Chaetognatha of the Brazil-Malvinas (Falkland) confluence: distribution and associations

Alina M. Crelier & María C. Daponte

Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pab. II, Ciudad Universitaria, C1428EHA, Buenos Aires, Argentina. (daponte@bg.fcen.uba.ar)

ABSTRACT. The planktonic chaetognaths from the Brazil-Malvinas (Falkland) confluence, extending between 36° 30' - 50° 5' S and 60° 33' - 41° 7' W, were studied. Ten species were found: *Eukrohnia hamata* (Möbius, 1875) (Eukrohniidae), *Pterosagitta draco* (Krohn, 1853) (Pterosagittidae), *Sagitta enflata* Grassi, 1881, *Sagitta gazellae* Ritter-Zahony, 1909, *Sagitta hexaptera* d'Orbigny, 1834, *Sagitta lyra* Krohn, 1853, *Sagitta minima* Grassi, 1881, *Sagitta planctonis* Steinhaus, 1896, *Sagitta serratodentata* Krohn, 1853, and *Sagitta tasmanica* Thomson, 1947 (Sagittidae). *Sagitta gazellae* was the most abundant species followed by *E. hamata*, *S. tasmanica* and *S. serratodentata*. The association analysis among the different species, salinity and temperature revealed two groups of species, or related to higher salinities and warmer waters (*P. draco*, *S. hexaptera* and *S. serratodentata*) and the other to lower salinities and colder waters (*E. hamata*, *S. gazellae* and *S. tasmanica*). The fact that *P. draco* and *S. hexaptera*, formerly defined as warm-water species, appeared further south than previously reported might be related to the existence of warm core eddies up to 46° S in September and October 1988.

KEYWORDS. Eukrohniidae, Pterosagittidae, Sagittidae, southwestern Atlantic, zooplankton.

INTRODUCTION

Chaetognaths are important members of the marine pelagic community; their biomass has been estimated in 30% of that of copepods (REEVE, 1970), and their energy transference to higher trophic levels is considered expressive (FEINGENBAUM, 1991), since they constitute a trophic link between the high number of copepods and larger predators. They can be found in all oceans, from bottom to surface waters, and their horizontal distribution can be affected, among other factors, by changes in the currents, salinity, and temperature. Chaetognaths have become useful as hydrological indicators due to their affinity for specific water types (BOLTOVSKOY, D., 1981; MAZZONI, 1983; MCLELLAND, 1984). As a rule, each water mass contains characteristic planktonic species, which can determine faunistic differences between neighboring areas. The existing information on the distribution and abundance of the different species of chaetognaths depends on the oceanographic regions considered. In the Southwestern Atlantic Ocean most of the studies were carried out in different areas of the continental shelf (Almeida Prado, 1961a, b, 1963, 1968; Mostajo, 1973, 1976; MAZZONI, 1983) or near the slope (BOLTOVSKOY & MOSTAJO, 1974; BOLTOVSKOY, D., 1975a, b, 1981). On the other hand, the investigations accomplished off the continental slope were sparse (BOLLMANN, 1934; THIEL, 1938), and the extensive distance between sampling stations has prevented a detailed analysis of the distribution of these organisms, mainly in hydrologically complex oceanic areas.

The present study aims to analyze the planktonic chaetognaths found in the Brazil-Malvinas (Falkland) confluence, where tropical and cold-water faunas converge. The composition and distribution of chaetognath associations were determined and their relations to surface salinity and water temperature investigated.

