Siphonophore assemblages along the east coast of South Africa; mesoscale distribution and temporal variations

DELPHINE THIBAULT-BOTHA[1,2,*], JOHANN R. E. LUTJEHARMS[3] AND MARK J. GIBBONS[1]

[1]ZOOLOGY DEPARTMENT, UNIVERSITY OF THE WESTERN CAPE, PRIVATE BAG X17, 7535 BELLVILLE, SOUTH AFRICA, [2]HAWAII INSTITUTE OF MARINE BIOLOGY, 46-007 LILIPUNA ROAD, KANEOHE, HI 96744, USA AND [3]DEPARTMENT OF OCEANOGRAPHY, UNIVERSITY OF CAPE TOWN, 7700 RONDEBOSCH, SOUTH AFRICA

*CORRESPONDING AUTHOR. PRESENT ADDRESS: LABORATOIRE D'OCÉANOGRAPHIE ET DE BIOGÉOCHIMIE, UMR 6535 CNRS/UNIVERSITÉ DE LA MEDITERRANÉE, OSU/CENTRE D'OCÉANOLOGIE DE MARSEILLE, CASE 901, MARSEILLE 13288 CEDEX 09, FRANCE. E-MAIL: botha@com.univ-mrs.fr

Using multivariate statistics we have examined spatio-temporal patterns in the distribution of siphono- phore assemblages along the east coast of South Africa, anticipating constancy in cross-shelf and alongshore structure that would mirror the hydrographic stability. Indeed, while the surface temperature of the Agulhas Current does vary on a seasonal basis, the position of its core is thought to have a stable trajectory year round, and its other physical and chemical characteristics are considered to be relatively aseasonal. Two clear aseasonal assemblages were observed, associated either with the nearshore waters in the extreme SW (Port Alfred upwelling cell), or with the Agulhas Current and inshore waters north of East London. Assemblages in the current-driven upwelling cell were characterized by low overall diversity and dense populations of Muggiaea atlantica (up to 28 000 ind. 1000 m^{-3}). Assemblages elsewhere in the region were dominated by Abylopsis eschscholtzi, A. tetragona, Bassia bassensis, Chelophyes contorta, Diphyes dispar, D. bojani, Eudoxoides spiralis, E. mitra, Lensia subtiloides and Sulculeolaria chuni. There is some evidence of both an alongshore and a cross-shelf pattern in the distribution of assemblages north of East London, but this is subordinate to a stronger seasonal signal. The impact of seasonality on regional assemblages is hypothesized to be reflected in significant changes in the upstream structure of Agulhas Current assemblages.

INTRODUCTION

The west coast of South Africa is a physically dynamic environment, which is characterized by coastal upwelling and the offshore advection of nearshore surface waters, and occasional downwelling and the onshore advection of oceanic waters (Shannon, 1985). Although wind stress across the region is markedly seasonal and upwelling tends to occur maximally in spring/summer, it is also very variable in time and space (Shannon, 1985). Upwelling is obviously accompanied by marked changes in the physical and chemical properties of the water column and these are reflected by similar micro- and mesoscale changes in zooplankton assemblages (Pagès and Gili, 1991b; Pagès *et al.*, 1991; Pagès, 1992; Gibbons and Buecher, 2001). While seasonality is apparent in the structure of Benguela zooplankton assemblages (Gibbons and Hutchings, 1996), it is largely linked to changes in upstream assemblages (and thereby to downwelling) and appears to be locally subordinate to cross-shelf and alongshore structuring (near-shore, mid-shelf and oceanic assemblages are clearly and consistently recognized), which reflects more directly the local variability in wind stress.

The east side of the South African coast is dominated by the south flowing warm Agulhas Current. This current is the major western boundary current of the South Indian Ocean (Lutjeharms, 1996). Its surface waters are warmer and saltier than ambient, being composed of Indian Sub-tropical Surface Water, with the occasional presence of Indian Tropical Surface Water on its inshore side (Gordon

et al., 1987). Seasonal variations in the surface temperature of the current are only 3–4°C; the maximum temperature being ~28°C. The core of the Agulhas Current has a maximum surface speed of 2 m s^{-1} (Wyrtki, 1973) and the current carries a volume of ~65 × 10^6 m^3 s^{-1} (Stramma and Lutjeharms, 1997). It reaches its maximum intensity in the region between Durban and Port Elizabeth (Lutjeharms, 1996), where its trajectory is very stable, meandering <15 km to either side (Gründlingh, 1983). The current tracks the edge of the shelf, which is narrow in the north and moves gradually offshore to the southwest. Apart from its surface temperatures, the Agulhas Current exhibits no clear seasonality in any of its characteristics [e.g. (Pearce and Gründlingh, 1982)]. Some of its surface waters may move onto the shelf on occasion, but these intrusions seem to occur with no clear seasonal pattern (Schumann and Van Heerden, 1988; Goshen and Schumann, 1990). Shelf-edge upwelling is observed on the inshore side of the Agulhas Current, and this is very site-specific, occurring almost exclusively just upstream of Algoa Bay [Fig. 1 (Lutjeharms *et al.*, 2000b)], where cooler Indian Ocean Central Water is moved onto the shelf and occasionally outcrops at the sea surface.

Siphonophores, like other gelatinous carnivores, tend to have limited mobility and they can be usefully employed as indicators of water masses and water mass movement (Mapstone and Arai, 1992; Pagès and Kurbjeweit, 1994;

Gibbons and Hutchings, 1996; Pagès, 1996; Gasca, 1999; Gibbons *et al.*, 1999). Our understanding of siphonophores (or indeed of any zooplankton) in the Agulhas Current is limited, though assemblages are clearly distinct from those present along the west coast of South Africa (Gibbons and Thibault-Botha, 2002). Given the lack of any strong seasonality in the hydrography of the Agulhas Current, it might be expected that the structure and composition of regional zooplankton assemblages would be similarly aseasonal, though cross-shelf and alongshore assemblages would be present, just as they are in the southern Benguela ecosystem. We test this hypothesis explicitly here by examining the siphonophores collected during a series of regional surveys conducted in 1990/1991 (Beckley and van Ballegooyen, 1992).

METHOD

Field sampling

Samples were collected during three ichthyoplankton surveys conducted on the *R.S. Sardinops* in late austral autumn and early winter (May/June 1990), spring (October 1990) and summer (February 1991). Samples were collected from four stations (located over 50, 100, 500 and 2000 m isobaths) across nine transects (Fig. 1) between Algoa Bay in the South (34°S, 26°E), and the Tugela River
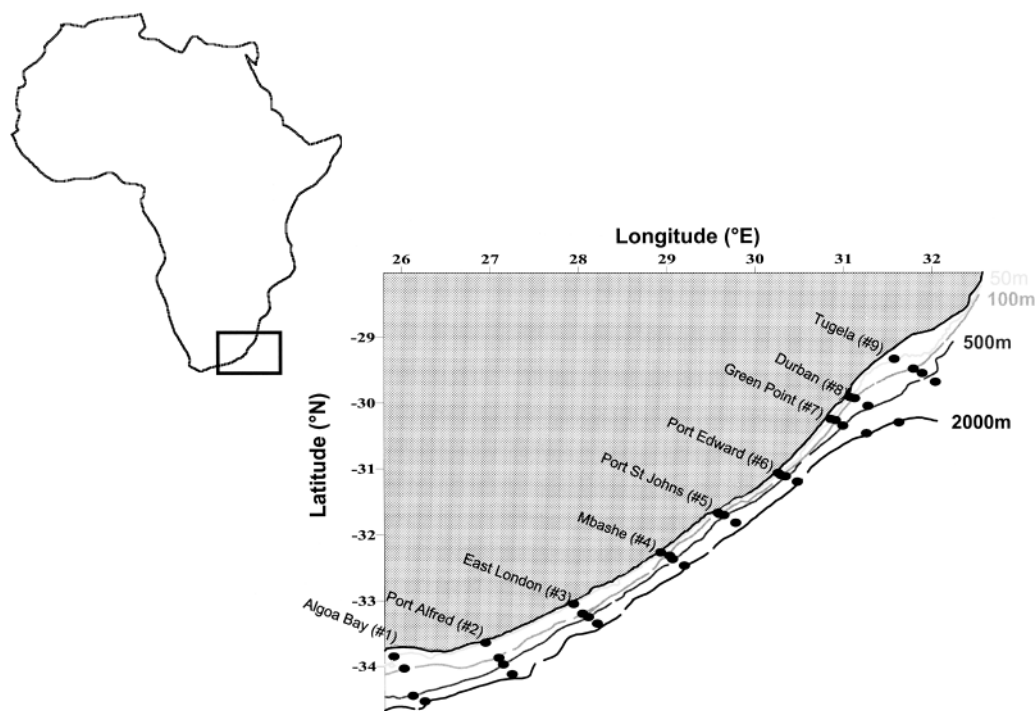

