Oblique plankton hauls were done from the surface to 5m off the ground, as calculated by wire length and angle. Towing time varied between 5 and 10 minutes, depending on depth, at approximately 1.5 knots. The water volume filtered through the net was measured for each haul with a 'Hydrobios' flowmeter, which was attached to the mouth of the net.

Treatment of samples: The samples were immediately fixed on board with a 4% formaldehyde solution, buffered with borax (2g at 98 ml commercial formaldehyde). After three months, they were transferred into a preservation solution as described in Steedman (1976).

The settled plankton volume was measured in 1000-ml sedimentation funnels, after a minimum settling time of 3 hours. Due to the high plankton volume, the samples were split using a Folsom-splitter, to obtain aliquots of 1/8 to 1/32 for further analysis.

All chaetognaths were removed from the aliquots and the numbers of chaetognaths were expressed as individuals per cubic meter.

Taxonomic identification: Juvenile chaetognaths were counted but not identified to species level.

The premature (showing developing reproductive organs) and mature chaetognaths were sorted and species specific features, such as length/maturity, length of ovaries, form of seminal vesicle, number of teeth and hooks, form of the eye-pigments and presence or absence of gut diverticle were analyzed under a microscope (Zeiss-Axioscop). Species were identified referring to descriptions and illustrations of papers on the taxonomy of chaetognaths (Alvariño 1963, 1967, 1969, Pathansali 1974, Pierrot-Bults 1974, Pierrot-Bults 1976, Pineda-Polo 1978, Srinivasan, 1979, Sund 1959, Sund 1961b).

Total length (excluding the caudal fin) was measured using an ocular micrometer.

Data treatment: Zooplankton biomass was determined from estimates of the individual volume of organisms assuming that the specific weight of the chaetognaths does not significantly differ from seawater considering that their water content is about 83-95% of wet weight (Ikeda & Kirkwood 1989). Estimations were done using a geometric form, similar to that of chaetognaths, which is made up of a cone (tail), barrel (trunk) and rotation ellipsoid (head). The individual volume is calculated with the following formula:

with

$$V = \underbrace{\frac{r^2 h}{3}}_{\text{(tail)}} + \underbrace{\pi \frac{h}{12} x (2D^2 + d^2)}_{\text{(trunk)}} + \underbrace{\frac{4}{3} a b^2}_{\text{(head)}}$$

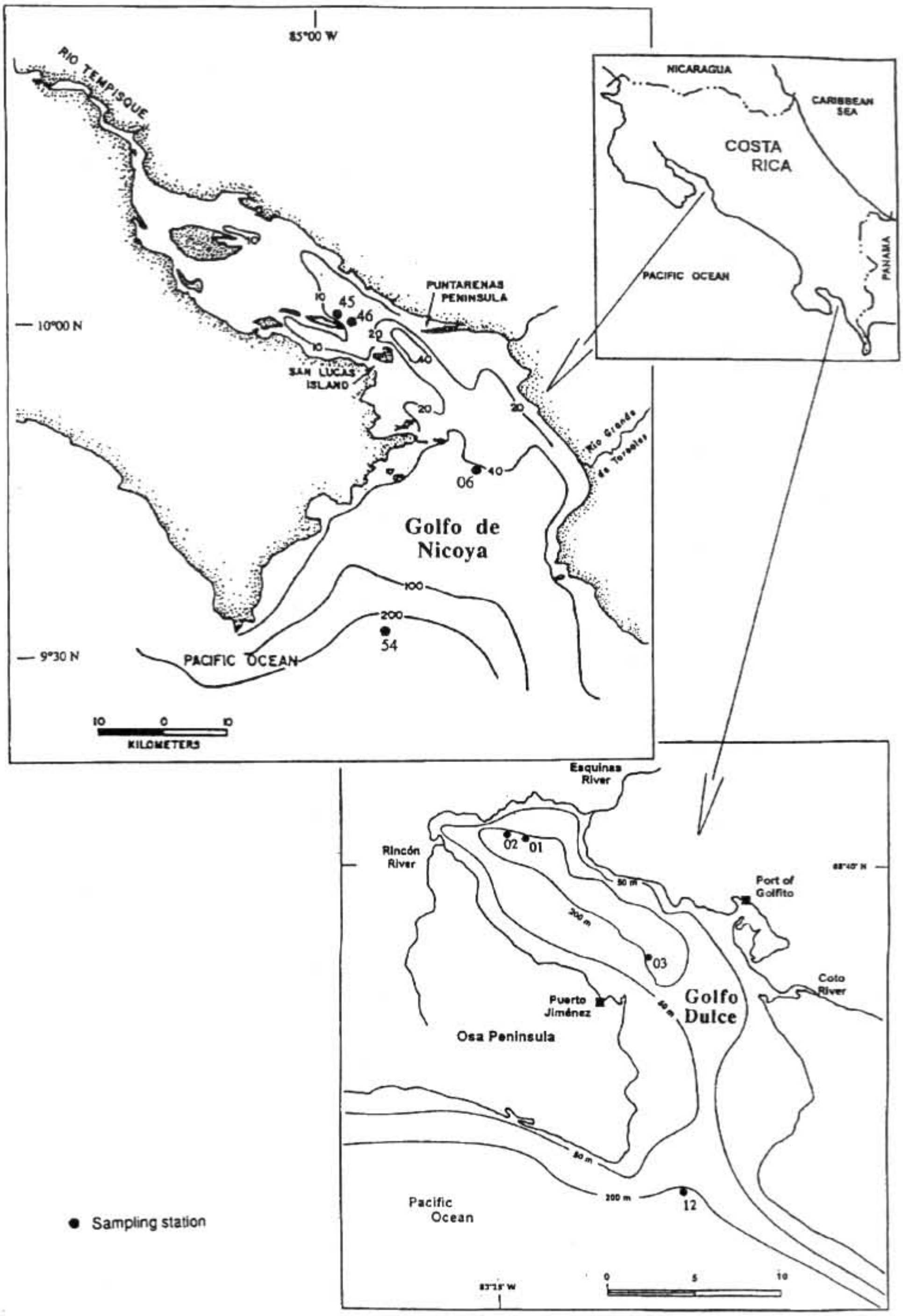


Fig. 1. The study areas Golfo de Nicoya and Golfo Dulce with the location of the sampling stations.

