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Interannual variation in the composition of the assemblages of medusae and ctenophores in St Helena Bay, Southern Benguela Ecosystem*

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SUMMARY: The assemblages of medusae and ctenophores were examined from samples collected each winter from St Helena Bay, over the 10-year period 1988-1997. A total of 50 hydromedusae, 1 scyphozoan and 2 ctenophore species were identified from 243 samples. Although the data set is characterised by great interannual variability, two main assemblages could be identified each year. These were characterised by either holoplanktonic medusae (e.g. *Liriope tetraphylla, Aglaura hemistoma*) or meroplanktonic medusae (e.g. *Mitrocomella millardae*, *Chrysaora hysoscella*) and ctenophores (e.g. *Pleurobrachia pileus*). The holoplanktonic medusae were typical of samples at the southern edge of the Bay, and were positively associated with both depth and temperature. Their abundances tended to increase during warm years (1992, 1993 and 1997) as warm surface water flooded the Bay. The meroplanktonic medusae and ctenophores were typical of samples collected within the Bay, and the density of species tended to be negatively correlated with temperature and depth. In spite of the eurythermal nature of the meroplanktonic species, they were more common during cold years (1990 and 1995). This paper represents the first Bay-wide, interannual study of any zooplankton group, and contributes important base line information on the structure of regional pelagic assemblages.

Key words: zooplankton, jellyfish, diversity, upwelling, South Africa.

INTRODUCTION

Coastal upwelling areas are of ecological interest, as well as economic importance, because of their enhanced primary productivity, which is generated by the vertical transport of nutrients to surface waters. The Benguela system along the southwest coast of Africa (~15°S to ~35°S) is one of the most important wind-driven coastal upwelling areas in the world. The region is bounded by two warm currents, the Angola Current in the north and the Agulhas Current in the south. This highly hydrodynamic area can be considered an unstable environment (Hart and Currie, 1960), where physical events can be evoked to explain the variability in species abundance and distribution (McGowan, 1974).

Cnidarians and ctenophores are thought to be good indicators of water mass movement (Colebrook, 1977; Raymont, 1983). Studies of their spatial distribution in and around the Benguela system have revealed the presence of distinct assemblages associated with both latitudinal and longitudinal gradients (Pagès and Gili, 1991a, 1991b; Pagès *et al.*, 1991; Pagès, 1992; Fearon *et al.,* 1992). Although the boundaries to these assemblages tend to agree with the regional oceanography, they vary

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with upwelling intensity. The diversity of the inner-shelf assemblages of gelatinous zooplankton is universally low (see also Gibbons and Hutchings, 1996). This contrasts with the pattern of numerical abundance, which tends to peak over the shelf and reflects spatial gradients of productivity.

Pelagic cnidarians are considered to be important predators in the pelagos (e.g. Matsakis and Conover, 1991; Purcell *et al.,* 1994). However, our understanding of their precise role in the region is still a product of postulation (e.g. Gibbons *et al.*, 1992). In sheltered bays and harbours, they have been shown to influence the abundance of some other zooplankton species (Fulton and Wear, 1985), and they have also been linked to fluctuations in wider-scale fisheries (Möller, 1984). Given the rapacious appetites of gelatinous carnivores (Costello, 1988; Gibbons and Painting, 1992), these impacts are primarily the result of a coincidence in time and space of predators and prey, which can be fostered by the sheltered nature of the environment. In pulsed and seasonal upwelling ecosystems, such as the Benguela, it is very difficult to disentangle the impact of pelagic cnidarians and ctenophores on zooplankton and fisheries from more general, wider environmental variability. This is because the distribution and abundance of plankton is dramatically altered with each upwelling pulse (Andrews and Hutchings, 1980).

It has recently been shown that inter-annual fluctuations in the abundance of commercial pelagic fishes in the southern Benguela are linked to changes in the environment (including the zooplankton food environment) (Verheye and Richardson, 1998; Verheye *et al.*, 1998). The present paper looks at interannual variability in the composition, abundance and distribution of medusae and ctenophores over a part of the same time period in an effort to improve our understanding of long term dynamics of ecosystems. This study describes the relationship between medusae and ctenophores with the environment, and so might enable us to make more direct links with fisheries in future.

MATERIALS AND METHODS

Study Site

St Helena Bay (~ 31°50'S - 32°50'S) (Fig. 1) is the broad shelf area to the north of Cape Columbine, which is one of the five major upwelling centres along the west coast of southern Africa (Shannon, 1985).

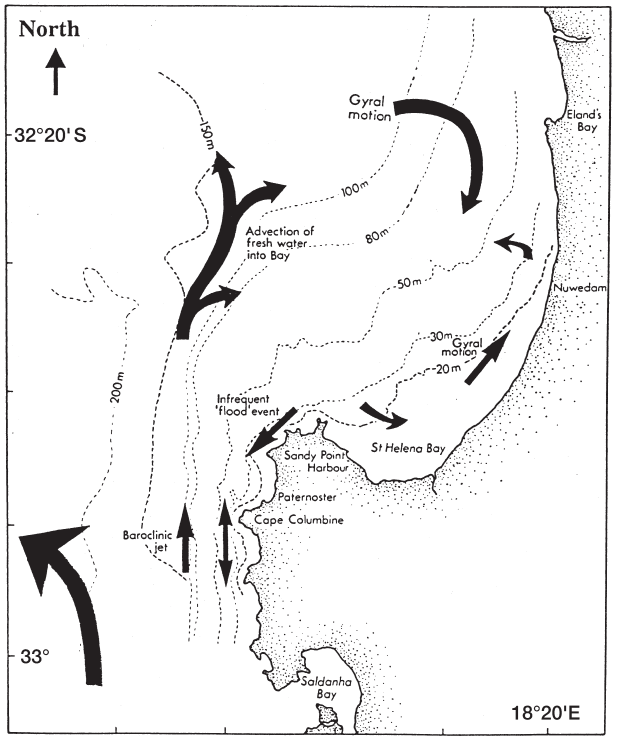

FIG. 1. – Map of the study area, showing generalised patterns of circulation (adapted from Chapman and Bailey, 1991)

Field Sampling

Ten to 44 stations 10 nautical miles apart were sampled each year by either the *FRS Africana* (1988-1994) or the *FRS Algoa* (1995-1997) during May and June from up to fifteen transects perpendicular to the shoreline of St Helena Bay (Table 1). The number of transects and the number of stations per transect varied each year according to the needs of the stock assessment surveys decided by Marine and Coastal Management. All stations were sampled during the day.