Fig. 1. Map of the study area showing the position of sampling stations and underlying bathymetry. Transect line numbers (#) in parentheses.

mouth in the North (29°S, 31°E). Full details of the sampling program and methodology can be found in Beckley and van Ballegooyen (Beckley and van Ballegooyen, 1992). Lutjeharms *et al.* (Lutjeharms *et al.*, 2000b) also gave a detailed description of the upwelling developing along the inshore edge of the Agulhas Current.

Samples were collected from each station using a paired Bongo net (57 cm mouth diameter) fitted with 500 μm mesh. The nets were towed obliquely at the slowest possible winch speed (1 m s^{-1}) in 5 m spans, from 80 m to the surface, except at the shallowest stations when only the upper 40 m was sampled. Both nets were equipped with calibrated flowmeters, mounted in the centre of each net mouth. The average volume of water filtered by the nets was 196.8 m^3. On retrieval, all samples were preserved in 5% saline formalin. This cruise was designed for sampling fish larvae, and was not at that time intended for studying gelatinous zooplankton. Therefore, large species of siphonophores are likely to be underrepresented. Hydrological information from the upper 200 m was collected at each station using a CTD profiler in May/June and October 1990, while the sampling was limited to the upper 80 m in February. Unfortunately, only SST data could be used here, as the balance of the data are lost. Although the February cruise provided synoptic results, there was a 2–3 weeks delay between the inshore and the offshore samples collected during May and October. Sampling was otherwise conducted on arrival at a station; slightly over 50% of the stations were sampled in daylight.

Laboratory analysis

The settled volume of zooplankton was measured for every pair of samples, and pairs showing large discrepancies (>20%) without major difference in the total volume of water filtered were excluded from further analysis. Samples that had been incompletely fixed and preserved were also discarded. All siphonophores from the remaining 105 samples were identified and counted using a dissecting microscope. The abundance of Calycophorae was determined from counts of the anterior nectophores only, and these were enumerated separately for the eudoxids. In the case of species from the family Hippopodiidae (Calycophorae), which are characterized by an irregular numbers of nectophores, we have used a figure of 10 per individual. When present, the pneumatophores of Cystonectae and Physonectae were counted. When the pneumatophores of these taxa were absent, estimates of abundance were made from the number of collected nectophores, gonophores and/or bracts, using information in Totton (Totton, 1965) and Pugh (Pugh, 1999). All abundance data were converted to density (ind. 1000 m^{-3}), using the volume of water filtered by the nets.

Numerical methods

Descriptive, multivariate statistics were used to identify assemblages in each season by examining relationships among samples. Rare species (present at <8 stations) have been ignored and the densities of the remaining dominant species were log $(x + 1)$ transformed. A similarity matrix was constructed between samples in each season using the Bray–Curtis Index (Field *et al.*, 1982). This matrix was then used to construct a plot classification diagram of percentage similarity between samples using complete linkage. All multivariate analyses were conducted using PRIMER software (Clarke and Warwick, 1994). Indicator species for each cluster were identified using the SIMPER routine within PRIMER. In order to determine how the distinct clusters identified by the multivariate analysis were associated with cross-shelf position (bottom depth), latitude (transect number) and season, as well as sea surface temperature, we used Kruskal–Wallis and ANOVA to test for significant differences in the median and mean (respectively) values for the non-parametric and parametric variables (respectively) of each sample cluster. ANOVA was also used to test for significant differences in density and richness of each sample cluster. These latter tests were performed using Statistica software.

RESULTS

Physical environment

Full details of the physical environment observed during the cruises have been reported by Beckley and van Ballegooyen (Beckley and van Ballegooyen, 1992). Aside from the fact that the temperature of Agulhas Current surface water was generally lower in spring (~23°C) than it was in either autumn (~24°C) or summer (~28°C), there is little clear evidence of seasonality in the general distribution of water masses across the sampling area (Fig. 2). Indeed, the overall patterns in the cross-shelf and alongshore distribution of sea surface temperature are persistent, as evidenced by the consistent patterns of stratification shown in Fig. 2.

Offshore water was consistently warmer than nearshore water across the sampling area, indicating the offshore presence of the Agulhas Current. The degree of cross-shelf variation in temperature was consistently lower north of East London (transect #3, see Fig. 1), implying the nearshore penetration of Agulhas Current water across the shelf to as far south as Mbashe (#4) at least in summer and autumn. During summer, this nearshore inundation by Agulhas Current water was facilitated by onshore Ekman transport caused by SW winds (Beckley and van Ballegooyen, 1992).
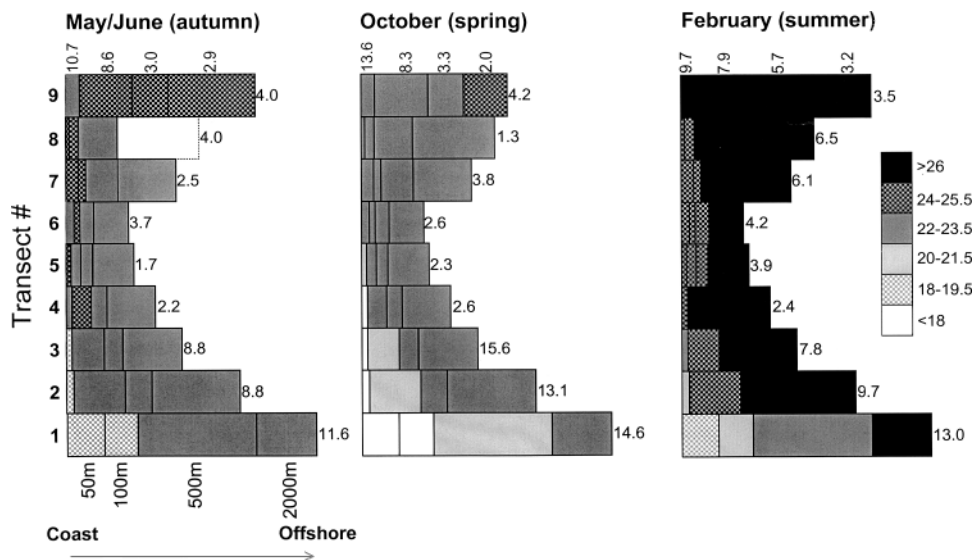
Fig. 2. Grid-maps showing the distribution of sea surface temperature (SST) across the study area in each season. The horizontal length of each grid-square is proportional to the distance between the different stations. Stations nearest to the shore are along the *y* axis. Dotted lines indicate no data. Also shown are the cross-shelf and alongshore coefficients of variation in SST (as percentages).

The degree of cross-shelf stratification (Fig. 2) was most marked in the extreme SW (11.6, 14.6 and 13.0°C in autumn, spring and summer, respectively), where cooler water was persistently observed throughout the year. The temperature of this water decreased and its coverage increased (offshore and northwards) during spring, when penetration of the Agulhas Current was observed to be least. The cool water in the SW was observed as a clear subsurface (∼30 m) thermal front at the 50 m station off Mbashe [see Fig. 5 in Beckley and van Ballegooyen (Beckley and van Ballegooyen, 1992)] in all three seasons, whilst at the 100 m stations during spring and summer, temperatures also tended to be <20°C at depths between 40 and 80 m. This is Indian Ocean Central Water and it contributes to the clearly delineated upwelling cell centred around Port Alfred (Lutjeharms *et al.*, 2000b). Beckley and van Ballegooyen (Beckley and van Ballegooyen, 1992) argued that the cold water observed inshore of the Agulhas Current at the three southernmost transects (with the coldest water over the greatest zonal extent at the last transect) represented the intermittent surface outcropping of upwelled water from the Port Alfred upwelling cell, and it was evident in some form or other, year-round. Goshen and Schumann (Goshen and Schumann, 1990) reported also several features that exist in the upper layer but some are not always reflected in the SST data.

