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Influence of Agulhas waters on the population structure of planktonic Cnidarians in the southern Benguela Region*

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SUMMARY: During the Austral summer the southern Benguela system receives large inputs of warm, saline water from the Agulhas Current. These intrusions exert an enormous influence on the hydrographic structure in the region between Cape Infanta and Cape Columbine. The advection of Agulhas water coincides with coastal upwelling in the region, and together they strengthen a thermohaline front that extends along the entire continental shelf. This mesoscale hydrographic configuration in turn regulates the structure of the zooplankton populations. Siphonophore and medusae populations in January 1978 were compared to those in August 1977, when intrusions by Agulhas water and upwelling were minimal, in order to determine the extent of the influence of this configuration on the gelatinous zooplankton in the region. More species and individuals were collected in January 1978 than in August 1977, because of the penetration by Agulhas water. There was a distinct inshore-offshore gradient, with more species and individuals offshore, primarily concentrated between Cape Agulhas and Cape Columbine, close to the front, along the edge of the continental shelf. The distribution pattern was the same in both months, though species abundances were varied. The relationship between the distribution pattern and mesoscale hydrographic structures and the possible effects of the gelatinous zooplankton on the abundance of other zooplankton are discussed.

Key words: Planktonic cnidarians, Zooplankton, community structure, southern Benguela, Agulhas waters.

INTRODUCTION

The waters of the Benguela System off the southwestern coast of Africa form one of the world's most productive regions (CRAWFORD *et al.*, 1987). A regime of episodic winds blowing along the coast towards the Equator drives semi-permanent upwelling (HART and CURRIE, 1960). The Benguela Current flows along the coast between 34° S and 17° S and is bounded by the Angola Current in the north and the Agulhas Current in the South (SHANNON, 1985). The Benguela System can be divided into northern and southern areas, each with its own oceanographic characteristics, separated by an area located off Lüderitz where the upwelling is permanent (SHANNON, 1985; AGENBAG and SHANNON, 1988).

The Southern Benguela is highly complex hydrographically, because South Atlantic Surface Water and the Agulhas Current meet and mix with South Atlantic Central Water upweller inshore (HUTCHINGS *et al.*, 1986; SHELTON, 1986). Upwelling in the Southern Benguela is seasonal, ocurring from September to April and reaching a peak in January and February (ANDREWS and HUTCHINGS, 1980). The upwelling regime and the inputs of Agulhas water are the two hydrodynamic features with the greatest impact on hydrographic structures in the region. During the Austral winter upwelling abates and the Agulhas Current water is barely detectable inshore, and consequently temperature and salinity gradients are weak. In contrast, during summer these factors peak

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and combine to give rise to a strong thermohaline front between Cape Agulhas and Cape Columbine along the edge of the continental shelf (HUTCHINGS *et al.*, 1986; SHELTON, 1986).

LUTJEHARMS (1981) developed a conceptual picture of the effect of the Agulhas Current on the Southern Benguela. The Agulhas Current is one of the most important western boundary currents in the Southern Hemisphere. It penetrates onto the continental shelf off eastern South Africa, and around 21-22° E turns southward under the influence of both the shelf topography and the southern Indian Ocean anticyclonic gyre. Eddies from the main current penetrate onto the Agulhas Bank and continue westward towards the Cape of Good Hope.

Hydrodynamic processes like the one described above have an important influence on the mesoscale structure of zooplankton communities, because the western boundary current area contains a highly diverse plankton community composed of a mixture of species from the Atlantic and Indian oceans (OLSON, 1986).

Earlier work on zooplankton in the region (e.g., DE DECKER, 1973, 1984) emphasised the importance of inputs by Agulhas Current water on increased zooplankton density and diversity in summer. This enrichment process affects the gelatinous zooplankton, which is particularly susceptible to mesoscale advective processes (COLEBROOK, 1977; GILI *et al*, 1991; PAGÈS and GILI, 1991). These organisms can have a major impact on the food web in littoral planktonic systems (ALLDREDGE, 1983), but their role in the planktonic system in the Benguela region is poorly known (SHANNON and PILLAR, 1986). The object of the present study is to examine the influence of Agulhas Current water on the main gelatinous zooplankton populations in the Southern Benguela (Fig. 1) and to compare the abundance and distribution patterns of these organisms during the Austral summer and Austral winter, when totally different hydrodynamic conditions prevail.

MATERIAL AND METHODS

The Southern Benguela was studied by means of monthly surveys under the Cape Egg and Larval Programe (CELP) from August 1977 to August 1978, continuing less regularly until November 1982 (SHELTON, 1986). The present paper considers surveys con-

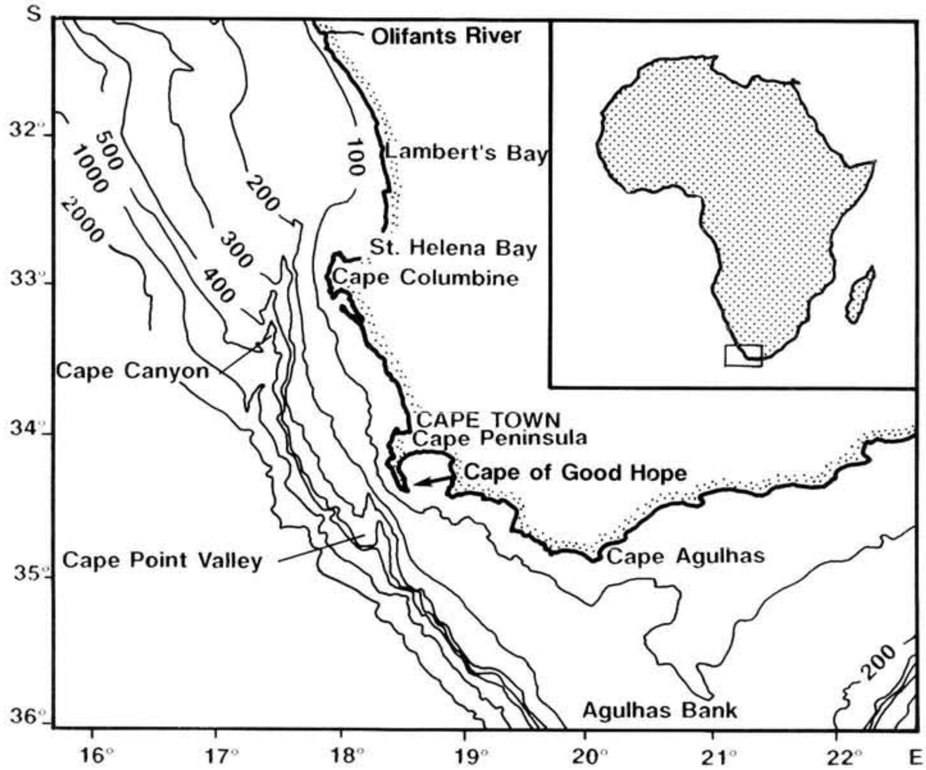

FIG. 1. — Cape Egg Larval Program (CELP) survey grid for the southern Benguela Current region sampled in August 1977 and January 1978 and general topography of the survey area (depth contours in metres).

