Composition of Trichiuridae and Gempylidae larvae (Teleostei) and their association with water masses in the Southwest Atlantic Ocean

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Abstract

In this paper the relationship between temporal changes in the occurrence of water masses and Trichiuridae and Gempylidae larvae composition and distribution in the Southwest Atlantic ocean were analysed between 25° and 40° S. Ichthyoplankton was collected during the three expeditions of the Subtropical Convergence Project: Winter and Spring 1977, Autumn 1978 and Summer 1981, realized in the Southwest Atlantic waters. Oblique tows were conducted using a Hensen net with 250 µm mesh size. Steep salinity and temperature gradient were found, where the

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river outflows from La Plata river (Argentina) and Patos Lagoon (Brazil) met the Tropical Water over the continental shelf between 32 and 36° S. We examined 524 Hensen-net samples that contained about 283 larvae from five species of Trichiuridae and Gempylidae. The most abundant and frequent species were *Trichiurus lepturus* Linnaeus 1758 and *Diplospinus multistriatus* Maul 1948. The mesopelagic species *D. multistriatus*, *Nealotus tripes* Johnson 1865 and *Lepidopus altifrons* Parin & Collette, 1993 were associated with Tropical Water. The benthopelagic *T. lepturus* and the epipelagic *Thyrsitops lepidopoides* (Cuvier 1832) were associated mainly with Coastal Water and Subtropical Shelf Water.

INTRODUCTION

The Scombroids fishes of the family Trichiuridae and Gempylidae are commonly known as Cutlassfish and Snake Mackerels, respectively, and are found in the midwaters of the entire world ocean (Nakamura & Parin 1993). Juvenile individuals inhabit waters to depths of up to 100 m, while adults inhabit water layers deeper than 400 m (Jackowski 1994 apud Trella 2004). Most mesopelagic species make extensive vertical migrations into the epipelagic zone at night, where they prey on plankton and each other, and thereafter migrate down several hundred meters to their daytime depths (Salvanes & Kristoffersen 2001). Many species of Trichiuridae and Gempylidae are important for commercial fisheries (Nakamura & Parin 1993), like the Snoek (*Thyrsites atun* (Euphrasen, 1791)) in New Zealand (Trella 2004). Here juvenile specimens first migrate from the spawning grounds to shallower waters (< 100 m) and later move to deeper waters (below 400 m) (Stevenson 1996). In the ecosystem of Benguela, South Africa, the spawning grounds of this fish are located at depths ranging from 150 to 400 m (Griffiths 2002).

This family Gempylidae is composed of approximately 20 genus and 24 species (Nakamura & Parin 1993, Salvanes & Kristoffersen 2001), from which nine species (*Diplospinus multistriatus* Maul 1948, *Epinnula orientalis* Gilchrist and von Bonde, 1924, *Gempylus serpens* Cuvier 1829, *Lepidocybium flavobrunneum* (Smith 1843), *Nealotus tripes* Johnson 1865, *Neseiarchus nasutus* Johnson 1862, *Promethichthys prometeus* (Cuvier 1832), *Ruvettus pretiosus* Cocco 1829 and *Thyrsitops lepidopoides* (Cuvier, 1832) occur in the Brazilian waters (Zavala-Camin 1981, Sato 1983, Nakamura & Parin 1993). The Trichiuridae family includes 9 genus and 32 species (Nakamura & Parin 1993, Salvanes & Kristoffersen 2001), of which only six species occur in the study area (*Aphanopus carbo* Parin and Becker 1972, *Benthodesmus tenuis* (Günther 1877), *Benthodesmus elongatus* Clarke 1879, *Evoxymetopon taeniatus* Gill 1863, *Lepidopus altifrons* Parin and Collette 1993 and *Trichiurus lepturus* Linnaeus 1758).

Despite the fact that some of the most important fishery resources of Brazil are found in its southern continental margin (Haimovici et al. 1989,

Krug&Haimovic 1991), little is known about the ichthyoplankton ecology of the shelf break region (Franco&Muelbert 2003). Also, very little is known about specific larval abundance and distribution patterns of trichiurid and gempylid in Brazil with the exception of the distribution and abundance of *Thyrsopterus lepidopoides* larvae along the Southern coast, investigated by Sato&Matsuura (1986). Recent studies about ichthyofauna of Southern and Northeastern Brazil also present information about the occurrence of Trichiuridae and Gempylidae larvae (Nonaka et al. 2000, Franco&Muelbert 2003). In the study region, ichthyoplankton distribution is influenced by the dynamic of the Subtropical Convergence, by freshwater inflow from the Patos Lagoon and Rio de la Plata, by wind action on the surface of the ocean (Gordon 1989, Olson 1988, Freitas&Muelbert 2004), and by mesoscale physical processes such as anticyclonic (Franco et al. 2006) and cyclonic eddies (Hubold 1980a). *In situ* hydrographic data, NOAA/AVHRR images and merged TOPEX/POSEIDON + ERS-1/2 satellite altimetry revealed an anticyclonic eddy dominating the shelf around 31° S, when the larval fish abundance was lower at the centre of this feature. This suggests that the eddy advected poorer offshore waters of tropical origin towards the inner shelf, concentrating the larvae around the eddy (Franco et al. 2006).