TABLE 1

Station data for the zooplankton samples collected in the Golfo de Nicoya and Golfo Dulce embayments dwing the RV Victor Hensen expedition, December 1993-February 1994

Golfo de Nicoya

Station	Position lat. / long.	Date	Time LT	Depth of haul (m)	Echo-Depth (m)	Tide	Temp. (°C)	Salinity (°/°°)	Watervol. filtered (m³)	Zooplankton volume (ml)	Zoopl. vol. (ml /m³)	subsample	no. of Chaetogn.	Chaet./m³
GN 45	10°03N / 085°00W	04.12.1993	14:21	3.0	6	high	29,7 - 28,9	28,5 - 29	20.43	30	1.47	1\ 8	144	56
GN 06	09°45N / 084°46W	03.12.1993	17:10	30-35	45	high	28 - 24	30,1 - 33,2	62.31	95	1.52	1\ 16	378	97
GN 54	09°33N / 084°50W	03.12.1993	15:56	150	270	high	28,7 - 12,8	29,3 - 34,6	217.72	56	0.26	1\ 16	222	16
GN 46	10°02N / 084°57W	02.02.1994	11:33	10	16	low	27,7 - 26,9	30,9 - 31,6	47.56	125	2.63	1\ 32	461	310
GN 54	09°33N / 084°50W	05.02.1994	10:39	180	300	low	27,3 - 13	32,3 - 34,7	155.57	105	0.67	1\ 8	190	10

Golfo Dulce

Station	Position lat. / long.	Date	Time LT	Depth of haul (m)	Echo-Depth (m)	Tide	Temp. (°C)	Salinity (°/°°)	Watervol. filtered (m³)	Zooplankton volume (ml)	Zoopl. vol. (ml /m³)	subsample	no. of Chaetogn.	Chaet./m³
GD 01	08°42N / 083°24W	08.12.1993	08:24	160	200	?	29 - 16	30,6 - 34,5	322.93	40	0.12	1\ 16	113	6
GD 03	08°35N / 083°16W	07.12.1993	16:47	145	190	high	29 - 16,2	31 - 34,5	123.02	42	0.34	1\ 16	53	7
GD 12	08°21N / 083°14W	07.12.1993	07:05	145	200	high	28,5 - 13,3	29,7 - 34,7	231.96	125	0.54	1\ 32	279	38
GD 02	08°42N / 083°25W	08.02.1994	16:53	160	199	low	29,7 - 16,3	31,9 - 34,7	163.46	50	0.31	1\ 4	64	2
GD 03	08°35N / 083°16W	08.02.1994	10:44	160	190	high	29,1 - 16,3	32 - 34,7	118.18	65	0.55	1\ 8	117	8
GD 12	08°21N / 083°14W	08.02.1994	06:26	140	205	high	28,6 - 13,4	32,2 - 34,8	325.05	300	0.92	1\ 32	283	28

Additional data from the Domo de Costa Rica in November 1981 (Segura *et al*, 1992):

geographical extension	surface temperature	salinity (superior)
7° and 9°N / 87° and 90° W	25.06 - 29.15°C	34 °/°°

Tail: r^2= tail width at septum, h= length of tail;
Trunk: h = length of trunk, D = largest width of trunk, d = width at anterior and posterior end of trunk (mean value);
Head: a =1/2 width of head, b =1/2 length of head.

To avoid measuring each individual, chaetognaths were summed up in length classes of logarithmic steps of 0,2. The length classes are:

I	<4000µm	IV	<16000µm
II	<6300µm	V	<25000µm
III	<10000µm	VI	<40000µm

Mean length per length class was then converted into mean volumes and, by multiplying with the number of individuals, total volume was calculated for each length class. Juveniles were not identified and volumes were calculated on the basis of the mean length of a length class (3250µm for length class I; 5150µm for length class II) for an average of at least 10 individuals per length class.

Biomass spectra for the chaetognaths were derived for the two gulf systems in both December 1993 and February 1994 (Fig. 4 and 5).

The biomass of each species is expressed for all stations in mg/1000m³ (Table 3).

RESULTS

Ten species of the genus *Sagitta* and *Krohnitta* were identified:

Sagitta enflata, S. hexaptera, S. pacifica, S. neglecta, S. regularis, S. bedoti, S. friderici, S. popovicii, S. pulchra and *Krohnitta pacifica.* The species group described as *S. friderici* probably includes *S. peruviana,* which has yet not been differentiated.

Distribution: In Golfo de Nicoya as well as in Golfo Dulce eight of ten species were found. There is no significant difference in diversity between the two gulf systems, instead a decrease in species richness from offshore to inshore (from seven to one/two species respectively) is observed in both areas.

The spatial and temporal distribution of species, according to their relative abundance and biomass in both gulf systems is illustrated in Fig. 2 (Golfo de Nicoya) and Fig. 3 (Golfo Dulce). The abundance and biomass of each species is shown in Table 3.

Sagitta enflata appears at all stations, except at the inner station of Golfo de Nicoya; it had the highest frequency of occurrence of all species in the study area. In Golfo de Nicoya it contributed 10-15% to the total numbers of chaetognaths at the central and offshore stations, while in Golfo Dulce it was much more abundant offshore as well as inshore. *S. enflata* was most abundant at the offshore stations of Golfo Dulce in December as well as February and made up more than 50% of the chaetognath biomass. In December, larger individuals were found offshore than inshore, while in February a shift of larger individuals to the inner gulf was observed.

Sagitta friderici was restricted to the central (GN 06) and inshore (GN45/46) stations of Golfo de Nicoya. In Golfo Dulce it appeared with few individuals at the central gulf station in December, whereas at GN 45/46 and GN 06 it appeared with high abundance and biomass. In both seasons, at the inner station of Golfo de Nicoya, it was the only species found and at GN 06 dominated the chaetognath biomass. During the end of the raing season, only juvenile individuals of *S. friderici* were registered at GN 45, while at GN 06 individuals of mature stages contributed half of the chaetognath biomass. During the dry season, mature individuals ranged to the inner gulf representing 23% of the total catch.

Sagitta popovicii was found at the central and inshore stations of Golfo Dulce in December. It appeared with a relative abundance of 90% at the innermost station (GD 01) but of only 10% in the central gulf (GD 03). In February the species was not recorded at these stations. All individuals found in the study area were mature stages and the maximum length of this tiny species didn't exceed 6 mm.

Sagitta bedoti appeared in 7 of the 11 sampling sites. It is present at all offshore stations and is also found in the central part of the gulfs (GN 06, GD 03), though here the abundance was much lower. In December the abundance of *S. bedoti* at the offshore station of Golfo de Nicoya was twice as high as at the inshore stations and in Golfo Dulce even 20-times higher offshore than inshore. In February less individuals were counted, but *S. bedoti* still represented 20% and 30% of the chaetognaths at the offshore stations of Golfo de Nicoya and Golfo Dulce, respectively.

TABLE 2

Occurrence of chaetognath species in Golfo de Nicoya (GN) and Golfo Dulce (GD) during the end of the rainy season (December 1993) and dry season (February 1994)

Species	Stations										
	December 1993						February 1994				
	GN 45	GN 06	GN 54	GD 01	GD 03	GD 12	GN 46	GN 54	GD 02	GD 03	GD 12
Sagitta enflata		X	X	X	X	X		X	X	X	X
Sagita hexaptera								X			X
Sagitta pacifica			X		X	X		X			X
Sagitta neglecta		X	X			X		X			X
Sagitta regularis			X			X		X			
Sagitta bedoti		X	X		X	X		X		X	X
Sagitta friderici	juv.	X			X		X				
Sagitta popovicii				X	X						
Sagitta pulchra			X								X
Krohnitta pacifica			X			X		X			X

Sagitta pacifica and *S. neglecta* were less abundant than *S. bedoti* but were also found at all offshore stations and, in addition, at one station in the central Golfo de Nicoya *(S. neglecta)* and Golfo Dulce *(S. pacifica)* in December.

