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SHORT-TERM EFFECTS OF COASTAL UPWELLING AND WIND REVERSALS ON EPIPLANKTONIC CNIDARIANS IN THE SOUTHERN BENGUELA ECOSYSTEM

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Patterns in the distribution of epiplanktonic cnidarians collected along the west coast of South Africa during June 1986 were examined. Upwelling-favourable south-easterly winds prevailed prior to sampling. These winds are believed to have transported coastal cnidarian assemblages offshore, resulting in a blurring of the inshore-offshore zonation of species. A wind reversal, to northerly winds in the north and north-westerly winds in the south, followed upwelling and persisted during sample collection. This resulted in the development of a distinct thermohaline front off Cape Columbine. Another consequence was the advection of oceanic water shorewards in the south, disrupting the original pattern of species zonation and redistributing cnidarian assemblages in a longshore pattern. Three different assemblages are differentiated: one north of Cape Columbine, consisting of coastal species, one south of Cape Columbine with a mixture of neritic and oceanic species, and one single-species community with coastal affinity inshore north of Cape Columbine. The effects of wind-driven onshore advection of offshore waters on the coastal communities of gelatinous zooplankters are discussed.

Patrone in die verspreiding van epiplanktoniese Cnidaria wat in Junie 1986 langs die weskus van Suid-Afrika versamel is, word ondersoek. Voor bemonstering het suidoostelike winde, wat gunstig vir opwellings is, oorheers. Daar word gemeen dat hierdie winde kusgemeenskappe Cnidaria seewaarts gedryf het en so die sonasie van spesies dwars tot die kus versluier het. 'n Windomkering, na noordewinde in die noorde en noordwestewinde in die suide, het op opwelling gevolg en voortgeduur tydens bemonstering. Dit het gelei tot die ontwikkeling van 'n termohaliene front teenoor Kaap Columbine. Nog 'n gevolg was die kuswaartse meevoering van oseaniese water in die suide, wat die oorspronklike soneringspatroon van spesies verbreek het en die Cnidaria-gemeenskap in 'n kuslangse patroon herrangskik het. Drie verskillende gemeenskappe word onderskei: een noord van Kaap Columbine wat uit kusspesies bestaan, een suid daarvan met 'n mengsel van neritiese en oseaniese spesies en aanlandig noord van Kaap Columbine een gemeenskap met 'n kus voorliefde en bestaande uit 'n enkele spesie. Die uitwerking van windgedrewe landwaartse meevoering van aflandige waters op die kusgemeenskappe van jellieagtige soöplankters word bespreek.

Coastal upwelling along the south-western tip of Africa is a result of longshore, equatorward winds driving surface water offshore. Upwelling in the southern Benguela system is controlled to a large extent by the bathymetry and the influence of the orography on the wind field (Shannon 1985). The region is complex in terms of topographic coastal irregularities, as mountainous capes or headlands alternate with low-lying coastal plains, ensuring a longshore variability in surface friction (Jury 1985).

Three sites, characterized by the tongue-like nature of the upwelling plume, have been identified as important upwelling centres. They are situated off the Cape Peninsula, off Cape Columbine and off Hondeklip Bay (Taunton-Clark 1985). During the process of upwelling, the upwelled water with its characteristic zooplankton community partially displaces the offshore surface water mass and its zooplankton community. The dynamics of this hydrographic event are portrayed in the distribution of the surface waters and the spatio-temporal distribution of the zooplankton (Andrews and Hutchings 1980). This is especially evident for gelatinous zooplankters on a mesoscale, because their distribution is directly influenced by the dynamics of the waters they inhabit, probably because of their poor swimming ability. Cnidarians, which constitute one of the dominant groups of gelatinous zooplankton, are particularly good indicators of recent hydrographic phenomena (Colebrook 1977, Gili *et al.* 1991). Despite their abundance in the Benguela system (Shannon and Pillar 1986), the role that cnidarians play within the zooplankton community of the Benguela ecosystem is currently unknown.