The present paper analyzed the occurrence of the Trichiuridae and Gempylidae larvae, spatial and temporal distribution patterns of the species and evaluated the influence of water masses on them in the Southwest Atlantic Ocean.

MATERIALS AND METHODS

A total of 524 zooplankton samples were collected during four oceanographic expeditions run between 1977 and 1981 by the “Diretoria de Hidrografia e Navegação” (DHN, 1982) of the Brazilian Navy, and conducted by the research vessel “NOc. Almirante Saldanha”. The expeditions were made August – September of 1977 (winter), October – November of 1977 (spring), April - June of 1978 (autumn) and January – March of 1981 (summer). The station grid (Fig. 1) was arranged in profiles perpendicular to the coast and covered the coastal, shelf and oceanic waters as far as 300 nautical miles offshore. The distance between stations and profiles was approximately 30 miles, and on the continental shelf, additional stations were made at the depth contours of 20, 50, and 100 meters and at the shelf edge (700 – 800 m depth). At each station temperature and salinity were measured, using the methods recommended by Strickland&Parsons (1968). Zooplankton was sampled with one oblique tow from 5 m above the bottom, or through the upper 200 m layer, using a Hensen net with 80 cm mouth diameter, 260 cm long, made of 250 µm

nylon gauze. The net was equipped with a 16 kg hydrodynamic depressor, a TSK maximum depth recorder and a flowmeter. Towing speed of the oblique net was estimated as 2 m s^{-1} during the ascending phase. Average wire angle on the haul was 70° . The samples obtained were preserved in 4% borax buffered formalin – seawater. Zooplankton displacement volume (ZDV) was measured with a precision of 1 ml according Ahlstrom&Thraillkill (1963). The values were standardized to ml per m^3 and represent the upper 200 m layer through which the nets were hauled. Large organisms such as jellyfish were removed and measured separately. All the trichiurids and gempylids larvae were removed from each sample and were identified to the lowest possible taxonomic level according to the morphological characteristics of each group: Trichiuridae (Tsukahara 1961, Robertson 1980) and Gempylidae (Strassburg 1964, Nishikawa 1987, Sato&Matsuura 1986). The number of fish larvae collected was standardized to 10 m^2 (Smith&Richardson 1979).

Fig. 1. Oceanographic station grid off Southwest Atlantic Ocean during CONVERSUT Cruises.

Data analysis

Maps of the horizontal distribution of fish larvae and zooplankton were made using Surfer for Windows (Kekler 1995). A Multiresponse Permutation Procedure (MRPP) analysis was utilized, in order to prove the existence of significant differences between periods in the composition of fish larvae (McCune&Grace 2002).

The Detrended Canonical Correspondence Analysis (DCCA) was performed with all oceanographic variables to investigate the gradient length. Since the gradient was below 4 (2.99) the Redundancy Analysis (RDA) was employed. The criteria adopted for determination of characteristic species of Trichiuridae and Gempylidae were a relative abundance greater than 3%. Prior to analysis, logarithmic transformation $\ln(x+1)$ of larval density (x) was performed to homogenize the variance. The matrix created with the oceanographic data was submitted to a square root transformation to reduce the effect of different scales. A forward selection procedure sequentially tested the statistical significance of oceanographic variables ($p = 0.02$) that contributed most strongly to the canonical model through 499 Monte Carlo permutations. This procedure yielded an RDA model based on a set of oceanographic variables: depth, temperature, salinity and ZDV.

RESULTS

Oceanographic characteristics

The distribution patterns of the environmental variables were based on values measured at 10 m depth. They are taken to represent the conditions of the mixture layer where the trichiurid and gempylid larvae are concentrated. The hydrographical data of the all positive stations are presented in Table 1. During the winter, the salinity minimum of 28.2 PSU was measured over the continental shelf off Chuí on the Uruguay coast (34° S). The maximum salinity of 36 PSU appears only in offshore stations. On the Argentinean shelf (36° S) near the De la Plata river estuary salinity was 31.1 – 31.4 PSU and the gradients coast-offshore were most expressive (31 to 36 PSU).

During the spring, the salinity ranged from 36 to 37 PSU in the north and decreased towards the coast and to the south. On the Brazilian coast between Mostardas (31° 20' S) and Santa Marta (28° 50' S), salinities ranged from 35.4 to 35.7 PSU, and north of Santa Marta from 34.2 to 34.9. Salinity gradients were most expressive over the continental slope between Rio de La Plata and Mostardas.

