Benguela Trophic Functioning
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MESOSCALE COUPLING BETWEEN PLANKTONIC CNIDARIAN DISTRIBUTION AND WATER MASSES DURING A TEMPORAL TRANSITION BETWEEN ACTIVE UPWELLING AND ABATEMENT IN THE NORTHERN BENGUELA SYSTEM

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The composition and spatio-temporal distribution of planktonic cnidarians in the northern Benguela system are described from plankton samples collected on four cruises between December 1981 and March 1982. The sampling period was characterized by initially active coastal upwelling, followed by abatement of upwelling. In all, 20 species of medusae and 24 species of siphonophores were identified. The most abundant medusae were *Chrysaora hysoscella*, *Aequorea aequorea* and *Liriope tetraphylla*, and the most abundant siphonophores were *Muggiaea atlantica*, *Abylopsis tetragona* and *Bassia bassensis*. Three assemblages of planktonic cnidarians were differentiated. The first was associated with coastal upwelling and consisted of the medusae *Proboscidactyla menoni*, *Aglauropsis edwardsii* and juvenile *C. hysoscella*, along with the siphonophore *M. atlantica*. The second assemblage was associated with oceanic water and the component species were indicative of the offshore influence of the Benguela system; *L. tetraphylla* and most of the siphonophores belonged to this assemblage. The third assemblage consisted of species typical of shelf fauna, namely *A. aequorea*, *Mitrocomella grandis* and adult *C. hysoscella*, all also typical of the northernmost waters of the Benguela system. Overall, there was coupling between mesoscale hydrographic features and the pattern of distribution of cnidarian populations, with a distinct cross-shelf gradient that was more pronounced during active upwelling.

Die samestelling en verspreiding oor ruimte en tyd van planktoniese Cnidaria in die noordelike Benguelastelsel word beskryf aan die hand van planktonmonsters op vier vaarte tussen Desember 1981 en Maart 1982 versamel. Die bemonsteringstydperk is gekenmerk deur aanvanklike aktiewe kusopwelling, gevolg deur verslapping van opwelling. Altesaam is 20 spesies medusae en 24 spesies sifonofore uitgeken. Die volopste medusae was *Chrysaora hysoscella*, *Aequorea aequorea* en *Liriope tetraphylla*, en die volopste sifonofore *Muggiaea atlantica*, *Abylopsis tetragona* en *Bassia bassensis*. Drie gemeenskappe van planktoniese Cnidaria is onderskei. Die eerste was geassosieer met kusopwelling en het uit die medusae *Proboscidactyla menoni*, *Aglauropsis edwardsii* en jong *C. hysoscella*, tesame met die sifonofoor *M. atlantica* bestaan. Die tweede gemeenskap het verband gehou met oseaniese water en die samestellende spesies het die aflandige invloed van die Benguelastelsel aangedui; *L. tetraphylla* en die meeste van die sifonofore het hieraan behoort. Die derde gemeenskap het uit spesies tipies van die vastelandsplatfauna bestaan, te wete *A. aequorea*, *Mitrocomella grandis* en volwasse *C. hysoscella*, wat almal ook tipies van die noordelikste waters van die Benguelastelsel is. Globaal was daar koppeling tussen mesoskaalse hidrografiese verskynsels en die verspreidingspatrone van die bevolkings van Cnidaria, met 'n duidelike gradiënt oor die dwarste van die plat, wat opvallender tydens aktiewe opwelling was.

The northern Benguela system is characterized by permanent coastal upwelling throughout the year, its intensity fluctuating between a maximum from October to December and a minimum in July and August (Stander 1964, Stetsjuk 1983, Shannon 1985). The location of upwelling centres along the coast varies, but certain more-permanent centres do exist. The most important such centre is located in the vicinity of Lüderitz at 26–28°S; other centres are located off Walvis Bay (23°S), Cape Frio (18°S) and the Cunene River (17°S).

During active upwelling the pattern of spatial distribution of zooplankton populations, composed primarily of secondary producers (Hutchings 1981, Madhupratap *et al.* 1990), displays a marked cross-shelf concentration gradient from inshore out towards the open ocean. Maximum densities occur in the coastal strip.

The gelatinous plankton is one of the least understood groups in upwelling regions (Thiriot 1978). However, certain workers have reported spatio-temporal distribution patterns consistent with prevailing environmental conditions and mesoscale water-mass dynamics (Pagès and Gili 1991a).

In recent years the growth of medusan populations in the northern Benguela system has been noteworthy. The two most common species, *Chrysaora hysoscella* and *Aequorea aequorea*, form huge swarms that hinder fishing operations by clogging trawlnets (pers. obs.). Concomitantly with the increase in medusan abundance, catches of the major commercial fish species have been in decline, and this has given rise to growing interest in the study of medusae in the region (Pagès 1991).

The object of the present study was to analyse the

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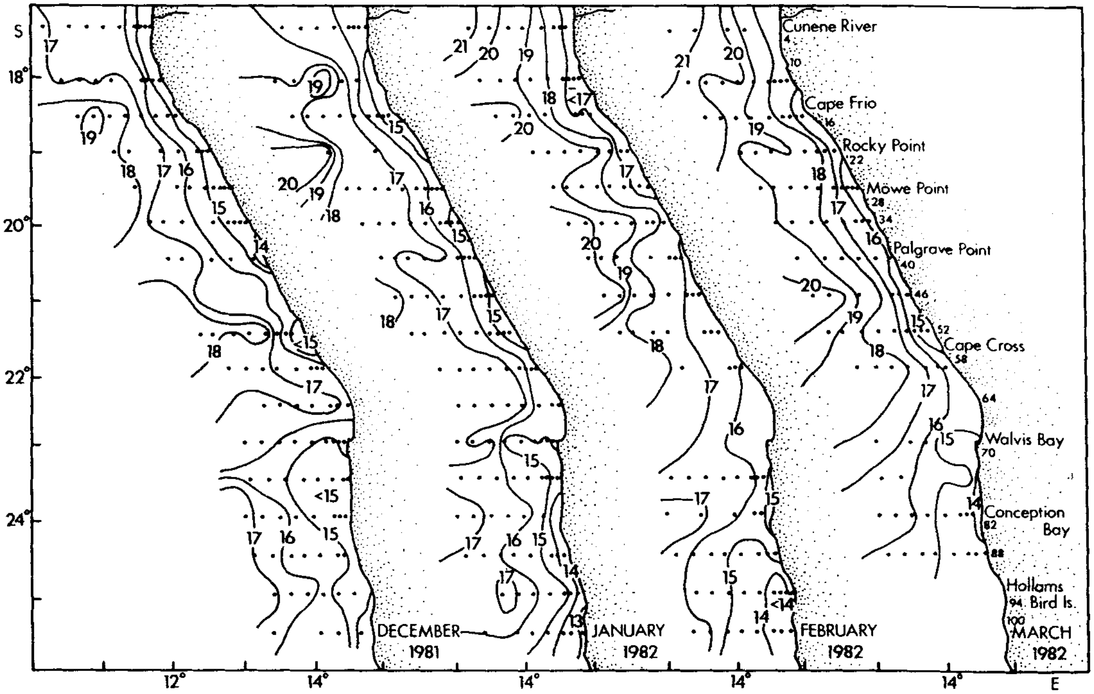