MATERIAL AND METHODS

Hydrology of the area. The surveyed area has a complex hydrological structure, characterized by the presence of different water masses and currents. Subantarctic waters are carried from the south in a northnortheastward direction along the Patagonian Shelf by the Malvinas (Falkland) Current (MC), a branch of the West Wind Drift (WWD) (PETERSON & STRAMMA, 1991; PIOLA & RIVAS, 1997), whereas the northern area is influenced by the tropical-subtropical waters of the Brazil Current (BC) (fig. 1). The WWD is constituted by pure and typical Subantarctic waters, with a minimum winter temperature of 3.5 °C and a minimum summer temperature of 5.5 °C (BOLTOVSKOY, E., 1970, 1981). The MC is characterized by salinities between 34 and 34.5 psu and temperatures below 10 - 11 °C (GONI et al., 1996; PROVOST et al., 1996; GUERRERO & PIOLA, 1997). However, its surface temperature depends on latitude and season (BOLTOVSKOY, E., 1970, 1981; LEGECKIS & GORDON, 1982). BC waters reach temperatures higher than 20 °C and salinities over 36 psu (Thomsen, 1962; Boltovskoy, 1970; Brandhorst & CASTELLO, 1971; CIOTTI et al., 1995; GONI et al., 1996; PROVOST et al., 1996). In its southern boundary, BC waters converge turbulently with the colder and less saline Subantarctic waters, loosing thereby warmth and salinity (PETERSON & STRAMMA, 1991) and giving rise to the Brazil-Malvinas (Falkland) confluence zone (BMCZ). The BMCZ is highly complex because of the presence of warm core eddies and meanders (BOLTOVSKOY, E., 1970, 1981; LEGECKIS & GORDON, 1982; GORDON, 1989). Their position oscillates between 38° and 46° S, depending on the season (LEGECKIS & GORDON, 1982).

The Subantarctic front (SAF) marks the southern limit of Subantarctic waters. Near Malvinas Plateau, the SAF sharply turns northward and reaches the BMCZ, then turns southward to finally deflect eastwards. Sampling design and data processing. The plankton samples were obtained by the Russian Research Vessel RTMA "EVRIKA" from August 1st through October 24th, 1988, in an oceanic sector located between 36° 30' - 50° 5' S and 60° 33' - 41° 7' W. Oblique tows were taken from 50 m of depth to surface with a Bongo net of 60 cm of mouth diameter and 500 μ m mesh. The filtered volume was determined with a digital DF-2030 flowmeter. Surface water temperature and salinity were registered in each station. The samples were fixed in 4% formaldehyde and deposited in the collection of the Department of Biodiversity and Experimental Biology, Universidad de Buenos Aires.

All chaetognaths were identified according to CASANOVA (1999). Density of the species found in each station was calculated as individuals 1000 m⁻³. The length and width of the smallest specimens collected with the net were measured. Horizontal distribution and abundance patterns were determined for each species, and their relationships with surface water temperature and salinity analyzed.

Similarities among sample units (s.u.) having chaetognaths were studied using Ochiai qualitative coefficient and Bray-Curtis quantitative index (LEGENDRE & LEGENDRE, 1998). The values obtained were grouped through the unweighted arithmetic average clustering method (UPGMA) (LEGENDRE & LEGENDRE, 1998). The greatest distance among clusters in the successive agglomeration steps was considered as the reference level (HAIR *et al.*, 1992). The results obtained from both indexes were compared with an exact test for 3x3 contingency tables (DIGBY & KEMPTON, 1994). In accordance to the clusters defined through the Ochiai index and UPGMA, the percentage of species present in each group was analyzed, and the fidelity degree of each species to each group (ZAIXSO, 1996) evaluated with a contingency table, using an RxC independence G test or a Fisher two tails exact test when any of the expected values was smaller than five (SOKAL & ROHLF, 1997). The preferential species of a group were defined as those positively and significantly associated to it (p < 0.05). The indicator species were defined as those preferential ones present in at least 75% of the s.u. in the group. The exclusive species were defined as those having a 100 % fidelity degree to a group (ZAIXSO, 1996).

Relationships among temperature, salinity and clusters (Ochiai-UPGMA) were studied through correspondence factorial analysis (BENZECRI, 1976; GAUCH, 1989) on a contingency table of groups and environmental factors (LEGENDRE & LEGENDRE, 1998; CARRASCO & HERNÁN, 1993). Three temperature intervals were defined for this analysis: temperature 1 (tem1) from 3 ° to 8 °C, temperature 2 (tem2) from 8 ° to 13 °C, and temperature 3 (tem3) from 13 ° to 18 °C. Three salinity intervals were also defined: salinity 1 (sal1) from 33.5 to 34.6 psu, salinity 2 (sal2) from 34.6 to 35.4 psu, and salinity 3 (sal3) from 35.4 to 36.2 psu.