During the summer the salinity ranged between 36.9 PSU in the north and 27.7 PSU off Rio de la Plata. The surface salinity was high (up to 36.0 PSU) in

the north oceanic area and on the Brazilian continental shelf between Santa Marta and Bom Abrigo. Salinities between 31.4 and 33.6 PSU were obtained at coastal areas off Chui and Mostardas. Over the shelf edge off Argentina and Uruguay, low salinity readings (below 31 PSU) were found.

During autumn the surface salinity was high (up to 36.9 PSU) in the oceanic areas beyond the continental shelf. In general, the 36.0 PSU isohaline closely followed the shelf edge and a steep salinity gradient towards the coastal waters was found over the shelf. Salinities between 33.1 and 34.9 PSU were found to the south of the La Plata estuary, and off the Uruguay and south Brazilian coasts salinities of 28.0 to 33.0 PSU were recorded. The salinity minimum was found close to the coast near Mostardas (26.0 PSU). The oceanic areas of relatively low salinity were observed at 52–53° W 38–40° S and 49° W 35° S with values between 34.4 and 35.7 PSU.

Temperatures of up to 24.2°C were measured in the north, during the spring, and the minimum temperature of 6.8°C occurred in the south, during the winter, over the edge of the continental shelf off Argentina. Steep temperature gradients were observed between 34° S and 40° S near the continental shelf and in the oceanic area at 50° W and 36° S.

Water temperature during summer ranged between 10.9 and 26.2°C, decreasing towards to the south. During summer the surface temperature was high (up to 24.0°C) in the north oceanic area and on the Brazilian continental shelf between Santa Marta and Bom Abrigo. Temperatures between 21 and 24°C were found between Chui and Mostardas. Over the shelf edge off Argentina and Uruguay, cold waters of 10.9 to 20.6°C were found.

During autumn, over the shelf edge off Argentina and the La Plata estuary, cold waters of 10.9 to 15.5°C were found. The shelf waters between La Plata and Santa Marta had 14.2 to 19.0°C, and a steep temperature gradient was found between the shelf and oceanic waters. The highest surface temperature was measured beyond the continental shelf off Chui at 23.4°C. High temperatures (between 18.4 and 22.5°C) were found in oceanic waters throughout the whole area.

Regarding the seasonal variation of the zooplankton biomass (ZDV), higher values were observed in summer and spring, mainly in the near shore zone.

Water masses

According to the T-S diagram, at the 10 m depth, four water masses were present (Fig. 2). The Tropical Water (TW) which is part of the southward flowing Brazil Current, was characterized by salinity >36 PSU and temperature >18.5°C (Campos et al. 1995). The South Atlantic Central Water (SACW) had salinity levels ranging from 34.2 to 36 PSU and temperatures between 6 and

Fig. 2. T-S diagrams for the positive oceanographic stations off Southwest Atlantic Ocean during CONVERSUT Cruises. (TW – Tropical Water, SACW – South Atlantic Central Water, STSW – Subtropical Shelf Water, CW – Coastal Water).

18.5°C (Silveira et al. 2001). The salinity of the Coastal Water (CW) oscillated between 31 and 35 PSU. Finally, Subtropical Shelf Water (STSW), characterized by the mixture of CW and SACW (Piola et al. 2000), had salinity levels ranging from 34 to 35.9 PSU and temperatures $>20^{\circ}\text{C}$.

CW and TW were found during all seasons (Table 1). During winter the Subtropical Shelf Water was observed in the convergence zone and extended towards the north under the Tropical Water layer at depths of 100 to 300 m. During spring, Tropical Water was found from Chuí in the south towards the north in a layer varying in thickness from 50 to 300 meters, indicating that the main branch of the Brazil Current flowed southwards, near the edge of the continental shelf, in eddies of 60 to 100 nautical miles, that cause upwelling of deep water layers in the centre of these cyclonic movements. These cyclonic eddies and resulting upwellings were observed in the oceanic parts of Subtropical Convergence along the 40°S latitude (Lenz 1975 apud Hubold 1980a). The STSW also approached the surface near Santa Marta, where a coastal upwelling area was also indicated by Castello and Moller (1977). Three principal water masses were identified during autumn: Tropical Water, South Atlantic Central Water and Coastal Water. The summer was characterized by three principal water masses: Tropical Water, Subtropical Shelf Water and Coastal Water. In both seasons direct mixing processes were observed between Tropical Water and Coastal Water.

Larvae composition

A total of 283 larvae representing two species of Trichiuridae (*Trichiurus lepturus* Linnaeus 1758 and *Lepidopus altifrons* Parin&Collette 1993) and three

Table 1

Position and hydrographical data of the positive stations on the Southwest Atlantic Ocean during CONVERSUT Cruises.