Zooplankton samples were collected at each station using paired vertical Bongo nets (57 cm mouth diameter), fitted with a 200 μm mesh (McGowan and Brown, 1966). The nets were lowered to 5 m above the sea floor (maximum depth for the studied area was 398 m in 1991) and hauled vertically at a speed of 1 m.s^{-1}. From 1988 to 1992, the volume filtered by the nets was calculated as a function of the mouth area and the sampling depth. From 1993 - 1997, the volume filtered by the nets was measured using an electronic flowmeter mounted in the mouth of one of the nets. On retrieval, all samples were immediately preserved in 5% buffered seawater formalin.

Crustacean mesozooplankton were identified and counted from replicate 5 ml subsamples. Numbers were converted to dry-weight using the equations of Painting (Painting *et al*., unpublished), prior to summation and the calculation of total mesozooplankton biomass (per m^2).

All medusae (hydromedusae and scyphomedusae) and ctenophores were identified and counted, without subsampling, and the data expressed as numbers per 100 m^3. A total of 243 samples were examined. Less than 0.5% of all the animals collected were too damaged to be identified.

A number of environmental parameters were measured at the same time as the zooplankton samples were collected. The speed and direction of near-surface currents (at 30-35 m depth) were determined on station, using a hull-mounted acoustic doppler current profiler (ADCP). Wind speed and direction were determined at each station using an anemometer mounted above the bridge of the research vessel. Although a conductivity-temperature-depth (CTD) instrument with a 12-bottle rosette was cast from the surface to close to the bottom at each station to provide profiles of salinity, temperature and Sigma-t, only surface values are presented here. Fluorescence profiles were obtained using a Chelsea Instruments Aquatracka submersible fluorometer mounted on a magnum rosette. Water samples were collected at the surface for the determination of size-fractionated chlorophyll *a* (total and > 10 μm), and to analyse the particle size composition of the water. Chlorophyll samples were analysed within 6 h following the method of Parsons *et al*. (1984), while a Coulter multisizer was employed to determine the particle-size composition of the water.

It should be noted that not all environmental parameters were collected across the whole grid each year (see Table 1).

Statistical analysis and data handling

Descriptive and multivariate statistics were used to examine relationships among the samples of medusae and ctenophores each year, in order to see whether there was any horizontal pattern to the assemblages observed. The densities of all species that contributed to greater than 10% of the numeric total in each sample (henceforth known as the dominant species), were root-root transformed and a similarity matrix was constructed between the samples using the Bray-Curtis Index (Field *et al*., 1982). These matrices were used to plot classification diagrams of percentage similarity between samples using group-average sorting. The identified clusters of samples (assemblages) were then superimposed onto maps of the sampling grid (Fig. 2). These analyses were conducted using PRIMER software.

"Indicator species" for each assemblage each year were identified using the SIMPER routine in PRIMER. This exploratory software routine calculates the contribution of each species **both** to the average Bray-Curtis dissimilarity **between** the identified assemblages (sample clusters), and to the average similarity **within** an assemblage. For ease of interpretation, the number of indicator species presented has been restricted to those species which contribute to 80% of the cumulative percentage similarity.

In an effort to determine which of the environmental parameters could "best explain" the pattern observed in the biological assemblages each year, the BIOENV proceedure in PRIMER was used. This software maximises a Spearman rank correlation between the environmental and biological similarity matrices (Clarke and Ainsworth, 1993). The environmental similarity matrices were constructed using normalised Euclidean distance whilst the Bray-Curtis Index was used to construct the similarity matrix for the biological data.

Hitherto, all the analyses have been conducted on the data collected each year. In an effort to detect any common patterns of association between the dominant species (those which were found in more than 10% of samples), Bray-Curtis similarity matrices were constructed from the whole 10-year data set and used to plot a classification diagram of percentage similarity using PRIMER.

Relationships between the abundance of the dominant species, and various environmental characteristics (temperature, depth and chlorophyll *a*) were examined using correlation analyses and multiple regression analyses of the untransformed data. These analyses were conducted using STATISTICA software on the whole 10-year data set.

RESULTS

The sea surface temperature (SST) during winter in St Helena Bay varied from a minimum of 10.9°C (in 1990) to a maximum of 18.9°C (in 1991). SST and sea surface salinity were lower near the coast and in the north (<14.0°C and < 35.0 psu), than offshore and in the south (>16.0°C and > 35.0 psu)