In the present paper, the spatial distribution of epiplanktonic cnidarians along the west coast of South Africa is examined. Sampling was performed after an upwelling event was followed by a wind reversal. Observations of the immediate effects produced by

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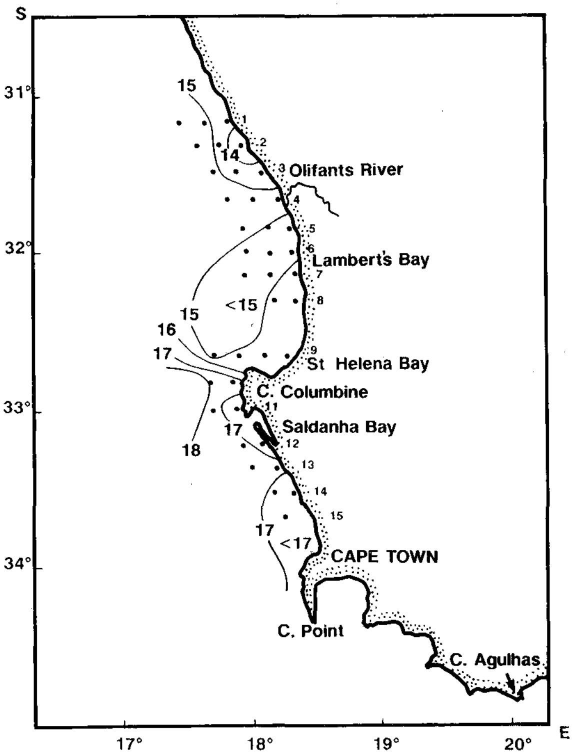

Fig. 1: Map of the South African west coast showing the grid of station positions sampled with the RMT-1 x 6 net system. Isolines of surface temperature are superimposed

such short-term hydrographic events on the gelatinous zooplankton assemblages are described.

MATERIAL AND METHODS

Data were collected along the west coast of South Africa between 31°10′ and 33°40′S during a survey of anchovy recruits aboard F.R.S. *Africana* from 13 to 16 June 1986. In all, 40 stations were occupied on a grid of 15 east-west transects (Fig. 1). Stations on each transect were 10 miles apart and, at each, a CTD/Rosette cast was made to near the bottom for water sampling, followed by zooplankton sampling in the upper 100 m of the water column. Sea surface temperature and salinity were monitored en route with a continuous thermosalinograph.

Zooplankton samples were collected in an obliquely towed 1 m^2 multiple opening-closing rectangular midwater trawl-net system (RMT-1×6) fitted with six nets of 200-μm mesh (Verheye and Hutchings 1988). Towing speed varied between 1,5 and 2,0 $m \cdot s^{-1}$. Depth, temperature, flow, net angle and net operations were monitored electronically. Usually, one sample was collected within, one above and one or two below the thermocline. Three depth intervals of approximately 20 m were sampled at the innermost station of each transect, and four strata of approximately 25 m each at the other stations. All zooplankton samples were preserved in borax-buffered 5-per-cent formaldehyde solution.

In the laboratory the zooplankton samples were halved with a Folsom plankton splitter and one half microscopically examined. All siphonophores and medusae were sorted and identified, and the data were expressed as number of individuals per 1 000 m^3.

To obtain an objective description of the distribution pattern of species, and to characterize assemblages of samples according to their affinity, based on species composition, a cluster analysis was made. Owing to the dominance of four species and the more sporadic presence of others, the matrix prepared contained an elevated number of zeros. Therefore, the matrix of Czekanowsky (Legendre and Legendre 1979) and the UPGMA algorithm (Sneath and Sokal 1973) were used.

RESULTS

Hydrography

Mesoscale thermal features of the study area are shown on the NOAA satellite image of 8 June 1986, five days prior to sampling (Fig. 2). The image is calibrated and corrected geometrically, giving temperatures accurate to within 0,5°C. A convoluted upwelling plume of 11–12°C water, with a small westward filament, was evident NNW off Cape Columbine. Upwelling-favourable south-easterly winds (4,1–7,1 $m \cdot s^{-1}$) had been recorded at this upwelling centre 3–4 days earlier (Fig. 3). On 8 June, the wind moderated and reversed to a northerly direction, which persisted until 13 June when sampling commenced. Wind speeds varied between 1,6 and 6,2 $m \cdot s^{-1}$ during this period. As a consequence, oceanic water was transported shorewards in the south, causing the development of a marked thermohaline front across the shelf from the coast outwards, forming an alongshore gradient (Figs 1 and 4). Although upwelling-favourable winds during the upwelling period were stronger (6,2–16,9 $m \cdot s^{-1}$) off Cape Point than off Cape Columbine (Fig. 3), there was little evidence of upwelling off the Cape Peninsula (Fig. 2).