Season	Stations	Latitude (S)	Longitude (W)	Local Depth (m)	Temperature (°C)	Salinity (PSU)	Volume filtered (m ³)	ZDV (ml 100 m ⁻³)	Water mass
Winter	4530	3816	5258	3500	10.31	34.43	658	23	SACW
	4561	3515	5228	590	16.53	33.21	518	39	STSW
	4563	3609	5021	3500	13.67	34.93	330	9	SACW
	4565	3556	4953	3500	14.06	35.08	676	14	SACW
	4585	3345	5046	1050	18.50	32.27	542	7	STSW
Spring	4586	3323	5117	100	16.30	30.30	232	13	CW
	4593	3305	5047	100	18.60	32.05	22	9	CW
	4605	3222	5028	102	19.33	32.43	171	28	CW
	4606	3214	5047	80	18.85	32.84	196	14	CW
	4607	3155	5107	50	17.33	35.12	144	22	SACW
	4610	3126	5043	53	16.83	35.58	219	41	SACW
	4622	3136	4911	3000	20.62	34.65	685	11	STSW
	4624	3105	4950	143	20.91	34.95	364	27	STSW
	4625	3056	5004	100	20.66	35.87	269	34	STSW
	4657	2921	4848	100	19.83	35.39	284	20	STSW
	4668	2815	4806	100	23.19	34.18	290	19	STSW
	4670	2900	4655	1500	23.91	36.44	393	12	TW
	4672	2936	4600	3000	23.12	36.35	293	23	TW
	4673	2955	4537	3000	23.41	36.34	552	8	TW
	4674	3013	4515	3000	23.08	36.55	484	9	TW
	4678	2904	4524	3000	23.89	36.98	534	7	TW
	4679	2846	4545	2800	23.60	36.90	584	6	TW
	4680	2833	4608	1500	24.16	37.06	526	6	TW
	4681	2813	4637	1500	24.14	37.00	564	6	TW
	4702	2657	4618	540	23.72	36.79	80	5	TW
	4703	2623	4725	97	22.84	35.62	30	19	CW
Autumn	4817	3605	5305	170	17.14	34.39	395	6	CW
	4830	3451	5250	100	17.25	34.03	148	21	CW
	4839	3429	5211	100	18.08	34.64	209	22	TW
	4846	3350	5142	100	20.70	35.90	166	16	TW
	4847	3400	5124	780	21.15	35.90	409	7	TW
	4864	3306	5040	100	20.54	36.42	211	6	TW
	4905	3036	4914	145	20.66	36.29	204	6	TW
	4934	3007	4639	2500	22.03	36.76	401	7	TW
	4935	2947	4707	2300	22.41	36.82	313	5	TW
	4936	2928	4735	1800	22.15	36.73	414	4	CW
	4939	2853	4826	98	17.37	31.70	186	15	CW
	4940	2839	4847	47	18.19	33.96	77	5	TW
	4944	2846	4721	780	22.50	36.54	178	9	CW
Summer	5685	3634	5451	58	20.66	31.41	118	32.3	CW
	5739	3315	5131	54	24.62	35.09	81	25	STSW
	5743	3234	5130	50	24.15	33.05	63	20.5	CW
	5744	3250	5105	60	25.04	34.39	386	4.7	STSW
	5745	3304	5040	100	25.44	35.05	182	23.1	STSW
	5757	3210	5049	80	24.56	34.99	93	19.8	STSW
	5758	3157	5109	50	24.33	33.65	53	35.8	CW
	5759	3153	5117	20	24.44	33.54	22	68.2	CW
	5761	3122	5044	50	25.00	34.69	70	39.3	STSW
	5762	3134	5036	100	24.60	34.22	92	41.5	STSW
	5775	3059	5006	98	24.88	34.83	306	22.2	STSW
	5776	3051	5017	51	25.19	34.84	58	32.9	STSW
	5791	3035	4756	988	26.14	36.61	264	6.4	TW
	5795	2937	4922	50	24.67	34.54	87	20.7	STSW
	5796	2923	4939	27	25.40	36.11	54	28.9	STSW
	5841	2811	4430	3358	24.88	36.30	18		TW

species of Gempylidae (*Diplospinus multistriatus* Maul 1948, *Thyrsopterus lepidopoides* (Cuvier 1832) and *Nealotus tripes* Johnson 1865) were identified in the Southwest Atlantic Ocean (Table 2). *T. lepturus* and *D. multistriatus* were the most dominant species (Table 2), comprising 82% of the larvae composition. *T. lepturus* was the most abundance species (48%), with a minimum density of 2.7 larvae 10 m⁻² during spring and maximum density of 89.2 larvae 10 m⁻² during summer. *D. multistriatus* was the second most abundant species (Table 2), representing 34.3% with a minimum density of 0 larvae 10 m⁻² during summer and a maximum density of 206.8 larvae 10 m⁻² during winter. *L. altifrons*, *T. lepidopoides* and *N. tripes* represented 8.1%, 7.8% and 1.8%, respectively. The MRPP analysis showed a significant difference ($p = 0.00174$) in the composition of fish larvae denoting temporal variability in the composition of trichiurid-gempylid larvae.