Fig. 1: Sea surface temperature (°C) during monthly SWAPELS cruises, December 1981–March 1982, showing the seasonal pattern of horizontal gradients

spatio-temporal distribution of epiplanktonic cnidarian populations in the northern Benguela system on four research cruises carried out between December 1981 and March 1982. Coastal upwelling gradually abates at that time of the year, its intensity falling off progressively from north to south along the coast of Namibia. An attempt is also made to describe the relationship between hydrographic characteristics of the water masses present in the northern Benguela system and the distribution pattern of cnidarian populations in the area. Elucidation of this relationship would enable the mechanisms responsible for conditioning the mesoscale distribution of cnidarians in the region to be defined.

MATERIAL AND METHODS

The planktonic cnidarian population of the northern Benguela system was studied by analysing the catches made during four SWAPELS (South West African Pelagic Egg and Larva Survey) cruises carried out between December 1981 and March 1982. Sampling covered the continental shelf off Namibia between the Cunene River (17°30′S, Line 4) and Spencer Bay (25°30′S, Line 100). On most lines nine stations were sampled. Inshore stations (1, 2, 3 and 4) were 2, 5, 10 and 15 nautical miles from the coast. Five offshore stations (6, 8, 10, 12 and 14) ranged 25–65 miles from the coast at 10-mile intervals.

The zooplankton samples were collected with a Bongo net 57 cm in mouth diameter fitted with 500- and 300-μm mesh nets. Oblique tows were carried out from a maximum of 100 m deep. A calibrated digital flowmeter was installed in the centre of the net mouth and used to measure the volume of water flowing through the net in each tow. All zooplankton samples were preserved in borax-buffered 5-per-cent formalin. Only the material collected by the 300 μm mesh net was sorted, but not all the samples were available to sort cnidarians in the laboratory. All siphonophores (both eudoxid and polygastric stages were considered) and medusae were identified, counted and the counts standardized to number of individuals per 1 000 m^3 of water, based on the actual volume of water filtered through the net during each tow. Data on the number of individuals of the species *Chrysaora hysoscella* and *Aequorea aequorea* >5 cm in diameter were accessed

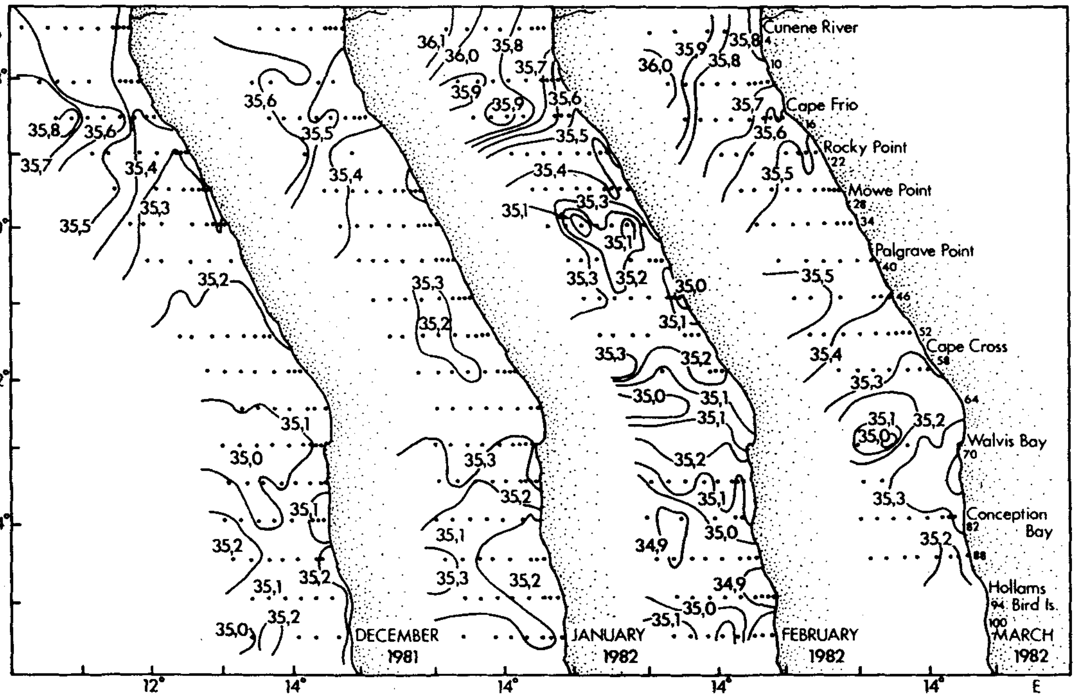

Fig. 2: Sea surface salinity (×10⁻³) during monthly SWAPELS cruises, December 1981–March 1982, showing the seasonal pattern of horizontal gradients

from the files of the Sea Fisheries Research Institute in Cape Town. Basic hydrographic data were also collected at each station by means of bathythermograph (BT) casts.

To obtain an objective description of the distribution pattern of species, and to characterize assemblages of samples according to their affinity based on the species composition, a cluster analysis was made for each month studied. The similarity coefficient of Jaccard (Margalef 1974) and the UPGMA algorithm (Sneath and Sokal 1973) were used.

RESULTS

Hydrographic features

Surface temperatures in December increased from inshore seawards, forming bands running north to south parallel to the coast over the continental shelf (Fig. 1). The 14°C isotherm was generally the band closest to shore and was indicative of upwelling (Boyd 1983), which was strongest between Palgrave Point and Cape Cross. A plume of warmer, more-saline Angolan water (salinity $>35,5 \times 10^{-3}$, temperature 18–19°C) was located north-west of Cape Frio (Fig. 2).