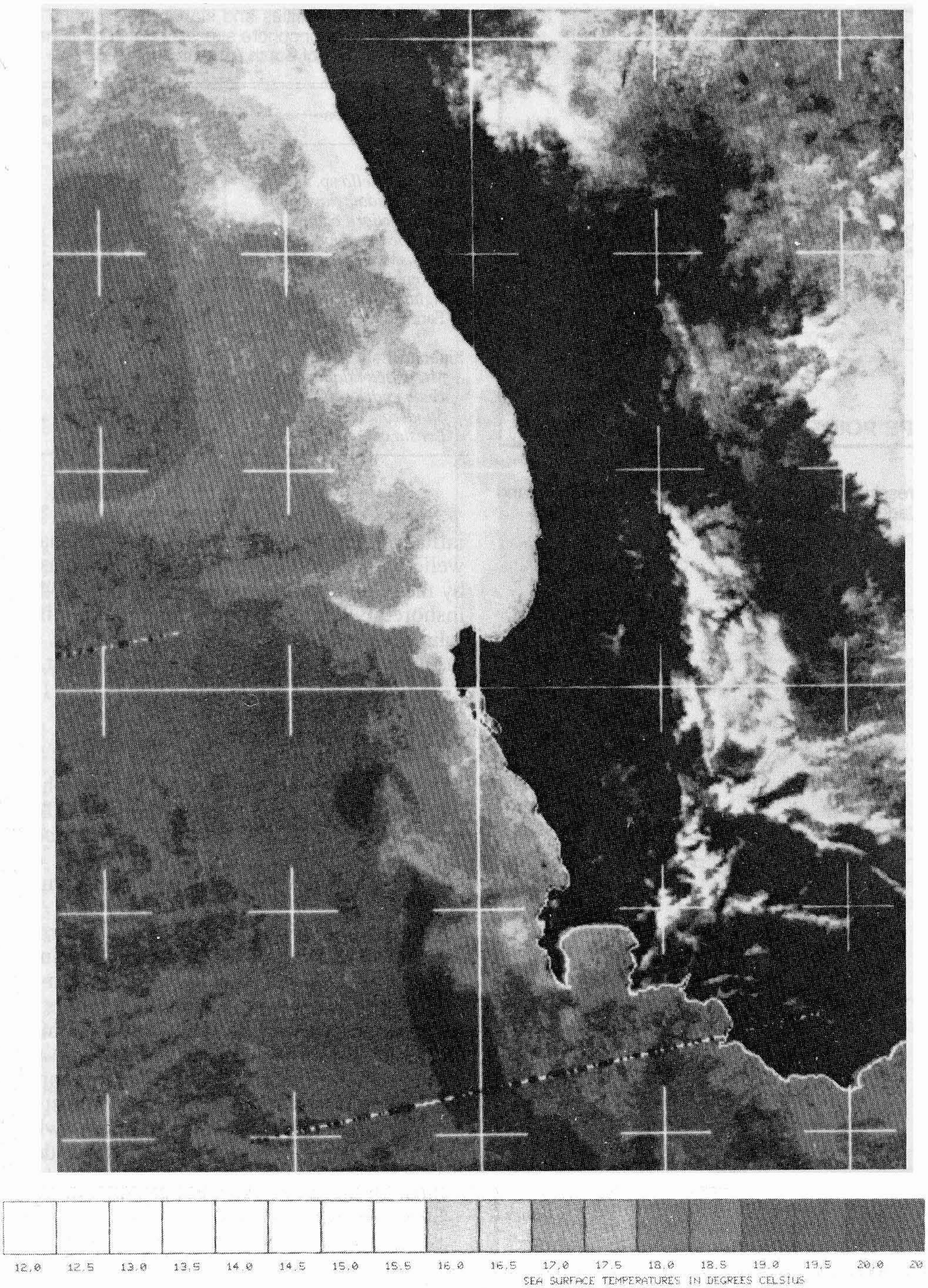

Fig. 2: NOAA-9 satellite image of the southern Benguela region, 8 June 1986 at 14h00, showing surface thermal features

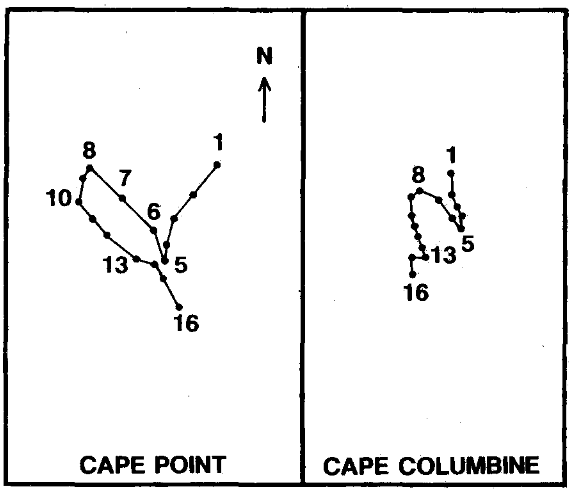

Fig. 3: Progressive wind vector diagrams from Cape Point and Cape Columbine for the period 1–16 June 1986

