

The match between ocean circulation and zoogeography of epipelagic siphonophores around southern Africa

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Published and unpublished records of epipelagic calycophoran siphonophores from around southern Africa were examined for zoogeographic structure. There is a close match between prevailing patterns of surface ocean circulation and zoogeography, which while similar to previous studies of intertidal taxa and euphausiids, is different from them in some key details. Separate subtropical provinces are associated with both the Angola and Agulhas Currents, and the latter system has a marked influence on the composition of (warm-temperate) assemblages along the south coast of South Africa. The nearshore waters in the Benguela upwelling ecosystem (cold temperate) are distinct, but the Lüderitz upwelling cell does not appear to act as an internal boundary within the Benguela ecosystem, as has been previously noted for benthic communities. Species richness is greater in oceanic than coastal waters, and peaks in subtropical waters. High diversity is also noted offshore in the area between Capes Agulhas and Columbine, where water of Indian, Southern and Atlantic Ocean interact. Indicator species for each major water mass were tentatively identified.

INTRODUCTION

It can be argued that a full understanding of zoogeography will only really arise when all co-occurring taxa are analysed together, because it is likely that inter-specific interactions have played some part in shaping the composition of assemblages. However, aside from any concerns about appropriate quantitative sampling, such analyses can only really take place when the taxonomic understanding of all taxa is equally good, and when all taxa have been subject to the same level of sampling intensity (areal coverage). This level of rigour might be realistic for a biota (on the macro-scale) that has been historically well studied, such as that of rocky sub- and inter-tidal substrata around southern Africa (Brown & Jarman, 1978; Millard, 1978; Kensley, 1981; Gosliner, 1987; Thandar, 1989; Emanuel et al., 1992; Williams, 1992). But it is unrealistic for any region (on the macro-scale) that has not been historically well studied—such as the pelagic environment around southern Africa. Furthermore, such a rigorous approach negates the value of comparative study, and fails to take into account systematic interest.

The east coast of southern Africa is bathed by the southward-flowing Agulhas Current whilst the west coast is bathed by both the northward-flowing Benguela Current (south of $\sim 20^{\circ}\text{S}$) and by the southward-flowing Angola Current (north of $\sim 20^{\circ}\text{S}$). Both the Agulhas and Angola Currents have a subtropical origin, and are associated with subtropical biogeographic provinces, albeit of Indian and Atlantic Ocean affinity, respectively. The Benguela Current is associated with dynamic coastal upwelling, which brings cold, Atlantic Ocean Central water to the surface (Shannon, 1985), and it is associated with a cold temperate province (Emanuel et al., 1992). The south coast of South Africa, unlike much of the rest of

regional coastline is characterized by a broad continental shelf, and is associated with a warm-temperate province.

Although there are some descriptive accounts of the distribution of pelagic taxa around South Africa (De Decker, 1984), only euphausiids have been subject to any semi-rigorous zoogeographic analysis (Gibbons et al., 1995). And while the biogeographic patterns generated from this latter work agree in part to those of the foregoing intertidal studies, our understanding could benefit from comparative work.

There are a number of factors that make Siphonophora a good taxon with which to make biogeographic comparisons with Euphausiacea. Both are exclusively marine taxa and most are pelagic. Both are of relatively large size and can be readily identified in plankton samples. However, there are some differences. Unlike euphausiids (Mauchline & Fisher, 1969), siphonophores are exclusively carnivorous and have generally poor powers of locomotion (Mackie et al., 1987). But most interestingly perhaps, they have widespread patterns of distribution (Alvarino, 1971), though they have been used as indicators of water mass (Russell, 1934, 1935).

The aim of this study is to describe the zoogeography of siphonophores around southern Africa, to examine pattern with respect to hydrological and biological features and to compare the resulting zoogeographic distribution with that of euphausiids. No attempt is made to interpret all species distributions, as comparative information is incomplete.

MATERIALS AND METHODS

The methods employed here follow those of Gibbons et al., 1995. Essentially the coastline between the mouths