The hydrographic situation in January was quite similar to that in the preceding month. Upwelling was taking place along the entire coast of Namibia, but it was strongest south of Hollams Bird Island. In the central part of the study area, salinity was slightly higher than in December.

Temperatures in February were 1–2°C higher than in January in the northern part of the study area and 3–4°C higher at oceanic stations. These higher temperatures were caused by penetration of warmer, more-saline Angolan water as a result of an abatement in coastal upwelling. The distribution pattern of surface isotherms was indicative of the displacement of warmer water south-eastwards towards the coast. The leading edge of the Angolan water was distinctly delimited by a salinity front located between Cape Frio and Rocky Point.

In March, there was no significant variation in either temperature or salinity with respect to February, reflecting a certain stability in hydrographic conditions.

Species distribution

A total of 20 species of medusae (Table I) and 24 siphonophorans (Table II) were taken on the four cruises considered here. On these surveys, 13, 13, 13 and 14 medusan and 12, 15, 17 and 18 siphonophoran species, respectively, were collected. Nearly half (9) of the medusan species and one-third (8) of the siphonophoran species were present on each of the monthly cruises, and these were clearly the most abundant species.

The cluster analysis for December 1981 distinguished three major sample groups (Fig. 3). Group O (Oceanic) consisted of the samples collected at the more-oceanic stations, in which *L. tetraphylla* and the siphonophores were the most abundant. Group C (Coastal) comprised the most-coastal samples and was subdivided into two subgroups (C1 and C2). Subgroup C1 consisted of the samples in which *M. atlantica* and *C. hysoscella* were almost exclusively the dominant species, whereas subgroup C2 included the same two species as well as all the other coastal ones. Group S (Shelf) comprised the samples in which *A. aequorea* occurred; they were located mainly along the outer continental shelf.

The cluster analysis for January 1982 distinguished the same three major sample groups as the previous month (Fig. 4).

The cluster analysis for February 1982 distinguished three main sample groups (C, A and O) — Fig. 5. Group C was again subdivided into two subgroups, C1 and C2. Subgroup C1 included the samples in which *M. atlantica* was almost unique. Subgroup C2 included the samples in which *M. atlantica* occurred with the rest of the coastal species, such as *C. hysoscella*, *P. menoni* and *A. edwardsii*. Group A (Angola) consisted of most of the samples in which *S. gracilis* and *C. appendiculata* occurred. They were located in a restricted area under the influence of Angolan water. A shelf group was not clearly distinguishable because

Table I: Mean abundance ± *SD* for medusae species collected by SWAPELS cruises off Namibia, December 1981–March 1982 (*n* = number of samples in each month)

Species	Mean abundance (individuals·1 000 m^{-3})			
	December (n = 112)	January (n = 118)	February (n = 96)	March (n = 92)
		Coastal species		
Bougainvillia macloviana	1,22 ± 6,30	1,00 ± 6,40	0,08 ± 0,94	0,03 ± 0,30
Clytia sp.	39,04 ± 170,60	1,80 ± 10,30	0	0
Obelia spp.	0	0	0	0,03 ± 0,31
Proboscidactyla menoni	43,64 ± 179,82	16,20 ± 48,70	7,57 ± 28,18	5,09 ± 14,60
Aglauropsis edwardsii	4,61 ± 14,80	1,20 ± 3,90	5,10 ± 40,20	0,55 ± 2,00
		Shelf species		
Leuckartiara octona	2,07 ± 13,14	0,22 ± 1,08	0,98 ± 5,60	0,09 ± 0,69
Aequorea aequorea	4,06 ± 14,46	5,82 ± 25,73	1,21 ± 8,96	3,10 ± 11,84
Mitrocomella grandis	14,19 ± 68,76	3,01 ± 15,89	13,70 ± 114,45	8,17 ± 23,45
Margalefia intermedia	0	0	0	0,06 ± 0,60
		Coastal-shelf species		
Chrysaora hysoscella	59,43 ± 550,16	52,50 ± 229,52	12,12 ± 51,18	9,25 ± 45,13
		Oceanic species		
Aglaura hemistoma	0,56 ± 2,70	0,34 ± 1,56	5,08 ± 25,85	28,58 ± 185,80
Liriope tetraphylla	8,68 ± 64,06	42,76 ± 198,14	39,00 ± 156,00	73,18 ± 340,13
Rhopalonema velatum	0,01 ± 0,18	0	0	0
Solmundella bitentaculata	0	0	0,02 ± 0,28	0,05 ± 0,50
Pegantha triloba	0	0	0,01 ± 0,18	0,03 ± 0,31
Pegantha martagon	0	0,02 ± 0,26	0,15 ± 1,60	0
Cunina peregrina	0,04 ± 0,46	0	0	0
Solmissus marshalli	0	0	0	0,12 ± 0,73
Discomedusa lobata	0,11 ± 0,96	0,04 ± 0,30	0,18 ± 1,70	0
Tetraplatia volitans	0	0,08 ± 0,97	0	0

the abundance of *A. aequorea* and *M. grandis* was the lowest of all four months considered in this study.

The cluster analysis for March 1982 distinguished four major sample groups (C, S, O and A) — Fig. 6. Group C consisted of the coastal samples in which *M. atlantica*, *C. hysoscella* and *P. menoni* were the most abundant species. Group S comprised the samples in which *M. grandis* was the dominant species and they were all located over the outer shelf. Group O consisted of the oceanic samples in which *L. tetraphylla* and most of the siphonophore species were collected. Group A comprised the samples containing *S. gracilis* and *C. appendiculata*; they were all located in the northern half of the sampling region.

The monthly distributions of cnidarians off Namibia therefore displayed a series of similarities, and the following four groups can be distinguished:

(i) species associated with inshore waters;

(ii) species distributed over the continental shelf, except in the coastal strip;

(iii) species associated with oceanic waters;

(iv) oceanic species associated with Angolan waters.

INSHORE SPECIES

This group of species consisted chiefly of meroplanktonic medusae whose lifecycle includes a polyp growth stage. *P. menoni* and *A. edwardsii* were two of the most dominant, being both abundant and endemic in the Benguela system. Densities were highest closest inshore and fell off abruptly offshore. *C. hysoscella* was associated with this group, because the highest concentrations of this species were recorded inshore (Fig. 7), where individuals were present in the form of ephyrae and juveniles.