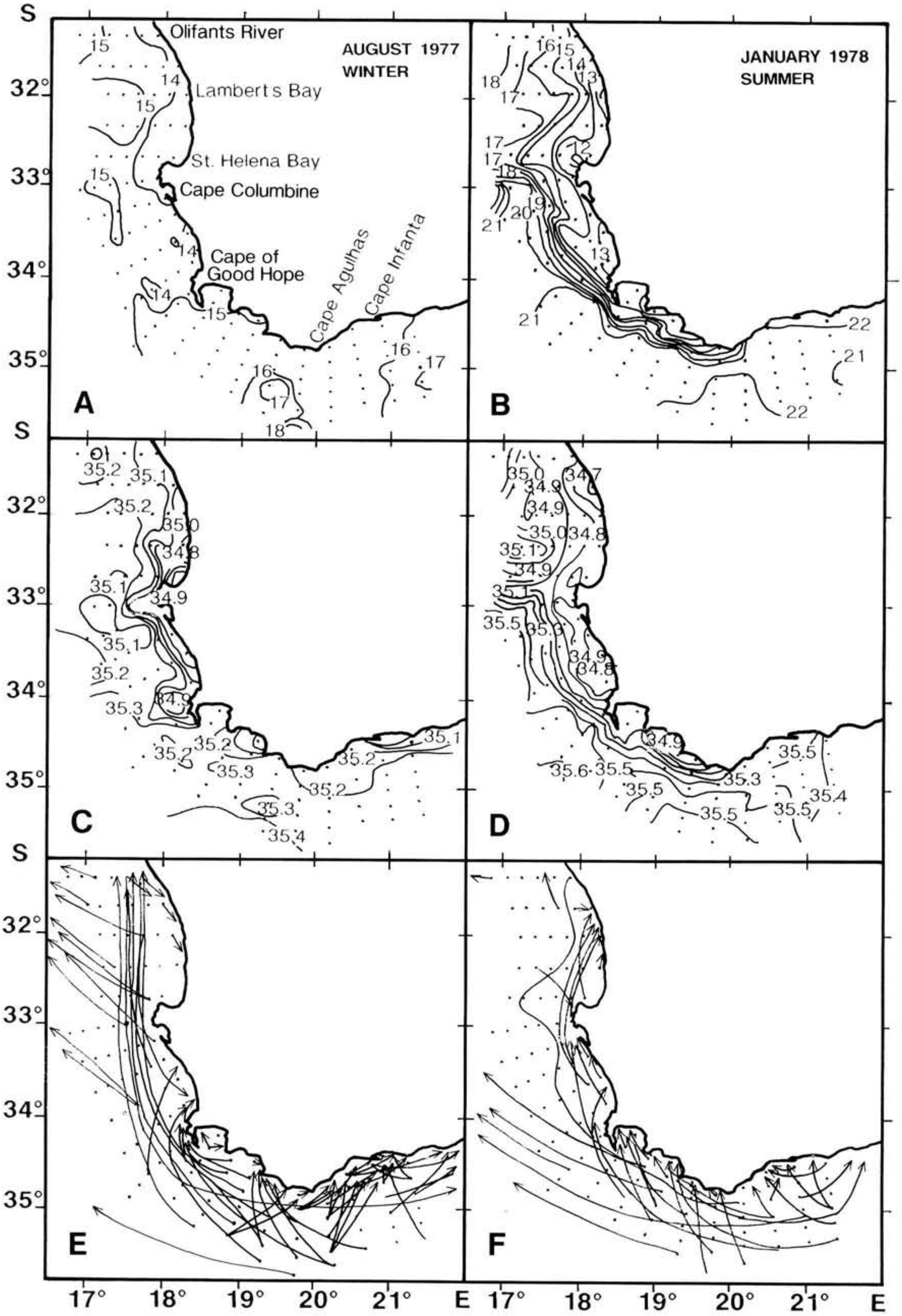

FIG. 2. — A and D: sea surface temperature measurements during the CELP surveys showing the seasonal pattern of horizontal gradients; B and E: surface salinity values; C and F: patterns of surface flow in the southern Benguela Current region in winter and summer gauged from drift-card recoveries from releases of 20 cards at each station in August 1977 and January 1978; arrows may represent more than one recovery and indicate general direction of flow (from SHELTON, 1986).

ducted from 19 to 28 August 1977 and from 7 to 20 January 1978. Sampling covered the continental shelf off South Africa between the Olifants River (31° 30′ S) and Cape Infanta (34° 30′ S) (Fig. 1).

The zooplankton samples were collected at 120 stations using a Bongo net 57 cm in diameter fitted with a 300 μm-mesh net. Oblique tows were carried out from a maximum depth of 100 m up to the surface. Samples were preserved in 5 % borax-buffered formaldehyde in sea water. A calibrated digitall flowmeter was installed in the centre of the mouth of the net and used to measure the volume of water flowing through the net in each tow. Basic hydrographic data were also collected at each station, temperature by means of bathythermograph (BT) casts and water samples for salinity by casts using 5-1 bottles.

Siphonophores and medusae were the predominant gelatinous organisms in all the samples. All individuals were separated and classified. Abundance was standardized to number of individuals per 1 000 m^3 of water.

Principal components analysis (PCA) (LEGENDRE and LEGENDRE, 1979) was applied to the survey data to provide an objective picture of the distribution pattern for the siphonophoran and medusan populations. The data were standardized by log transformation, and the correlation matrix was calculated and employed as the basic input data for the PCA. A Spearman rank correlation (CONOVER, 1980) was used to relate the f-scores for each station and the surface temperature and salinity values and thereby establish the relationship between these two hydrographic factors and species abundance. The f-scores were also correlated with the number of species and number of individuals at each station to complement the PCA results.

HYDROGRAPHY OF THE AREA

The hydrographic characteristics of the study area have been partially described by ANDREWS and HUTCHINGS (1980), SHANNON (1985), and HUTCHINGS *et al.* (1986). SHELTON (1986) described the hydrographic situation in August 1977 and January 1978, the two months considered here.

Differences in surface temperature over the entire area did exceed 4 °C (Fig. 2A) in August 1977 (Austral winter) but reached 10 °C in January 1978 (Fig. 2B). The vertical gradient in August was also weaker than in January (15 °C at the surface, 8 °C on the bottom). In January 1978 (Austral summer) the surface temperature values over practically the entire area between 33° S and 36° S were the highest recorded all year (Fig. 2B). Solar heating of surface water and intrusions of warm Agulhas Current water resulted in temperatures higher than 21 °C. Temperature differences in the area exceeded 10 °C, with the maximum gradient located across the continental shelf. In this area, the advection of Agulhas water coincides with coastal upwelling in the region, and together they strengthen a thermohaline front. The vertical temperature gradient revealed a strong thermocline at about 40 m in depth throughout the entire area, between the front and the edge of the continental shelf with a large temperature difference between the surface (22 °C) and the bottom (8 °C).

In August and hardly any upwelled water was detected inshore, in contrast to January (Fig. 2C and 2D). High salinity water (> 35.4) retreats to the north or to the east in winter. The warmest, most saline water flows in a northwesterly direction along the oceanic side of the front. In contrast, less saline, recently upwelled water is located inshore north of Cape Columbine (Fig. 2D). Active upwelling takes place between the coast and the front, with water temperatures lower than 15 °C in that area. Winds from the southeast drive the upwelling and push the inshore water mass oceanwards. Below the surface the jet current associated with the front (BANG and ANDREWS, 1974) flowed in a northwesterly direction. In August SE winds which blow offshore from Cape Columbine are much less frequent than the westerly onshore winds, due to the passage of easterly moving cyclones past the southern tip of Africa. Nevertheless, much of the near surface drift appears to move around from the western Agulhas Bank to the north, with a divergence near Cape Columbine (Fig. 2C). Water from the offshore area of the grid appears to move further offshore, while nearshore drift is towards the coast. In January, SE winds predominate, and there is more offshore drift from the western Agulhas Bank to the west (Fig. 2F). The front between Cape Agulhas and Cape Columbine also weakens at this time of year and shifts shorewards, and it is not detectable at the surface.

RESULTS

In August 1977 seven species of medusae and twenty siphonophores were collected while in January 1978, 21 medusa species and 28 siphonophore

TABLE 1. — Maximum number, minimum number, percentage, mean average and standard deviation of individuals per 1000 m^3 for the medusae species collected during CELP cruises in August 1977 and January 1978.

Species	August 1977					January 1978				
	Max. No.	Min. No.	%	X	SD	Max. No.	Min. No.	%	X	SD
Dipurena halterata	—	—	—	—	—	2	12	0.02	0.12	1.19
Dipurena sp.	—	—	—	—	—	479	3	0.69	85.88	812.0
Euphysa aurata	—	—	—	—	—	11	7	0.03	0.18	1.29
Bougainvillia macloviana	—	—	—	—	—	8	8	0.01	0.08	0.79
Leuckartiara octona	277	4	55.10	14.83	37.20	113	3	0.70	4.84	13.93
Leuckartiara sp.	—	—	—	—	—	6	3	0.02	0.09	0.89
Calicopsidae	—	—	—	—	—	4	3	0.01	0.07	0.49
Cytaeis tetrastyla	44	4	8.14	2.19	6.82	10	1	0.02	0.11	0.99
Laodicea undulata	—	—	—	—	—	5	3	0.02	0.17	0.76
Mitrocomella grandis	—	—	—	—	—	8	8	0.01	0.08	0.79
Mitrocomella sp.	34	31	5.14	1.38	6.57	42844	3	64.09	444.12	4244.44
Tiaropsidium roseum	—	—	—	—	—	3	3	0.01	0.03	0.30
Proboscidactyla menoni	55	4	13.83	3.72	10.82	2553	3	4.33	30.03	253.20
Proboscidactyla stellata	—	—	—	—	—	19	19	0.03	0.19	1.88
Rhopalonema velatum	—	—	—	—	—	11	1	0.05	0.35	1.43
Persa incolorata	—	—	—	—	—	25	3	0.07	0.50	3.07
Aglaura hemistoma	72	4	7.98	2.15	10.54	1499	3	21.22	147.02	286.88
Liriope tetraphylla	22	4	8.46	2.28	4.42	442	3	7.63	52.86	79.33
Solmundella bitentaculata	—	—	—	—	—	138	2	1.05	7.27	20.77
Aegina citrea	—	—	—	—	—	3	3	0.01	0.09	0.51
Chrysaora hysoscella	17	4	1.34	0.36	2.45	—	—	—	—	—

TABLE 2. — Maximum number, minimum number, percentage, mean average and standard deviation of individuals per 1000 m^3 for the siphonophores species collected during CELP cruises in August 1977 and January 1978.