RESULTS AND DISCUSSION

Chaetognaths were found in 70 out of 110 oceanographic stations. Only those samples containing

well-preserved specimens were considered (n=63). The species found in the study area were: Eukrohnia hamata (Möbius, 1875) (Eukrohniidae), Pterosagitta draco (Krohn, 1853) (Pterosagittidae), Sagitta enflata Grassi, 1881, Sagitta gazellae Ritter-Zahony, 1909, Sagitta hexaptera d'Orbigny, 1834, Sagitta lyra Krohn, 1853, Sagitta minima Grassi, 1881, Sagitta planctonis Steinhaus, 1896, Sagitta serratodentata Krohn, 1853, and Sagitta tasmanica Thomson, 1947 (Sagittidae) (tab. I). Sagitta gazellae was the most frequent (45%), followed by S. serratodentata (20%), S. hexaptera (19.1%), P. draco (18.25%), and S. tasmanica (15.5%). The most abundant species were S. gazellae (up to 1062 ind.1000 m⁻³), E. hamata (788 ind.1000 m⁻³), S. tasmanica (153 ind. 1000 m⁻³), and S. serratodentata (up to 73 ind.1000 m⁻³) (figs. 2, 3). The densities of P. draco, S. lyra, S. minima, S. enflata, S. hexaptera and S. planctonis were lower than 55 ind.1000 m⁻³ (figs. 4, 5).

The net probably failed to catch specimens having maximum diameter smaller than 500 μ m. Such diameter corresponds to total lengths <7.5 mm (n=15) for *S. minima* and up to 35 mm for *S. gazellae* (n=100).

Sagitta gazellae was found all over the sampling area, being most abundant between 40 and 50° S and having low densities between 36° 30' and 39° S. The northern area, which presented the lowest densities, was warmer (13° - 15.2 °C) and more saline (35 - 35.7 psu). High densities were found at temperatures between 3.6 °C and 13.0 °C and salinities between 34 and 35 psu (fig. 6). These values are typical of Subantarctic waters and fall within the limits reported in the literature (DAVID, 1955). The low densities of *S.* gazellae in the northern area may reflect certain environmental conditions (salinity >35.0 psu) that are unsuitable for the development of this species.

Eukrohnia hamata was found south of 42° S. The temperature-salinity-density diagram (T-S-D) shows the highest abundances at 3.6° - 8.7 °C and 34 - 34.4 psu (fig. 6), corresponding to the location of the WWD (fig. 1). Its absence northward may indicate its sinking to deeper layers at these latitudes, according to its mesoplanktonic nature at intermediate latitudes (PIERROT-BULTS & NAIR, 1991).

Sagitta tasmanica extends northward up to 38° 50' S, at temperatures of 5° - 14.6 °C and salinities of 34.1 - 35.1 psu (fig. 7). The highest densities were found between 7.8 and 10.0 °C, and between 34.4 and 34.6 psu. The highest salinities correspond to mixed waters, thus indicating certain tolerance of this species to warmer conditions. DADON & BOLTOVSKOY (1982) also reported the presence of *S. tasmanica* in transitional waters that reach the northern boundary of the BMCZ.

Sagitta serratodentata was found at temperature and salinity ranges oscillating between 9.1 and 16.7 °C and between 34.5 and 35.9 psu (fig. 7), whereas the highest densities and frequencies were found at temperatures and salinities above 14 °C and 35.0 psu.

Pterosagitta draco was found at temperatures ranging between 6.7 and 16.7 °C, and salinities between 34.1 and 35.9 psu (fig. 8). However, in agreement with the authors who characterized it as a warm-water species (GRANT, 1991; LIANG & VEGA-PÉREZ, 2001), the

Table I. Oceanographic data and planktonic chaetognath species found in each sampling station of Russian Research Vessel RTMA "EVRIKA" from Brazil-Malvinas (Falkland) confluence, August 1st through October 24th, 1988 (Eh, *E. hamata*; Pd, *P. draco*; Se, *S. enflata*; Sg, *S. gazellae*; Sh, *S. hexaptera*; Sl, *S. lyra*; Sm, *S. minima*; Sp, *S. planctonis*; Ss, *S. serratodentata*; St, *S. tasmanica*).