Several mesoscale structures (such as meanderings and eddies) led to the intrusion of warm waters onto the shelf around Port Alfred (#2) in autumn, between

Port St Johns (#5) and Mbashe (#4) in spring, and between Port St Johns and East London (#3) in summer. Other, smaller scale meanderings were noted at several stations over the 500 m isobaths (Beckley and van Ballegooyen, 1992).

Assemblages

Fifty-nine species of siphonophore were collected during the study (Table I). Calycophorae accounted for between 81–89% of the species collected, whilst 9 species of Physonectae were recovered. The low number of Cystonectae (species and individuals) precludes detailed comment: a maximum of five individuals were sampled at any one station (data not shown). Sixty percent of the species were recorded in all three seasons, 20% were found in two seasons and the remainder was collected only in one season. The greatest number of species was observed in autumn and summer (49 and 51, respectively), and least was seen in spring (42). Most species were observed at a few stations, especially during spring. Species with the widest distribution also tended to be the most abundant over the study area, as indicated by the positive relationship ($r = 0.71$, $P < 0.01$) between total abundance and frequency of occurrence (data not shown). Only 49 taxa (including the eudoxid stages of five Abylid genera/species) occurred at more than 10 stations and were included in further analyses; these are highlighted in Table I.

Examination of Fig. 3 reveals a number of distinct clusters of samples (assemblages) arranged in a hierarchical

Table I: Alphabetical list of siphonophore species, by Order, collected during these surveys

Cystonectae			Calycophorae (cont)		
	Rhizophysa	*eysenhardti*		**Enneagonum**	**hyalinum***
	Rhizophysa	*filiformis*		**Eudoxoides**	**mitra**
				Eudoxoides	**spiralis**
Physonectae				**Hippopodius**	**hippopus**
	Agalma	**elegans**		**Lensia**	**campanella**
	Agalma	**okemi**		*Lensia*	*conoidea*
	Apolemia	*uvaria*		**Lensia**	**cossak**
	Arthorybia	*rosacea*		**Lensia**	**fowleri**
	Forskalia	*contorta*		**Lensia**	**gnanamuthui**
	Forskalia	**leuckarti**		*Lensia*	*hardy*
	Forskalia	**tholoides**		**Lensia**	**hotspur**
	Halistema	**rubrum**		*Lensia*	*hunter*
	Physophora	**hydrostatica**		**Lensia**	**meteori**
				Lensia	**multicristata**
Calycophorae				*Lensia*	*panikkari*
	Abyla	**bicarinata**		**Lensia**	**subtilis**
	Abyla	**haeckeli**		**Lensia**	**subtiloides**
	Abyla	**trigona**		**Muggiaea**	**atlantica**
	Abylopsis	**eschscholtzi***		*Muggiaea*	*kochi*
	Abylopsis	**tetragona***		**Nanomia**	**bijuga**
	Amphycaryon	**acaule**		**Praya**	**dubia**
	Amphycaryon	**ernesti**		**Praya**	**reticulate**
	Bassia	**bassensis***		**Rosacea**	**plicata**
	Ceratocymba	*dentata*		**Sphaeronectes**	**gracilis**
	Ceratocymba	*leukarti*		**Sulculeolaria**	**biloba**
	Ceratocymba	*sagittata*		**Sulculeolaria**	**chuni**
	Chelophyes	**appendiculata**		**Sulculeolaria**	**monoica**
	Chelophyes	**contorta**		**Sulculeolaria**	**quadrivalvis**
	Dimophyes	*arctica*		**Sulculeolaria**	**turgida**
	Diphyes	**bojani**		**Vogtia**	**glabra**
	Diphyes	**chamissonis**		*Vogtia*	*pentacantha*
	Diphyes	**dispar**			

Bold typeface indicates those taxa that were recorded in eight or more samples and which have been used in analyses of assemblage structure.
*Indicates taxa where eudoxids were enumerated separately and where counts of these stages have been included in addition to polygastric stages.

structure (levels). The characteristics of these groups and their environments are summarized in Table II, whilst the species that most contribute (>4%) to their structure are shown in Table III. It should be noted at the outset that the greatest level of similarity between individual samples was generally <85%. Such a high level of heterogeneity in sample composition (attributable to the generally low densities at which most species occur) generates considerable 'noise' and forces us to focus our efforts only on the more obvious patterns in assemblage distribution.

Level I structure of the cluster analysis is independent of season and contrasts assemblages collected in the extreme nearshore waters of the SW (Group I-B) with the balance (Group I-A) of the sampling grid (Fig. 3). The former samples are characterized by high density and very low diversity (they are typically dominated by *Muggiaea atlantica*, responsible for 94% of the structure of Group I-B) and are associated with significantly cooler, shallower water than the remainder of the area (Table II). It should be noted that Group I-B reflects the seasonal shift in the northward extent of cold water during spring (sample O 4 50), and also, interestingly, that May samples are absent from this group.

Level II structure also reflects alongshore pattern, and it is again independent of season (Fig. 3). Group II-A samples are of significantly lower diversity than Group II-B samples; they are associated with a lower ambient temperature and tend to occur (on average) further
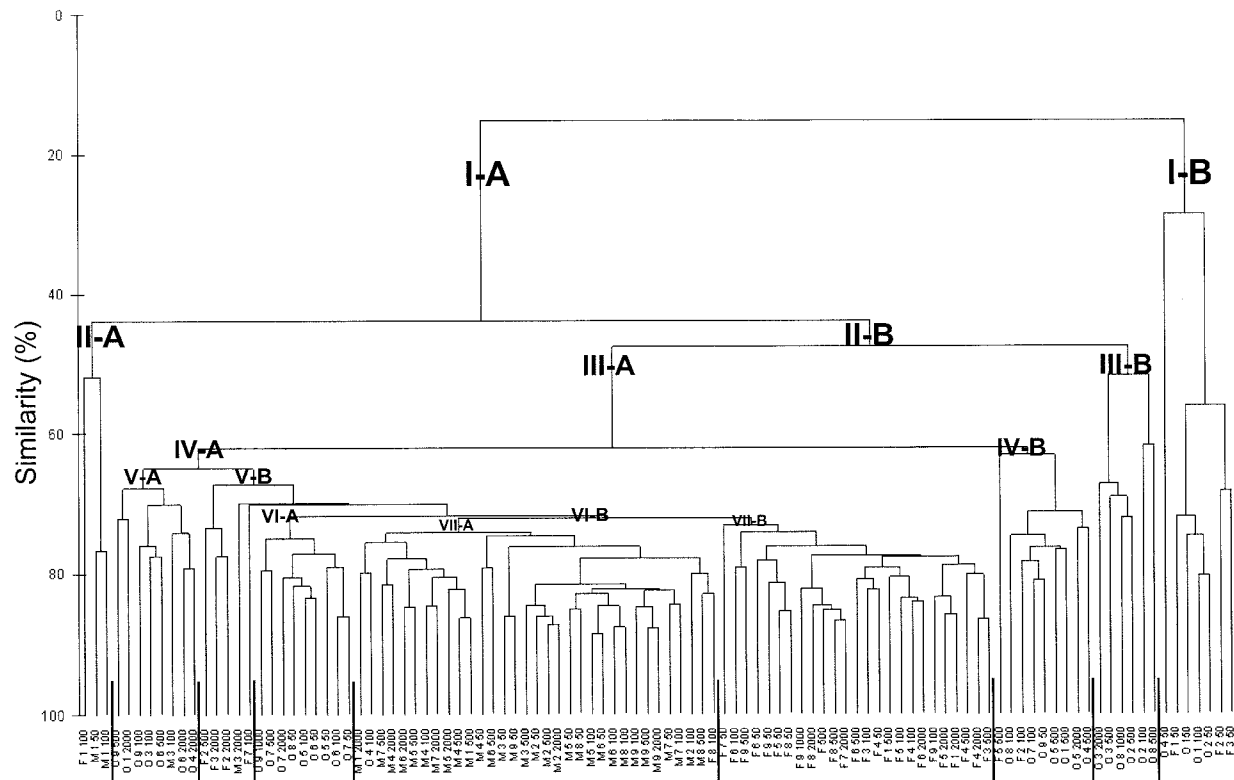
Fig. 3. Dendrogramme of percent similarity (Bray–Curtis measure) between all samples. Levels of similarity and cluster identities shown above branching points in bold typeface (see text). Samples identifiable by month (October, May, February), transect line (#1–9, see Fig. 1), and depth (50, 100, 500 and 2000 m).