Species	August 1977					January 1978				
	Max. No.	Min. No.	%	X	SD	Max. No.	Min. No.	%	X	SD
Rhizophysa filiformis	4	4	0.01	0.04	0.42	3	3	0.01	0.06	0.43
Agalma okeni	—	—	—	—	—	3	3	0.01	0.06	0.43
Agalma elegans	—	—	—	—	—	1	1	0.01	0.01	0.10
Nanomia bijuga	—	—	—	—	—	147	3	0.36	5.13	17.95
Amphicaryon acaule	—	—	—	—	—	3	3	0.01	0.03	0.31
Amphycaryon ernesti	—	—	—	—	—	3	3	0.01	0.03	0.31
Hippopodius hippopus	4	4	0.01	0.09	0.59	—	—	—	—	—
Sulculeolaria quadrivalvis	4	4	0.01	0.09	0.59	5	1	0.01	0.17	0.78
Sulculeolaria chuni	—	—	—	—	—	38	3	0.08	1.09	4.29
Sulculeolaria monoica	—	—	—	—	—	7	3	0.01	0.14	0.83
Diphyes dispar	—	—	—	—	—	7	2	0.02	0.34	1.27
Diphyes bojani	12	4	0.1	0.60	1.97	12	2	0.06	0.91	2.15
Diphyes chamissonis	—	—	—	—	—	8	8	0.01	0.15	0.92
Lensia conoidea	107	4	1.06	8.04	24.55	165	3	0.69	10.00	25.89
Lensia campanella	4	4	0.06	0.53	1.70	17	17	0.01	0.18	1.73
Lensia hardy	5	4	0.01	0.09	0.59	19	1	0.02	0.32	2.02
Lensia hotspur	101	5	0.18	2.48	13.00	113	3	0.16	2.25	12.02
Lensia multicristata	4	4	0.01	0.04	0.42	—	—	—	—	—
Lensia subtilis	38	4	0.16	1.41	5.33	54	1	0.14	2.01	7.53
Lensia subtiloides	—	—	—	—	—	6	3	0.02	0.24	0.98
Muggiaea atlantica	7040	4	95.65	653.74	1103.58	14380	3	95.95	1386.21	2591.17
Dimophyes arctica	9	4	0.02	0.14	1.02	19	4	0.02	0.31	2.06
Chelophyes appendiculata	28	4	0.02	1.43	4.25	61	3	0.11	1.57	7.02
Chelophyes contorta	9	4	0.04	0.29	1.40	31	1	0.09	1.29	4.04
Eudoxoides spiralis	152	3	1.76	12.64	23.76	65	3	0.42	6.03	10.17
Eudoxoides mitra	18	4	0.19	1.37	3.09	26	3	0.17	2.45	5.47
Abylopsis tetragona	9	3	0.06	0.44	1.42	22	3	0.13	1.94	4.49
Abylopsis eschscholtzi	33	3	0.26	1.84	4.90	78	3	0.42	6.13	11.04
Bassia bassensis	21	4	0.20	1.40	3.90	237	2	1.05	15.13	37.32
Enneagonum hyalinum	4	4	0.02	0.13	0.71	6	3	0.03	0.49	1.28

species were taken (Tables 1 and 2). The number of medusa species found at the sampling stations in August 1977 was very similar (Fig. 7) but in January 1978, greater number of species were found on the Agulhas Bank and on the shelf off the Cape of Good Hope.

Two distribution trends for medusae were recorded in both months, one for coastal species, some of

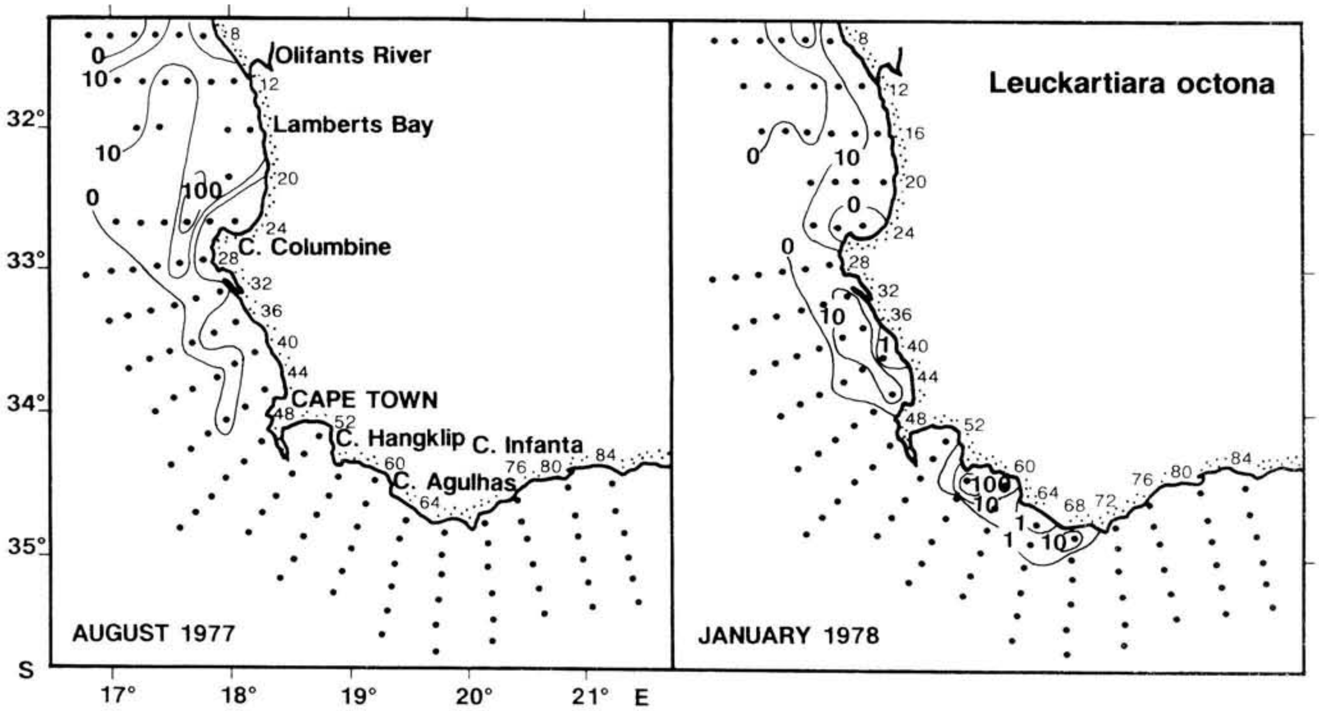

FIG. 3. — Geographic distribution and abundance (number of individuals per 1000 m³) of *Leuckartiara octona* in August 1977 and January 1978.