Sagitta hexaptera, S. pulchra and *S. regularis* appeared sporadically with a relative abundance of 1-3% at the offshore stations of both gulfs. The occurrence of *Krohnitta pacifica* was also restricted to the offshore stations, but the relative abundance, varying between 3 and 35%, was higher. No significant differences in biomass were found for these species between the two seasons.

The biomass of juveniles (Fig. 2, 3) was higher in Golfo de Nicoya than in Golfo Dulce. Juveniles dominated the biomass of the inner stations in Golfo de Nicoya, decreasing to the mouth of the gulf. In Golfo Dulce, an increase of juveniles from the inner to the outer gulf can be observed, but the biomass represents less than 10% of the total.

Biomass distribution: The chaetognath biomass in Golfo de Nicoya during the rainy season was highest at the central station, where it exceeded seven times the biomass of both inshore and offshore stations. Inshore biomass was represented by small individuals, with an individual body weight of less than 2 mg. (Table 4). At the central and offshore station, a wider range of body mass was found with a shift towards larger individuals. At both of these stations, biomass was higher in the size groups of larger individuals and maximum biomass was found for the size group < 2 mg. During the dry season the biomass spectrum was similar to that of the rainy season, with small individuals dominating the inshore and larger the offshore stations (Fig. 4a, 5a). However, inshore biomass was nineteen times higher compared to that of the offshore biomass and nearly double the amount of that in the rainy season. The average biomass, pooled over all stations in Golfo de Nicoya, showed a flat slope in the rainy season and a negative slope in the dry season (Fig. 4c, 5c).

In Golfo Dulce, the reverse was found: biomass was higher offshore than inshore and the size spectrum at all stations had a wider range. During the rainy season, the offshore biomass was 39-times higher than inshore and 3 fold of that of the central station. Large individuals dominated offshore, whereas smaller individuals (< 6 mg) represented the inshore biomass. During the dry season all stations showed similar biomass spectra, with larger individuals dominating the biomass and a wide range of size spectrum (Fig. 4b, 5b). Larger individuals appeared more often at the inshore and central station than offshore, but the biomass of the latter was highest (nearly 4-times higher than inshore). The biomass spectrum, pooled over all stations, showed a wide size range with larger individuals dominating the gulf system. This was more pronounced during the dry season than during the end of the rainy season (Fig. 4d, 5d).

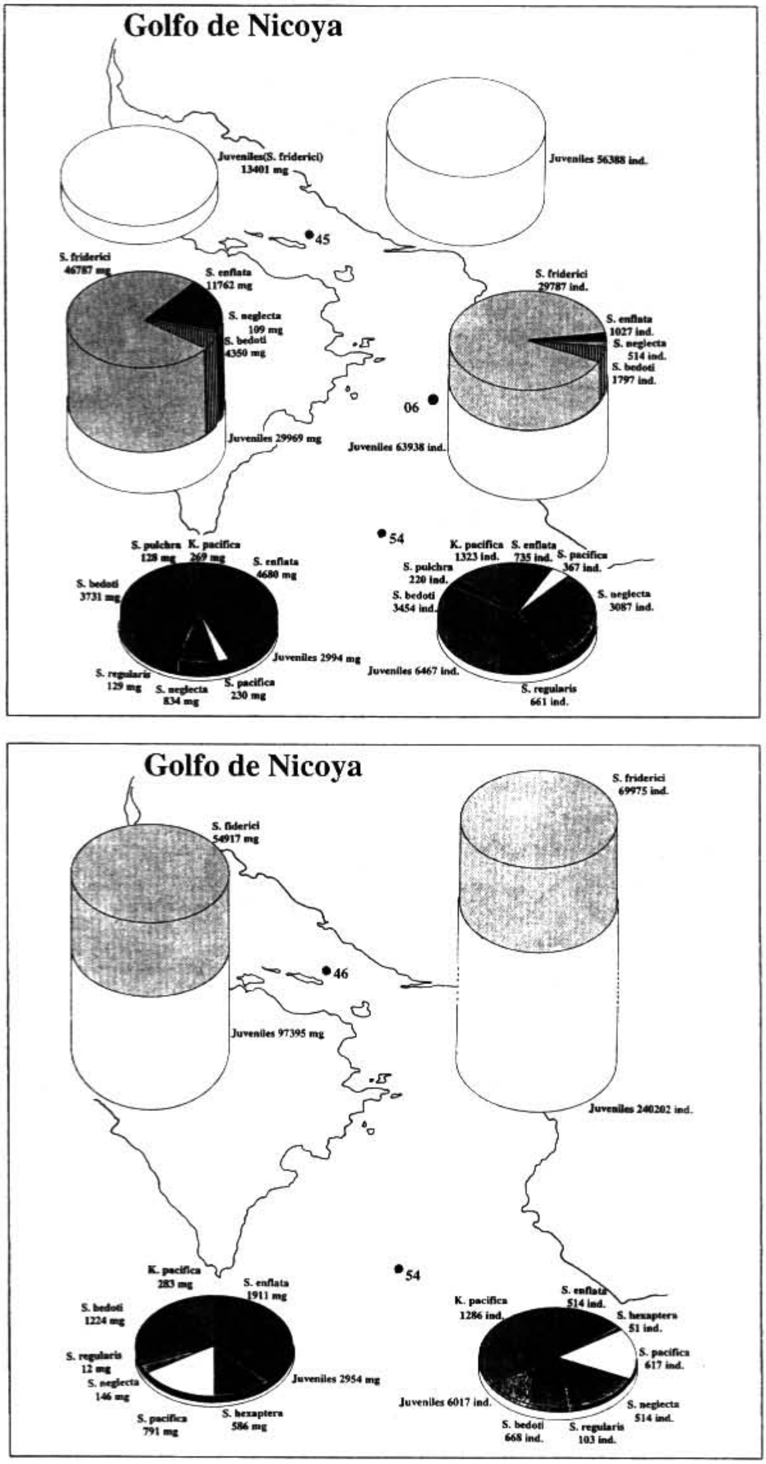
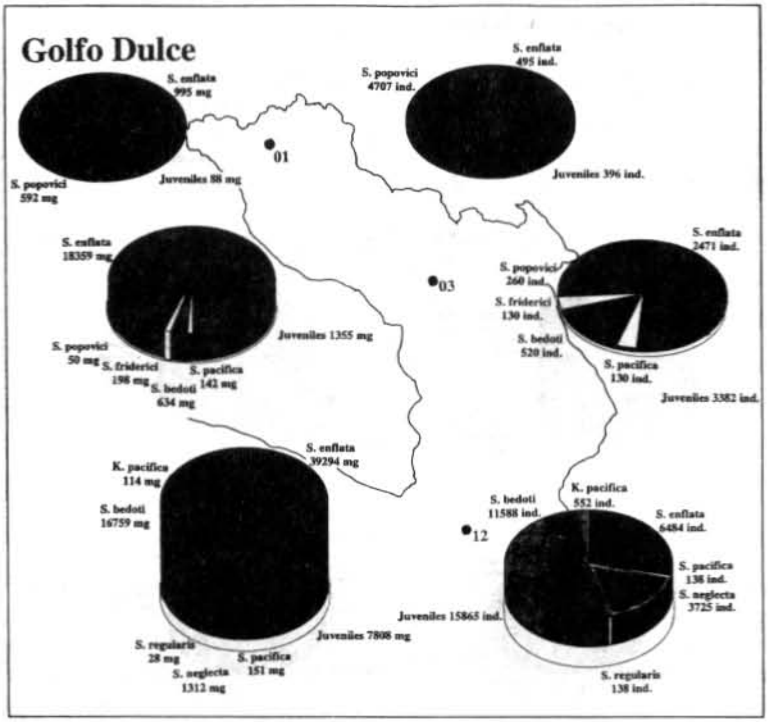