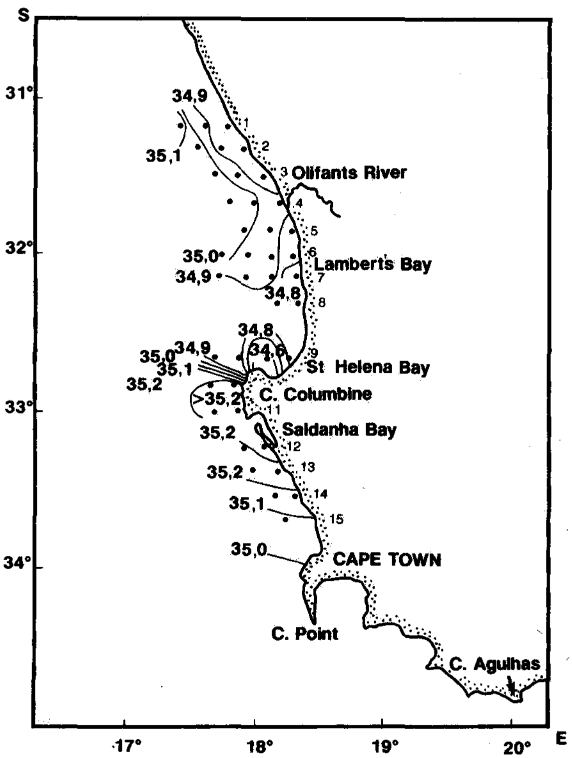

Fig. 4: Surface salinity distribution superimposed onto the station grid

Table I: Mean densities and standard deviations of medusae and siphonophore species collected off the west coast of South Africa in June 1986 (n = 95)

Taxon	Mean density (individuals · 1 000 m^{-3})	*SD*
Medusae		
Mitrocomella sp.	1 636,9	9 114,4
Proboscidactyla menoni	67,7	202,3
Leuckartiara octona	35,8	96,2
Liriope tetraphylla	3,2	16,1
Chrysaora hysoscella (ephyrae)	1,5	11,3
Aglaura hemistoma	1,2	6,5
Pandeidae	0,1	0,9
Siphonophora		
Muggiaea atlantica	463,3	1 316,2
Eudoxoides spiralis	0,4	4,8
Sphaeronectes gracilis	0,2	1,6
Lensia conoidea	0,1	1,9

Surface salinity data during the cruise suggest an influx of oceanic water mixing with the maturing upwelled water north of Cape Columbine, as indicated by the relatively low values of salinity ($<34,9 \times 10^{-3}$) inshore (Fig. 4). South of Cape Columbine surface salinities were much higher ($>35,0 \times 10^{-3}$), suggesting the presence of oceanic water near the coast.

Species distribution pattern

Seven species of medusae and four siphonophores were collected in the samples (Table I). Among the medusae, *Proboscidactyla menoni*, *Mitrocomella* sp. and *Leuckartiara octona* were the most dominant. *Muggiaea atlantica* was the most abundant siphonophore.

The results of the cluster analysis are given in Figure 5. The analysis distinguished three major sample groups. Group C was segregated from Groups A and B because it included the samples in which *Mitrocomella* sp. was the dominant and almost unique cnidarian. Group A was subdivided into three subgroups (A1, A2 and A3). Subgroup A1 contained the samples in which *P. menoni* was the most abundant. Samples dominated by *L. octona* and which were collected farther offshore and at greater depths than those in Subgroup A1 were grouped in Subgroup A2. Subgroup A3 consisted of a few samples which were isolated both geographically and bathymetrically, with *M. atlantica* and *L. octona* as the common species. Three subgroups (B4, B5 and B6) were also distinguished in Group B. Subgroup B4 contained the samples in which *M. atlantica* was the most prominent species and which were collected in the three upper