Table 2

List of Gempylidae taxa, their origin (MP - mesopelagic; EP - epipelagic), period, abundance, minimum and maximum density (larvae 10 m⁻²) and frequency of occurrence (%) on the Southwest Atlantic Ocean during CONVERSUT Cruises.

Taxa	Origin	Period	Abundance	Minimum density	Maximum density	Frequency of occurrence
<i>T. lepturus</i>	Benthopelagic	Spring	24	2.7	81.8	9.5
		Summer	94	3.3	89.2	6.7
		Autumn	18	3.6	21.7	5.3
<i>L. altifrons</i>	Benthopelagic	Spring	14	2.3	24.0	8.4
		Autumn	9	9.2	18.8	2.3
<i>D. multistriatus</i>	Mesopelagic	Winter	83	5.6	206.8	6.3
		Spring	8	2.8	15.2	8.4
		Summer	6	0.0	158.3	1.0
<i>T. lepidopoides</i>	Epipelagic	Spring	5	2.3	6.7	3.2
		Summer	17	4.6	14.1	1.5
<i>N. tripes</i>	Mesopelagic	Spring	5	10.8	19.2	2.1
Total			283			

Spatial and temporal distribution of species

The trichiurid larvae were collected more frequently in the shelf break region of the Southwest Atlantic. However, gempylid larvae were collected more within the oceanic zone (Fig. 3). *Trichiurus lepturus* Linnaeus 1758 presented a large distribution occurring in the neritic region, during spring, summer and autumn. The maximum density was verified during summer on the continental shelf between Santa Marta and Rio Grande. *Diplospinus multistriatus* Maul 1948 larvae were collected in winter, spring and summer, with the maximum density during winter in the oceanic south area between

Fig. 3. Spatial distribution of Trichiuridae and Gempylidae larvae on the Southwest Atlantic Ocean.

Chuí and La Plata River. *Thyrstips lepidopoides* (Cuvier, 1832) larvae were found predominantly in the neritic stations during spring and summer. The highest density occurred between Patos Lagoon and La Plata River during summer. *Lepidopus altifrons* Parin&Collette, 1993 occurred mainly in the oceanic stations, between Bom Abrigo and Santa Marta, during spring and autumn. *N. tripes* occurred only in spring in Santa Marta.

Table 3

Range of area, depth, temperature, salinity, zooplankton displacement volume and water mass, on the four periods and in the presence of trichiurid and gempylid larvae.

Period	Area (° S - ° W)	Depth (m)	Temperature (°C)	Salinity (PSU)	ZDV (ml 100 m ⁻³)	Water mass
Winter 1977	35.0 – 40.0	19 – 4300	6.8 – 19.0	28.2 – 36.0	3.0 – 78.0	CW, STSW, TW SACW
Spring 1977	25.0 – 35.0	20 – 3800	16.0 – 24.2	29.0 – 37.1	1.0 – 98.0	CW, STSW, TW
Autumn 1978	28.0 – 40.0	15 – 5000	10.9 – 23.4	26.0 – 36.9	1.0 – 258.0	CW, STSW, TW
Summer 1981	26.0 – 40.0	20 – 4198	19.7 – 26.1	27.7 – 36.9	1.4 – 274.7	CW, STSW, TW
<i>T. lepturus</i>						
Spring	30.5 – 33.4	50 – 1050	16.3 – 20.9	30.3 – 35.9	7.0 – 41.0	CW, STSW
Summer	29.2 – 33.1	20 – 100	24.2 – 26.2	33.1 – 36.1	4.7 – 68.2	CW, STSW, TW
Autumn	28.4 – 36.0	47 – 700	17.1 – 21.2	31.7 – 36.3	4.0 – 22.0	CW, STSW, TW
<i>L. altifrons</i>						
Spring	26.6 – 31.4	100 – 3000	19.8 – 24.2	35.0 – 37.1	5.0 – 27.0	TW, STSW
Autumn	28.5 – 30.1	780 – 2500	22.0 – 22.4	36.5 – 36.8	4.0 – 9.0	TW
<i>D. multistriatus</i>						
Winter	35.3 – 38.0	590 – 3500	10.3 – 16.5	33.2 – 35.1	9.0 – 39.0	SACW
Spring	28.0 – 30.0	1500 – 3000	22.8 – 24.0	34.2 – 36.0	6.0 – 9.0	TW, STSW
Summer	28.0 – 30.3	988 – 3358	24.9 – 26.1	36.3 – 37.1	6.4	TW
<i>T. lepidopoides</i>						
Spring	27.2 – 31.0	100	19.8 – 23.2	34.2 – 35.9	19.0 – 34.0	STSW
Summer	31.3 – 36.3	50 – 60	20.7 – 25.0	31.4 – 34.7	4.7 – 39.3	CW
<i>N. tripes</i>						
Spring	29.0 – 29.5	1500 – 3000	23.1 – 23.9	36.3 – 36.4	12.0 – 23.0	TW