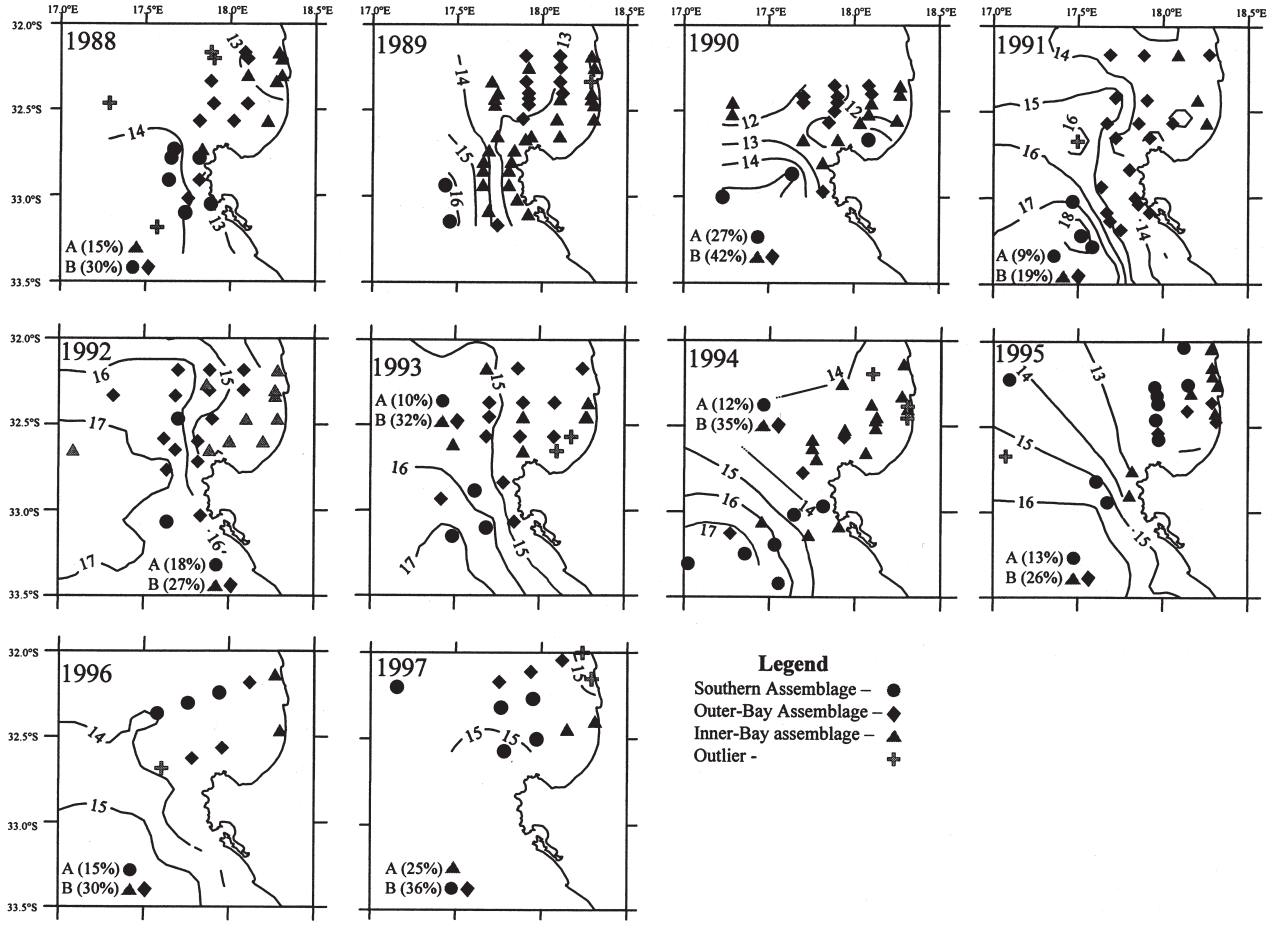

FIG. 2. – The different assemblages of medusae and ctenophores, identified by cluster analysis and superimposed upon maps of the study area each year. Contours represent the position of surface isotherms (°C), while the percentage value indicates the Bray-Curtis level of similarity between the assemblages.

TABLE 1. – List of parameters measured by Marine and Coastal Management during the Recruit Survey, by year: * indicates parameters measured for all samples; # indicates parameters available only for some of the samples. Zooplankton biomass and dry weight were measured for all the zooplanktonic groups, non-crustacean and gelatinous zooplankton.

	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
Sea surface temperature (SST)	*	*	*	*	*	*	*	*	*	*
Sea surface salinity	*	*	*	*	#	#		#		
Currents at 30-35 m depth (ADCP)			#	#	#	#	#	#	#	#
Sea surface fluorimetry				*	*	*				
Wind speed and direction				*	*	*	*	*	*	
Total Chlorophyll *a*	*	*	*	*	*	*	*	*		
Chlorophyll a < 10µm	*	*	*	*	*	*	*	#		
% Chlorophyll a < 10µm	*	*	*	*	*	*	*	#		
% Chlorophyll a > 10µm	*	*	*	*	*	*	*	#		
Biomass and dry weight zooplankton	#	#	#	#	#	*	*	*	*	
Maximum depth noted during the survey	318 m	365m	216m	398m	313m	202m	201m	202m	166m	148m
Mean temperature	13.3°C	13.1°C	12.2°C	14.3°C	15.4°C	15.6°C	14.3°C	13.0°C	13.6°C	15.3°C
Number of transects	11	15	8	8	9	7	8	9	2	3
Number of samples collected	29	44	27	29	32	25	29	29	10	12

(Fig. 2). The coldest year was 1990, with a mean SST of 12.2°C. By contrast, 1992 and 1993 were the warmest years and the mean SST reached 15.4°C and 15.6°C respectively (Table 1).

A total of 50 hydromedusae species (29 anthomedusae, 13 leptomedusae, 3 limnomedusae, 1 narcomedusae and 4 trachymedusae), 1 scyphomedusa species and 2 ctenophores species (1 tentacula-

TABLE 2. – Species of medusae and ctenophores collected from 1988 to 1997 and the total number of each species collected in the Survey. Species preceded by # are holoplanktonic (totally pelagic), whereas the others are either known, or assumed to be meroplanktonic (with a benthic stage).