Table II: Mean assemblage and environmental characteristics of each cluster identified in Fig. 3

Level	Cluster	N	Density (ind. m^{-3})	Richness	Depth (m)	Month	Transect	Temp (°C)
Level I	A	98	**89**	**25**	**644**	5.5	**5.2**	**23.7**
Level I	B	7	**3461**	**3**	**57**	6.6	**2.0**	**19.0**
Level II	A	3	232	**12**	83	4.0	**1.0**	**19.0**
Level II	B	95	84	**26**	662	5.6	**5.4**	**23.9**
Level III	A	89	**87**	**27**	654	**5.3**	5.4	**23.9**
Level III	B	6	**36**	**12**	767	**10.0**	4.3	**22.4**
Level IV	A	80	87	**28**	674	4.9	5.5	**24.1**
Level IV	B	9	93	**18**	483	8.2	5.1	**22.7**
Level V	A	8	**38**	**22**	913	**9.4**	5.1	**22.5**
Level V	B	72	**92**	**28**	647	**4.4**	5.5	**24.3**
Level VI	A	9	**249**	**22**	433	**10.0**	6.7	**22.6**
Level VI	B	58	**73**	**29**	622	**3.7**	5.5	**24.4**
Level VII	A	33	82	30	570	**5.1**	5.3	**23.1**
Level VII	B	25	61	29	692	**2.0**	5.8	**26.2**

Data in bold typeface indicate significant differences (*P* < 0.05) between characteristics of samples (A and B) within any given level of similarity (I–VIII). Number of samples within each cluster also shown (*n*). Significance determined by ANOVA (density, richness, temperature) or Kruskal–Wallis (depth, month, transect line) tests.

Table III: List of dominant species identified by SIMPER as responsible for differences in the structure of the clusters (by Level) shown in Fig. 3

Level	Genus	Species	Mean density		Contribution (%)
			Cluster A	Cluster B	
I	*Muggiaea*	*atlantica*	837	8542	6.53
I	*Bassia*	*bassensis*	163	1	6.20
I	*Abylopsis*	*eschscholtzi**	170	0	5.95
I	*Eudoxoides*	*spiralis*	232	5	5.90
I	*Bassia*	*bassensis**	180	1	5.79
I	*Chelophyes*	*contorta*	82	0	5.07
I	*Abylopsis*	*eschscholtzi*	72	1	5.02
I	*Diphyes*	*dispar*	41	0	4.77
I	*Eudoxoides*	*mitra*	39	1	4.29
I	*Diphyes*	*bojani*	34	1	4.01
II	*Muggiaea*	*atlantica*	2711	778	6.79
II	*Abylopsis*	*eschscholtzi*	2	74	5.96
II	*Eudoxoides*	*spiralis*	14	238	4.98
II	*Diphyes*	*dispar*	2	42	4.75
II	*Abylopsis*	*eschscholtzi**	16	175	4.49
II	*Sulculeolaria*	*chuni*	0	26	4.22
II	*Bassia*	*bassensis**	14	185	4.08
II	*Eudoxoides*	*mitra*	2	40	4.01
III	*Abylopsis*	*eschscholtzi**	185	0	7.71
III	*Bassia*	*bassensis**	196	1	7.46
III	*Muggiaea*	*atlantica*	822	8	5.52
III	*Diphyes*	*bojani*	37	2	4.83
III	*Lensia*	*subtiloides*	68	1	4.77
III	*Abylopsis*	*tetragona**	17	0	4.02
IV	*Muggiaea*	*atlantica*	757	1410	6.70
IV	*Sulculeolaria*	*turgida*	16	0	4.41
IV	*Lensia*	*campanella*	21	1	4.23
V	*Muggiaea*	*atlantica*	12	839	6.49
V	*Lensia*	*subtiloides*	6	82	4.75
VI	*Muggiaea*	*atlantica*	4240	389	8.53
VI	*Enneagonum*	*hyalinum**	0	19	4.68
VI	*Chelophyes*	*appendiculata*	4	37	4.25
VI	*Chelophyes*	*contorta*	26	120	4.20
VII	*Muggiaea*	*atlantica*	513	235	5.63
VII	*Diphyes*	*chamissonis*	59	0	5.56
VII	*Chelophyes*	*appendiculata*	7	79	4.40

The mean density (ind. 1000 m^{-3}) of each species in each assemblage (cluster A, B) is also shown, as are their proportional contribution to dissimilarity (only species with at least a contribution of 4% are reported here). * indicates eudoxid stage, else all are polygastric.

south than the balance of samples (Table II). Essentially Group II-A samples occur immediately offshore of Group I-B samples and act as a buffer region between the cold upwelled water that lies close inshore in the south and the warmer water further offshore and to the north. Group II-A samples have a higher diversity than Group I-B samples (Table II), but they are still dominated by *M. atlantica* (Table III).

Level III structure reflects also alongshore patterns and separate spring samples (Group III-B) that occur directly offshore of Group I-B as well as further north (transect #8) with the balance of samples. They are of low diversity and density (<10 ind. m^{-3}) of all species and associated with lower temperature (Table III).

Level IV structure again reflects alongshore pattern and seasonality, and contrasts spring (Group IV-B) with the balance of samples (Group IV-A) (Fig. 3). The former are associated with significantly lower water than the latter, and although they tend to have a less diverse assemblage of species, individual populations occur at the same density (Table II). *M. atlantica* again occurs at higher densities in Group IV-B than Group IV-A samples (Table III).

There is no clear explanation for the Level V structure, though it separates spring mainly offshore samples with the balance of the samples; the density and diversity of assemblages is nevertheless significantly lower in Group V-A than Group V-B (Table II).

Patterns are at Levels VI and VII under temporal separation. We can also see that at both the Level VI-A (spring) and the Level VII (VII-A: autumn; VII-B: summer) clusters, there is a fairly clear cross-shelf, but not an alongshore structure (Table II). In the case of Level VI, samples are located in cooler water and directly north of the extended upwelled region. They are also associated with significantly higher density (largely dominated by *M. atlantica*) but lower diversity. Level VII summer samples are associated with a more pronounced onshore–offshore thermal gradient (Fig. 2), which is missing in the autumn samples. There is no significant difference between Group VII-A and Group VII-B in terms of either diversity or overall density, though the autumn samples (Group VII-A) support greater numbers of *M. atlantica* (but lower densities of other species) (Table III). Within Level VII-A, separation appears between samples offshore in the southern transect (#1) and centre of the study area and those inshore and extending to offshore ones at transect #2, 3 and 9. In summer (Group VII-B), stations located mainly offshore in the south and over the whole centre of the region contrasted with the balance of stations.

Comments on individual species

Muggiaea atlantica (Calycophorae, Diphyidae) was the most numerous and widely distributed species collected during the study. It was also the species that was most responsible for the structure of the regional assemblages (Table III). This typical coastal species was persistently abundant in near-shore waters (<100 m), and was particularly common in the south, where it extended offshore during all three seasons (Fig. 4a) although it reached greatest densities (28 406 ind. 1000 m^{-3}) during spring.