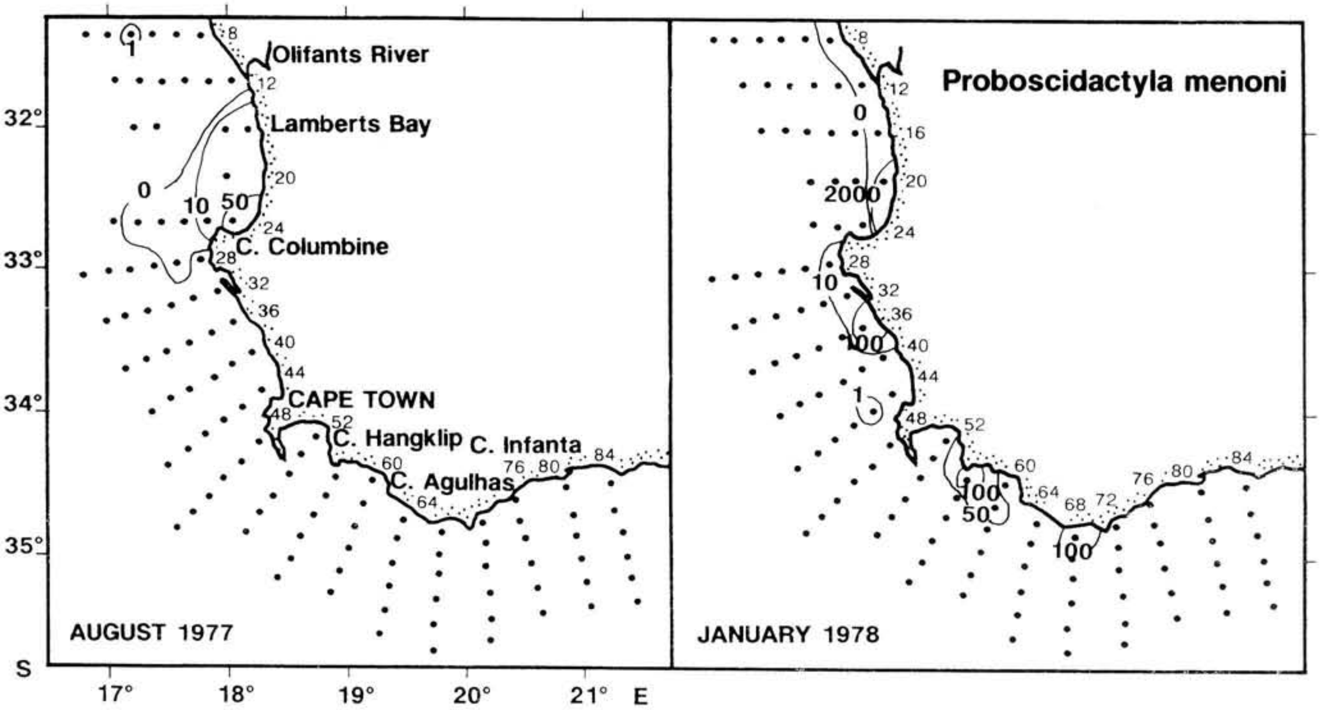

FIG. 4. — Geographic distribution and abundance (number of individuals per 1000 m³) of *Proboscidactyla menoni* in August 1977 and January 1978.

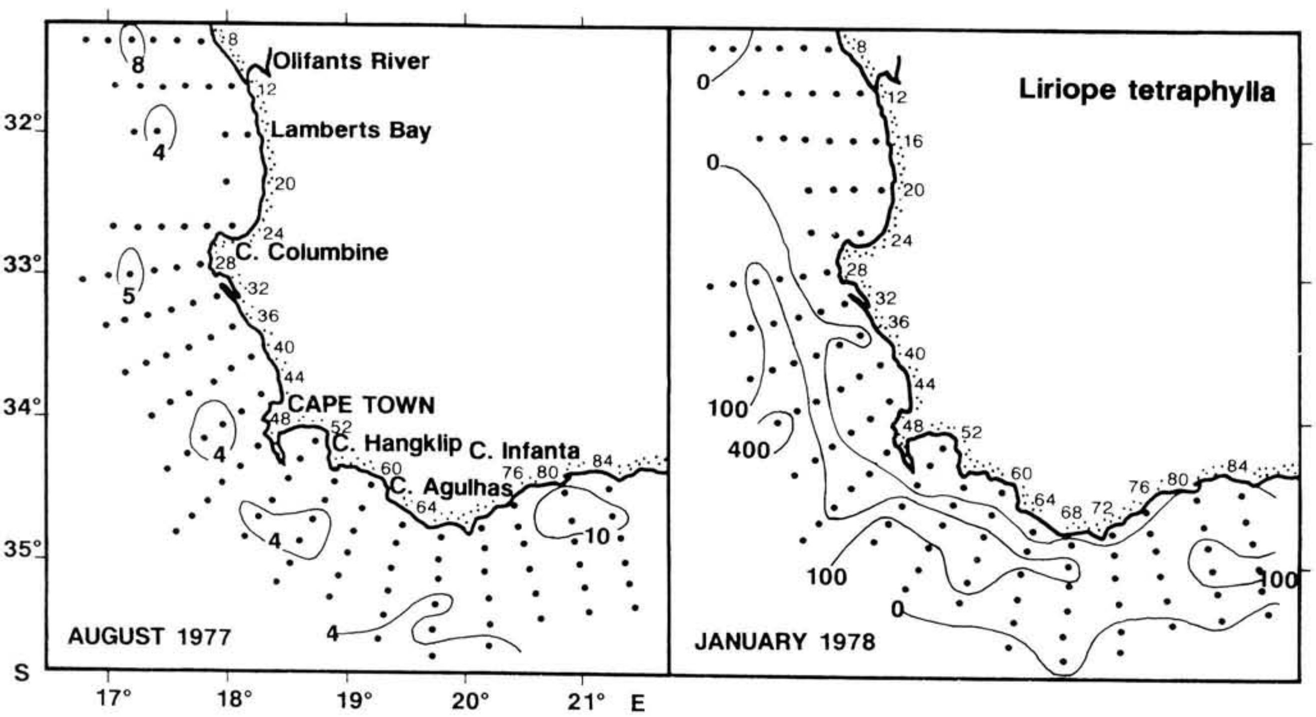

FIG. 5. — Geographic distribution and abundance (number of individuals per 1000 m^3) of *Liriope tetraphylla* in August 1977 and January 1978.

which were associated with upwelled water, and the other for oceanic species, found mainly on the Agulhas Bank and over the continental shelf from the Cape of Good Hope to Cape Columbine. In August 1977 the medusae of *Leuckartiara octona* (Fig. 3) and *Proboscidactyla menoni* (Fig. 4) were abundant and restricted to the coast and continental shelf north of Cape Columbine. In contrast, *Liriope tetraphylla* was distributed along the edge of the shelf in oceanic water throughout the study area and was more abundant in summer (January) (Fig. 5). In January 1978 *Leuckartiara octona* was concentrated in the inshore zone between Cape Agulhas and the northwestern tip of the area associated with upwelling (Fig. 3). In contrast, *L. tetraphylla* abundance rose substantially from the southeastern border of the area to the vicinity of Cape Columbine, with concentrations of this species sometimes in excess of 400 individuals per 1000 m^3.

The distribution patterns for *Aglaura hemistoma* and *Solmundella bitentaculata* (Fig. 6) were similar to that for *L. tetraphylla*, with maximum densities at the edge of the continental shelf off the Cape of Good Hope and inshore only in the southeastern part of the area. *Mitrocomella sp.* was the most abundant species in January 1978 (Table 1), but all the individuals were collected in a few stations close to shore south of Cape Columbine, with densities of more than 40 000 individuals 1000 m^{-3} in a single station.

The distribution of siphonophores was oceanic, except for that of *Muggiaea atlantica*, which was distributed inpatchess throughout the study area in both months (Fig. 8). This species accounted for over 95.5 % of the total number of siphonophoran individuals in both surveys. In August 1977 high densities were recorded for this species at the northwestern and southeastern borders of the study area, with over 3000 individuals 1000 m^{-3} being found at some stations. Considerably lower densities were present in the central portion of the area. In January 1978 densities at certain stations exceeded 5000 individuals per 1000 m^3. Maximum densities were recorded on the Agulhas Bank and over the continental shelf off the Cape of Good Hope in association with the intrusion of Agulhas water, while densities were rather low in the northwestern half of the study area.

In August 1977 all the other siphonophore species were located over the continental shelf, particularly near its edge. However, density values of most species were verey low in the northwestern third of the area, north of Cape Columbine. *Eudoxoides spiralis*, with densities greater than 100 individuals (nectophores) per 1000 m^3 in some cases, was representa-