Species	Years /occurrences 88	89	90	91	92	93	94	95	96	97	Total number
PHYLLUM CNIDARIA											
CLASS HYDROZOA											
Subclass Hydroidomedusae											
Order Anthomedusae											
Dicodonium sp.	•										1
Dipurena halterata (Forbes, 1846)		•									1
Dipurena ophiogaster Haeckel, 1879				•							1
Sarsia nipponica Uchida, 1927								•			1
Sarsia resplendens Bigelow, 1909								•			1
Ectopleura dumortieri (van Beneden, 1844)		•	•	•			•				14
Euphysa aurata Forbes, 1848	•	•	•	•	•	•	•	•	•	•	763
Euphysilla pyramidata Kramp, 1955	•			•	•		•	•			6
Euphysomma brevia (Uchida, 1947)			•	•			•				3
Euphysora gracilis (Brooks, 1882)	•										1
Euphysora furcata Kramp, 1948				•							1
Hybocodon unicus (Browne, 1902)	•		•		•						4
Pennaria sp.	•										1
Zanclea costata Gegenbaur, 1856			•	•	•		•				5
Zancleopsis gotoi Uchida, 1927					•						1
Zancleopis tentaculata Kramp, 1928								•			2
Staurocladia vallentini (Browne, 1902)							•				1
Turritopsis nutricula McCrady, 1856								•			1
Podocoryne minuta (Mayer, 1900)	•			•		•					3
Podocoryne carnea M. Sars, 1846	•										1
Bougainvillia macloviana Lesson, 1836		•	•	•	•	•	•				125
Lizzia blondina Forbes, 1848					•	•					3
Nemopsis sp.			•								1
Amphinema dinema (Péron & Lesueur, 1809)							•				2
Amphinema rugosum (Mayer, 1900)	•										1
Pseudotiara tropica Bigelow, 1912		•									1
Leuckartiara octona (Fleming, 1823)	•	•	•	•	•	•	•	•	•	•	469
Urashimea globosa Kishinouye 1910				•		•					45
Heterotiara sp.		•									1
Order Leptomedusae											
Krampella sp.	•										1
Staurodiscus sp.		•									1
Mitrocomella grandis Kramp, 1965		•	•		•	•			•	•	149
Mitrocomella millardae Pagès *et al.*, 1992	•	•	•	•	•	•	•	•	•	•	3 089
Obelia spp.	•	•	•	•	•	•	•	•	•	•	1 752
Clytia folleata (McCrady, 1857)								•			4
Clytia hemispherica (Linné, 1767)	•		•	•	•	•	•	•	•	•	67
Clytia simplex (Browne, 1902)			•			•					6
Eucheilota paradoxica Mayer, 1900								•			2
Cirrholovenia polynema Kramp, 1959		•									1
Phialella quadrata (Forbes, 1848)				•	•		•				4
Eirene menoni Kramp, 1953		•			•						2
Aequorea aequorea (Forskål, 1775)	•		•		•	•					5
Order Limnomedusae											
Cubaia aphrodite Mayer, 1894									•		1
Proboscidactyla menoni Pagès *et al.*, 1992	•	•	•	•	•	•	•	•	•	•	547
Proboscidactyla stellata (Forbes, 1846)		•									1
Order Narcomedusae											
#Solmundella bitentaculata (Quoy & Gaimard, 1833)	•	•		•	•	•	•	•	•	•	35
Order Trachymedusae											
#Liriope tetraphylla (Chamisso & Eysenhardt, 1821)	•	•	•	•	•	•	•	•			111
#Aglaura hemistoma Péron & Lesueur, 1809	•	•	•	•	•	•	•	•			790
#Persa incolorata McCrady 1857	•	•	•		•				•		26
#Rhopalonema velatum Gegenbaur, 1856	•	•			•			•			17
CLASS SCYPHOZOA											
Order Semaeostomae											
Chrysaora hysoscella (Linné, 1766) (ephyra)	•	•	•		•	•				•	851
PHYLLUM CTENOPHORA											
CLASS TENTACULATA											
Order Cydippida											
#Pleurobrachia pileus (O.F. Müller, 1776)	•	•	•	•	•	•	•	•	•	•	5 288
CLASS NUDA											
Order Beroida											
#Beroe spp.	•	•	•	•	•	•	•		•	•	290
Number of species collected per year	24	23	21	21	24	19	19	18	12	11	24 512

ta and 1 nuda) were collected over the course of the 10-year survey (Table 2). The maximum number of species recorded in any one year was 24 in 1988 and 1992, and the minimum number observed was 11 in 1997 (Table 2). Many of the species recovered have previously been recorded from the region (Millard, 1975, Pagès *et al.*, 1992; Bouillon, 1999), but there are 21 new records for the southern Benguela. These include *Sarsia resplendens*, *Euphysilla pyramidata*, *Euphysoma brevia*, *Zancleopsis tentaculata* and *Urashimea globosa*.

Although *Euphysa aurata*, *Leuckartiara octona*, *Mitrocomella millardae*, *Obelia* spp., *Proboscidactyla menoni* and *Pleurobrachia pileus* were the only species to be caught every year (Table 2), their abundances were highly variable. For example, the average abundance of *E. aurata* in 1991 was 69.86 ind. m^{-3} (± 248.86), but during 1995 only 0.33 ind. m^{-3} (± 0.75) were recorded.

Mitrocomella millardae was the most abundant species and 5 269.36 ind. m^{-3} were collected in 1994. *Pleurobrachia pileus* was the second most abundant species in St Helena Bay. By contrast, other species such as *Podocoryne carnea* (in 1988) and *Staurocladia vallentini* (in 1994) were recorded only once during the entire survey (Table 2). These and the other uncommon species listed in Table 2 were ignored in all subsequent analyses, which were confined to the dominant 12 species.