This cold-water species was routinely uncommon (<55 ind. 1000 m^{-3}) in the core of the Agulhas Current (2000 m) and failed to show any distinct seasonality in distribution. Examination of Fig. 4a suggests that the inshore population has two centres of high density; north (Port Edward #6) and south (Algoa Bay #1) of Mbashe (#4).

The abundance and distribution of the other calycophoran species (Fig. 4b) showed a pattern that was largely opposed to that of *M. atlantica*; in other words, there was a general decrease in abundance towards the SW. During autumn, the highest densities of other calycophoran siphonophores were recorded at the innermost stations along the coast, and at offshore stations in the north and south. There was a good match between the distribution of other calycophoran siphonophores and the position of the shelf break, with larger offshore populations observed where the shelf is wide (90% of the population found offshore at Algoa Bay) in May/June. This trend appeared to be less obvious during the two other seasons. Densities across the region were lowest during spring, and patches of relatively high abundance were restricted to offshore waters in the northern half of the study area. During summer, highest species densities were recorded offshore and in the north, and a tongue of high-density water penetrated inshore to East London (#3). The calycophoran species that made a significant contribution to the total density of siphonophores in the study area were mostly widely spread over the region, being present in at least 30 stations. *Abylopsis eschscholtzi*, *Bassia bassensis*, *Chelophyes contorta*, *Eudoxoides mitra*, *E. spiralis* and *Lensia subtiloides* were abundant (average density >40 ind. 1000 m^{-3}) all year round, whilst *Sulculeolaria chuni* was present at similar densities except during spring. These species were found across the shelf, but often reached highest densities in the region of the shelf break.

Physonectae (data not shown) were observed mainly in the northern part of the study area and along the coast where they were restricted to 50–100 m isobath stations; they tended to be more common during the warmer seasons. The maximum number of individuals observed was ~100 ind. 1000 m^{-3} in summer (96) and autumn (129), while no more than 25 ind. 1000 m^{-3} were reported in spring. The distribution of Physonectae during spring appeared to follow the inshore edge of the Agulhas Current.

DISCUSSION

Although there is little comparative information on the siphonophores of the Western Indian Ocean, most species are thought to be widely distributed (Pugh, 1999). There is,
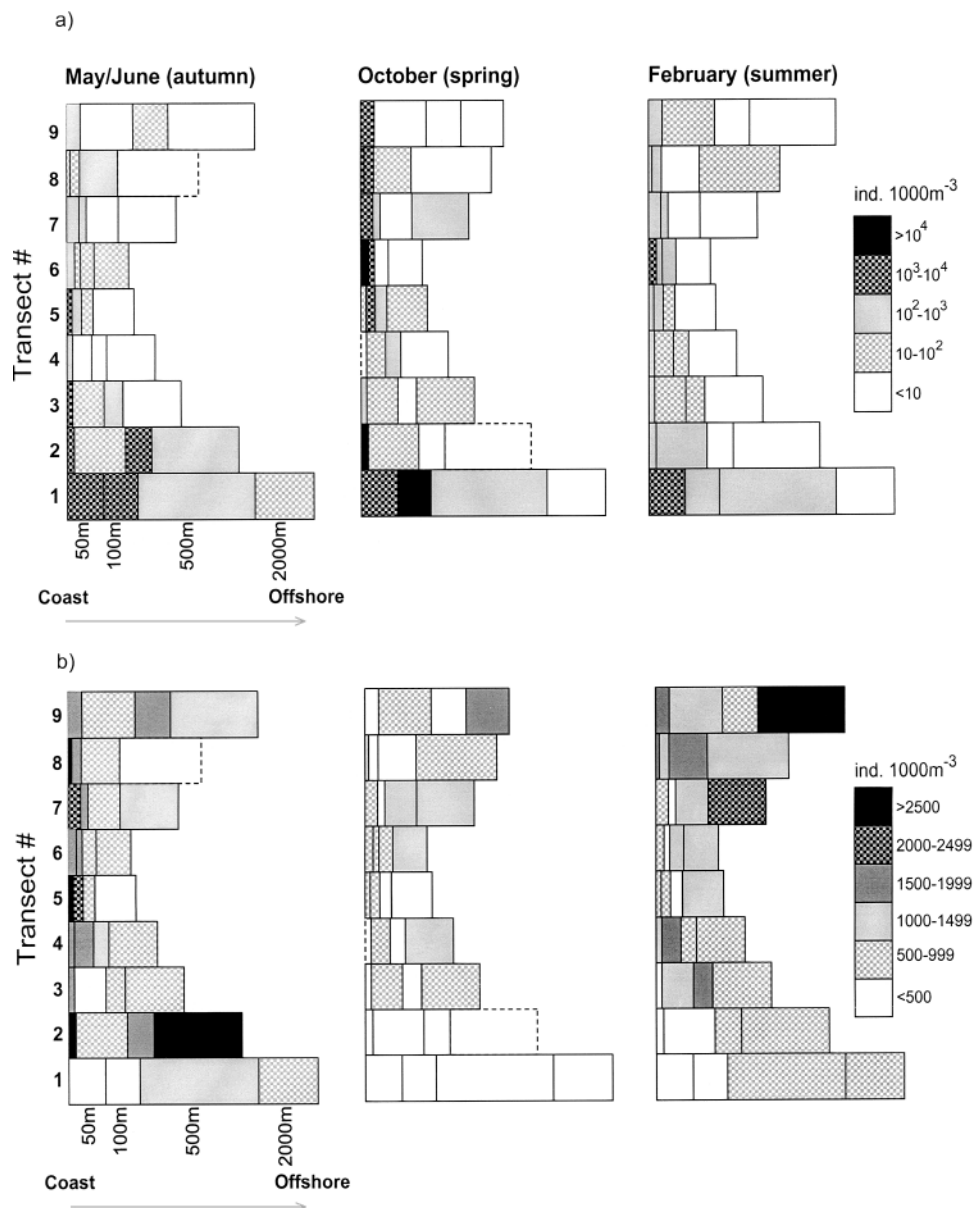
Fig. 4. Grid-maps showing the distribution of siphonophore across the study area in each season. Data for *Muggiaea atlantica* (**a**) and other calycophoran species (**b**) have been shown separately. Dotted lines indicate no data.

therefore, a broad similarity between the compositions of the assemblages observed here and those reported from surrounding areas. Of the 59 species recorded during this survey (Table I), 23 species are shared with the east coast of India (Daniel and Daniel, 1963), and between 44–50 have been noted in the Indian Ocean and along the east coast of Africa (Daniel, 1974). That a greater proportion was not similar may reflect the fact that our net collections spanned only the upper 200 m, and meso- and bathypelagic taxa would have been missed. Although assemblages along the east coast of South Africa have been identified as conspicu-

ously different from those along the west coast (Gibbons and Thibault-Botha, 2002), 44 species in the present collections have previously been reported from the Benguela Current (Pagès and Gili, 1992) and 53 have been observed in the wider South Atlantic Ocean (Pugh, 1999).

The results presented here suggest that regional siphonophore assemblages reflect the persistent mesoscale (alongshore and cross-shelf) features of the hydrography, and that while important, seasonality plays a role only in structuring assemblages more directly under the influence of the Agulhas Current. Thus we can see the permanent

influence of the upwelling cell at Port Alfred (and seasonal changes in its distribution) on the structure of siphonophore assemblages, which are characterized by extremely low diversity and a high abundance of *M. atlantica*. We can also note the distinctive, mixed nature of assemblages in the buffer zone between newly upwelled water and that further offshore and to the north. The former assemblages are characterized by moderately low diversity, and moderately high densities of *M. atlantica*, while those of the latter typically have a high diversity and low overall abundance, especially of *M. atlantica*. The spatial pattern of these results is in general agreement with those observed in the southern Benguela upwelling region (Pagès and Gili, 1991a, b; Pagès *et al.*, 1991; Pagès, 1992), as well as in upwelling areas elsewhere (Dessier and Donguy, 1985; Smith *et al.*, 1986; Nogueira and Oliveira, 1991; Seridji and Hafferssas, 2000).