Fig. 2. Distribution of chaetognath species, according to their relative abundance (right) and relative biomass (left) in Golfo de Nicoya. Total abundance and biomass of chaetognaths are illustrated as height of pie chart, including juveniles, not distinguished to species level. Top: Distribution of chaetognaths during the end of the rainy season (December 1993). Bottom: Distribution of chaetognaths during the dry season (February 1994).



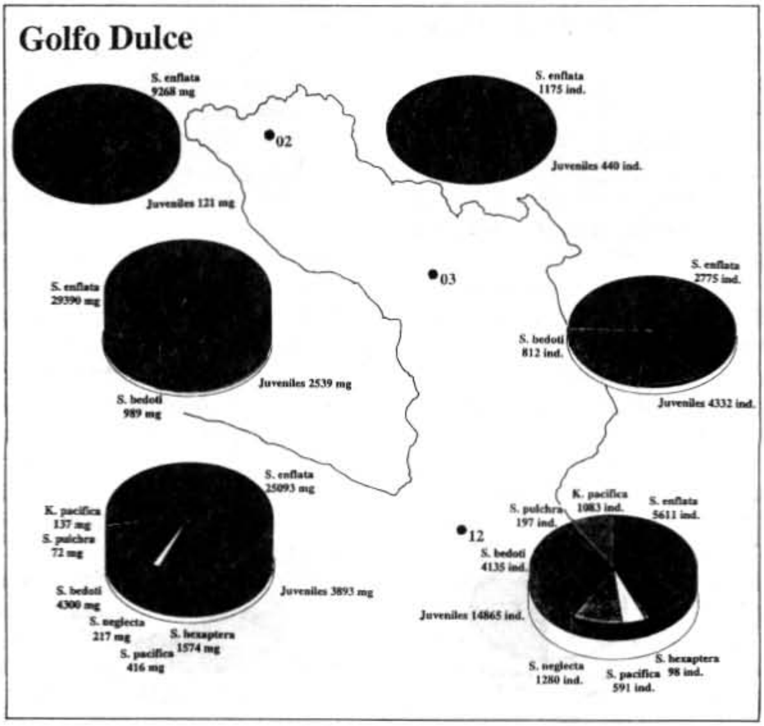


Fig. 3. Distribution of chaetognath species, according to their relative abundance (right) and relative biomass (left) in Golfo Dulce. Total abundance and biomass of chaetognaths are illustrated as height of pie chart, including juveniles, not distinguished to species level. Top: Distribution of chaetognaths during the end of the rainy season (December 1993). Bottom: Distribution of chaetognaths during the dry season (February 1994).

TABLE 3

Abundance and biomass of chaetognath species in Golfo de Nicoya and Golfo Dulce during the end of the rainy season (December 1993) and dry season (February 1994)

Golfo de Nicoya - December 1993

Species	GN 45		GN 06		GN 54	
	n/1000m³	mg/1000m³	n/1000m³	mg/1000m³	n/1000m³	mg/1000m³
Sagita enflata			1027	11762	735	4680
Sagitta hexaptera						
Sagitta pacifica					367	230
Sagitta neglegta			514	109	3087	834
Sagitta regularis					661	129
Sagitta bedoti			1797	3417	3454	4350
Sagitta friderici			29787	46787		
Sagitta popovicii						
Sagitta pulchra					220	128
Krohnitta pacifica					1323	269
Juvenile	56388	13401	63938	29969	6467	2994
Sum	**56388**	**13401**	**97063**	**92045**	**16314**	**13615**

Golfo de Nicoya - February 1994

Species	GN 46		GN 54	
	n/1000m³	mg/1000m³	n/1000m³	mg/1000m³
Sagita enflata			514	1911
Sagitta hexaptera			51	586
Sagitta pacifica			617	791
Sagitta neglegta			514	146
Sagitta regularis			103	12
Sagitta bedoti			668	1224
Sagitta friderici	69975	54917		
Sagitta popovicii				
Sagitta pulchra				
Krohnitta pacifica			1286	283
Juvenile	240202	97395	6017	2954
Sum	**310177**	**152312**	**9770**	**7905**

Golfo Dulce - December 1993

Species	GD 01		GD 03		GD 12	
	n/1000m³	mg/1000m³	n/1000m³	mg/1000m³	n/1000m³	mg/1000m³
Sagita enflata	495	995	2471	18359	6484	39294
Sagitta hexaptera						
Sagitta pacifica			130	142	138	151
Sagitta neglegta					3725	1312
Sagitta regularis					138	28
Sagitta bedoti			520	634	11588	16759
Sagitta friderici			130	198		
Sagitta popovicii	4707	592	260	50		
Sagitta pulchra						
Krohnitta pacifica					552	114
Juvenile	396	88	3382	1355	15865	7808
Sum	**5598**	**1676**	**6893**	**20737**	**38490**	**65466**

Golfo Dulce - February 1994

Species	GD 02		GD 03		GD 12	
	n/1000m³	mg/1000m³	n/1000m³	mg/1000m³	n/1000m³	mg/1000m³
Sagita enflata	1175	9268	2775	29390	5611	25093
Sagitta hexaptera					98	1574
Sagitta pacifica					591	416
Sagitta neglegta					1280	217
Sagitta regularis						
Sagitta bedoti			812	989	4135	4300
Sagitta friderici						
Sagitta popovicii						
Sagitta pulchra					197	72
Krohnitta pacifica					1083	137
Juvenile	440	121	4332	2539	14865	3893
Sum	**1615**	**9389**	**7919**	**32919**	**27860**	**35702**