Although there was no underlying relationship between total species richness and either temperature or depth (Table 3), an examination of the data by life-cycle reveals two contrasting patterns. The species richness of the meroplanktonic assemblage (comprised of species with an attached polyp stage during the life cycle) was negatively correlated with both temperature and depth, but it was positively correlated with total chlorophyll *a*. By contrast, the richness of the holoplanktonic assemblage of medusae (medusae with a totally pelagic life cycle) was positively correlated with temperature and depth, and negatively correlated with total chlorophyll *a*. *In other words the meroplanktonic species reached peak richness in cold, chlorophyll a-rich shallow water, whilst the holoplanktonic species were more diverse in warm, oligotrophic deep water.*

The total abundance of medusae and ctenophores was negatively correlated with bottom depth and surface temperatures (Table 3). Although the abundance of holoplanktonic ctenophores was also correlated negatively with depth and temperature, the abundance of meroplanktonic medusae was significantly, and negatively, correlated with depth. The abundance of holoplanktonic medusae was positively correlated with temperature but not with depth or total chlorophyll *a* (Table 3).

TABLE 3. – Correlation coefficients between species richness and abundance, and various parameters of the physical environment. Data expressed as totals and subdivided by life-cycle type and taxonomic group. Level of significance indicated: ** $p < 0.05$, * $p < 0.10$.

	Temperature	Depth	Total chlorophyll *a*
Total Abundance	-0.14*	-0.19**	0.02
Total Species Richness	-0.06	-0.07	0.08
Holo-Abundance	0.16**	-0.03	0.06
Holo- Richness	0.51**	0.55**	-0.18**
Mero- Abundance	-0.13	-0.16**	0.08
Mero- Richness	-0.25**	-0.27**	0.18**
Antho- Abundance	-0.06	-0.09	0.08
Antho- Richness	-0.12	-0.05	0.17**
Lepto- Abundance	-0.10	-0.12	0.05
Lepto- Richness	-0.25**	-0.27**	-0.01
Trachy- Abundance	0.15**	-0.04	0.07
Trachy- Richness	0.48**	0.52**	-0.17
Cteno- Abundance	-0.12	-0.15*	-0.03

The results of the cluster analysis suggest that each year two distinct groups of samples could be identified. These clusters roughly correspond to samples collected within, and to the south of, St Helena Bay; their positions have been mapped in Figure 2. The percentage similarity between these two main groups varied between 9% (in 1991) to 27% (in 1990). The samples collected within St Helena Bay (hereafter referred to as "Bay" samples) could usually be further subdivided into two subgroups that corresponded to inshore-and outer-shelf-samples. It is important to note that while all three assemblages could be identified each year, their positions varied from one year to the next (Fig. 2). There were also a number of outlying samples (Fig. 2), which showed a limited degree of similarity with any others and these have been ignored here as uninformative.

The BIOENV procedure suggested that surface temperature and/or water column depth and/or chlorophyll *a* were the environmental variables that best explained the pattern observed each year in the assemblages (Table 4). However, the same variables, or combination of variables, did not always provide the best explanation for the pattern observed amongst the assemblages each year. For example, water column depth and chlorophyll *a* best explained the pattern observed in 1988, whilst temperature alone explained the pattern observed in 1994.

TABLE 4. – Harmonic correlations between environmental parameters which, either singularly or in combination, were significantly correlated (*: $p < 0.05$) with the structure of the medusa and ctenophore assemblages identified by cluster analysis and indicated on Fig. 2. The analysis was conducted using the BIOENV procedure in PRIMER (see text). There were insufficient data during 1996 and 1997 to conduct these analyses.

	1988	1989	1990	1991	1992	1993	1994	1995
Temperature		*	*	*		*	*	*
Depth	*		*	*	*	*		*
Total Chlorophyll	*	*				*		
Correlation factor	0.30	0.40	0.33	0.50	0.20	0.15	0.18	0.37

TABLE 5. – Specific composition of the two main assemblages (Southern and "Bay" assemblages) and of the two sub-groups (inshore-and outer-shelf- assemblages) which compose the "Bay" assemblage. Only species responsible for contributing to 80 % of the assemblage identity are included. The average abundances are indicated in brackets (ind. 100 m^{-3}).

	Southern assemblage	"Bay" assemblage	Inshore assemblage	Outer-shelf assemblage
1988	*P. menoni* (11.6) *Obelia* spp. (109.2) *P. incolorata* (2.6) *P. pileus* (33.2)	No significant species	*C. hysoscella* (1239.9)	*P. menoni* (10.1) *P. pileus* (19.9)
1989	No significant species	*P. menoni* (23.3) *L. octona* (17.7) *P. pileus* (49.9) *Beroe* sp. (14.2)	*P. pileus* (68.7) *P. menoni* (26.3) *L. octona* (16.6)	*L. octona* (20.7) *P. menoni* (15.3) *E. aurata* (5.6)
1990	*P. pileus* (20.7)	*P. pileus* (1275.6) *P. menoni* (25.9) *Obelia* spp. (373.7) *C. hemispherica* (11.7)	*P. pileus* (2318.5) *Obelia* spp. (699.3) *P. menoni* (40.1) *Beroe* sp.(87.1) *C. hemispherica* (19.3)	*P.pileus* (128.4) *E. aurata* (8.4) *P. menoni* (10.3)
1991	*L. tetraphylla* (6.8) *E. aurata* (15.2) *A. hemistoma* (0.8)	*E. aurata* (89.8) *P. menoni* (22.9) *P. pileus* (189.7)	*P. menoni* (23.4) *Obelia* spp. (49.4)	*E. aurata* (104.7) *P. pileus* (221.3) *L. octona* (3.04)
1992	No significant species	*E. aurata* (31.4) *R. velatum* (56.7) *A. aequorea* (16.56) *L. blondina* (9.9) *L. tetraphylla* (66.5)	*A. hemistoma* (97.5) *E. aurata* (36.9) *L. octona* (5.7)	*C. hysoscella* (120.9) *P. menoni* (32.2) *B. macloviana* (90.0) *P. pileus* (185.8) *Beroe* sp. (42.4) *C. hemispherica* (21.5)
1993	A. hemistoma *(4.4)*	*P. pileus* (706.8) *C. hysoscella* (19.1) *Obelia* spp. (292.2) *P. menoni* (6.9) *L. octona* (9.0)	*P. pileus* (128.1) *P. menoni* (8.9) *L. octona* (14.5) *C. hysoscella* (15.8) *E. aurata* (10.6)	*Obelia* spp. (86.4) *P. pileus* (32.5)
1994	*L. tetraphylla* (6.9) *A. hemistoma* (10.9)	*P. menoni* (26.5) *L. octona* (45.6) *E. aurata* (39.0)	*P. pileus* (470.8) *P. menoni* (30.0) *Obelia* spp. (16.5)	*L. octona* (54.4) *P. menoni* (25.8) *E. aurata* (46.0)
1995	*L. octona* (4.9) P. menoni *(4.5)*	*Obelia* spp. (56.3) *M. millardae* (23.3) *P. pileus* (14.6)	*Obelia* spp. (56.3) *M. millardae* (23.3) *P. pileus* (14.6)	*M. millardae* (26.9) *P. pileus* (5.8)
1996	*E. aurata* (7.0) *L. octona* (7.8)	*P. pileus* (88.7) *M. millardae* (927.8) *C. hemispherica* (4.8)	No significant species	*P. pileus* (65.6) *M. grandis* (8.8)
1997	*L. octona* (11.6)	No significant species	No significant species	*E. aurata* (87.1) *L. octona* (5.7)