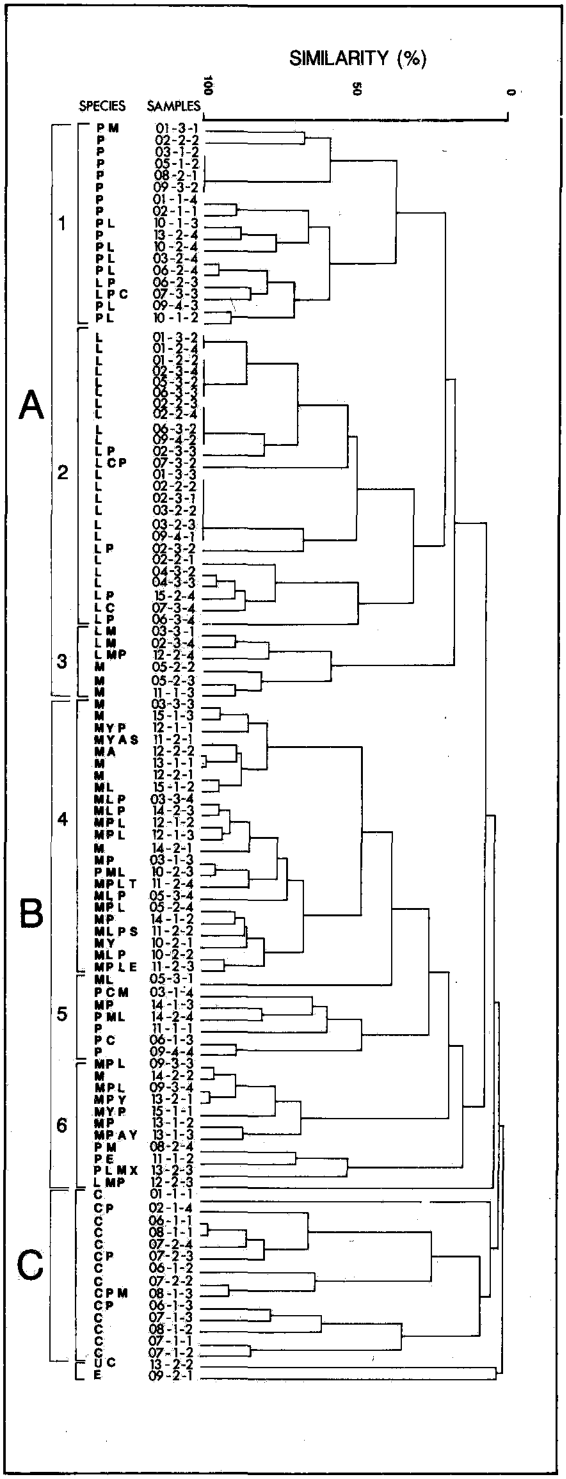

Fig. 5: Dendrogram of similarities (using the Czekanowsky index) between the 105 samples collected during the cruise on the basis of the distribution of 11 cnidarian taxa. The first letter in the species column refers to the dominant species, where P is *Proboscidactyla menoni*, L is *Leuckartiara octona*, C is *Mitrocomella* sp., M is *Muggiaea atlantica*, A is *Aglaura hemistoma*, Y is *Liriope tetraphylla*, S is *Sphaeronectes gracilis*, X is *Lensia conoidea*, U is *Eudoxoides spiralis*, T is Pandeidae, and E is ephyrae of *Chrysaora hysoscella*. Sample code: transect (01–15)-station position (1–4)-depth stratum (1–4). Groups were estimated considering a similarity level >20%

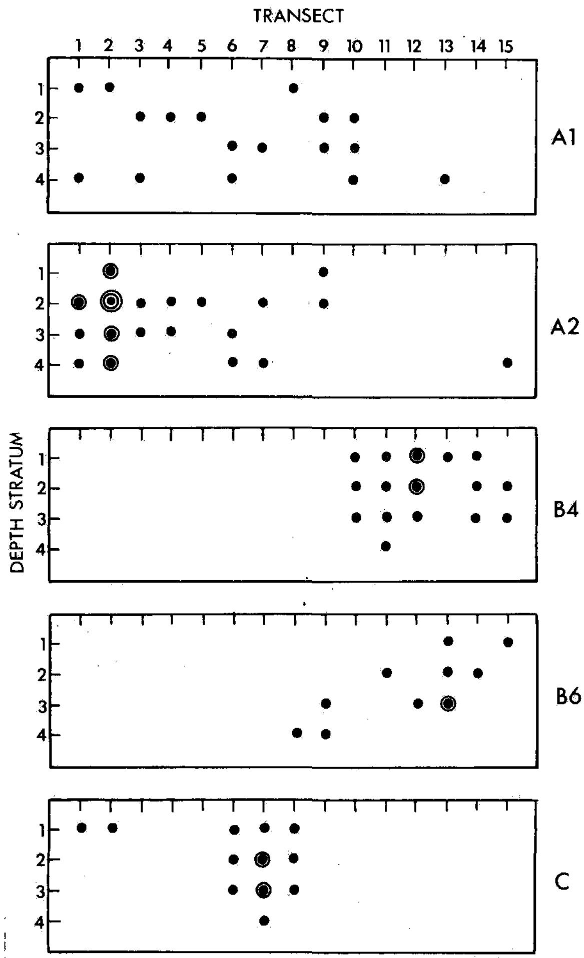

Fig. 6: Relationships between latitudinal distribution (transect) and depth (depth stratum) for each of the principal subgroups (A1, A2, B4, B6, C) distinguished by cluster analysis. Each graph represents the distribution of the dominant species belonging to the respective subgroup: A1 – *Proboscidactyla menoni*; A2 – *Leuckartiara octona*; B4 – *Muggiaea atlantica*; B6 – *M. atlantica*-*P. menoni*-*Liriope tetraphylla*-*Aglaura hemistoma*-*Eudoxoides spiralis*; C – *Mitrocomella* sp.