Although data on record at the Sea Fisheries Research Institute in Cape Town on the size and numbers

Table II: Mean abundance ± *SD* for siphonophoran species collected by SWAPELS cruises off Namibia, December 1981–March 1982 (*n* = number of samples in each month)

Species	Mean abundance (individuals·1 000 m^{-3})			
	December (n = 112)	January (n = 118)	February (n = 96)	March (n = 92)
	Inshore species			
Muggiaea atlantica	877,00 ± 1 971,90	138,32 ± 569,45	1 283,18 ± 5 083,60	1 267,97 ± 4 383,70
	Shelf species			
Hippopodius hippopus	0	0	0	0,10 ± 0,77
Ceratocymba dentata	0	0	0,02 ± 0,28	0,05 ± 0,51
	Oceanic species			
Agalma elegans	0,48 ± 3,64	0,44 ± 1,72	1,30 ± 1,74	0,31 ± 1,00
Agalma okeni	0	0	0	0,09 ± 0,47
Physophora hydrostatica	0	0,21 ± 1,48	0,02 ± 0,28	0,15 ± 0,91
Forskalia leuckarti	0,36 ± 1,35	0,31 ± 1,15	0,24 ± 1,01	0,43 ± 1,49
Amphicaryon acaule	0	0,02 ± 0,26	0,02 ± 0,28	0
Rosacea plicata	0	0,21 ± 1,48	0,17 ± 0,95	0,03 ± 0,30
Sulculeolaria quadrivalvis	0	0	1,07 ± 6,81	0,32 ± 1,62
Sulculeolaria turgida	0	0	0,01 ± 0,18	0,06 ± 0,43
Sulculeolaria monoica	0	0	0	0,06 ± 0,60
Diphyes dispar	0	0	0;34 ± 2,32	0
Lensia campanella	0,09 ± 0,55	0	0,02 ± 0,28	0
Lensia conoidea	0,06 ± 0,38	0,02 ± 0,26	0	0,03 ± 0,30
Lensia hardy	0	0,02 ± 0,26	0	0
Lensia hotspur	0	0,02 ± 0,26	0	0
Lensia subtilis	0,03 ± 0,37	0,15 ± 1,29	0	0
Chelophyes appendiculata	0,59 ± 2,16	0,41 ± 1,50	1,56 ± 8,66	1,02 ± 3,37
Eudoxoides spiralis	0,05 ± 0,39	0,04 ± 0,32	0,07 ± 0,56	0,06 ± 0,43
Abylopsis tetragona	2,38 ± 7,86	3,19 ± 11,71	5,31 ± 15,97	5,19 ± 13,11
Bassia bassensis	1,43 ± 5,96	9,81 ± 42,76	12,70 ± 61,33	11,58 ± 48,33
Enneagonum hyalinum	0,02 ± 0,27	0	0,51 ± 4,81	0,15 ± 0,91
Sphaeronectes gracilis	1,31 ± 5,46	0,34 ± 1,97	5,37 ± 20,00	5,26 ± 17,10

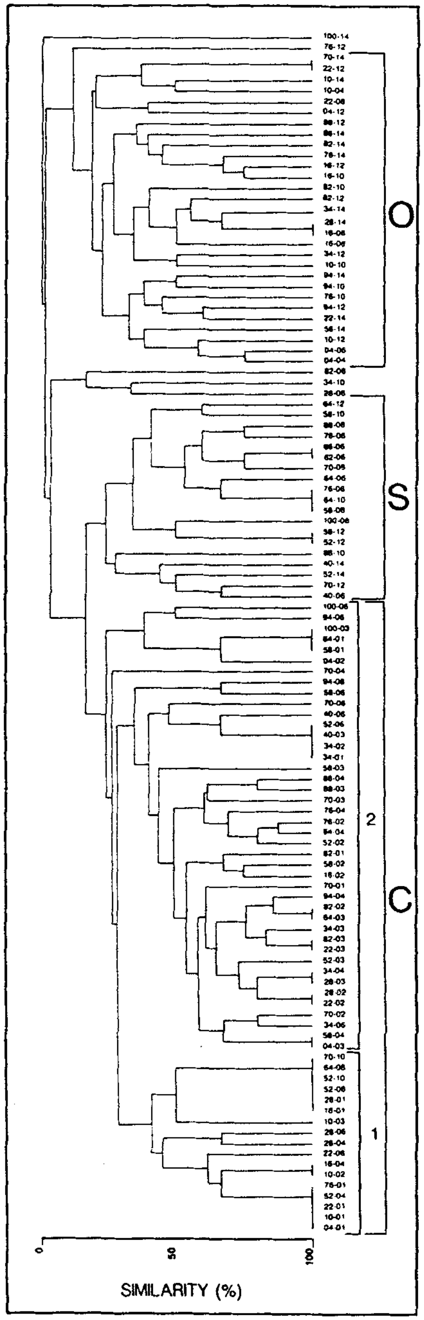

Fig. 3: Dendrogram of similarities (using the Jaccard index) between the 112 samples collected during December 1981 on the basis of the distribution of 25 cnidarian species. Sample code — Line (04–100) — Station (01–14). Groups were estimated considering a similarity level >20 per cent. The letters refer to the dominant water mass, where C is coastal, S is shelf and O is oceanic

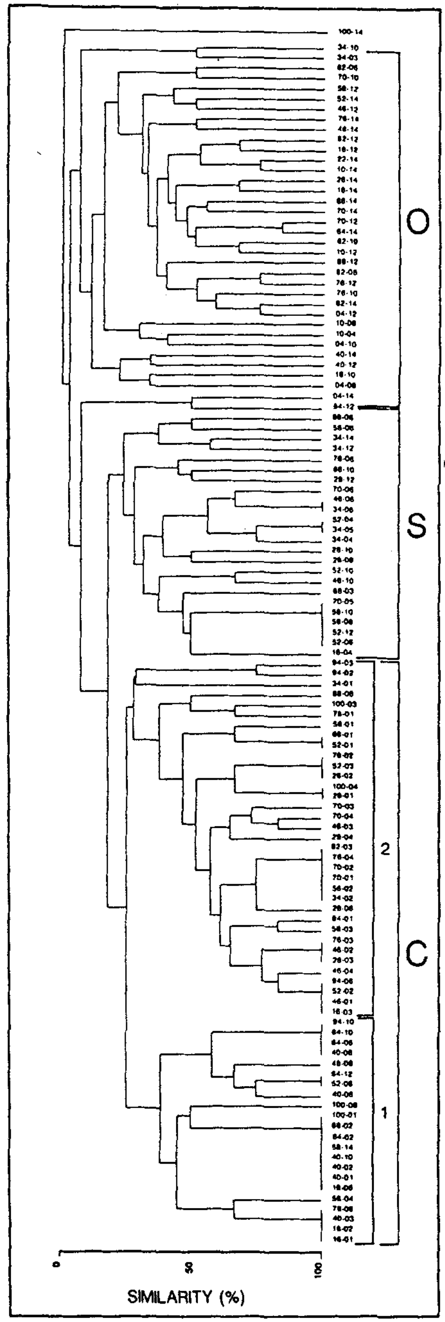

Fig. 4: Dendrogram of similarities (using the Jaccard index) between the 118 samples collected during January 1982 on the basis of the distribution of 28 cnidarian species. Sample code — Line (04–100) — Station (01–14). Groups were estimated considering a similarity level >10 per cent. The letters refer to the dominant water mass, where C is coastal, S is shelf and O is oceanic