The dominant species that could be used to identify the different assemblages each year tended to vary (Table 5). For example, during 1988 the southern assemblage was identifiable by relatively high numbers of *Proboscidactyla menoni*, whilst in 1994 it was identifiable by large numbers of *Liriope tetraphylla*. Although many of the species were found in more than one assemblage, some species tended

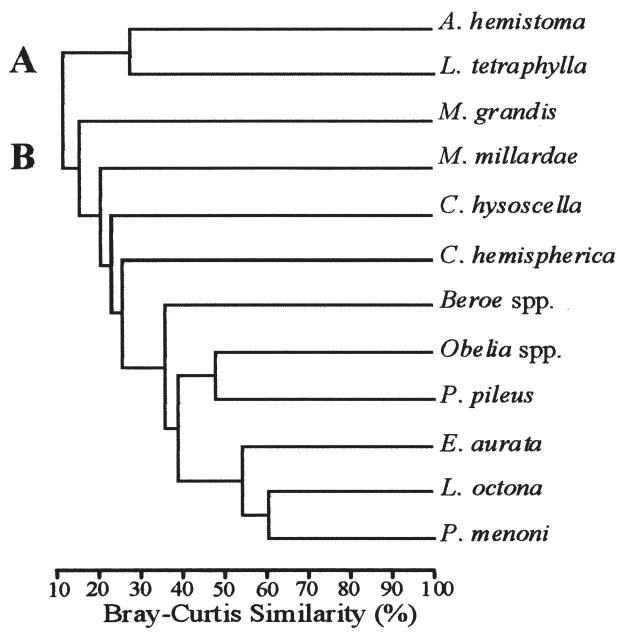

FIG. 3. – Dendrogram of percent similarity (Bray-Curtis Index) between the dominant species of medusae and ctenophores collected during winter in St Helena Bay, over the period 1988-1997. Two clusters can be seen that correspond to warm and deep water species (A), and cooler and shallow water species (B).

to be consistently present in some assemblages but absent in others. For example, *Liriope tetraphylla* was a conspicuous component of the southern assemblage, whilst *Pleurobrachia pileus* and *Mitrocomella millardae* were more characteristic of the Bay assemblages.

The dendrogram of percent similarity amongst the dominant gelatinous zooplankton delimits two main clusters at the 10% level (Fig. 3). These two clusters indicate species-groups whose members tended to be found together in samples, and whose abundances tended to fluctuate in tandem with each other. The greater the similarity between members the more frequently they were found together. The two clusters identified were of very unequal size and correspond to holoplanktonic medusae (group A), and meroplanktonic medusae and holoplanktonic ctenophores (group B). Although the level of similarity between associated species was generally low, these two clusters roughly correspond to the southern and "Bay" assemblages identified previously (Fig. 3, Table 5).

Owing to the fact that generally too few samples of any one species were collected in any one year, it was necessary to look at species-specific responses to the physical environment using the entire data set. The results of the correlation analyses reveal that the abundances of only seven of the 12 dominant species could be linked to the environment. The abundances of the two holoplanktonic species (group A) were both positively correlated with temperature and/or depth. The abundance of group B species was all negatively correlated with either temperature and/or depth, although it should be noted that congruence in the pattern of response was not constant between species. However, from multiple regression analyses done with the species and the environmental parameters (temperature, depth and concentration on chlorophyll *a*), the abundance of only three of the dominant species could be significantly explained (at least at the 0.01 level) by linear combinations of the environment. Of these dominant species, *Liriope tetraphylla* and *Aglaura hemistoma*, group-A members, had their abundances linked to temperature and depth (but not chlorophyll *a*). The remaining species (*Clytia hemispherica*) was from group B, and was negatively affected by temperature.

DISCUSSION

In order to explain the interannual patterns in assemblage composition, abundance and distribution, it is necessary to try to appreciate the environment in which they occur. The western coast of South Africa is subject to SE winds, which quickly result in coastal upwelling. This is particularly pronounced where the shelf-edge lies close to the coastline and in the vicinity of capes (such as Cape Columbine) and peninsulas. Although the newly upwelled water is cold and nutrient-rich, it gradually warms as it moves offshore (by Ekman transport), and phytoplankton populations bloom at the surface. The upwelling front that develops may, if the SE winds are strongly sustained, eventually be coincident with the shelf-edge front that separates coastal waters from warm, chlorophyll-poor oceanic waters. Onshore winds result in the fairly rapid movement of the oceanic water over the shelf, which leads to an increase in SST there and downwelling (Shannon, 1985; Boyd *et al.*, 1992). The system is characterized by much variability, and by rapid changes in the physical environment.