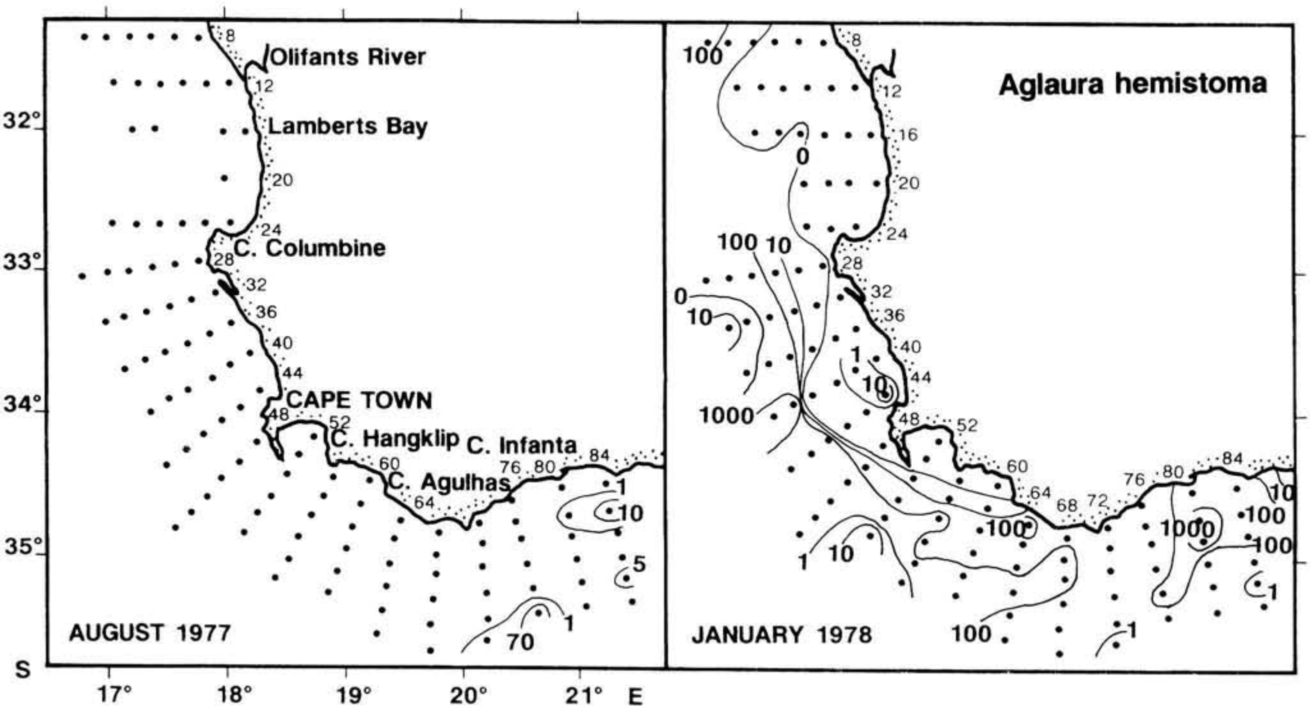

FIG. 6. — Geographic distribution and abundance (number of individuals per 1000 m³) of *Aglaura hemistoma* in August 1977 and January 1978, exemplifying the distribution pattern of other less abundant species as *Solmundella bitentaculata*.

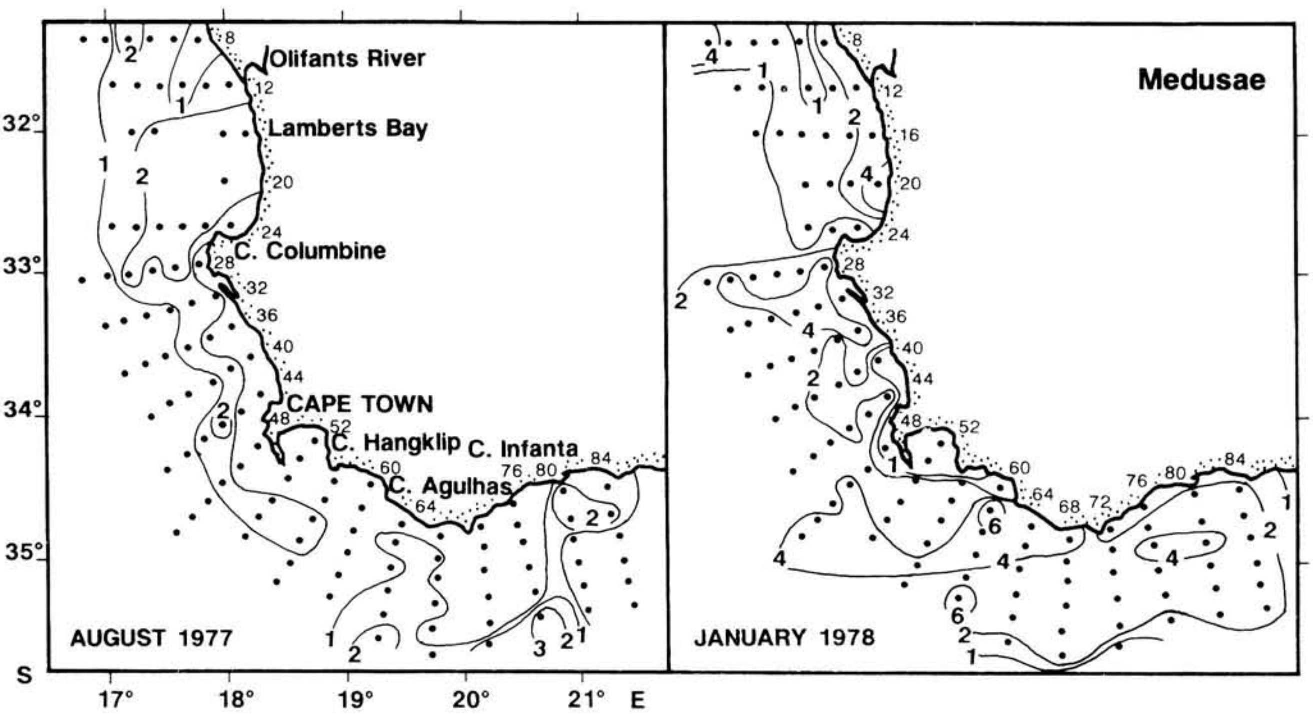

FIG. 7. — Number of medusae species at each sampling station of the CELP grid in August 1977 and January 1978.

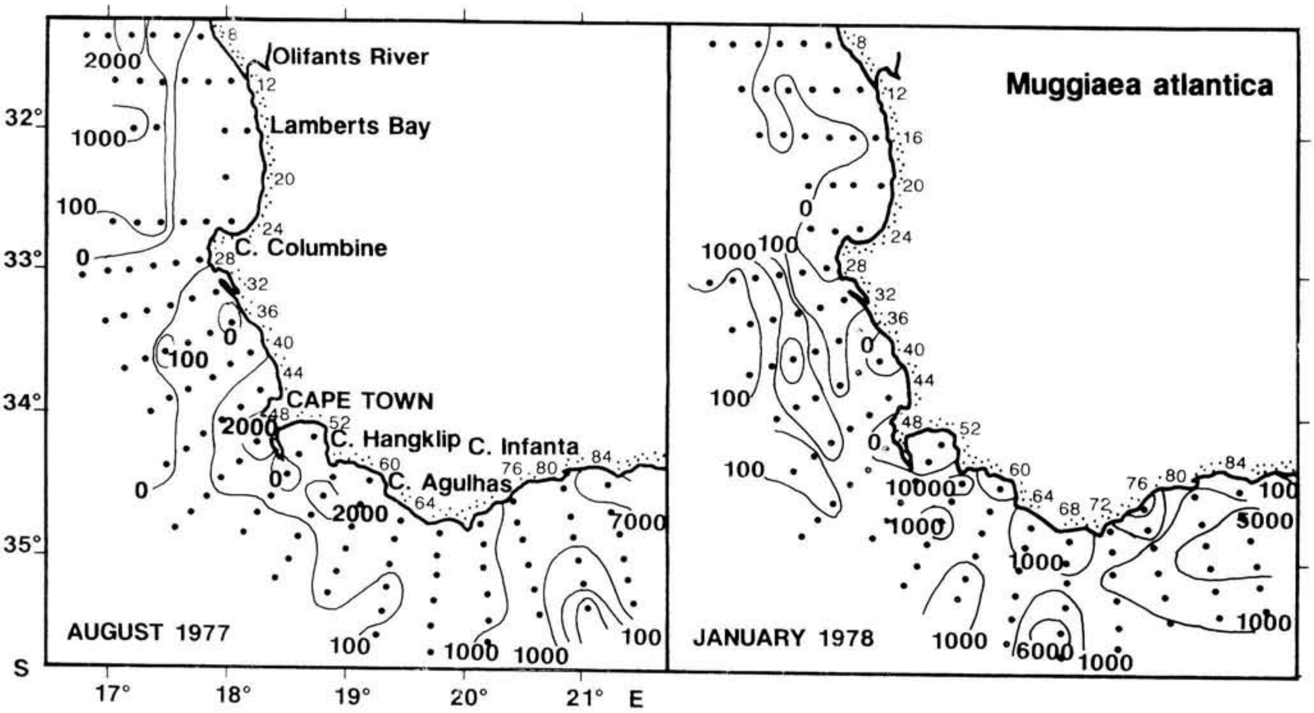

FIG. 8. — Geographic distribution and abundance (number of individuals per 1000 m³ of *Muggiaea atlantica* in August 1977 and January 1978; Only the poligastric stage has been considered.