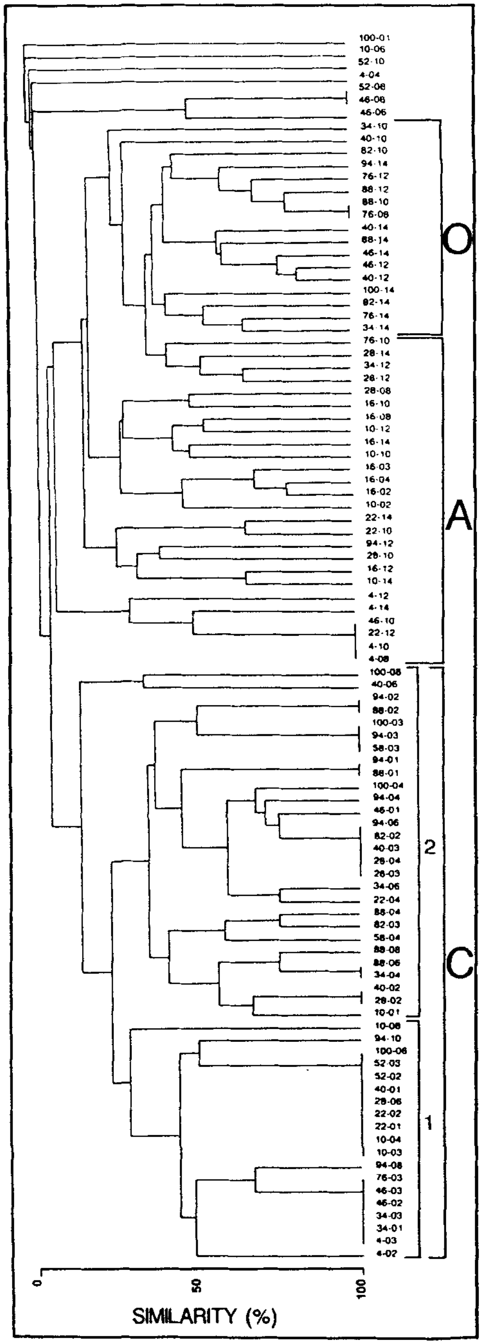

Fig. 5: Dendrogram of similarities (using the Jaccard index) between the 96 samples collected during February 1982 on the basis of the distribution of 30 cnidarian species. Sample code — Line (04–100) — Station (01–14). Groups were estimated considering a similarity level >10 per cent. The letters refer to the dominant water mass, where C is coastal, A is Angolan and O is oceanic

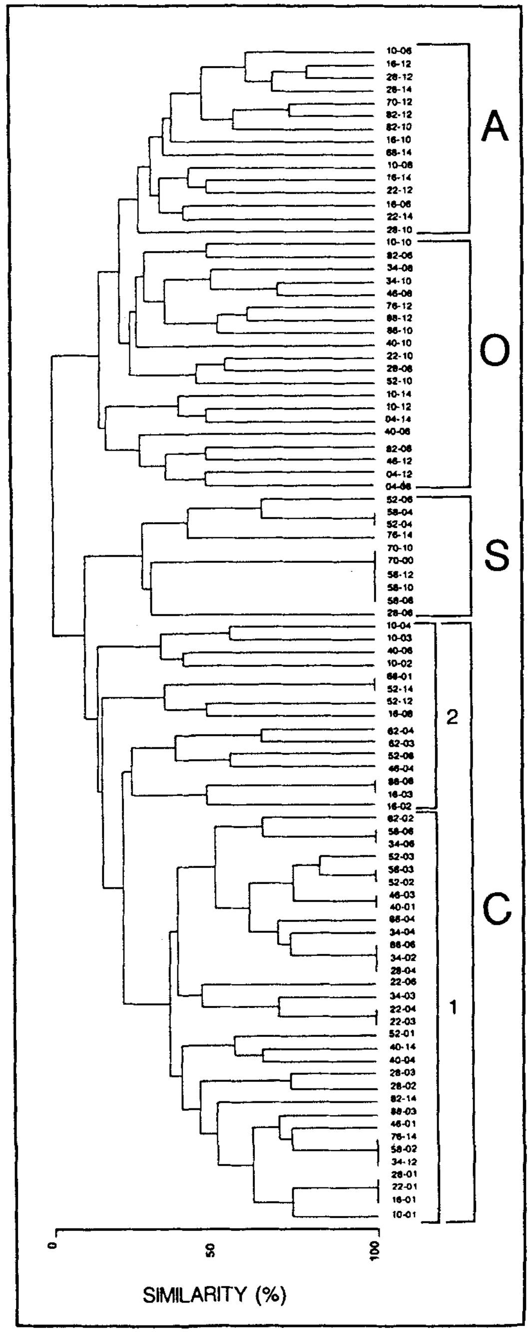

Fig. 6: Dendrogram of similarities (using the Jaccard index) between the 92 samples collected during March 1982 on the basis of the distribution of 32 cnidarian species. Sample code — Line (04–88) — Station (01–14). Groups were estimated considering a similarity level >15 per cent. The letters refer to the dominant water mass, where C is coastal, S is shelf, A is Angolan and O is oceanic