Station	Date	Positi	on	Temperature (°C)	Salinity (psu)	Species		
1	01/08	36°30' S 50°31' W		14.00	35.19	Pd, Sg, Sh, Ss		
2	02/08		49°51' W	12.64	34.53	Pd, Se, Sg, Sh, Ss		
4	03/08		48°30' W	16.66	35.91	Pd, Sh, Sp, Ss		
5	03/08		47°57'W	15.63	35.73	Pd, Sh,		
6	03/08		47°30' W	15.06	35.59	Sg, Sh, Ss		
7	04/08		48°01' W	15.20	35.67	Pd, Sg, Sh, Ss		
8	04/08		48°30' W	14.80	35.65	Sh		
9	04/08		49°44' W	14.74	35.56	Pd, Sh, Sm, Ss		
10	04/08		50°59' W	14.03	35.36	Pd, Sg, Sh, Sp, Ss		
11	05/08		51°30' W	14.64	35.53	Pd, Sg, Sh, Ss		
12	05/08		51°52' W	14.81	35.60	Pd, Sg, Sh, Ss		
14	05/08		53°09' W	12.20	34.83	St		
16	06/08		53°00' W	14.79	35.65	Sh		
17	06/08		52°08' W	14.70	35.56	Sh		
19	07/08		50°43' W	15.00	35.70	Sh, Ss		
20	07/08		50°10' W	15.06	35.66	Pd, Sg, Sh, Sm, Ss		
21	07/08		49°18' W	15.09	35.76	Sh		
23	08/08		48°00' W	14.74	35.69	Pd, Sh, Ss		
24	08/08		47°30' W	12.78	35.27	Pd, Sg, Ss		
27	08/08		47°17'W	10.43	34.69	Sg		
29	11/08		44°12' W	11.78	35.03	Sg, St		
32	11/08		44°53' W	14.27	35.59	Pd, Sh, Ss		
33	12/08		45°57'W	11.20	34.90	Sg, Ss		
34	13/08		47°00' W	9.78	34.64	Pd, Sg, Ss		
37	16/08		50°29' W	9.38	34.45	Pd, Sg		
39	17/08		51°44' W	14.35	35.49	Se, Sg, Ss		
40	17/08		52°40' W	14.50	35.58	Sg, Sh, Ss		
42	18/08		54°27'W	7.00	34.11	Sg		
46	21/08		55°27' W	6.22	34.05	Sg		
47	22/08		54°30' W	6.96	34.09	Eh, Pd, Sg, St		
50	23/08		51°37' W	9.30	34.32	Sg		
51	23/08		50°30' W	9.37	34.50	Sg, St		
52	23/08		49°35' W	9.85	34.60	Sg, St		
53	24/08		48°31' W	14.35	35.55	Sg, Ss		
55	25/08		45°00' W	9.05	34.57	Sg, Ss		
61	04/09		54°33' W	5.83	34.24	Sg		
62	04/09		54°28' W	6.13	34.14	Sg Sg Sg		
66	06/09		58°31' W	4.32	34.07	Sg		
69	06/09		60°01' W	5.66	34.01	Sg		
73	08/09		59°00' W	4.06	34.08	Sg		
75	08/09		57°41' W	5.04	34.08	Sg, St		
77	09/09		56°38' W	9.04	34.60	Eh, Sg, St		
80	10/09		54°37' W	11.71	35.03	Pd, Sp, St		
85	11/09		50°25' W	10.72	34.91	Pd, Sg, Sp		
86	12/09		50°52' W	11.74	35.12	Pd, Sg, St		
90	14/09		58°27' W	4.49	34.09	Sg		
91	15/09		58°59' W	4.62	34.12	Eh, Sg		
106	07/10		50°00' W	8.31	34.59	Sg, St		
107	07/10		50°00' W	11.39	35.10	Eh, Sl, Ss		
108	07/10		50°01' W	8.26	34.48	Sg, St		
109	08/10		50°02' W	10.96	35.00	Sg, Sh, Sp		
111	09/10		50°01' W	3.71	34.05	Eh, Sg		
112	10/10		49°18' W	3.63	34.03	Eh, Sg		
113	10/10		48°13' W	6.26	34.21	Sg		
114	10/10		47°10' W	8.67	34.48	Eh, Sg		
115	11/10		46°01' W	7.70	34.48	Eh, Sg, St		
118	12/10		44°59' W	7.84	34.41	Sg, St		
119	12/10	43°59' S	45°01' W	8.02	34.43	Sg, St		
121	13/10		45°00' W	10.20	34.68	Sg, St		
122	13/10	42°29' S	44°57' W	11.80	34.87	Pd, Sg, Sp, St		
123	13/10		45°00' W	11.80	34.87	Sg, Sp, St		
124	14/10	40°27' S	44°58' W	14.60	35.07	Sg, Sh, Sm, Sp, St		