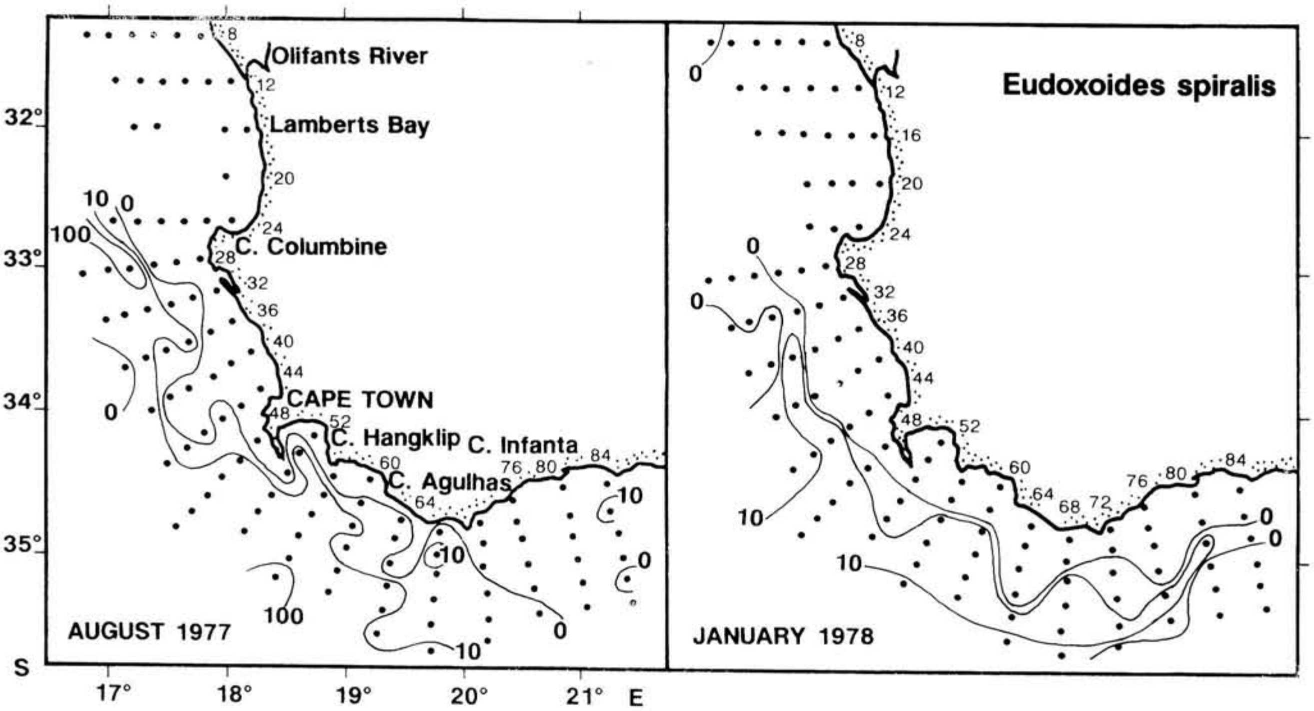

FIG. 9. — Geographic distribution and abundance (number of individuals per 1000 m³) of *Eudoxoides spiralis* in August 1977 and January 1978; only the polygastric stage has been considered.

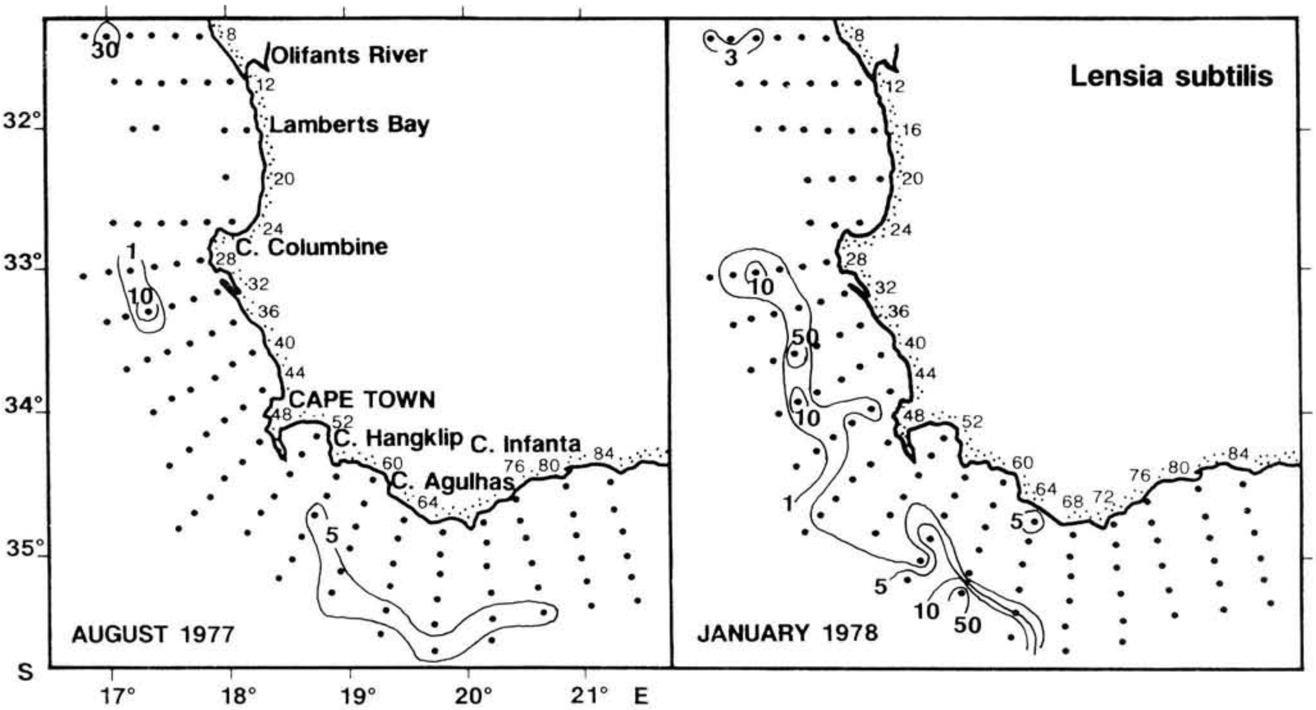

FIG. 10. — Geographic distribution and abundance (number of individuals per 1000 m^3) of *Lensia subtilis* in August 1977 and January 1978. Only the polygastric stage has been considered, exemplifying the distribution pattern of other less abundant species as *Abylopsis eschscholtzi* and *Bassia bassensis*.

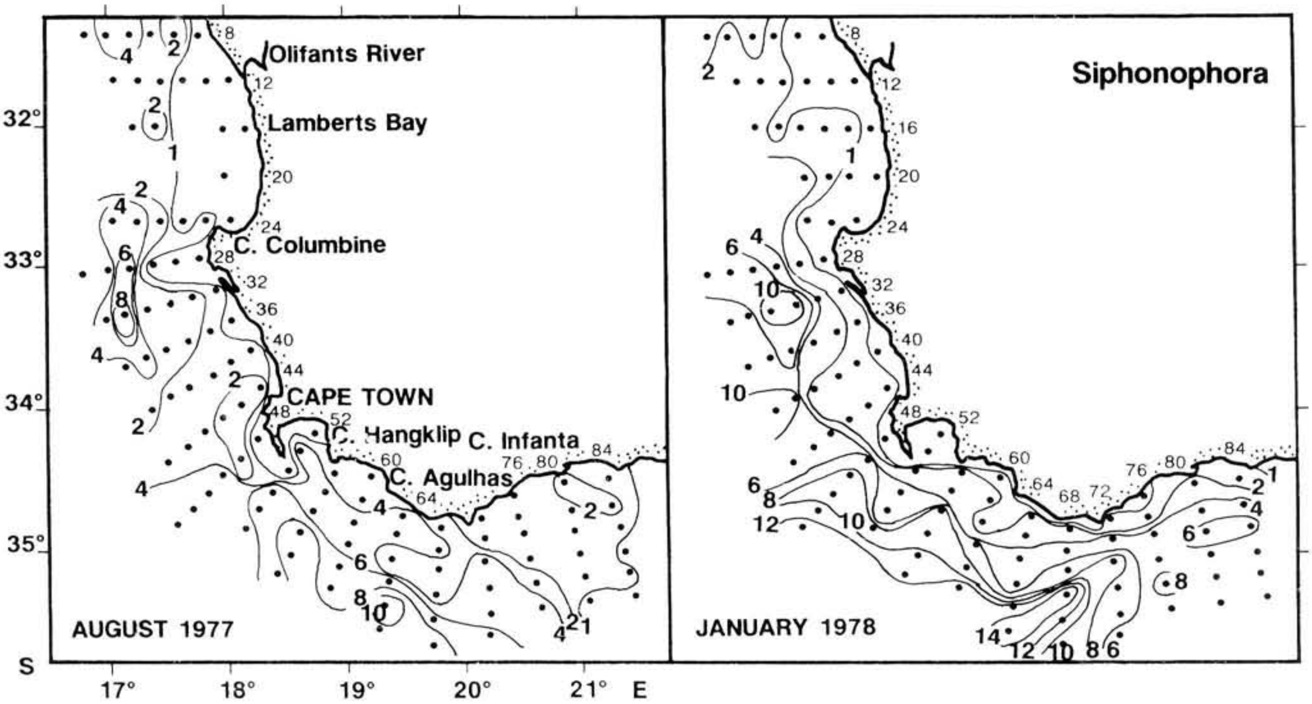

FIG. 11. — Number of siphonophoran species at each sampling station of the CELP grid in August 1977 and January 1978.