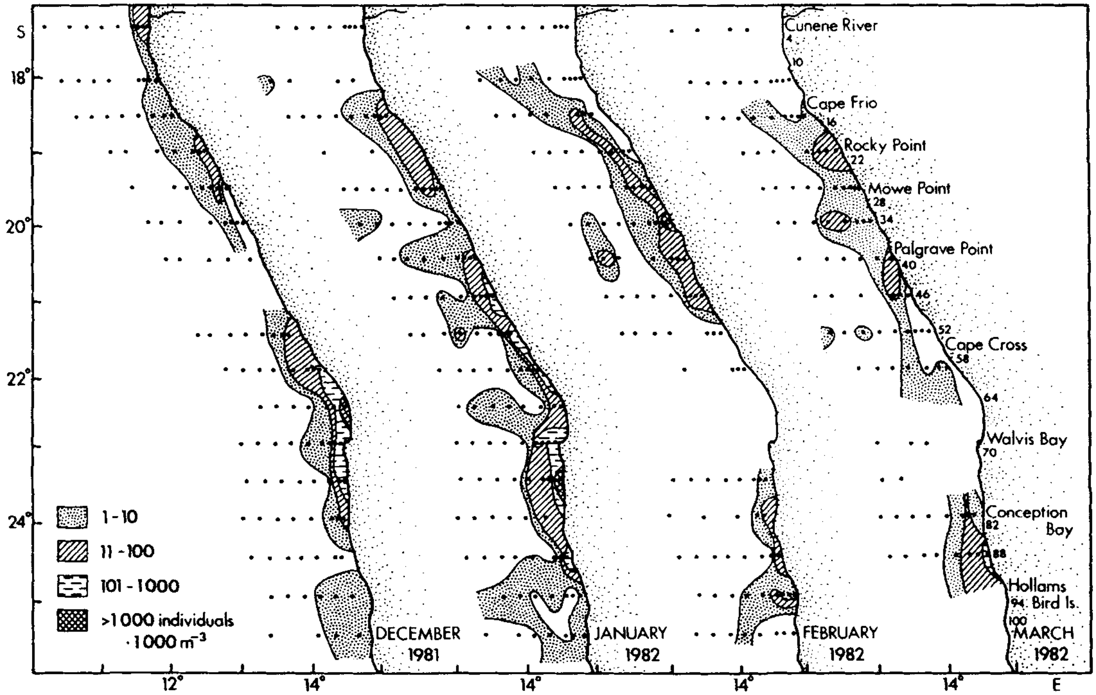

Fig. 7: Horizontal distribution and abundance of *Chrysaora hysoscella* off Namibia, December 1981–March 1982

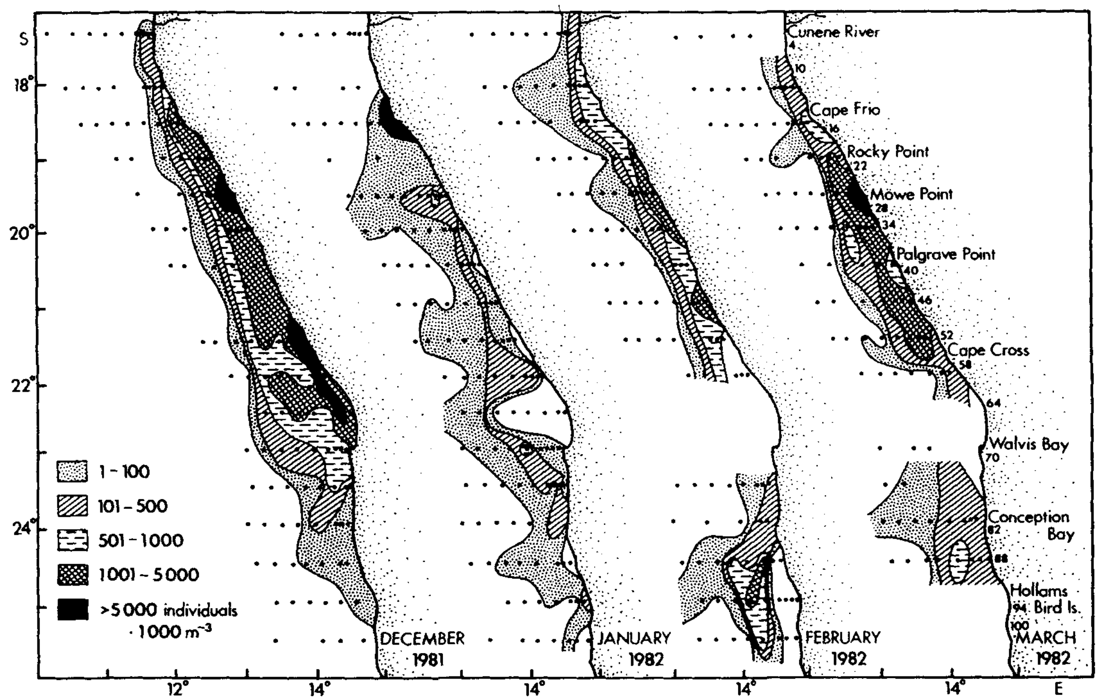

Fig. 8: Horizontal distribution and abundance of *Muggiaea atlantica* off Namibia, December 1981–March 1982