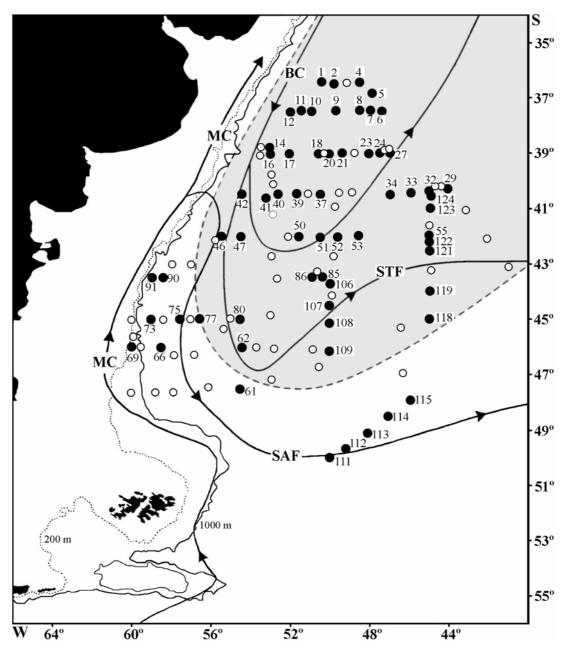


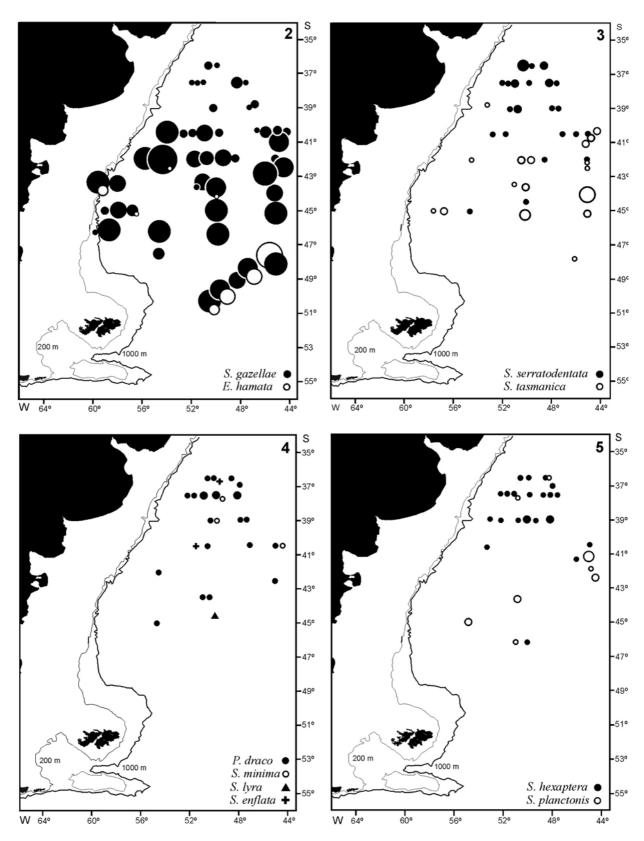
Fig. 1. Schematic representation of the surface hydrology of the surveyed area (adapted from PETERSON & STRAMMA, 1991) and position of sampling stations of Russian Research Vessel RTMA "EVRIKA" from August, 1st through October, 24th, 1988 (BC, Brazil current; MC, Malvinas (Falkland) current; SAF, Subantarctic front; STF, Subtropical Front; Grey area, Brazil-Malvinas (Falkland) confluence; black circles, chaetognath presence; white circles, chaetognath absence.

highest densities were found above 14 °C and 35.4 psu. Although the boundary of its southern distribution was established at 40° S (ALVARIÑO, 1969; PIERROT-BULTS & NAIR, 1991), we report its presence up to 45° 02' S.