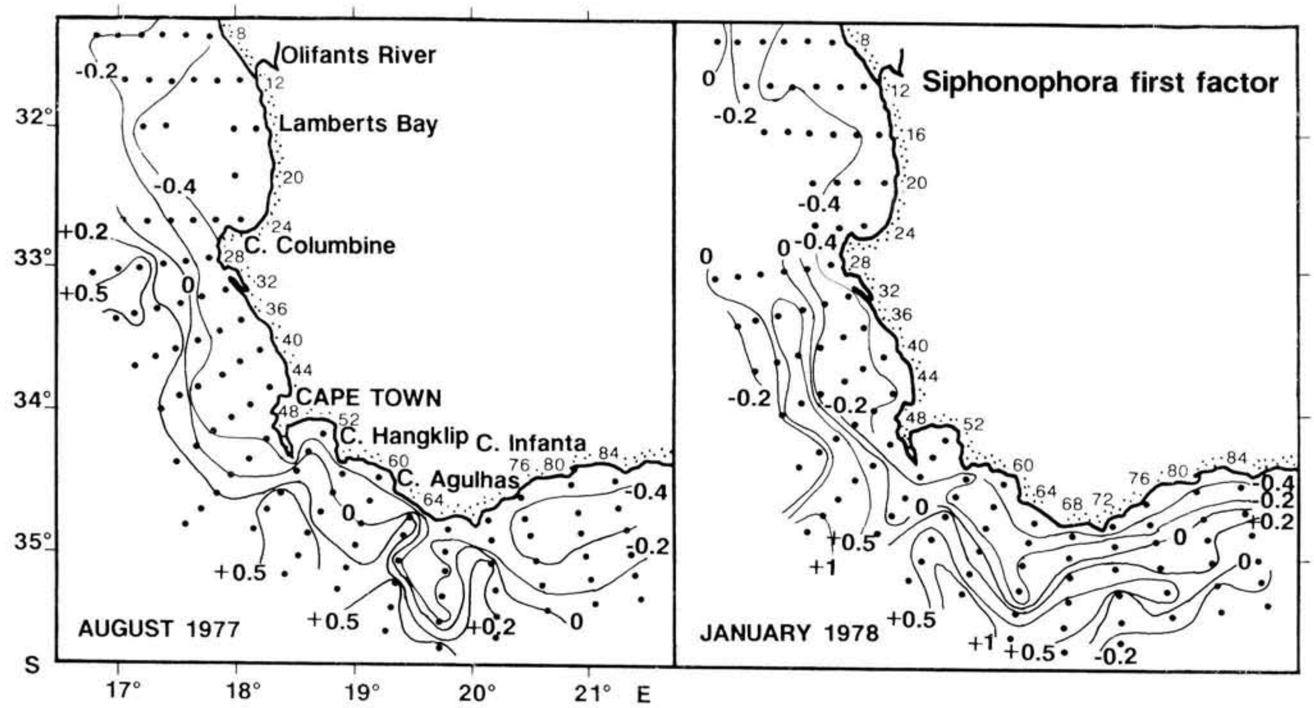

FIG. 12. — Distribution of f-score values for factor 1 from principal component analysis (PCA) for medusae in August 1977 and January 1978. Positive values correspond to high number of species, whereas negative values correspond to low number of species.

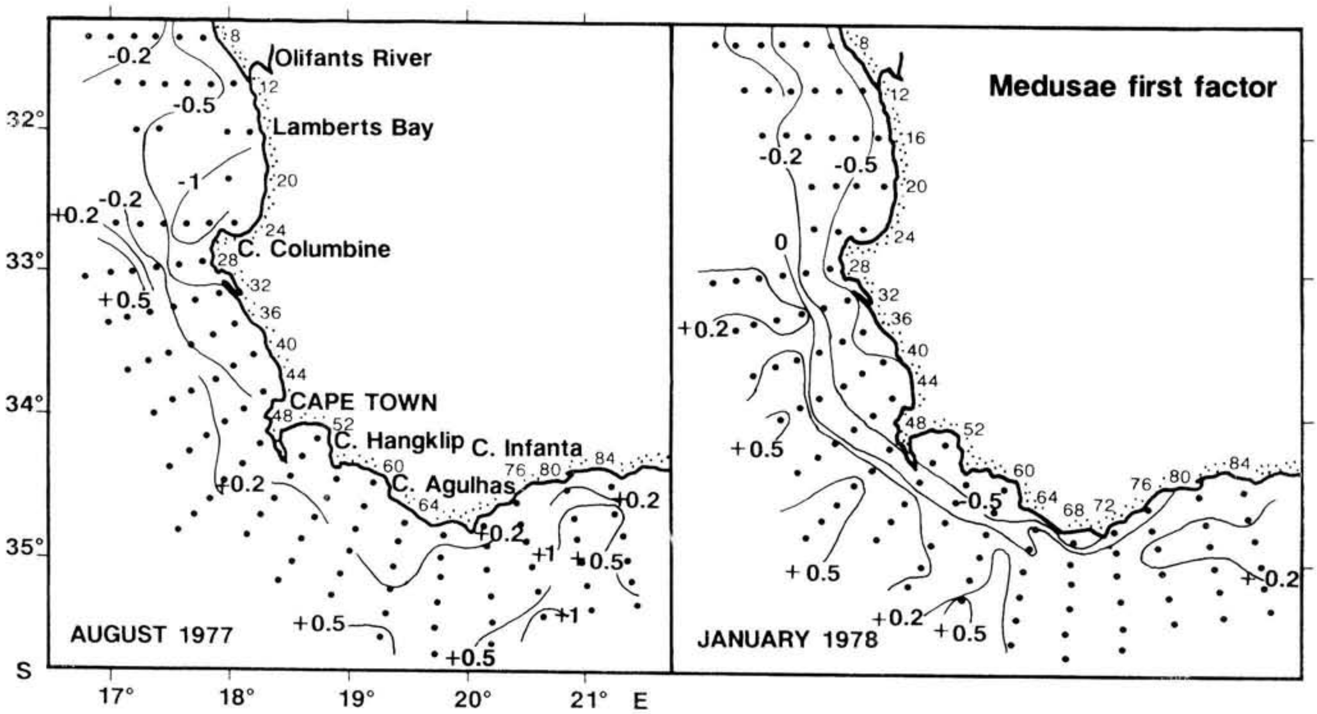

FIG. 13. — Distribution of f-score values for factor 1 from principal component analysis (PCA) for siphonophores in August 1977 and January 1978. Positive f-score values correspond to high number of species, whereas negative f-score values correspond to low number of species.

tive of this overall pattern (Fig. 9). The distribution of *E. spiralis* was the same in both months considered, but the frequency of occurrence and abundance decreased in January 1978. *Lensia subtilis, Abylopsis eschscholtzi,* and *Bassia bassensis* followed similar patterns (Fig. 10). The greater abundance of *Bassia bassensis* in January 1978 (Table 2) was due to increased numbers of eudoxids (sexual stage) associated with the intrusion of Agulhas water. This intrusion brought other species to the Agulhas Bank area, and some reached as far as Cape Columbine. For example, *Chelophyes contorta, Enneagonum hyalinum, Diphyes bojani, D. dispar,* and *Lensia hotspur,* which in August 1977 were present only south east of the Cape of Good Hope, were more frequent in January 1978 and present off Cape Columbine. *Eudoxoides mitra* followed the same pattern as these last-mentioned species, though in January 1978 more eudoxids (sexual stage) than nectophores were collected.

In summary, in January 1978 higher numbers of siphonophores species were recorded from the Agulhas Bank to Cape Point and off Cape Columbine, with concentrations always located near the edge of the continental shelf, but the area of highest diversity was the same as in August 1977, i.e., the Agulhas Bank (Fig. 11).

Plotting the f-scores for PCA factor 1 for all medusae on the station grid yielded quite similar patterns for both months (Fig. 12). In August 1977 (when factor 1 explained 50 % of the variance) and in January 1978 (when it accounted for 28 % of the variance), the highest positive values coincided with the highest values for number of species (Table 3). The area of negative vallues coincided with the colder and less saline upwelled water (Table 3). The area of positive values coincided with warmer, more saline water in which most of the abundant species, like *Liriope tetraphylla,* were found.