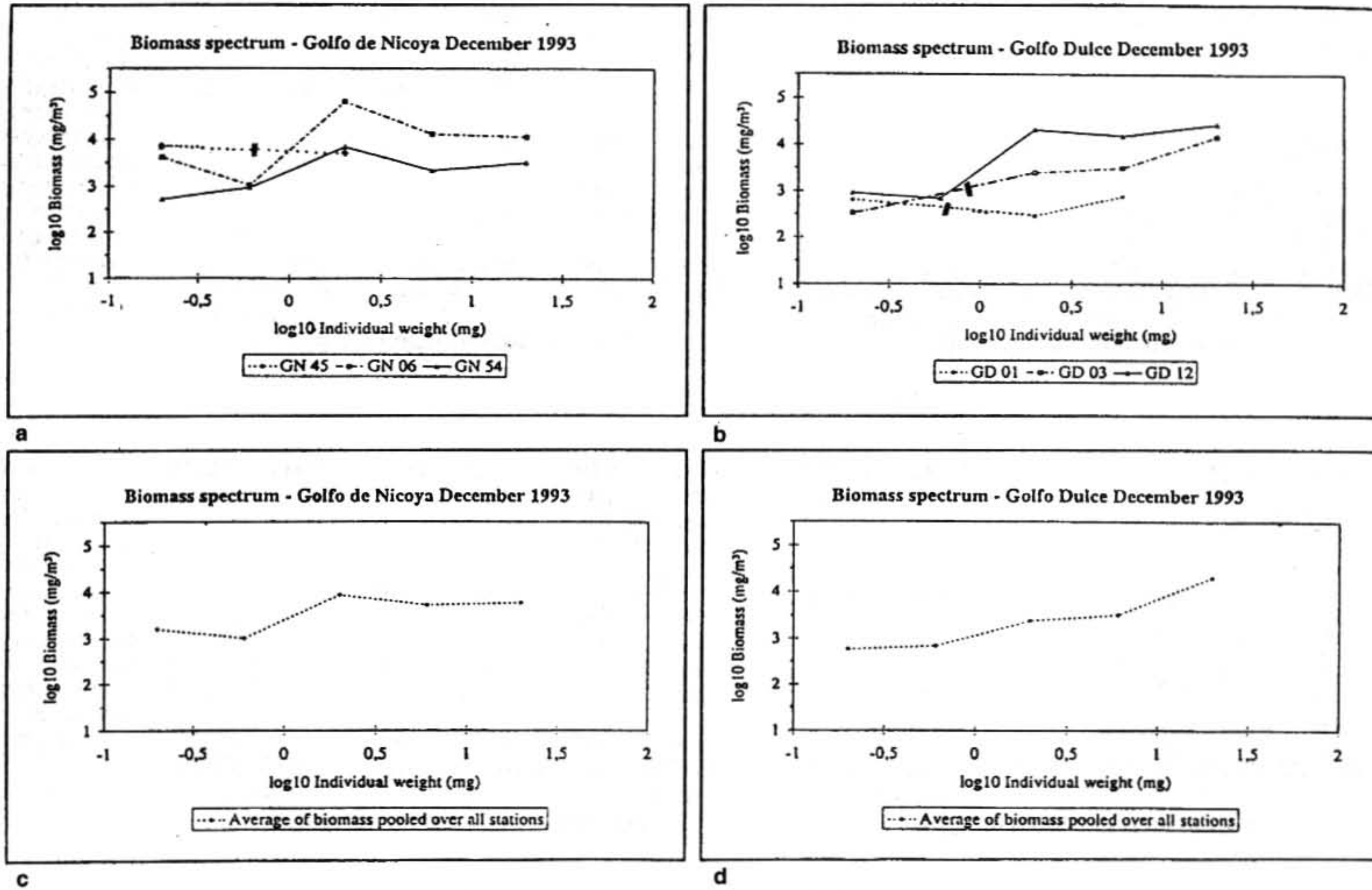


Fig. 4 a, b. Biomass spectra of all stations in Golfo de Nicoya and Golfo Dulce during the end of the rainy season (December 1993). Fig.c, d. Biomass spectra for all samples pooled in Golfo de Nicoya and Golfo Dulce during the end of the rainy season (December 1993).

TABLE 4

Biomass of chaetognath species according to their distribution in the size groups at all stations

Species	Individual bodyweight < 0.2 mg mg/1000m³	log biom.	< 0.6 mg mg/1000m³	log biom.	< 2 mg mg/1000m³	log biom.	< 6 mg mg/1000m³	log biom.	< 20 mg mg/1000m³	log biom.	< 60 mg mg/1000m³	log biom.	Sum
GN45-Dec 93													
Sagitta enflata													0
Sagitta hexaptera													0
Sagitta pacifica													0
Sagitta neglegta													0
Sagitta regularis													0
Sagitta bedoti													0
Sagitta friderici													0
Sagitta popovicii													0
Sagitta pulchra													0
Krohnitta pacifica													0
Juveniles	7500	3.88			5901	3.77							13401
Sum	7500	3.88			5901	3.77							13401
GN06-Dec 93													
Sagitta enflata							769.84	2.89	10992.21	4.04			11762
Sagitta hexaptera													0
Sagitta pacifica													0
Sagitta neglegta			109.12	2.04									109
Sagitta regularis													0
Sagitta bedoti					1251.40	3.10	2165.86	3.34					3417
Sagitta friderici			948.33	2.98	35993.53	4.56	9845.23	3.99					46787
Sagitta popovicii													0
Sagitta pulchra													0
Krohnitta pacifica													0
Juvenile	4112.14	3.61			25856.70	4.41							29969
Sum	4112	3.61	1057	3.02	63102	4.80	12781	4.11	10992	4.04			92044
GN54-Dec 93													
Sagitta enflata							1539.69	3.19	3140.63	3.50			4680
Sagitta hexaptera													0
Sagitta pacifica			69.65	1.84	160.61	2.21							230
Sagitta neglegta	48.74	1.69	483.62	2.68	301.95	2.48							834
Sagitta regularis	8.26	0.92	121.13	2.08									129
Sagitta bedoti					3731.14	3.57	618.82	2.79					4350
Sagitta friderici													0
Sagitta popovicii													0
Sagitta pulchra			31.22	1.49	97.03	1.99							128
Krohnitta pacifica	36.92	1.57	231.59	2.36									269
Juvenile	426.88	2.63			2567.38	3.41							2994
Sum	521	2.72	937	2.97	6858	3.84	2159	3.33	3141	3.50			13615
GD01-Dec 93													
Sagitta enflata					252.27	2.40	742.88	2.87					995
Sagitta hexaptera													0
Sagitta pacifica													0
Sagitta neglegta													0
Sagitta regularis													0
Sagitta bedoti													0
Sagitta friderici													0
Sagitta popovicii	592.50	2.77											592
Sagitta pulchra													0
Krohnitta pacifica													0
Juvenile	54.48	1.74			34.00	1.53							88
Sum	647	2.81			286	2.46	743	2.87					1676
GD03-Dec 93													
Sagitta enflata					396.71	2.60	3115.32	3.49	14846.62	4.17			18359
Sagitta hexaptera													0
Sagitta pacifica					142.04	2.15							142
Sagitta neglegta													0
Sagitta regularis													0
Sagitta bedoti					633.62	2.80							634
Sagitta friderici					198.07	2.30							198
Sagitta popovicii	49.74	1.70											50
Sagitta pulchra													0
Krohnitta pacifica													0
Juvenile	285.90	2.46			1069.29	3.03							1355
Sum	336	2.53			2440	3.39	3115	3.49	14847	4.17			20737
GD12-Dec 93													
Sagitta enflata					982.62	2.99	10744.86	4.03	27566.18	4.44			39294
Sagitta hexaptera													0
Sagitta pacifica					150.78	2.18							151
Sagitta neglegta			556.44	2.75	755.91	2.88							1312
Sagitta regularis			28.43	1.45									28
Sagitta bedoti					12103.36	4.08	4655.18	3.67					16759
Sagitta friderici													0
Sagitta popovicii													
Sagitta pulchra													0
Krohnitta pacifica	13.88	1.14	100.40	2.00									114
Juvenile	909.66	2.96			6898.64	3.84							7808
Sum	924	2.97	685	2.84	20891	4.32	15400	4.19	27566	4.44			65466

continued table 4....