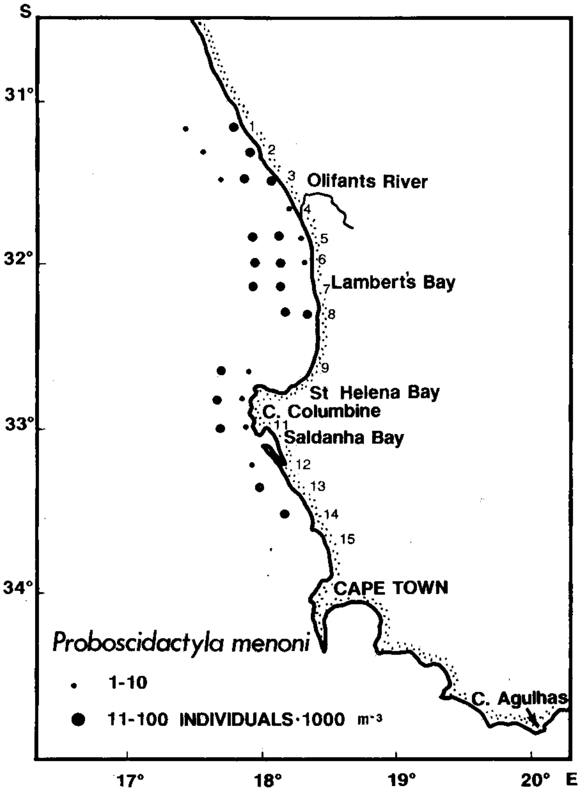

Fig. 7: Horizontal distribution and abundance of *Proboscidactyla menoni* averaged over the water column at each station

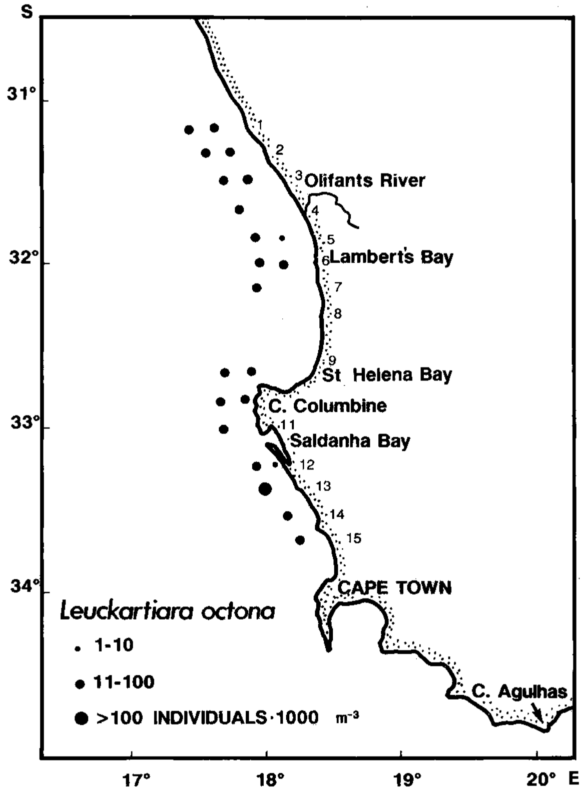

Fig. 8: Horizontal distribution and abundance of *Leuckartiara octona* averaged over the water column at each station

depth strata of the water column. A few samples which were heterogeneous both in terms of number of species and geographical position were pooled in Subgroup B5. Subgroup B6 included samples in which *M. atlantica* predominated, but which were further characterized by the presence of the allochtonous siphonophores *Eudoxoides spiralis* and *Lensia conoidea* and medusae *Aglaura hemistoma* and *Liriope tetraphylla*.