Sagitta minima appeared in three stations with mixed water characteristics (14 - 15 °C, 35.5 - 35.6 psu) (fig. 8), in agreement with the observations by ALVARINO (1965, 1969). A low density of Sagitta lyra (9 ind. 1000 m⁻³) was found in only one station (44° 29' S), at 11.39 °C and 35.1 psu (fig. 8). Very few specimens of *S. enflata* were found in the study area, in two stations north of 41° S, at temperatures fluctuating between 12.6 and 14.4 °C and salinities between 34.5 and 35.5 psu (fig. 8).

Sagitta hexaptera was allocated north of 41° S, except for one specimen recorded at 46° 10' S, and its densities were low (<16 ind.1000 ⁻³). This species generally appeared in mixed waters with subtropical influence (13° - 16.7 °C, 35.4 - 35.9 psu) (fig. 9).

Sagitta planctonis was found in waters at 10.7 - 16.7 °C with salinities of 34.9 - 35.9 psu (fig. 9). The highest temperatures and salinities correspond to the northern stations. The present results confirm the presence of this species over the BMCZ, in the surface layers and in mixed water, especially regarding salinity, which in all of the stations exceeded the typical values for subantarctic waters.



Figs. 2-5: Distribution and abundance of the chaetognath species from Brazil-Malvinas (Falkland) confluence zone (from August, 1^{st} through October, 24^{th} , 1988). 2: *S. gazellae* and *E. hamata*; 3: *S. tasmanica* and *S. serratodentata*; 4: *P. draco, S. minima*, *S. lyra* and *S. enflata*; 5: *S. hexaptera* and *S. planctonis*. Ind./1000 m³:



	Α	group	В	group	C group		
Species	Presence (%)	Fidelity (%)	Presence (%)	Fidelity (%)	Presence (%)	Fidelity (%)	
Eukrohnia hamata	0	0	0	0	23	100 (0,0112)**	
Pterosagitta draco	70	70 (3,6.10-5)	13	5	16	25	
Sagitta gazellae	75	31	25	4	100	65 (1,8.10 ⁻⁵)*	
S. tasmanica	0	0	0	0	45	100 (4,2.10-6)**	
S. serratodentata	100	95 (6,7.10 ⁻¹⁶)*	13	5	0	0	
S. hexaptera	70	64 (0,0002)	100	36 (0,0001)*	0	0	
S. planctonis	15	43	13	14	10	43	
S. minima	10	100**	0	0	0	0	
S. enflata	10	100**	0	0	0	0	

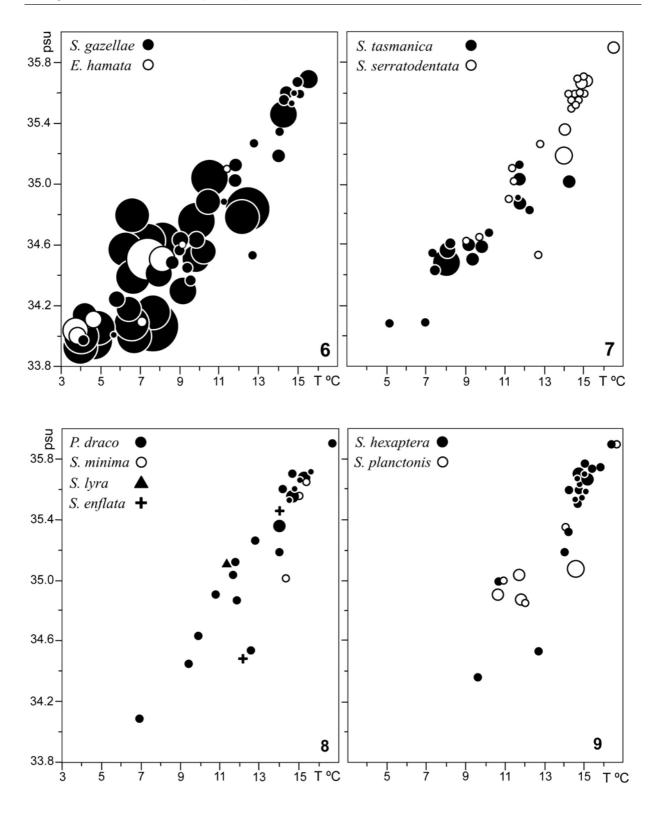
Table II. Presence and fidelity degrees between each species and each group (Ochiai-UPGMA). The probabilities of the positive significant associations (p<0,05) between species and group are in brackets; preferential species in bold; *, indicator species; **, exclusive species. *S. lyra* was found in a single outlier sample and is not indicated in the table.