Plotting the f-scores for PCA factor 1 for all the siphonophores on the station grid also yielded similar patterns for both months (Fig. 13). In August 1977 (when factor 1 explained 31 % of tahe variance) and in January 1978 (when it accounted for 28 % of the variance), the positive values coincided with high values for number of species (Table 3). The overall pattern in August 1977 was poorly correlated with the temperature and salinity distributions (Table 3), because the most abundant species, *Muggiaea atlantica,* was present throughout the entire area (Fig. 8). The area of negative f-scores for August matched the distribution of *M. atlantica.* The area of positive values showed a greater resemblance to the distributions of the other, more oceanic, species like *Eudoxoides spi-*

TABLE 3. — Spearman rank correlation between f-scores for factor 1 from principal component analysis and the surface Temperature and Salinity, number of species and number of individuals for both medusae and siphonophores. Correlations significant at $^{*}p \leq 0.05$ and $^{**}p \leq 0.001$.

Medusae		PCA axis 1	Temperature	Salinity	Number of species	Number of individuals
August 1977	PCA axis 1	1				
	Temperature	0.73**	1			
	Salinity	0.60**	0.76**	1		
	N species	0.52**	0.05	0.25	1	
	N individuals	0.39*	0.26	0.49**	0.47**	1
January 1978	PCA axis 1	1				
	Temperature	0.55**	1			
	Salinity	0.69**	0.77**	1		
	N species	0.54**	0.25	0.33*	1	
	N individuals	0.59**	0.34*	0.36*	0.65**	1
Siphonophora		**PCA axis 1**	**Temperature**	**Salinity**	**Number of species**	**Number of individuals**
August 1977	PCA axis 1	1				
	Temperature	–0.14	1			
	Salinity	–0.15	0.60**	1		
	N species	0.89**	0.28	0.60**	1	
	N individuals	0.32*	0.49*	0.11	–0.01	1
January 1978	PCA axis 1	1				
	Temperature	0.61**	1			
	Salinity	0.57**	0.69**	1		
	N species	0.94**	0.58**	0.35*	1	
	N individuals	0.59**	0.54**	0.23	0.48*	1

ralis (Fig. 9). The overall distribution pattern for the siphonophores in January 1978 showed a good correlation with the temperature and salinity distributions (Table 3). The area of positive f-score values coincided with the area influenced by the warmer, more saline Agulhas water, where the greatest numbers of species were collected.

DISCUSSION

The Southern Benguela is a region of considerable hydrographic complexity and one of the most important areas of species interchange in the Southern Hemisphere. The interaction between mesoscale hydrographic structures, generated by the Benguela and Agulhas currents, and biological factors is responsible for the region's special characteristics. The region is affected by intrusions by the Agulhas Current, which are subject to annual variations caused by large-scale climatic and hydrographic fluctuations in the Southern Indian Ocean (LUTJEHARMS, 1981), and the intensity of the intrusions by Agulhas water into the region regulates the extent of the interchange and dispersal of species between the two oceans. Three types of species make up the structure of zooplankton communities in western boundary current regions: species endemic to one ocean, species common to both oceans, and cosmopolitan species. The abundance and distribution of the first two types of species with respect to the cosmopolitan species provides key information indicative of the degree of interchange occurring at any given time.

The siphonophores and medusae in the Southern Benguela system in August 1977 were mostly cosmopolitan. Hydrographic conditions, particularly the absence of Agulhas water, lead to the broad distribution throughout the area of a small number of spethat are highly abundant in both oceans, for example *Muggiaea atlantica*. Current flow out towards the open ocean in August 1977 (SHELTON, 1986) (Fig. 2C) also contributed to the low number of species on the shelf. In addition, the current flow east of Cape Agulhas in an easterly direction towards the coast helped prevent penetration into the area by Indian Ocean species. Finally, low upwelling intensity greatly reduced the presence of coastal medusan species.

In January 1978, a higher number of species and individuals were detected. This result was consistent with a peak in zooplankton biomass reported in the area at the end of the Austral spring and during the Austral summer (DE DECKER, 1973; HUTCHINGS, 1981). The inflow of Agulhas water carried Indian Ocean species, for example *Chelophyes contorta* and *Diphyes chamissonis* (which were scarce in the Atlantic Ocean), into the Southern Benguela. These species were distributed over the Agulhas Bank and the continental shelf off the Cape of Good Hope by the current that flowed in a westerly direction along the edge of the shelf under the influence of the topography of the region (NELSON and HUTCHINGS, 1983). High concentrations of gelatinous zooplankton and high species diversity have been recorded in this same area during the Austral summer (HUTCHINGS, 1979). DE DECKER (1973) and SCHLEYER (1985) reported high densities of Thaliacea, Appendiculata, and Chaetognatha, which form dense swarms of thousands of individuals per m^2. Furthermore, in contrast to the situation prevailing in August 1977, the current that flowed towards the coast east of Cape Agulhas was weaker, and hence the flow of Indian Ocean waters towards the Agulhas Bank was stronger (SHELTON, 1986).

In January 1978 atlantic species, for example *Lensia hardy* (which was scarce in the Indian Ocean), where found in the same area were the Indian Ocean species aggregated at the edge of the continental shelf from the Agulhas Bank to Cape Columbine. Their abundance there seems to have been due to the convergence between South Atlantic Surface Water and the Agulhas Current west of the Agulhas Bank. The convergence of these water masses beyond the continental shelf makes the area between Cape Agulhas and Cape Columbine into a mixing area for water and thus for species. The major number of species and individuals were present in this area (on the Agulhas Bank towards the northwest in association with surface waters) in both August 1977 and January 1978. Maximum zooplankton diversity values have also been reported in this area (HUTCHINGS, 1988; DE DECKER, 1984), as have maximum density values for fish larvae in the Austral summer (SHELTON AND HUTCHINGS, 1990). In the summer the nutrients are stripped out early by phytoplankton which support growth of zooplankton populations (SHELTON, 1986). The relationship between fish larvae and the planktonic cnidarians is an interesting issue, since the maximum abundance of all three occur in the same area at the same time of year. Planktonic cnidarians often prey on fish larvae or compete with fish larvae for mesozooplankton prey (PURCELL, 1985). Thus, the impact of cnidarians on fish larvae in the region may affect the recruitment success of fish species.

Upwelled water was recorded inshore of the front located north of Cape Columbine in January 1978. The temperature (12 °C) and salinity (34.89) of the upwelled water were consistent with those for South Atlantic Centrall Water (HUTCHINGS *et al.*, 1986). The upwelled water exhibited low species diversity and contained some of the species endemic to the region. Such species as *Proboscidactyla menoni*, *Mitrocomella* sp., and *Dipurena* sp. were taken solely in the upwelled water near the west coast of South Africa (PAGÈS *et al.*, in press).

HUTCHINGS (1979) reported differences in the species composition of zooplankton between the inshore zone off the coast of South Africa (low diversity) and the area over the shelf offshore of the front. Earlier, DE DECKER (1973) and THIRIOT (1978) had also recorded low species diversities inshore. The confinement of upwelled water inshore during the Austral summer probably favours the growth of species that spawn at this time, such as certain anthomedusae, copepods (DE DECKER, 1984) and fish larvae (SABATÉS and OLIVAR, 1990).

In this upwelling area, the distribution of zooplankton biomass follows a clear inshore-offshore gradient, with the highest biomass values, to which crustaceans make a significant contribution, inshore (ANDREWS and HUTCHINGS, 1980). As discussed herein, the pattern for the planktonic cnidarians is the exact opposite, with the highest densities and species diversity values recorded at the edge of the shelf. Although this is not so similar to that for copepods and probably other crustaceans (DE DECKER, 1984). This difference between the cnidarians and crustaceans may be because hervivorous crustaceans respond more immediately to the input of nutrients carried by the upwelled water inshore, thereby attaining high biomass levels-grazing phytoplankton, while carnivorous gelatinous organisms are much slower to respond. The cnidarians are more abundant in water that may offer a more stable environment than upwelled water does. In a conceptual model of the zooplankton in the Benguela system, SHANNON and PILLAR (1986) reported that large populations of gelatinous zooplankton inhabit the Agulhas Bank because of the hydrographic special conditions there during the Austral summer. Conditions are also optimal in the Austral winter, when large poulations also follow the same distribution pattern as in summer. There was practically no change in this pattern between August 1977 and in January 1978, though in this latter month both the number of species and the number of individuals increased appreciably.

In conclusion, the gelatinous zooplankters, are abundant in areas of stability with locally persisten hydrographic conditions, as recently pointed out by SHELTON and HUTCHINGS (1990) for anchovy populations in the area. It is the close interleaving of stable, food-poor oceanic water with rich coastal upwelling waters at the front which stimulates the production of prey species and allows the gelatinous predators to develop high populations densities. The development of dense populations of medusae and siphonophores may be an important source of larval fish mortality if both types of organism coincide in space and in time.

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