Species	< 0.2 mg		< 0.6 mg		< 2 mg		< 6 mg		< 20 mg		< 60 mg		Sum
	mg/1000m³	log biom.	mg/1000m³	log biom.	mg/1000m³	log biom.	mg/1000m³	log biom.	mg/1000m³	log biom.	mg/1000m³	log biom.	
GN46-Feb 94													
Sagitta enflata													0
Sagitta hexaptera													0
Sagitta pacifica													0
Sagitta neglegta													0
Sagitta regularis													0
Sagitta bedoti													0
Sagitta friderici			22988.04	4.36	28703.10	4.46	3225.82	3.51					54917
Sagitta popovici													0
Sagitta pulchra													0
Krohnitta pacifica													0
Juvenile	19965.06	4.30			77429.66	4.89							97395
Sum	19965	4.30	22988	4.36	106133	5.03	3226	3.51					152312
GN54-Feb 94													
Sagitta enflata					104.77	2.02	1078.38	3.03	728.06	2.86			1911
Sagitta hexaptera									585.74	2.77			586
Sagitta pacifica					790.99	2.90							791
Sagitta neglegta	20.45	1.31	54.56	1.74	70.52	1.85							146
Sagitta regularis	11.65	1.07											12
Sagitta bedoti					500.80	2.70	722.89	2.86					1224
Sagitta friderici													0
Sagitta popovici													0
Sagitta pulchra													0
Krohnitta pacifica	20.72	1.32	261.90	2.42									283
Juvenile	347.13	2.54			2606.43	3.42							2954
Sum	**400**	**2.60**	**316**	**2.50**	**4074**	**3.61**	**1801**	**3.26**	**1314**	**3.12**			**7905**
GD02-Feb 94													
Sagitta enflata					249.21	2.40	1174.24	3.07	7337.66	3.87	507.27	2.71	9268
Sagitta hexaptera													0
Sagitta pacifica													0
Sagitta neglegta													0
Sagitta regularis													0
Sagitta bedoti													0
Sagitta friderici													0
Sagitta popovici													0
Sagitta pulchra													0
Krohnitta pacifica													0
Juvenile	53.85	1.73			67.13	1.83							121
Sum	**54**	**1.73**			**316**	**2.50**	**1174**	**3.07**	**7338**	**3.87**	**507**	**2.71**	**9389**
GD03-Feb 94													
Sagitta enflata					482.15	2.68	1419.87	3.15	23197.85	4.37	4290.63	3.63	29390
Sagitta hexaptera													0
Sagitta pacifica													0
Sagitta neglegta													0
Sagitta regularis													0
Sagitta bedoti					989.42	3.00							989
Sagitta friderici													0
Sagitta popovici													0
Sagitta pulchra													0
Krohnitta pacifica													0
Juvenile	127.48	2.11			2411.20	3.38							2539
Sum	**127**	**2.11**			**3883**	**3.59**	**1420**	**3.15**	**23198**	**4.37**	**4291**	**3.63**	**32919**
GD12-Feb 94													
Sagitta enflata					2102.55	3.32	4717.91	3.67	18272.77	4.26			25093
Sagitta hexaptera									1574.17	3.20			1574
Sagitta pacifica			93.40	1.97	322.32	2.51							416
Sagitta neglegta	91.50	1.96	125.47	2.10									217
Sagitta regularis													0
Sagitta bedoti					4024.05	3.60	275.65	2.44					4300
Sagitta friderici													0
Sagitta popovici													0
Sagitta pulchra			71.84	1.86									72
Krohnitta pacifica	89.13	1.95	47.77	1.68									137
Juveniles	1870.18	3.27			2022.81	3.31							3893
Sum	**2051**	**3.31**	**336**	**2.53**	**8472**	**3.93**	**4994**	**3.70**	**19847**	**4.30**			**35702**