The clustering of sample units (s.u.) according to the Ochiai qualitative index and UPGMA yielded three groups: A, B and C (fig. 10). Two outlier s.u. (stations 14 and 107) were excluded from the clustering. At the same time, the clustering using the Bray-Curtis quantitative index and UPGMA yielded three groups, which significantly corresponded with the ones found through the qualitative index ($p < 1.10^{-7}$). We preferred to use an index based on presence-absence data since such kind of indices generally produce more forceful results than quantitative ones, with regards to sampling biases and mistakes (GREEN, 1979). Moreover, the temporal or spatial dominance of a species or a small number of species does not involve changes in the qualitative composition of a community (Pérès & PICARD, 1964).

The analysis of presence and fidelity degree of the groups obtained with the Ochiai index (tab. II) yielded: group A (20 s.u.) with *S. serratodentata* as the indicator species, *P. draco* and *S. hexaptera* as preferential species, and *S. minima* and *S. enflata* as exclusive species. Group B (9 s.u.) only had *S. hexaptera* as indicator species. Group C (32 s.u.) had *S. gazellae* as indicator species, and *E. hamata* and *S. tasmanica* as preferential and exclusive species.

factorial The analysis of multiple correspondences of the contingency table among the groups of s.u., which were found with the Ochiai index and UPGMA, and salinity and temperature yielded a biplot (fig.11), which indicates that: group A was associated to the highest temperatures and salinities (13 - 18.0 °C and 35.4 - 36.2 psu); group B was also related to high temperatures and salinities; and group C was associated with the lowest temperatures and salinities in the studied area (3 - 8.0 °C and 33.5 - 34.6 psu). From these analysis it can be concluded that group C is highly differentiated from groups A and B. The differences between groups A and B may obey to the different proportions of slightly euryoecious species in both groups (best represented in A than in B). Sagitta hexaptera and P. draco were present in both groups, but A also included S. minima and S. *planctonis*. The relatively warm and saline conditions associated to groups A and B are related to waters influenced by the Brazil Current. The last conclusion allows us to consider groups A and B together, forming a great assemblage of stations associated to the same environmental (temperature and salinity) conditions. In contrast, the lower salinities and temperatures associated to group C would be typical of subantarctic waters.

Concerning S. gazellae, classified as an indicator species in group C, its presence in the other groups again reveals its wide tolerance to environmental conditions. Therefore, it cannot be considered as an indicator species of subantarctic water masses. Since S. serratodentata, classified as an indicator species in group A, was not detected in the group associated to cold water conditions, it can be properly defined as an indicator species of subtropical water masses, as pointed out by DADON & BOLTOVSKOY (1982). The mapping of the groups according to Ochiai-UPGMA shows two well-differentiated areas (fig. 12), one made up by the stations of groups A and B, scattered in the northern region of the sampled area and related to subtropical water conditions, and another one made up by the stations of group C, to the south and representing Subantarctic water conditions. The distribution of the different species of chaetognaths depends, among other factors, on the temperature and salinity of the water mass. Their highest densities are found under optimal development conditions, and decreased when approaching their distribution boundary. This fluctuation in density as well as in reproductive stages must be taken into account when determining the allocation range of the species. Accordingly, if specimens are found at very low densities or sterile, they might be considered expatriated organisms and may not reflect the real species range. In the area under analysis, the existence of species associated with higher temperatures and salinities (groups A and B), which were surrounded by species related to lower temperatures and salinities (group C), would indicate the presence of warm core eddies up to 46° S approximately, between September and October 1988 (fig. 12). These eddies would allow the presence of *P. draco* and *S. hexaptera* southward. The distribution patterns of the species detected confirm the hydrological complexity of the area analyzed.