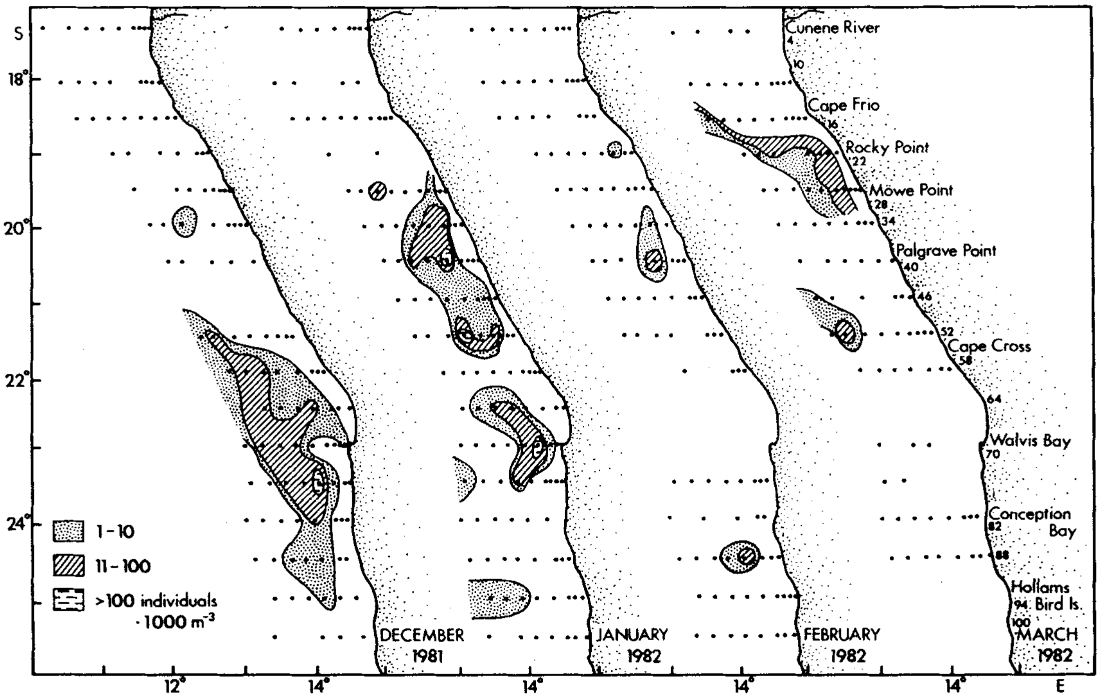

Fig. 9: Horizontal distribution and abundance of *Aequorea aequorea* off Namibia, December 1981–March 1982

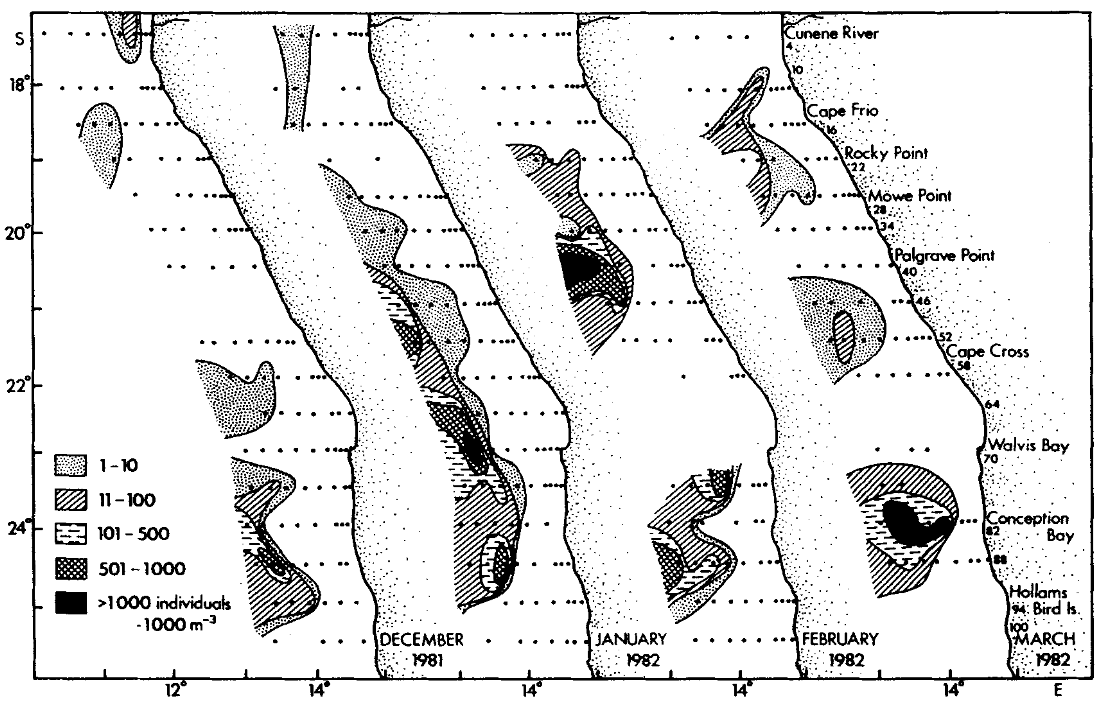

Fig. 10: Horizontal distribution and abundance of *Liriope tetraphylla* off Namibia, December 1981–March 1982

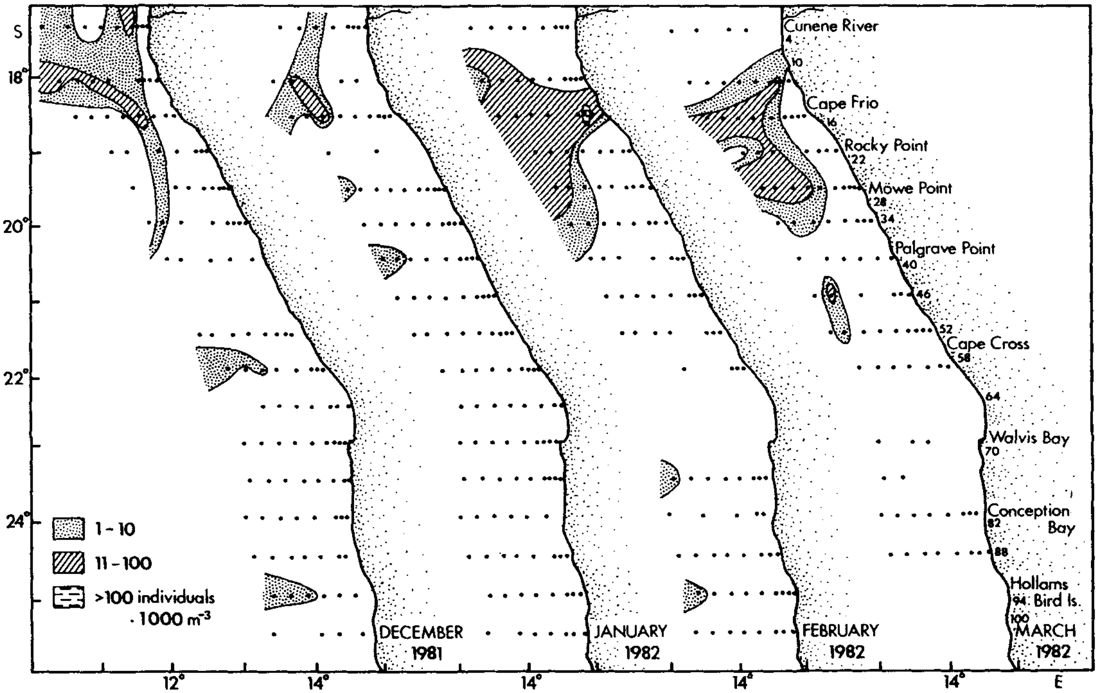

Fig. 11: Horizontal distribution and abundance of *Sphaeronectes gracilis* off Namibia, December 1981–March 1982

of specimens caught and discarded are not indicative of significant differences in the size of individuals taken at coastal and at oceanic stations, direct examination of zooplankton samples clearly showed a progressive decrease in the number of juveniles from inshore seawards. Concomitantly, *M. atlantica* was the most abundant siphonophore on the survey and the only one to exhibit a strictly inshore distribution (Fig. 8). This neritic species was found all along the coast, with concentrations highest inshore and falling off progressively in a seaward direction.