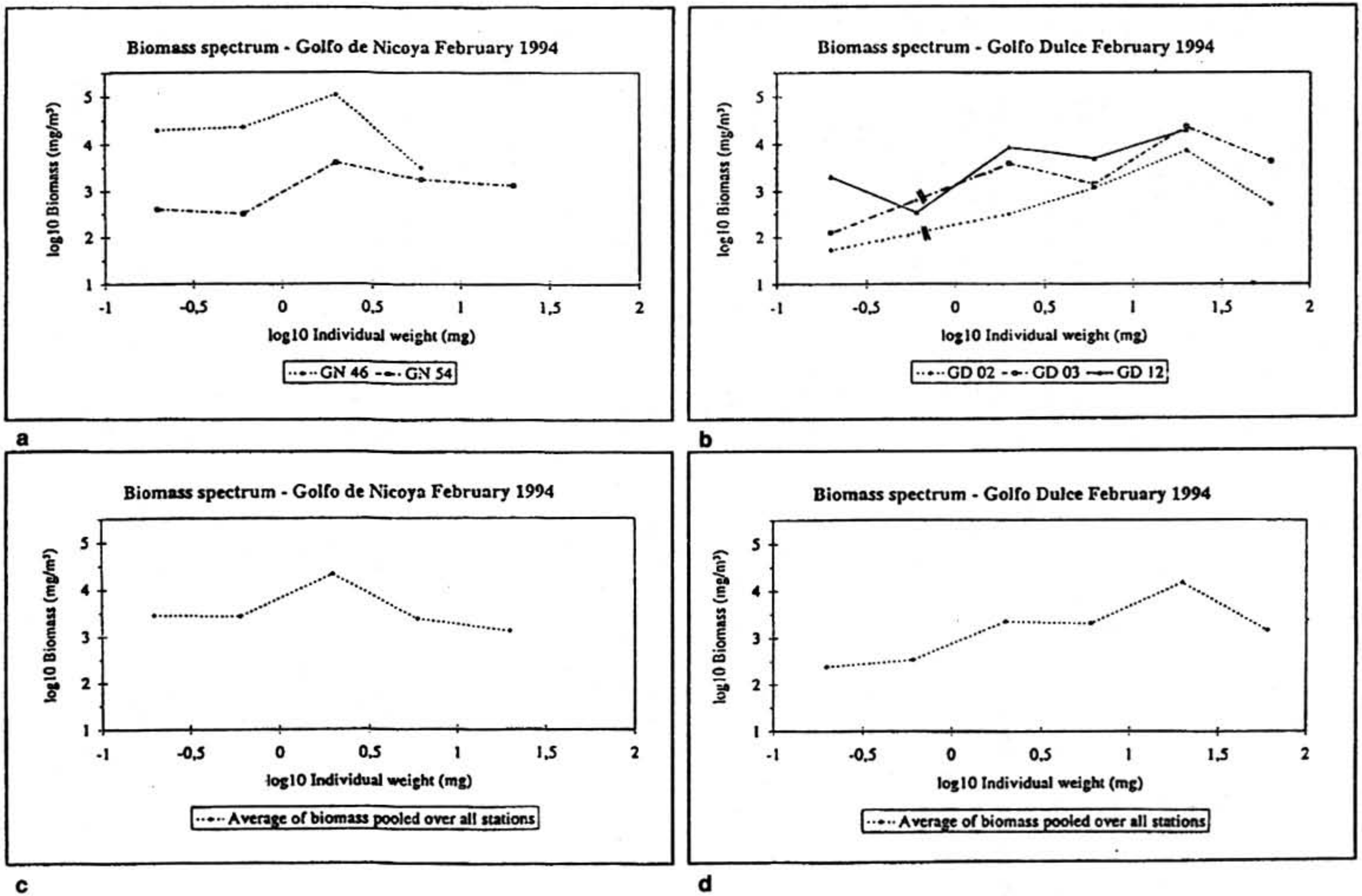


Fig. 5. a, b. Biomass spectra of all stations in Golfo de Nicoya and Golfo Dulce during the dry season (February 1994). Fig. 5 c, d. Biomass spectra for all samples pooled in Golfo de Nicoya and Golfo Dulce during the dry season (February 1994).

Comparing both systems, the inshore biomass of Golfo de Nicoya in the rainy season was eight times higher than in Golfo Dulce and sixteen fold in the dry season.

DISCUSSION

The decrease in species richness from offshore to inshore found in both gulf systems clearly indicates the preference of the holoplanktonic chaetognaths to oceanic water. Some species, however, are more tolerant to changes in temperature, salinity and nutrient loads, typical for nearshore and estuarine environments. Accordingly, the species found in the study area can be devided into three ecological groups: 1. neritic species, 2. semi-neritic species, 3. oceanic species.

Sagitta friderici and *S. popovicii*, both known from neritic waters in the tropical Pacific, form one group of species, restricted to the inner stations of both gulfs. Only *S. friderici*, usually associated with lower salinity and near-shore waters (McLelland 1989) occupies the inshore part of Golfo de Nicoya as unique species, indicating the estuarine character of the inner gulf, which is influenced by the river Tempisque and it also supports the reports of many authors (Alvariño 1972, Boltovskoy 1975). During the rainy season a prevalence of juvenile individuals is observed in the inshore gulf and a group of larger individuals of mature stages appear solely at the central station. An invasion of larger individuals of mature stages in the inshore gulf is observed during the dry season, when the river influence in this area is supposedly less pronounced. It can thus be argued, that a prevalence of juveniles indicates areas with estuarine character and that in gulf systems with distinct hydrographic boundaries juvenile and mature individuals (or individuals of different sizes) occupy different regions.

In Golfo Dulce the tiny species *S. popovicii* was found in the central and inshore gulf, with a prevalence at the innermost station (GD 01). It was first described by Sund (1961b) for the area, near the entrance to the Port of Talara in Peru and has been found also north of the studied area, in neritic regions of Guatemala and in the Gulf of Tehuantepec (Alvariño 1972). In this study, it exclusively appears during the rainy season at the Golfo Dulce stations. The increase of individuals towards the inner gulf and the dominance of this species at station GD 01 may indicate the estuarine character of this area during the rainy season, which is influenced by the rivers Río Rincón and Río Esquinas (Fig. 1). The lack of *S. popovicii* at the corresponding stations in February hints to a change in water conditions during the dry season. An analysis of additional stations, nearshore and closer to the mouth of the rivers may proof, if this species still appears at the river influenced zones in the gulf.

Sagitta popovicii occurs together with *S. enflata*, but it was found that as *S. popovicii* increased in abundance inshore, while the reverse was found for *S. enflata*. In February, *S. popovicii* was not recorded and *S. enflata* dominated the inshore Golfo Dulce. This may indicate a kind of niche competition between the two species. In neritic waters of the South American Atlantic coast, Boltovskoy (1975) found a similar but opposite alternation between *S. enflata* and *S. tenuis*, the latter being a tiny species like *S. popovicii*. He assumed, that the dominance of either of these species was determinated by some local environmental factor and that probably only in neritic waters *S. tenuis* can compete with *S. enflata*, because the latter does not reach large sizes in this zone.

A size decrease from offshore to inshore waters proved for *S. enflata* during the rainy season in Golfo Dulce and the shift of large individuals towards the inner gulf during the dry season may indicate that larger individuals are more associated with oceanic waters, which during the dry season extend to the inshore regions. *S. enflata* is described as oceanic and semi-neritic species (McLelland 1989) with a wide tolerance to environmental changes, which seems confirmed by this study. In the region of the Domo de Costa Rica it has been found wide spread with an abundance of 82-729 ind/1000 m^3 (Segura *et al.* 1992). *S. bedoti*, also known as a semi-neritic species, showed a similar distributional pattern to that of *S. enflata*. A clear preference to higher abundance at the offshore stations was recorded for both gulf systems. An increase in abundance of *S. bedoti* towards the coastal area was reported by Segura *et al.* (1992) for the region of the Domo de Costa Rica, but numbers are not nearly as high as those found in this study. This confirms the semi-neritic character of this species and it is suggested, that highest concentrations are probably to be found close to the coast. Due to its high abundance at the offshore stations, *S. neglecta* as well can be characterized as a semi-neritic or nearshore species. This is also found for the region of the Domo de Costa Rica, where major concentrations of *S. neglecta* were localized in the coastal area (Segura *et al.* 1992).

S. hexaptera, S. pulchra, S. regularis and *Krohnitta pacifica* form a group of oceanic species, exclusively found at the outer gulf stations, low in abundance and biomass. These species are known for the region of the Domo de Costa Rica (Segura *et al.*, 1992), although they seem to appear more frequently and in higher abundance in the open Pacific Ocean.

The dominance of juveniles and small individuals at the inshore station in Golfo de Nicoya reflects high reproduction rates and a high energy flow through chaetognaths in this system. The estuarine character is reflected in the predominance of the neritic species *S. friderici.* The enormous increase of chaetognath biomass from December to February (change of seasons) points to high zooplankton production during that time, probably caused by strong winds leading to mixing of the water column and inshore movement of oceanic water.

The high abundance (90%) of the neritic species *S. popovicii* suggests the neritic character of the inshore part of Golfo Dulce during the rainy season, though the co-occurrence of small individuals of *S. enflata* in this area may indicate an oceanic water influence as well. *S. enflata* dominates the biomass at the offshore station with large individuals, decreasing towards inshore. The appearance of large individuals at the inshore station during the dry season points to an invasion of oceanic water in the inner gulf. The absence of *S. popovicii* during that time confirms this conclusion. Low chaetognath reproduction as determined by the low contribution of juveniles to the biomass, also points to the more oceanic character of this gulf. Thus the picture emerges, that the pelagic environment of Golfo Dulce is rather stable and structured through predation of larger over smaller plankton organisms revealed by the wide and more continuous chaetognath biomass spectrum and the biomass dominance of larger over smaller individuals. The broad biomass spectrum also suggests that chaetognaths may feed on several trophic levels in this system and therefore play a mayor role in structuring the zooplankton community as a top predatory component.