Correlations between fish larvae and water masses

The benthopelagic *Trichiurus lepturus* Linnaeus 1758 and the epipelagic *Thyrsitops lepidopoides* (Cuvier 1832) were associated mainly with Coastal Water and Subtropical Shelf Water. The mesopelagic *Diplospinus multistriatus* Maul 1948 was associated with Tropical and Subtropical Water and occasionally with South Atlantic Central Water (winter). The benthopelagic *Lepidopus altifrons* Parin&Collette, 1993 and the mesopelagic *N. tripes* were associated with Tropical Water (Table 3).

The higher *T. lepturus* densities were found in a wide temperature range between 16.3 and 26.2°C. The salinity of all positive stations varied from 30.3 to 36.3 PSU and ZDV variation was between 4 and 68.2 ml 100 m⁻³. Temperature variation in positive stations of *T. lepidopoides* was between 19.8 and 25.0°C. Salinity variation was between 31.5 and 35.9 PSU. ZDV variation was between 4.7 and 39.3 ml 100 m⁻³. The higher *D. multistriatus* densities

occurred between 10.3 to 26.1°C. The salinity variation was between 33.2 and 37.1. *D. multistriatus* larvae were found in ZDV range between 6 and 39 ml 100 m⁻³. The higher *L. altifrons* densities were found in a wide temperature range between 16.3 and 20.9°C. The salinity of all positive stations varied from 35.0 to 37.1 PSU and ZDV variation was between 4 and 27 ml 100 m⁻³. Temperature variation in positive stations of *N. tripes* was between 23.1 and 23.9°C. Salinity variation was between 36.3 and 36.4 PSU. ZDV variation was between 12 and 23 ml 100 m⁻³ (Table 3).

A Redundancy Analysis based on a reduced set of 4 environmental variables (depth, temperature, salinity and ZDV) was performed to verify the existence of an ordination between species and respective samples. Eigenvalues, measures of importance for RDA axes that may vary between zero and one, ranged from 0.274 for RDA 1 to 0.001 for RDA 4 (Table 4). Species-environment correlations were high for the two first RDA axes, ranging from 0.826 to for RDA 1 to 0.475 for RDA 2. The combined sum of canonical eigenvalues (0.337) equalled 33.7% of that for all eigenvalues (1.0), showing the effect of adequately building environmental relationships into the RDA model. The cumulative percentage of species variance (CPSV) accounted for the RDA totalling 33.7% for the first four RDA axes. Furthermore, the first two RDA axes explained 98.6% of the cumulative percentage of the species-environment (CPSE). Because the first two RDA axes explained 33.3% of the CPSV and 98.6% of the CPSE, the latter two RDA axes were not further interpreted.

The low multiple regression coefficients of environmental variables indicated that there were not collinear variables. This result is important because

Table 4

Results from Redundancy Analysis (RDA) of 4 cases of species occurrence in 55 collections of ichthyoplankton from the South Atlantic Ocean.

AXES	RDA			
	1	2	3	4
Eigenvalues	0.274	0.059	0.004	0.001
Species-environment correlations	0.826	0.475	0.134	0.090
Cumulative percentage variance of species data	27.4	33.3	33.6	33.7
Cumulative percentage variance of species-environment relation	81.2	98.6	99.7	100
Sum of all eigenvalues			1.000	
Sum of all canonical eigenvalues			0.337	

multicollinear variables must be deleted from the analysis, since collinear variables can influence the canonical coefficients (Ter Braak 1986). The plot of RDA sample and species scores illustrates their dispersion pattern, and the plot of environmental variables vectors illustrates the directions and strengths of environmental relationships within the first two dimensions of the RDA ordination (Fig. 4). Strong environmental gradients were important correlates with the abundance of trichiurid-gempylid larvae in the RDA. The depth, ZDV and salinity correlated particularly well with the RDA axis 1 and the temperature water correlated well with the RDA axis 2. These environmental gradients also reflected the spatial and temporal changes in the species density. *T. lepidopoides* was negatively correlated with the first and second RDA axes. *D. multistriatus* was positively correlated with the first and second RDA axes. *L. altifrons* was positively correlated with the first axis and negatively correlated with the second axis and *T. lepturus* was negatively correlated with the first axis and positively correlated with the second RDA axis. This implied that *T. lepidopoides* and *T. lepturus* occurred mostly at high water temperature and ZDV during summer. *D. multistriatus* appeared preferentially during the winter at high depth and low temperature and ZDV, whereas *L. altifrons* predominantly occurred at high salinity and depth during spring and autumn (Fig. 4).