Our understanding of the role that seasonality plays on assemblages under the more direct influence of the Agulhas Current is still not clear, given the relatively small database. However, it would appear that there are some fundamental changes in overall assemblage composition associated with seasonal changes in the thermal (and other) characteristics of this water mass, and in the way that it interacts with shelf waters. During summer and autumn, when penetration of the shelf by the Agulhas Current is most extensive and when therefore interactions with shelf water are likely to be most pronounced, there would appear to be distinct assemblages associated with the core of the current (occurring in deeper water), and with the spill-over on the shelf. These different assemblages are characterized by similar levels of diversity. Cross-shelf structure, while not completely lacking in spring, is nevertheless weaker than it is at other times, and this may reflect the weaker cross-shelf thermal gradient north of Port Alfred (Fig. 2), which is associated with a reduced influence of the Agulhas Current.

That a seasonal pattern is observed is perhaps not surprising given the seasonal changes in the thermal properties of the Agulhas Current itself, and this must reflect upstream changes in population and assemblage processes. Although we are largely ignorant of seasonal changes in the structure and composition of zooplankton assemblages in the East Madagascar and Mozambique currents, which provide the source water for the Agulhas Current, seasonality is evident in their physical and chemical characteristics (Lutjeharms *et al.*, 2000c) and in their biological processes (Longhurst, 1998). It is not unlikely, therefore, that these changes will be reflected in the structure of their respective zooplankton assemblages: weak patterns of seasonality have been observed in zooplankton biomass within the core of the Gulf Stream (Allison and Wishner, 1986). These results are partly at odds with the findings of McGowan and

Walker (McGowan and Walker, 1979, 1985) from the North Pacific Gyre, who noted a general lack of seasonal signal in the structure of copepod assemblages. Such was evidenced, in part, by a seasonal consistency in their rank order of dominant species. Given that the Agulhas Current forms the western part of the South Indian Gyre, similar consistency might have been expected here. And to a certain extent it is—seven of the dominant 10 species from the Agulhas Current identified during autumn (cluster VII-A, Fig. 3) were also among the dominant 10 species identified during summer (cluster VII-B, Fig. 3). Dominant species reported in spring (cluster VI-A) were also similar to the two other seasons. Although rare species were generally rare in both sets of seasonal samples, there was little agreement in the intermediate dominance structure (Table IV). This could reflect seasonal changes in the interactions between species within the zooplankton [about which, like McGowan and Walker (McGowan and Walker, 1979), we are unable to comment], but is probably attributable to the generally low abundances of most taxa, as noted previously. This would suggest that perhaps examinations of higher trophic levels are not amongst the most useful in disproving seasonality in the open ocean.

That a cross-shelf pattern in assemblage structure is observed, with nearshore assemblages supporting greater densities of siphonophores (at least in autumn), is also not surprising given the generally more productive nature of nearshore than offshore waters [e.g. (Brown *et al.*, 1991; Pitcher *et al.*, 1992)]. Having said that, it does now imply a role for local population processes, including the possibility of *in situ* population growth following earlier (summer) seeding from offshore waters—as has been shown for the salp *Thalia democratica* off the SE coast of the USA, subsequent to its nearshore seeding by the Florida Current (Paffenhöfer and Lee, 1987). Such cross-shelf changes in overall abundance are commonly reported in the literature (Raymont, 1980). The absence of any change in the richness of siphonophore assemblages in nearshore and offshore waters during both summer and autumn reflects the extent to which the species-rich Agulhas Current penetrates inshore (Schumann and Van Heerden, 1988; Lutjeharms *et al.*, 1989b). This shoreward penetration of Agulhas Current water is also evidenced in the close clustering of offshore and nearshore samples in the results presented by Gibbons and Thibault-Botha (Gibbons and Thibault-Botha, 2002).

However, what is perhaps surprising is the general lack of cohesion between seasons in the hierarchical structure of the nearshore and offshore assemblages. *Muggiaea atlantica*, *Enneagonum hyalinum* and *Chelophyes*

Table IV: Mean density (ind. 100 m^{-3}) and dominance rank of all species from Agulhas Current water in summer (cluster VII-B), Autumn (cluster VII-A) and Spring (cluster VI-A)

Species	Summer (cluster VII-B)		Autumn (cluster VII-A)		Spring (cluster VI-A)	
	Mean density	Rank	Mean density	Rank	Mean density	Rank
Eudoxoides spiralis	267.6	**1**	237.9	**5**	306.6	**2**
Muggiaea atlantica	234.9	**2**	513.2	**1**	4240.4	**1**
*Bassia bassensis**	180.9	**3**	291.8	**3**	233.8	**3**
Chelophyes contorta	179.8	**4**	77.4	**8**	26.0	**10**
*Abylopsis echschlotzi**	179.5	**5**	296.5	**2**	104.8	**5**
Bassia bassensis	142.7	**6**	287.4	**4**	166.0	**4**
Chelophyes appendiculata	78.6	**7**	7.0	23	3.8	21
Abylopsis echschlotzi	76.9	**8**	105.1	**7**	65.9	**7**
Diphyes dispar	65.5	**9**	42.0	11	45.3	**9**
Diphyes bojani	48.8	**10**	35.0	13	65.7	**8**
Sulculeolaria chuni	36.2	11	36.7	12	23.4	12
Lensia subtiloides	35.2	12	146.3	**6**	24.2	11
Eudoxoides mitra	27.8	13	42.5	**10**	66.7	**6**
Lensia campanella	20.4	14	26.2	14	17.9	15
Lensia multicristata	16.6	15	1.1	34	2.2	27
Sulculeolaria turgida	16.3	16	21.5	17	10.4	17
*Abylopsis tetragona**	14.6	17	20.4	19	19.8	14
Abylopsis tetragona	14.5	18	16.9	21	21.9	13
Sulculeolaria quadrivalvis	13.0	19	1.5	32	2.1	28
*Enneagonum hyalinum**	12.7	20	24.4	15	0.0	35
Nanomia bijuga	6.8	21	4.3	26	6.3	18
Enneagonum hyalinum	6.6	22	20.6	18	6.3	19
Lensia hotspur	6.3	23	19.3	20	15.9	16
Praya dubia	5.7	24	22.1	16	0.0	36
Lensia gnanamuthui	4.2	25	0.1	39		
Lensia subtilis	4.1	26	15.3	22	3.9	20
Agalma elegans	4.1	27	3.6	29	0.2	34
Sulculeolaria monoica	3.0	28	4.2	27	0.6	32
Agalma okemi	2.9	29	0.9	36	0.0	37
Sulculeolaria biloba	2.4	30	0.8	37	3.0	24
Praya reticulata	2.1	31	0.6	38		
Sphaeronectes gracilis	1.7	32	1.2	33		
Rosacea plicata	1.6	33	5.3	24	0.0	38
Lensia cossak	1.6	34	4.9	25	3.4	22
Amphycaryon ernesti	1.2	35	1.0	35		
Hippopodius hippopus	0.8	36	2.5	30	0.6	33
Abyla trigona	0.6	37	1.7	31		
Diphyes chamissonis	0.0	38	59.2	**9**	1.2	31
*Agalma sp.**	0.0	39	4.1	28		

*Indicates eudoxid stage, else all are polygastric. Bold, rank ≤10.

appendiculata showed similar patterns of cross-shelf abundance in each season (*M. atlantica* and *E. hyalinum* were more common inshore than offshore, whilst *C. appendiculata* was more common offshore than inshore). It would be premature (with the exception of *M. atlantica*—see below) to suggest that these taxa are indicative of nearshore and offshore waters (Gibbons and Thibault-Botha, 2002). The seasonal inconsistencies in the structure of

the nearshore and offshore assemblages can probably be attributed to the seasonal changes in the composition of the Agulhas Current assemblages.