Figs. 6-9: Temperature-salinity-density (T-S-D) diagram of the chaetognath species from Brazil-Malvinas (Falkland) confluence zone (from August, 1st through October, 24th, 1988). 6: *S. gazellae* and *E. hamata*; 7: *S. tasmanica* and *S. serratodentata*; 8: *P. draco*, *S. minima*, *S. lyra* and *S. enflata*; 9: *S. hexaptera* and *S. planctonis*. Ind./1000 m³:

• ▲ + 1-9; ● 10-49;	• 50-99;		100-199;		200-499;		500-999;		≥ 1000.	
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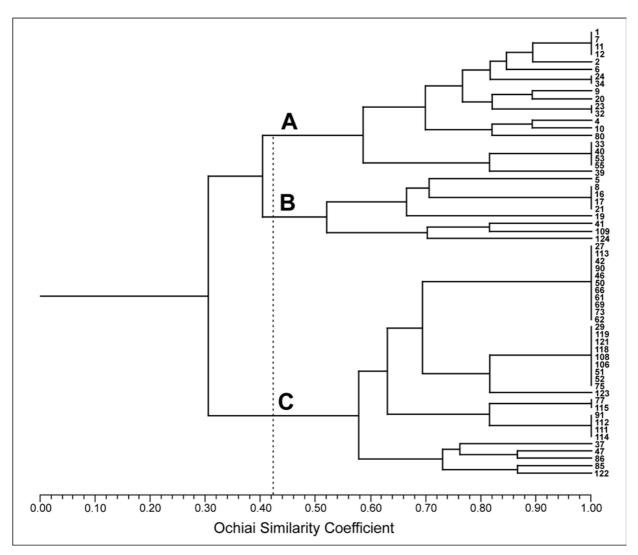


Fig. 10. Cluster analysis of sample units according to Ochiai index and UPGMA. Dot line: reference level.

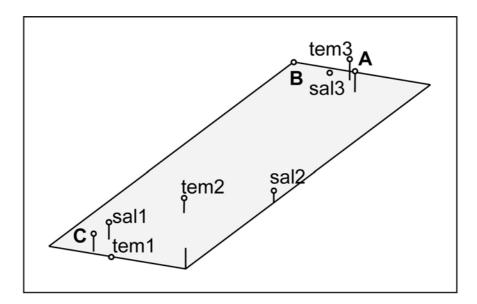


Fig. 11. Correspondence biplot among sample units groups (A, B and C), temperature and salinity (tem1, 3.0-8.0 °C; tem2, 8.0-13.0 °C; tem3, 13.0-18.0 °C; sal1, 33.5-34.6 psu; sal2, 34.6-35.4 psu; sal3, 35.4 - 36.2 psu).

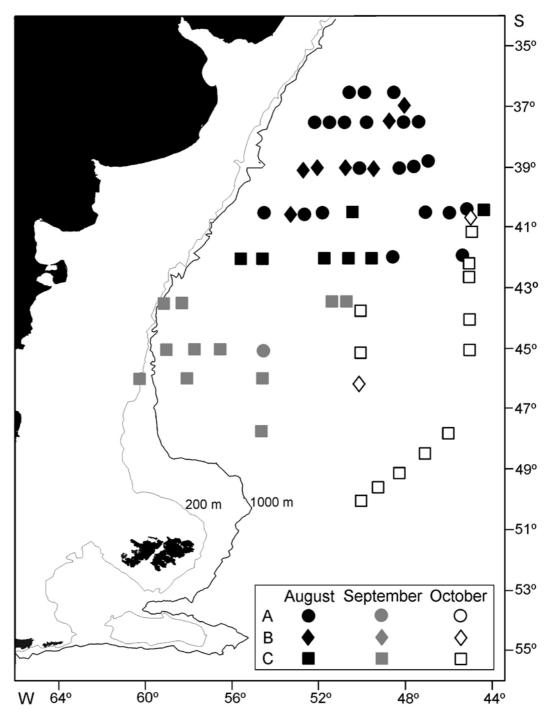


Fig. 12. Mapping of the sample unit groups (A, B, C) according to Ochiai-UPGMA in August, September and October 1988.

Acknowledgments. To Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) from Mar del Plata, Argentina, for providing the material studied and H. E. Zaixso, for the statistic advice.

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Recebido em outubro de 2003. Aceito em setembro de 2004. ISSN 0073-4721