Fig. 4. Ordination diagram of the Redundancy Analysis (RDA) (1-Winter, 2-Spring, 3-Autumn, 4-Summer).

DISCUSSION

The Brazil Current carries Tropical Water southwards along the Brazilian continental slope and meets the subantarctic Malvinas (Falkland) Current off the Rio de la Plata estuary between 35° and 40° S (Hubold 1980a). The meeting zone is considered the western extreme of the Brazil-Falkland confluence zone (Goni et al. 1996, Willson&Rees 2000). The seasonal shifting of the convergence affects the shelf and coast waters of Argentina, Uruguay and southern Brazil (Hubold 1980a). When the BC leaves the South Brazil Bight, just north of the study area, it bifurcates into two branches. One branch flows along the 2000-m isobath carrying most of the current volume. A weaker inshore branch flows along the 100-m isobath as a coastal component of the BC and may induce the formation of small eddies (~100 km radius) through shear instability process (Soares&Mooller 2001, Souza&Robinson 2004, Franco et al. 2006). These eddies, of 60 to 100 nautical miles diameter, cause upwelling of deep water layers in the centers of cyclonic movements (Hubold 1980a). The water mass that upwells in the Brazilian southwest coast is the South Atlantic Central Water (Ciotti et al. 1995, Resgalla Jr. et al. 2001).

The thermal structure of the region varied between 6.8° and 26.2°C, with a maximum to the northeast of the study area associated with waters of salinity values higher than 36 PSU. These values indicated the influence of Tropical Water (TW) transported by the Brazil Current (BC). The TW was found above the South Atlantic Central Water (SACW, 6-20°C and 34.5-36 PSU). The Subtropical Shelf Water (STSW) was observed over the shelf and shelf break. It was also possible to verify the existence of a Coastal Water (CW) mass with warmer and less saline waters (31 – 34 PSU). The thermohaline characteristics of the Coastal Water (CW) vary according to the annual cycle of river runoff and mixing with offshore waters (Ciotti et al. 1995). The Scombroids were associated with water masses from the Southwest Atlantic Ocean. *Trichiurus lepturus* Linnaeus 1758 and *Thyrsitops lepidopoides* (Cuvier 1832) were associated mainly with Coastal Water and Subtropical Shelf Water. The *Diplospinus multistriatus* Maul 1948 was associated with Subtropical Water and occasionally with South Atlantic Central Water. *Lepidopus altifrons* Parin&Collette, 1993 and *Nealotus tripes* Johnson 1865 were associated with Tropical Water. Batch spawning of most Scombroids species takes place in tropical and subtropical waters, frequently inshore (Collette&Nauen 1983). Mesopelagic fishes exhibit batch spawning with repeated spawning throughout a prolonged season of several months (Salvanes&Kristofersen 2001).

The chlorophyll *a* concentration at the surface varied from 0.02 mg m⁻³ to 3.4 mg m⁻³ during the spring, from 0.02 to 22.4 mg m⁻³ during the winter and from 0.02 to 9.54 mg m⁻³ during the autumn. The low values (0.02 -0.5 mg m⁻³)

were found in the oceanic parts of the area. High values ($>2.0 \text{ mg m}^{-3}$) were localized on the continental shelf between Santa Marta and Rio Grande and on the Uruguayan coast and in the La Plata estuary (Hubold 1980a,b). In spring and autumn *T. lepturus* and *T. lepidopoides* larvae occurred mostly at areas with high ZDV and chlorophyll *a* concentrations on the continental shelf between Santa Marta and Rio Grande. The weak offshore Ekman transport in the interior regions of the Bight associated with a closed geostrophic circulation prompt the suggestion that spawning in this coastal region would be favorable to the reproductive success of fish species inhabiting the southeastern and southern continental shelf of Brazil (Bakun&Parish 1990, Freitas&Muelbert 2004). *D. multistriatus* larvae were also found during winter in oceanic areas with high ZDV and chlorophyll *a* concentrations but *L. altifrons* and *N. tripes* appeared only in the north oceanic areas with low ZDV and chlorophyll *a* concentrations. Other authors, too, observed a tendency for spatial segregation between the abundance of zooplankton and larval fish (Katsuragawwa et al. 1993, Resgalla Jr et al. 2001).