Muggiaea atlantica is a common component of near-shore zooplankton assemblages in cool, productive waters (Russell, 1934) and can often reach very high abundance, 1400 ind. 1000 m^{-3} in Friday Harbor (Purcell, 1982), 2399 ind. 1000 m^{-3} in the Humboldt Current system (Pagès *et al.*, 2001), but values as high as those observed in Algoa Bay (~28 ind. m^{-3}) have never been reported for the open ocean, although populations up to 500 ind. m^{-3} were reported during the German Bight invasion in 1989 (Greve, 1994). The near complete domination by this species of the inner stations to the extreme south of the study area and offshore in Algoa Bay reflects the upwelling environment in this region and the optimal thermal conditions for this species (16–19°C). Although a few warmer stations also appear to support large populations of this species (Figs 2 and 4a), this might be related to the presence of IOCW at the bottom of the sampling depth (Beckley and van Ballegooyen, 1992). Stations that had a high abundance of *M. atlantica* were generally associated with low overall diversity, and a low abundance of other species. While it is tempting to interpret this mutually exclusive pattern in terms of competitive exclusion, it is more likely to reflect the limited thermal tolerance of the other species. However, *M. atlantica* was not entirely confined to the cooler, most southern stations, and was also recorded on the shelf and shelf-edge further to the north at high abundance in all three seasons. *M. atlantica* was absent or present in very low numbers from most of the outermost stations in the north that are indicative of purer Agulhas Current water; therefore inshore populations in the north are unlikely to have been seeded by that current. The fact that the Agulhas Current itself cannot provide the source of individuals implies that the northern populations of *M. atlantica* were able to maintain themselves along the inner shelf despite occasional flushing by the Agulhas Current. The mechanism for this maintenance is unknown, but it is probably linked to the St Lucia upwelling cell (Carter and Schleyer, 1988; Lutjeharms *et al.*, 1989a) at the northern end of the Natal Bight (29°S, Fig. 1). This cell has very similar characteristics to that at Port Alfred, except that is more intense and durable (Lutjeharms *et al.*, 2000a). A preference for cool and productive waters in the region has already been demonstrated for adult sardine (*Sardinops sagax*) and copepods (Carter, 1977; Beckley and Hewitson, 1994), although the mechanisms involved varied between the dynamic upwelling south of Mbashe and (presumed) topographic upwelling north of Tugela. *M. atlantica* also failed to display any distinct seasonality in distribution over

the shelf and offshore, which is in good agreement with the aseasonal nature of the current. However, inshore stations show higher abundance in October when the intensity of both the northern and southern upwelling cells is stronger.

This study has shown that siphonophores can be very numerous along the east coast of South Africa. Elsewhere, these organisms are often considered to play an important role in the structuring of pelagic food webs (Reeve and Walter, 1978; Purcell, 1981, 1982; Alldredge, 1984; Feigenbaum and Marris, 1984; Miller and Daan, 1989; Pagès *et al.*, 2001), and may have a significant impact on prey populations. Using our abundance estimates for just one species, *M. atlantica*, in conjunction with previously published predation rates for this species [(Purcell, 1982): 5.5–10.5 copepods siphonophore^{-1} day^{-1}], it is clear that the number of copepods required to sustain local populations ranges from 1.9 (spring) to 31.1 (summer) m^{-3}. These estimates are based on average (shelf-wide) densities of *M. atlantica*, and ignore localized peaks in abundance. Maximum predation impact would have been achieved in Algoa Bay during October, when *M. atlantica* reached a density of ~14 ind. m^{-3}; this species would then have been able to remove up to 300 copepods m^{-3} day^{-1}. Unfortunately there are no quantitative data on either the abundance, or production, of copepods along the east coast of South Africa, and further work will obviously be needed to determine the potential impact of *M. atlantica* and other species of siphonophores in the region. Purcell (Purcell, 1982) reported that *M. atlantica* exerted little pressure on the copepod population (0.1–0.2%) in the surface waters at Friday Harbour, Washington. On the other hand, Pagès *et al.* (Pagès *et al.*, 2001) noted that up to 69.3% of the small copepods in the Humboldt Current system could be fed upon by *Bassia bassensis* (a species that is also common and abundant along the east coast of South Africa). Large numbers of carnivores ultimately require an elevated level of primary production. Although the waters along the east coast of South Africa are thought to be fairly uniform and to support a small phytoplankton biomass showing a low production [e.g. (Carter and Schleyer, 1988; Probyn *et al.*, 1995)], the data presented here suggest that inshore conditions, especially in Algoa Bay, must be quite different from the rest of the shelf, as noted over the East Agulhas Bank by Probyn *et al.* (Probyn *et al.*, 1995).

REFERENCES

Alldredge, A. L. (1984) The quantitative significance of gelatinous zooplankton as pelagic consumers. In Fasham, M. J. R. (ed.), *Flows of Energy and Materials in Marine Environments*. Plenum Publishing Corporation, pp. 407–433.

Allison, S. K. and Wishner, K. F. (1986) Spatial and temporal patterns of zooplankton biomass across the Gulf Stream. *Mar. Ecol. Prog. Ser.*, **31**, 233–244.

Beckley, L. E. and van Ballegooyen, R. C. (1992) Oceanographic conditions during three ichtyoplankton surveys of the Agulhas current in 1990/91. *S. Afr. J. Mar. Sci.*, **12**, 83–93.

Beckley, L. E. and Hewitson, J. D. (1994) Distribution and abundance of clupeoid larvae along the East coast of South Africa in 1990/91. *S. Afr. J. Mar. Sci.*, **14**, 205–212.

Brown, P. C., Painting, S. J. and Cochrane, K. L. (1991) Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. *S. Afr. J. Mar. Sci.*, **11**, 537–564.

Carter, R. A. (1977) *The Distribution of Calanoid Copepoda in the Agulhas Current System off Natal, South Africa.* Oceanographic Research Institute, University of Natal, Durban, 165 pp.

Carter, R. A. and Schleyer, M. H. (1988) Plankton distributions in Natal coastal waters. In Schumann, E. H. (ed.), *Coastal Ocean Studies off Natal, South Africa.* Springer-Verlag, Berlin. Lecture notes on Coastal and Estuarine Studies, **26**, pp. 152–177.

Clarke, K. R. and Warwick, R. M. (1994) *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*, Plymouth Marine Laboratory, Plymouth, 144 pp.

Daniel, R. (1974) Siphonophora from the Indian Ocean. *Mem. Zool. Survey India*, **15**, 1–242.

Daniel, R. and Daniel, A. (1963) On the siphonophores of the Bay of Bengal I. Madras Coast. *J. Mar. Biol. Assoc. India*, **5**, 185–220.

Dessier, A. and Donguy, J.-R. (1985) Planktonic copepods and environmental properties of the eastern Equatorial Pacific: seasonal and spatial variations. *Deep-Sea Res.*, **32**, 1117–1133.

Feigenbaum, D. L. and Marris, R. C. (1984) Feeding in the chaetognatha. *Oceanogr. Mar. Biol. Annu. Rev.*, **22**, 343–392.

Field, J. G., Clarke, K. R. and Warwick, R. M. (1982) A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.*, **8**, 37–52.

Gasca, R. (1999) Siphonophores (Cnidaria) and summer mesoscale features in the gulf of Mexico. *Bull. Mar. Sci.*, **65**, 75–89.

Gibbons, M. J. and Buecher, E. (2001) Short-term variability in the assemblage of medusae and ctenophores following upwelling events in the southern Benguela ecosystems. *Mar. Ecol. Prog. Ser.*, **220**, 169–177.

Gibbons, M. J. and Hutchings, L. (1996) Zooplankton diversity and community structure around southern Africa, with special attention to the Benguela upwelling system. *S. Afr. J. Sci.*, **92**, 63–76.

Gibbons, M. J. and Thibault-Botha, D. (2002) The match between ocean circulation and zoogeography of epipelagic siphonophores around southern Africa. *J. Mar. Biol. Assoc. UK*, **82**, 801–810.

Gibbons, M. J., Gugushe, N., Boyd, A. J., Shannon, L. V. and Mitchell-Innes, B. A. (1999) Changes in the composition of the non-copepod zooplankton assemblage in St Helena Bay (southern Benguela ecosystem) during a six day drogue study. *Mar. Ecol. Prog. Ser.*, **180**, 111–120.

Gordon, A. L., Lutjeharms, J. R. E. and Gründlingh, M. L. (1987) Stratification and circulation at the Agulhas Retroflection. *Deep-Sea Res.*, **34**, 565–599.