Each year, the assemblages of gelatinous zooplankton could be divided into two groups on the basis of similarities in their specific composition (Fig. 2): a cool, shallow water assemblage (identified as "Bay") and a warmer, deeper water assemblage (identified as "southern"). These groups were

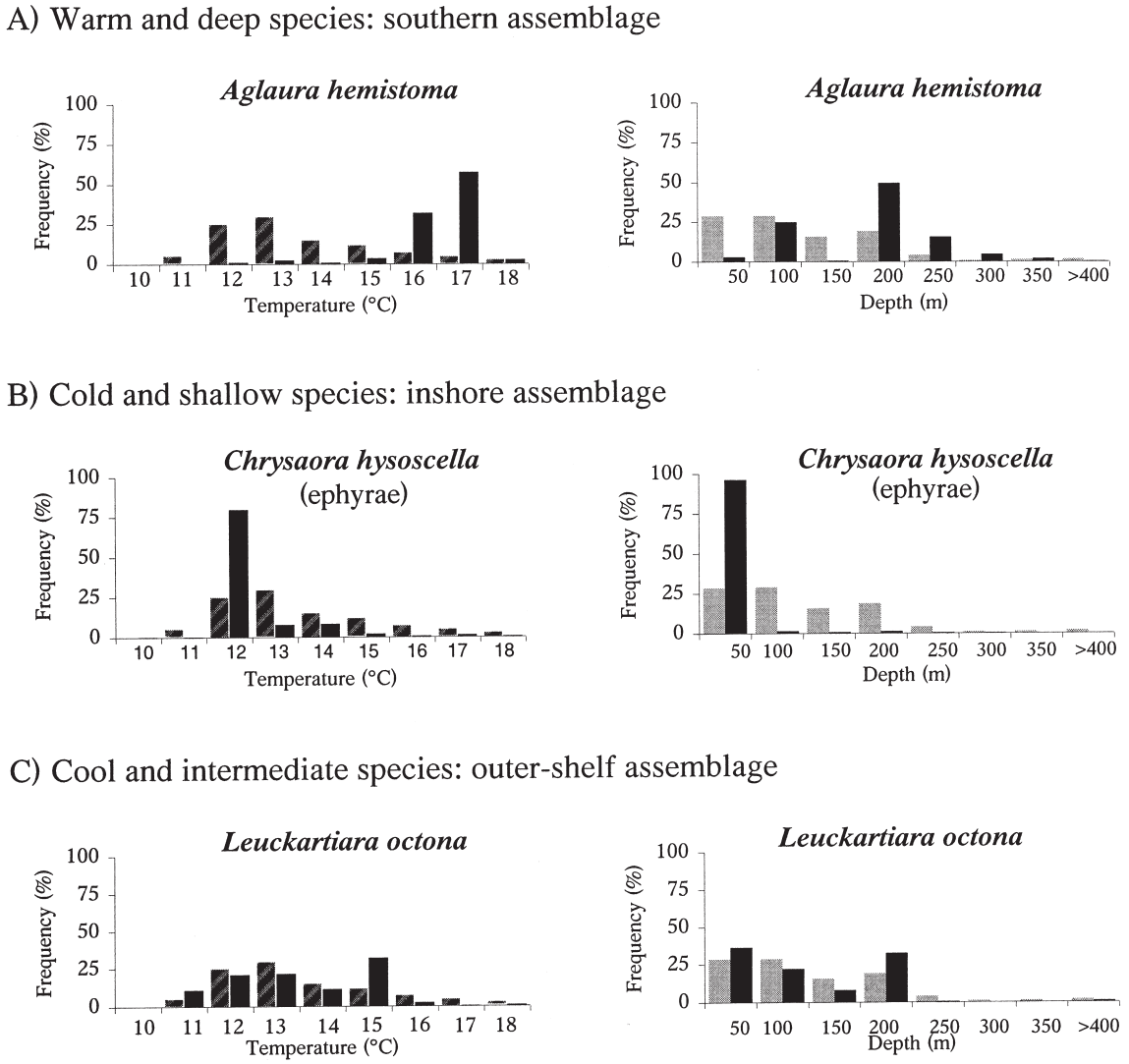

FIG. 4. – Frequency distributions of three species of medusae (black bars) plotted against frequency distribution of temperature (striped grey bars) and depth (light grey bars). Each species is characteristic of one of the three different assemblages identified in St Helena Bay during winter. The frequency distributions were calculated with all the results from the survey. For example: between 1988 and 1997, 24.8% of the samples were collected at temperatures between 10 and 11°C and 79.7% of the ephyrae of *Chrysaora hysoscella* were collected at these temperatures.

"best" explained in terms of the structure of the biophysical environment (temperature, and/or depth, and/or chlorophyll *a*) (Table 4). The spatial limits of the groups varied from year to year, presumably in accordance with the prevailing circulation (Shannon, 1985), and with the water masses present.

The southern assemblage was characterised by holoplanktonic species of medusae, whose richness increased in the warm, chlorophyll-poor offshore waters (Table 2). The dominant species of this assemblage (*Liriope tetraphylla* and *Aglaura hemistoma*) are typical of oceanic waters (Russell, 1953). Their abundance was positively correlated with temperature (Fig. 4) and they tended to be more common during warm years. For example, the mean abundance of *A. hemistoma* in the southern assemblage during 1992 (an El Niño year), was 60.1 ind. m^{-3} but was only 0.1 ind. m^{-3} in 1990. Their greater overall abundance during warm years reflects the greater area of St Helena Bay inundated with warm water then. Pagès *et al.* (1991) described both these species as indicators of oceanic water in the southern Benguela. These authors noted that although they were generally rare, they were occasionally common components of the inshore biota south of Cape Columbine, which was postulated to follow the mixing of shelf and oceanic waters there.