P. menoni was widely distributed over the area sampled, but it was most abundant north of Cape Columbine, where it was found throughout the water column (Fig. 6). In the southern part of the study area, although less abundant, it occurred mainly in the surface layer where it was most prominent offshore (Fig. 7). The distribution of *L. octona* also covered both the northern and southern parts of the study area (Fig. 8). However, *L. octona* was found mainly offshore at subsurface depths within and below the thermocline (Fig. 6). The siphonophore *M. atlantica* was more abundant south of Cape Columbine (Fig. 9), particularly at the offshore stations of the grid. Its abundance was greatest near the surface and rapidly decreased with depth. A few individuals were also collected at four offshore stations in the north. A variety of oceanic species of both medusae (*A. hemistoma*, *L. tetraphylla*) and siphonophores (*E. spiralis*, *L. conoidea*) appeared in the samples taken at those stations where *M. atlantica* was most abundant, i.e. essentially south of Cape Columbine (Fig. 6). The distribution of *Mitrocomella* sp. was clearly different from that of all other cnidarians. It was found in much higher densities (75 073 individuals·1 000 m^{-3} in the upper 15 m at the innermost station of Transect 7). Its distribution was restricted to a very limited area off Lambert's Bay (Transects 6, 7 and 8, Fig. 6) with abundances decreasing steeply with distance offshore. The species was also found sporadically in some samples farther north (maximum

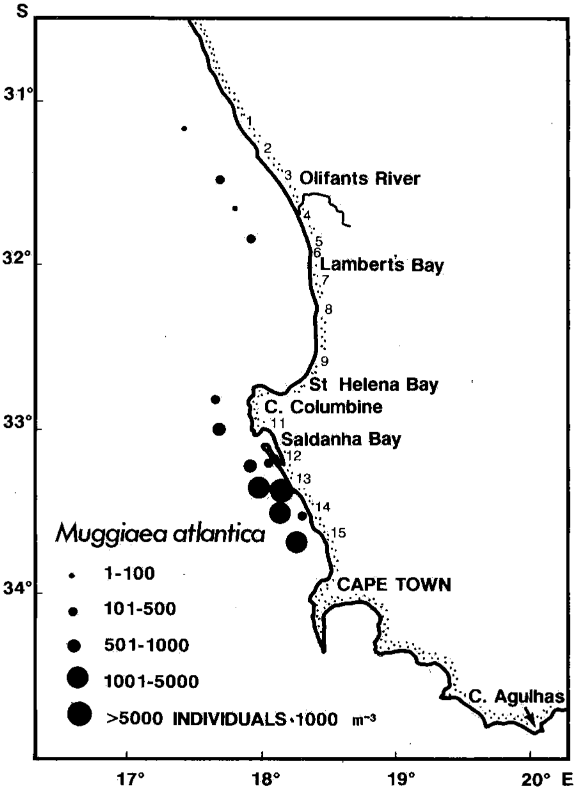

Fig. 9: Horizontal distribution and abundance of *Muggiaea atlantica* averaged over the water column at each station

305 individuals·1 000 m^{-3}).

DISCUSSION

The patterns observed in the distribution of the dominant cnidarian species are the result of a series of short-term hydrographic events related to upwelling and the subsequent wind reversal. During upwelling, wind-driven advection of surface water transports surface-dwelling zooplankters such as juvenile stages of copepods (Verheye 1989, Verheye *et al.* in press), larval euphausiids (Pillar *et al.* 1989) and certain gelatinous zooplankters, such as *Muggiaea atlantica*, offshore. This siphonophore is widespread in coastal/shelf waters (Daniel 1974, Alvariño 1980, Gili *et al.* 1988). In both the northern and southern Benguela systems, it is generally very abundant inshore and forms dense aggregations which result in a high degree of patchiness (Pagès in prep.). The absence of *M. atlantica* in the coastal zone north of Cape Columbine and its patchy distribution offshore suggest that surface Ekman transport took place during the upwelling event prior to the cruise.

The disappearance of *M. atlantica* from the coastal zone in the north coincided with the presence of large concentrations of recently released hydromedusae (2–3 mm diameter) of *Mitrocomella* sp. and *Proboscidactyla menoni*. Densities of those species were far in excess of their concentrations generally encountered in the region (Pagès in prep.). It is therefore suggested that some upwelling-associated environmental trigger was responsible for the release of hydromedusae from the hydroids. Such a mechanism, together with the concomitant disappearance from the coastal zone of *M. atlantica*, which is an important trophic competitor preying heavily on copepods (Purcell 1982), would favour rapid development and survival of the hydromedusae whenever upwelling occurs. Because of their suspected residence at depth during the first few days of their planktonic existence, as has been documented for the Scyphomedusa *Chrysaora quinquecirrha* (Littleford 1939), newly released hydromedusae would not be swept offshore with the upwelling plume. Moreover, as a result of the wind reversal following the upwelling event, onshore transport of surface waters further prevented these hydromedusae from being lost from the coastal zone.