Goshen, W. S. and Schumann, E. H. (1990) Agulhas Current variability and inshore structures off the Cape Province, South Africa. *J. Geophys. Res.*, **95**, 667–678.

Greve, W. (1994) The 1989 German Bight invasion of *Muggiaea atlantica*. *ICES J. Mar. Sci.*, **51**, 355–358.

Gründlingh, M. L. (1983) On the course of the Agulhas Current. *S. Afr. Geog. J.*, **65**, 49–57.

Longhurst, A. R. (1998) *Ecological Geography of the Sea*, Academic Press, New York, 398 pp.

Lutjeharms, J. R. E. (1996) The exchange of water between the South Indian and South Atlantic oceans. In Wefer, G., Berger, W. H., Siedler, G. and Webb, D. J. (eds), *The South Atlantic: Present and Past Circulation.* Springer-Verlag, Berlin Heidelberg, pp. 123–162.

Lutjeharms, J. R. E., Gründlingh, M. L. and Carter, R. A. (1989a) Topographically induced upwelling in the natal Bight. *S. Afr. J. Sci.*, **85**, 310–316.

Lutjeharms, J. R. E., Catzel, R. and Valentine, H. R. (1989b) Eddies and other boundary phenomena of the Agulhas Current. *Cont. Shelf Res.*, **9**, 597–616.

Lutjeharms, J. R. E., Valentine, H. R. and van Ballegooyen, R. C. (2000a) The hydrography and water masses of the natal Bight, South Africa. *Cont. Shelf Res.*, **20**, 1907–1939.

Lutjeharms, J. R. E., Cooper, J. and Roberts, M. (2000b) Upwelling at the inshore edge of the Agulhas Current. *Cont. Shelf Res.*, **20**, 737–761.

Lutjeharms, J. R. E., Wedepohl, P. M. and Meeuwis, J. M. (2000c) On the surface drift of the East Madagascar and Mozambique Currents. *S. Afr. J. Sci.*, **96**, 141–147.

Mapstone, G. M. and Arai, M. N. (1992) Abundance and vertical distribution of siphonophores (Cnidaria) from the central Strait of Georgia, British Columbia, during spring and summer. *Contrib. Natural Sci.*, **15**, 1–8.

McGowan, J. A. and Walker, P. W. (1979) Structure in the copepod community of the north Pacific gyre. *Ecol. Monogr.*, **49**, 195–226.

McGowan, J. A. and Walker, P. W. (1985) Dominance and diversity maintenance in an oceanic ecosystem. *Ecol. Monogr.*, **55**, 103–118.

Miller, R. J. and Daan, R. (1989) Planktonic predators and copepod abundance near the Dutch coast. *J. Plankton Res.*, **11**, 263–282.

Nogueira, C. R. and Oliveira, S. R., Jr (1991) Siphonophora from the coast of Brazil (17°S to 24°S). *Biol. Inst. Oceanogr. Sao Paulo*, **39**, 61–69.

Paffenhöfer, G.-A. and Lee, T. N. (1987) Development and persistence of patches of Thaliacea. *S. Afr. J. Mar. Sci.*, **5**, 305–318.

Pagès, F. (1992) Mesoscale coupling between planktonic cnidarians distribution and water masses during a temporal transition between active upwelling and abatement in the northern Benguela system. *S. Afr. J. Mar. Sci.*, **12**, 41–52.

Pagès, F. (1996) Distribution patterns of the mesozooplankton, principally siphonophores and medusae, in the vicinity of the Antarctic Slope front (eastern Weddell Sea). *J. Mar. Sys.*, **9**, 231–248.

Pagès, F. and Gili, J.-M. (1991a) Effects of large-scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. *Mar. Ecol. Prog. Ser.*, **75**, 205–215.

Pagès, F. and Gili, J.-M. (1991b) Vertical distribution of epipelagic siphonophores at the confluence between Benguela waters and the Angola current over 48 hours. *Hydrobiol.*, **216–217**, 355–362.

Pagès, F. and Gili, J.-M. (1992) Siphonophores (Cnidaria, Hydrozoa) of the Benguela Current (southeastern Atlantic). *Sci. Mar.*, **56**, 65–112.

Pagès, F. and Kurbjeweit, F. (1994) Vertical distribution and abundance of mesoplanktonic medusae and siphonophores from the Weddell Sea, Antarctica. *Polar Biol.*, **14**, 243–251.

Pagès, F., Verheye, H. M., Gili, J.-M. and Flos, J. (1991) Short-term effects of coastal upwelling and wind reversals on epiplanktonic cnidarians in the southern Benguela ecosystem. *S. Afr. J. Mar. Sci.*, **10**, 203–211.

Pagès, F., Gonzalez, H. E., Ramón, M., Sobarzo, M. and Gili, J.-M. (2001) Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Bassia bassensis* (Siphonophora: Calycophorae). *Mar. Ecol. Prog. Ser.*, **210**, 13–24.

Pearce, A. F. and Gründlingh, M. L. (1982) Is there a seasonal variation in the Agulhas Current? *J. Mar. Res.*, **40**, 177–184.

Pitcher, G. C., Brown, P. C. and Mitchell-Innes, B. A. (1992) Spatiotemporal variability of phytoplankton in the southern Benguela upwelling system. *S. Afr. J. Mar. Sci.*, **12**, 439–456.

Probyn, T. A., Mitchell-Innes, B. A. and Searson, S. (1995) Primary productivity and nitrogen uptake in the subsurface chlorophyll maximum on the Eastern Agulhas Bank. *Cont. Shelf Res.*, **15**, 1903–1920.

Pugh, P. R. (1999) Siphonophorae. In Boltovskoy, D. (ed.), *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, The Netherlands, pp. 467–511.

Purcell, J. E. (1981) Feeding ecology of *Rhizophysa eysenhardti*, a siphonophore predator of fish larvae. *Limnol. Oceanogr.*, **26**, 424–432.

Purcell, J. E. (1982) Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham 1893). *J. Exp. Mar. Biol. Ecol.*, **63**, 39–54.

Raymont, J. E. G. (1980) *Plankton and Productivity in the Oceans. Volume 2. Zooplankton*, Jefferies, R.L. and Davy, A.J. (eds), Pergamon, Oxford, 824 pp.

Reeve, M. R. and Walter, M. A. (1978) Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores. *Limnol. Oceanogr.*, **23**, 740–751.

Russell, F. S. (1934) On the occurence of the siphonophores *Muggiaea atlantica* Cunningham and *Muggiaea kochi* (Will) in the English Channel. *J. Mar. Biol. Assoc. UK*, **19**, 555–558.

Schumann, E. H. and Van Heerden, I. L. (1988) Observations of Agulhas Current frontal features south of Africa, October 1983. *Deep-Sea Res.*, **35**, 1355–1362.

Seridji, R. and Hafferssas, A. (2000) Copepod diversity and community structure in the Algerian Basin. *Crustaceana*, **73**, 1–23.

Shannon, L. V. (1985) The Benguela ecosystem. Part 1. Evolution of the Benguela, physical features and processes. *Oceanogr. Mar. Biol. Annu. Rev.*, **23**, 105–182.

Smith, S. L., Jones, B. H., Atkinson, L. P. and Brink, K. H. (1986) Zooplankton in the upwelling fronts off Pt. Conception, California. In Nihoul, J. C. J. (ed.), *Marine Interfaces Ecohydrodynamics*. Vol., **42**, pp. 195–214.

Stramma, L. and Lutjeharms, J. R. E. (1997) The flow field of the subtropical gyre in the South Indian Ocean. *J. Geophys. Res.*, **102**, 5513–5530.

Totton, A. K. (1965) *A synopsis of the Siphonophora*, History, Trustees of the British Museum (Natural History) (ed), London, 230 + 40 plates pp.

Wyrtki, K. (1973) Physical oceanography of the Indian Ocean. In Zeitzschel, B. (ed.), *The Biology of the Indian Ocean*. Springer-Verlag, Berlin Heidelberg New York, pp. 18–36.