The "Bay" assemblages were less clearly defined in terms of actual species than the southern assem-

blages. However, they were characterised by meroplanktonic medusae and holoplanktonic ctenophores, whose abundance and diversity increased in cold, shallow and chlorophyll-rich waters (Table 5; Fig. 3, Group B). The dominant species were negatively correlated with temperature and tended also to be more abundant during cold years. For example, *Mitrocomella millardae* reached a mean density of 11.1 ind. m^{-3} in 1990, but only 0.5 ind. m^{-3} in 1992.

Meroplanktonic medusae are common in shelf waters (Goy, 1997), because (in part) of their sessile polyp stages which require some sort of substratum for larval settlement. Pagès *et al*. (1991) noted that although shelf assemblages north of Cape Columbine (which largely correspond to the "Bay" assemblage here) were characterised by meroplanktonic medusae, their composition varied with upwelling intensity. These authors also noted that the shelf assemblages in St Helena Bay could be subdivided into two that broadly corresponded to inshore and offshore regions. They found that *Leuckartiara octona* was characteristic of the offshore samples, which is in agreement with the results observed here for that species (Fig. 4).

Although the overall abundance and diversity of the meroplanktonic taxa were negatively linked to temperature and depth (Table 3), correlations between individual species abundance and the physical environment were low. Indeed, it is fair to state that most of the species failed to show any abundance response to the physical environment, and could be found anywhere within the Bay at any time. The lack of observed response at the species level has its origins in a number of factors, enumerated below.

The species (as *Obelia* spp. or the ephyrae of *Chrysaora hysoscella*) could be eurythermal (as opposed to the holoplanktonic species in group A), and showed common responses across the low temperature range observed in the Bay throughout the study period. This is supported by the fact that most of the dominant species recovered here have been widely recorded elsewhere in the world (Kramp, 1961), where they are able to survive and grow in a wide variety of thermal environments.

Alternatively, it should be realised that the occurrence of a medusa in the Bay must reflect the environmental conditions at some stage prior to sampling, while the observed distribution of the species should reflect the oceanographic processes that have taken place in the interim.

The polyp stages of meroplanktonic species have certain, specific environmental cues to which medusa release is the response. These cues include temperature (Werner, 1961) and food (Roosen-Runge, 1970), but may also be light (Costello, 1988) or phases of the lunar cycle (Goy, 1973), or any combination of these (and other) factors (Arai, 1992). However, the precise and relevant cues are not known for most species. Should any factor not be present, then the pelagic stage will not occur in the water column and the species will not be recovered from samples. A species might also be present in low numbers, and not collected by net sampling. However, should the environment have been favourable for medusa release, then although the species blooms (typically in an episodic fashion) the historical cues linking abundance to the environment are missed. Especially in the once-a-year surveys employed here. Pagès *et al*. (1991) encountered a similar problem in their study of the pelagic cnidarians in the Benguela ecosystem and postulated that the overwhelming abundance of some occasional species in St Helena Bay was probably due to an upwelling event prior to the survey that triggered their release.

Tracking the fate of the newly released medusae by backtracking changes in the physical environment in a dynamic environment such as St Helena Bay, is clearly not possible at this stage. However, this very dynamism can account for the poor degree of similarity amongst meroplanktonic associates (Fig. 3), as well as the low correlation coefficients between species abundances and the environment. It can also explain the inter-annual inconsistencies among the environmental parameters that best explain the patterns in assemblage composition (Table 4) and the variable indicator species (Table 5), as well as the variable "boundaries" that were observed to the identified assemblages from one year to the next (Fig. 2).

Comparative studies of interannual variations in the abundance and distribution of zooplankton in the region are sadly lacking. From a long-term study of changes in copepod biomass conducted at a station off the Cape Peninsula, Verheye *et al*. (1998) have recently shown a net increase in the copepods biomass (10 fold) between 1951 and 1996. These authors found a marked increase in the abundance of copepods < 0.9 mm prosome length and a decrease in the numbers of those > 1.0 mm prosome length. It was suggested that these changes in the composition of the communi-

ty might have allowed a regime-shift from sardine to anchovy. These authors postulated that this increase in small-animal biomass could reflect biological responses to the long-term intensification of upwelling in the Benguela ecosystem as well as a reduction in predation pressure due to a decrease in pelagic fish biomass (Verheye and Richardson, 1998).

Long-term studies have begun to show that shifts in the structural composition of pelagic communities might be "normal" for the pelagic marine ecosystem (Russell *et al.,* 1971; Southward, 1980; 1984; Southward *et al.,* 1988). Aside from work on fishes and copepods, there are few pluriannual observations of gelatinous zooplankton. In the Mediterranean Sea, an alternation of gelatinous species has been observed over at least a 17 y period (Morand and Dallot, 1985; Buecher *et al.*, 1997). The species that have replaced each other have the same ecological role but differences in the physical environment (temperature, turbidity) and/or the biological environment (food availability, predation pressure) favours blooming of one species rather than another. Explaining these specific alternations as normal characteristics for the dynamics of gelatinous zooplankton, Boero (1991) described an "internal circannual clock" which either activates some resting stage or stimulates reproduction, and so favours the proliferation of one species over another species. This activation, which may induce pulsations in the abundance of some species (as for *Mitrocomella millardae* in 1994), as well as differential thermal sensitivity, could explain the succession of species observed in St Helena Bay over the 10-year period of observations.

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