During winter and spring the convergence zone of Tropical and Subantarctic Water (Brazil Current and Malvinas Current) was localized at 53° W and $35 - 39^\circ \text{ S}$, in a northeast to southwest extension (Hubold 1980a), and the mixed waters were defined as Subtropical Water where *D. multistriatus* larvae were found in high densities. The STSW front, characterized by an accentuated termohaline gradient, promotes stability along the water column favoring the aggregation of planktonic organisms. In this way, the shelf break region generates favorable areas for the spawning of fish and for the development of early larval stages of some families (Franco&Muelbert 2003).

During autumn the convergence zone was localized at $53 - 55^\circ \text{ W}$ and $35 - 40^\circ \text{ S}$, in a northeast to southwest extension. The position of the convergence varied less than 2° in latitude between the research periods, but during autumn, due to the strong influence of the Tropical water beyond the continental shelf in the entire area, the oceanic parts of the Subtropical Convergence were shifted southwards out of the investigation area (Hubold 1980b) and no Trichiurid-Gempylid larvae were captured in the convergence zone.

In the Southwest Atlantic Ocean five species of Trichiurid-Gempylid larvae were identified, with *T. lepturus* and *D. multistriatus* being the most dominant species. Each species showed a preference for a particular season; *T. lepturus* and *T. lepidopoides* for summer, *D. Multistriatus* for winter and *L. altifrons* and *N. Tripes* for spring. This study showed that the Scombroids fishes presented similar reproductive strategies, spawning at a favorable period for each species, adjusting their reproductive patterns to the environmental factors. *T. lepturus* and *T. lepidopoides* larvae had the highest densities in less saline waters and in

higher temperatures and ZDVs in comparison to the *L. altifrons*, *D. multistriatus* and *N. tripes*. There was spatial and temporal variation in the distribution and abundance, and possibly in the reproductive cycle of the Trichiurid-Gempylid species. Variation in the oceanographic environment may cause interannual changes in both the distributional range of the adult fish and in the features of their spawning environment (Doyle et al. 1993). Examining the spatial and temporal patterns in the distribution and abundance of ichthyoplankton in relation to the oceanographic conditions may provide insight into the adaptation of the spawning strategies to the prevailing physical and biological processes as well as into the effect of the variability in these processes on year – class strength (Somarakis et al. 2002).

All Trichiurid-Gempylid adult fishes have a subtropical pelagic distribution between epi- benthic- and mesopelagic habitats. *T. lepturus* Linnaeus 1758 (Largehead hairtail) has a benthopelagic distribution to 350 m in the Western North Atlantic (WNA) from Cape Cod to Brazil (Nakamura&Parin 1993). *L. altifrons* Parin&Collette, 1993 (Crested scabbardfish) is a benthopelagic species from the Western Atlantic off the Scotian Shelf of Canada to off southern Brazil. *T. lepidopoides* (Cuvier 1832), the White snake mackerel, is an epipelagic species from the South Atlantic Ocean (Sato&Matsuura 1986). *N. tripes* Johnson 1865 (Black snake mackerel), a vertical migrant, in the WNA from the Grand Banks to Brazil, is epi- to mesopelagic to 600 m (Nakamura&Parin 1993). *D. multistriatus* Maul 1948 (Striped scolar) is mesopelagic to 1000 m in the WNA from the Grand Banks to Brazil (Zavala-Camin 1981, Nakamura&Parin 1993). The fish stocks and their relation to the Subtropical Water seem to be a promising aim for fisheries prospection (Hubold 1980a).

In the Santa Marta Grande Cape (29° S), the continental shelf gradually narrows (Castro&Miranda 1998), allowing the influence of the SACW in the area. This could be identified by low temperature (21°C) and salinity higher than 34 closer to the shore (Freitas&Muelbert 2004). The study area, between 27° S to 31° S, is characterized by an upwelling process over the continental shelf (Castello&Moller 1977; Hubold 1980a, 1980b; Odebrecht&Djurfeldt 1996; Resgalla Jr. et al. 2001). In this coastal region, wind action can promote an offshore displacement of water masses by Ekman transport, and when this happens, upwelling of deep waters to the euphotic zones may occur, resulting in modifications in the structure of pelagic communities (Resgalla Jr. et al. 2001). If spawning occurred during the strong upwelling season, larvae would be carried offshore (Freitas&Muelbert 2004). Normally the early life stages of epipelagic populations are passively transported long distances which means high advective loss, but no particular long-distance drift patterns are yet known

for mesopelagic fishes and this may reflect lower advective loss (Salvanes&Kristofersen 2001).

The results of this study demonstrate that the water masses appear to influence the abundance of the Scombroids species, allowing that each species had a period and place more favourable to spawn in the Southwest Atlantic Ocean.

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