CONTINENTAL SHELF SPECIES

The shelf group consisted of few species. Although the group was not very well defined, it did possess certain characteristics that separated it from the other species groups. For instance, the distribution of this group of species was closely associated with the Benguela system. The group consisted mainly of the medusae *A. aequorea* (Fig. 9), *M. grandis* and adult *C. hysoscella*. *A. aequorea* and *C. hysoscella* are the most abundant species throughout the Benguela, forming dense swarms that interfere with fishing operations by clogging trawlnets (pers. obs.).

OCEANIC SPECIES

This was the most numerous group and consisted primarily of siphonophores. The distribution pattern of this group took the form of a strip, with some discontinuities, running from north to south and encompassing the stations farthest offshore, reflecting the boundary between the waters of the Benguela and strictly Atlantic Ocean waters. Siphonophoran abundance was more consistent over the four-month period of study, whereas there were fewer medusae in terms of both number of species and number of individuals. Only the trachymedusa *L. tetraphylla* was consistently present in concentrations comparable to those of the siphonophores (Fig. 10). The remaining medusans fluctuated with time over the study period, displaying different populations each month.

ANGOLAN OCEANIC SPECIES

This group was made up of species mainly restricted to oceanic stations in the northern half of the sampling area, i.e. those influenced by Angolan waters. The siphonophores *Sphaeronectes gracilis* (Fig. 11) and *Chelophyes appendiculata* were the most abundant species.

DISCUSSION

The distribution patterns of temperature and salinity recorded over the sampling period delineated different mesoscale water masses. These patterns enabled the boundaries between the areas of influence of the Benguela system off Namibia to be discerned. The northern edge of the Benguela met the waters of the Angola Current, whereas offshore the boundary coincided with the oceanic thermal front. South of Lüderitz this front runs along the edge of the continental shelf, but in the north its location has not yet been established precisely (Shannon 1985).

O'Toole (1980) described the existence of three masses of surface water off Namibia, and this finding has subsequently been corroborated by other workers (Badenhorst and Boyd 1980, Le Clus and Kruger 1982, Olivar and Barangé 1990). These three water masses are: cold, weakly saline surface water (12–18°C; $34{,}9–35{,}1 \times 10^{-3}$) characteristic of upwelling or freshly upwelled water; warm, highly saline water (17–22°C; $35{,}5–35{,}9 \times 10^{-3}$) advancing in a south-easterly direction towards the coast, particularly at the end of the austral summer when upwelling intensity abates; water with an intermediate range of temperature and salinity (16–20°C; $35{,}2–35{,}5 \times 10^{-3}$) originating from mixing of cold Benguela and warm Angolan water.

The spatial distribution pattern of the zooplankton populations considered was closely associated with the hydrographic features in the northern Benguela. Earlier, Pagès and Gili (1991a) had stressed the importance of intrusions of Angolan water on the distribution of the gelatinous zooplankton in the study area.

Comparison of the different water masses described by O'Toole (1980) with the distribution patterns of medusae and siphonophores off Namibia during the period December 1981 – March 1982 suggests that the boundaries separating the water masses in the northern Benguela closely matched the distribution patterns of planktonic cnidarians in the study area. Like the four different water masses referred to above, four species associations were distinguishable.

Inshore species associated with upwelled water

These species were located chiefly in the coastal strip, with density increasing during periods of active upwelling. Their increase in abundance may be due either to environmental conditions conducive to release of the benthic polyp stage of the medusa or to higher concentrations of potential prey organisms brought about by upwelling, which enhances the survival of these cnidarian species.

The group's abundance and the extent of their distribution decreased progressively from December to March, as upwelling intensity diminished at the end of summer. Concentrations of the siphonophore *M. atlantica* did not decrease over the four-month study period, and this was apparently related to the holoplanktonic lifecycle of this species, which does not seem to be affected by the upwelling regime.

Shelf species associated with the Benguela

This species group consisted of species such as *A. aequorea* and *M. grandis*, adults of *C. hysoscella*, *M. intermedia* and possibly *L. octona*. They were particularly abundant in a broad intermediate strip separating the coastal from the oceanic water.

There are two possible explanations for their pattern of distribution. As all these species pass through a polyp stage during their lifecycles, they may have been carried by Ekman transport from inshore out to the oceanic front, which would then act as a barrier to further drift. The other possibility is that they may have been transported from the south by the Benguela system. If their presence was due to Ekman transport, individuals should have been caught close inshore, but only *C. hysoscella* was collected inshore. The polyps of these species may dwell over the shelf, but in that case medusae should have appeared inshore, carried along by upwelled water. The most convincing possibility is that these species were transported from the south by the main body of the Benguela, and that their presence delimits the northernmost extent of the influence of those waters.

Oceanic species associated with South Atlantic Central Water

This species group comprised the trachymedusae, narcomedusae and most of the siphonophores collected, species common in the oceanic waters of the South-East Atlantic (Pagès 1991). Their longitudinal geographic distribution was basically bounded by the edge of the continental shelf and therefore coincided with the boundary between South Atlantic Central Water and the Benguela. Because temperature variations at the oceanic stations over the sampling period were slight, particularly in the southern half of the study area, the presence and abundance of these species remained constant over the four months considered.

Warm-water oceanic species associated with the Angolan Current

In this species group were mainly *S. gracilis* and *C. appendiculata*. They were present offshore when upwelling was most active, but as upwelling slackened they were transported shorewards by Angolan water. They would seem to be good indicators of penetration by Angolan water into the Benguela system, as occurred during a strong intrusion during 1986. Then they formed dense concentrations in the surface layers (Pagès and Gili 1991b).

CONCLUSIONS

The mesoscale distribution pattern of water masses off Namibia is clearly responsible for both the extent and the limits of the distribution of epiplanktonic species of cnidarians in the region. The location of distributional boundaries is closely linked with the intensity of upwelling, which gives rise to hydrographic and biological gradients between the coast and the open ocean. It also affects penetration by Angolan water from the north and by oceanic water onto the shelf, as well as the extent of the Benguela off Namibia.

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