During the period of north-westerly winds, intrusions of oceanic surface water south of Cape Columbine, seen as a dark band extending quite close to the coast in Figure 2, were accompanied by onshore transport of high densities of *M. atlantica* (>8 000 individuals·1 000 m^{-3}). These were supposedly displaced offshore during upwelling. North of Cape Columbine, *M. atlantica* was not collected because of the northerly direction of the winds (Fig. 3). Andrews and Hutchings (1980) described a similar phenomenon of onshore-offshore shifting of zooplankton in the Cape Peninsula region, which caused large fluctuations in zooplankton stocks. In their study, sustained upwelling resulted in the offshore displacement of zooplankton, whereas intrusions of warm water restricted the zooplankton to the inshore zone. Likewise, Hutchings (1981, 1988), in analysing short-term variations of zooplankton biomass off the Cape Peninsula, noted that variations in wind speed and direction determined the extent of offshore dispersion and onshore concentration of copepods. If during upwelling, south-easterly winds, which normally persist for 4–6 days in the area, can displace zooplankton patches up to 90 km offshore (Hutchings 1981, 1988), then north-westerly winds of similar strength and duration, which were evident immediately prior to the present study, can also transport zooplankters such as epiplanktonic cnidarians shorewards over similar distances.

The joint presence of the oceanic species *Aglaura hemistoma*, *Liriope tetraphylla* and *Sphaeronectes gracilis* south of Cape Columbine suggests that the oceanic intrusions are of South Atlantic Surface Water origin and not of Agulhas Bank/Current origin. This hypothesis is corroborated by the lack in the samples of the common Indian Ocean species and the much larger species diversity which is typical of Agulhas waters (Pagès unpublished data). Although the three oceanic species mentioned are very common in the Benguela system, over the shelf and beyond the shelf break (Pagès in prep.), they did not occur at any of the stations north of Cape Columbine. This can be ascribed to the lack there of oceanic water (indicated by salinity $>35{,}2 \times 10^{-3}$).

In a comprehensive mesoscale study of the horizontal distribution of medusae and siphonophores along the Namibian coast, Pagès (in prep.) has observed a clear inshore-offshore zonation of the same species under upwelling conditions. *M. atlantica*, *P. menoni* and *Leuckartiara octona* were always most abundant close inshore, whereas *A. hemistoma* and *L. tetraphylla* showed a typical oceanic distribution. It is surmised here that this pattern of cross-shelf distribution of species assemblages approximated that during the upwelling period prior to the study. Subsequently, the five-day period of onshore winds just prior to the study and the accompanying intrusion of oceanic water disrupted this inshore-offshore zonation pattern. The inshore zone south of Cape Columbine was re-populated by an offshore species assemblage. Therefore, the sequence of upwelling and wind reversal caused a change from an inshore-offshore to a longshore zonation pattern of cnidarian species assemblages. The front which formed off Cape Columbine as a result of hydrographic changes represented a boundary between the northern *Proboscidactyla-Leuckartiara-Mitrocomella* assemblage and the southern *Muggiaea-Liriope-Aglaura-Lensia-Eudoxoides-Sphaeronectes* assemblage.

It must be pointed out, however, that such redistribution of species or assemblages is likely to be of a very short-term or transitional nature, given the rapid changes in wind speed and direction which may occur in the area (Andrews and Hutchings 1980, Taunton-Clark 1985, Hutchings 1988). Therefore, the incidence of this phenomenon of displacement of coastal species offshore and subsequent replacement with offshore species will depend on the duration of a wind reversal. Such short-term changes would be beneficial to offshore species in that they are brought from an oligotrophic offshore environment into a coastal zone where prey density is higher.

In conclusion, short-term changes in the distribution of water masses cause a great deal of heterogeneity in the assemblages of gelatinous zooplankton. In an area of large hydrodynamic variability, such as the southern Benguela upwelling system, this zooplanktonic heterogeneity is reflected in the longshore redistribution of species assemblages, with well-defined boundaries, but with a low species diversity that increases as a result of intrusions of offshore water. These intrusions are accompanied by an influx shorewards of oceanic and shelf species, and they can have an important impact on the composition of coastal communities. The frequency and the intensity of such intrusions seem to be limiting for the proliferation of coastal species, which depend on the periodicity of intrusions and the residence time of these foreign water masses near the coast. Whereas the north-westerly wind regime mainly affects the coastal populations south of Cape Columbine, it seems to be advantageous for the development and maintenance of coastal populations in the north. This is partly because of the peculiar orographic characteristics (Jury 1985) and the circulation system (Holden 1985) of the St Helena Bay region. In this manner, north-westerly winds facilitate retention of pools of maturing upwelled water and their zooplankton communities, compensating for the losses suffered during upwelling and contributing further to the stability of zooplankton assemblages in St Helena Bay.

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