ACKNOWLEDGEMENTS

I especially thank Matthias Wolff for his support and advice, as well as Helga Kapp for her friendly help in identifying the chaetognath species and Claudio Richter for critical reviews of the first manuscript drafts.

RESUMEN

Se analizó el gremio de los quetognatos con base en el muestreo hecho por el buque RV Victor Hensen al Pacífico costarricense en diciembre de 1993 y febrero de 1994. Se identificaron las siguientes diez especies de los géneros *Sagitta y Krohnitta: S.enflata, S. hexaptera, S. pacifica, S. neglecta, S. regularis, S. bedoti, S. friderici, S. popovicii, S. pulchra y K. pacifica.* Sus patrones de distribución indican que pertenecen a los grupos ecológicos neríticos, seminerítícos y oceánicos. En ambos golfos hubo un marcado gradiente de riqueza de especies desde mar afuera hacia la costa (8 a 1, respectivamente) Los quetognatos de la parte interna fueron principalmente juveniles y adultos de *S. friderici* en el Golfo de Nicoya y *S. popovicii* en el Golfo Dulce. Los espectros de biomasa fueron más contínuos y de mayor ámbito en el área del Golfo Dulce, donde dominaron las especies más grandes, lo que sugiere un sistema pelágico más desarrollado en el Golfo Dulce, donde los quetognatos más grandes pueden definir la estructura de la comunidad del plancton mediante fuerte presión de depredación desde la parte superior del sistema.

REFERENCES

Alvariño, A. 1963. Quetognathos epiplanctónicos del Mar de Cortés. Rev. Soc. Mex. Hist. Nat. 24: 97-203.

Alvariño, A. 1967. The Chaetognatha of the NAGA Expedition (1959-1961) in the South China Sea and the Gulf of Thailand, Part 1: Systematics. NAGA Report 4: 1-197.

Alvariño, A. 1969. Los Quetognathos del Atlántico. Distribución y notas esenciales de sistemática. Inst. Esp. Ocean. Madrid. 37: 1-290.

Alvariño, A. 1972. Zooplankton del Caribe, Golfo de México y regiones adyacentes del Pacífico. Mem. IV Congr. Nac. Ocean. México: 223-247.

Boltovskoy, D. 1975. Some biometrical, ecological, morphological and distributional aspects of Chaetognatha. Hydrobiologia 46: 515-534.

Bone, Q., Kapp, H. & A.C. Pierrot-Bults (eds.) 1991. The biology of chaetognaths. Oxford University Oxford. 173p.

Ikeda, T. & R. Kirkwood. 1989. Metabolism and elemental composition of a giant chaetognath *Sagitta gazellae* from the southern ocean. Mar. Biol. 100: 261-267.

McLelland, J.A. 1989. An illustrated key to the Chaetognatha of the northern Gulf of Mexico with notes on their distribution. Gulf Res. Rep. 8: 145-172.

Pathansali, D. 1974. Chaetognatha in the coastal waters of peninsular Malaysia with descriptions of two new species. Fish. Bull. Min. Agric. Rural. Dev. Malaysia. 2: 1-30.

Pearre, S. Jr. 1980. Feeding by Chaetognatha: The relation of prey size to predator size in several species. Mar. Ecol. Prog. Ser. 3: 125-134.

Pierrot-Bults, A.C. 1974. Taxonomy and zoogeography of certain members of the "*Sagitta serratodentata*-group" (Chaetognatha). Inst. Taxon. Zool., Univ. Amst. 44: 215-234.

Pierrot-Bults, A.C. 1976. Histology of the seminal vesicles in the "*Sagitta serratodentata*-group" (Chaetognatha). Bull. Zool. Museum, Univ. Amst. 5: 19-29.

Pineda-Polo, F. 1978. Taxonomy of the chaetognaths of the Bight of Panamá. 2. The *Sagitta friderici* Ritter-Zahony, 1913, and its relatives *S. peruviana* Sund, 1961, and *S. euneritica* Alvariño, 1961. Bol. Dept. Biol. Universidad de Valle, Colombia: 371-439.

Reeve, M.R. 1970. The biology of Chaetognatha. I. Quantitative aspects of growth and egg production in *Sagitta hispida*, p. 168-89. *In* J.H. Steele (ed.). Marine food chains. Oliver & Boyd, Edinburgh.

Richards, F.A., J.I. Anderson & J.D. Cline. 1971. Chemical and physical observations in Golfo Dulce, an anoxic basin on the Pacific coast of Costa Rica. Limnol. Oceanogr. 16: 43-50.

Segura, L., R. Hernández & L. Morones. 1992. Distribución y abundancia de los quetognathos (Chaetognatha) en la región del Domo de Costa Rica. Rev. Biol. Trop. 40: 35-42.

Srinivasan, M. 1979. Taxonomy and ecology of Chaetognatha of the west coast of India in relation to their role as indicator organisms of watermasses. Zoological Survey of India, Technical Monograph 3: 1-47.

Steedman, H.F. 1976. Miscellaneous preservation techniques, p. 175-181. *In* H.F. Steedman (ed.). Zooplankton fixation and preservation. UNESCO, Paris.

Sund, P.N. 1959. A key to the Chaetognatha of the Tropical Eastern Pacific Ocean. Pac. Sci. 13: 269-285.

Sund, P.N. 1961a. Some features of the autecology and distributions of Chaetognatha in the Eastern Tropical Pacific. Inter-Amer. Trop. Tuna Com. Bull. 5: 307-331.

Sund, P.N. 1961b. Two new species of Chaetognatha from the waters off Peru. Pac. Sci. 15: 105-111.

Sund, P.N. & A. Renner. 1959. The Chaetognatha of the Eastropac Expedition with notes as to their possible value as indicators of hydrographic conditions. Inter-Amer. Trop. Tuna Com. Bull. 9: 115-216.

Voorhis, A., C.E. Epifanio, D. Maurer, A. Dittel & J.A. Vargas. 1983. The estuarine character of the Gulf of Nicoya, an embayment on the Pacific coast of Central America. Hydrobiologia 99: 225-237.

Wangelin, M. von & M. Wolff. 1996. Comparative biomass spectra and species composition of the zooplankton community of the Golfo Dulce and Golfo de Nicoya ecosystems. Rev. Biol. Trop. 44. Suppl. 3: 135-155.

Wolff, M. & J.A. Vargas 1994. Macroscale evaluation: overview on oceanographical conditions: 5-10. *In*: RV Victor Hensen Costa Rica Expedition 1993/1994 - Cruise Report, ZMT Contribution 2. Center for Tropical Marine Ecology, Bremen.