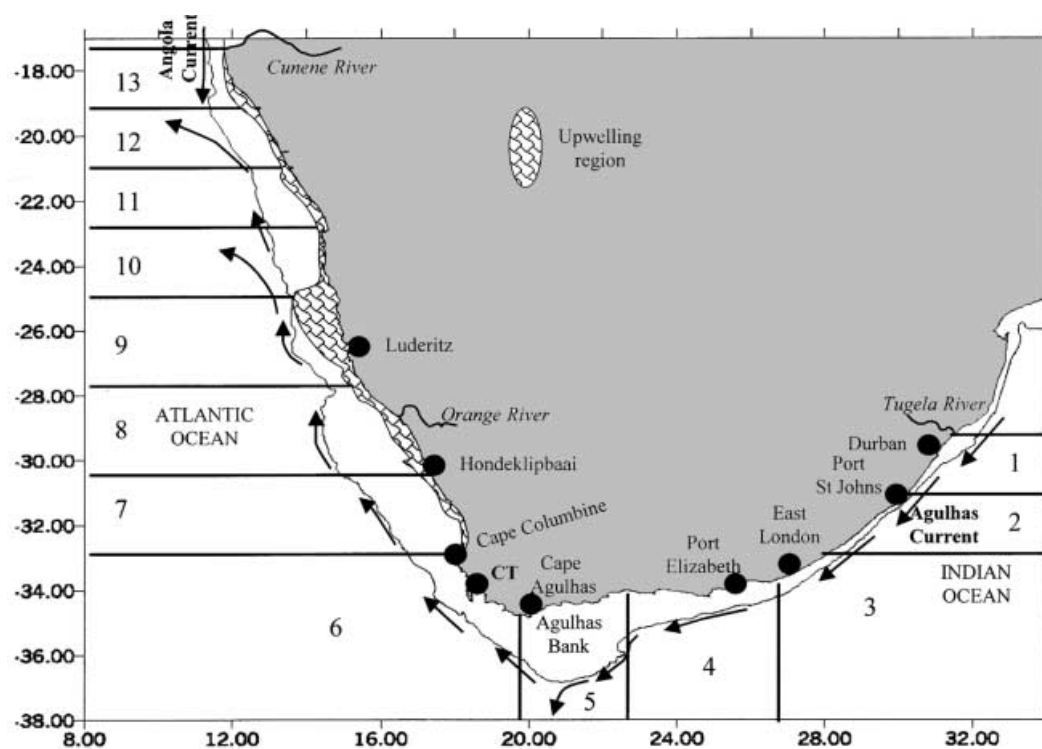


Figure 1. Map of study area showing position of the 13 grid squares, and major oceanographic features (modified from Gibbons et al., 1995). The 200 m isobath is illustrated.

of the Tugela River on the east coast ($29^{\circ}20'S$ $31^{\circ}35'E$) and the Cunene River on the west coast of southern Africa ($17^{\circ}20'S$ $11^{\circ}40'E$) was divided into 13 zones. Each of these zones corresponds roughly to a polygon $\sim 2^{\circ}$ of latitude wide (Figure 1). The edge of the continental shelf is considered to be a major ecological boundary and as a consequence, each 2° grid square (GS) was subdivided at the 200 m depth contour into a shelf (inshore) and oceanic (offshore) component. The distribution ranges of siphonophores were then plotted onto this grid, by scoring their presence/absence in each 2° square.

The distribution data that were used here originated in a number of published and unpublished sources in which data have been collected over the top 200 m (most of them being collected between 0–80 m). Unlike the previous study of euphausiids (Gibbons et al., 1995), we have not used information residing in relevant historic data sets (Moser, 1925; Leloup, 1934; Leloup & Hentschel, 1938; Totton, 1941, 1954; Alvarino, 1971), owing to their oceanic focus and scattered nature. For the west and south coasts of the region, we have primarily used the extensive recent records provided in Pagès & Gili, 1992. Supplementary unpublished data from along the south coast were provided by an analysis of samples collected during the Agulhas Bank Boundary Processes cruise [see Verheye et al., 1994 for details on the stations sampled and cruise characteristics], which extended from (34° to $27.2^{\circ}E$ and 18.5 to $36.5^{\circ}S$). For the east coast, we have examined the siphonophores from ~ 100 of the samples collected by Beckley & Hewitson (1994). The grid surveyed by the latter authors extended from Port Elizabeth in the south to the Tugela River mouth in the north, and samples were collected across transects perpendicular to the coast

extending from 50 m to 2000 m depth. Not all records of siphonophores from the above mentioned data sets have been used in the analyses, and we have ignored Cystonectae and Physonectae to eliminate bias caused by their scattered nature, and deep distribution (Mackie et al., 1987; Pugh, 1999), respectively. In order to minimize errors resulting from poor areal coverage, gaps in the distribution record of some species have been filled in when possible. This interpolation was confined to gaps of single 2° GS flanked on both side by at least one positive record.

To examine zoogeographic structure, the entire data matrix was subject to cluster analysis (Clarke & Warwick, 1994), based on link-average grouping using the Bray-Curtis Index of similarity (Field et al., 1982). Classification diagrams (dendrograms) were then constructed to visualize the similarities. Analyses were conducted separately on the inshore and offshore data, as well as on the combined data, using Plymouth Routines in Multivariate Ecological Research software (PRIMER for Windows v5.2).

RESULTS AND DISCUSSION

Diversity

A total of 54 species of epipelagic Calycophorae were used in the current analyses (Table 1). This does not reflect the true diversity of Calycophorae recorded from around southern Africa, because a further 18 (Table 2) were variously noted by Alvarino (1971), Leloup (1934), Leloup & Hentschel (1938), Moser (1925), and Totton (1941, 1954). Most of these species (Table 2) are uncommon

Table 1. Distribution of epipelagic, calycophoran siphonophores amongst the inshore (0–200 m) and offshore (>200 m) grid squares (see Figure 1) around southern Africa. Data as presence (1) or absence (0). Highlighted species were present in more than 10 grid squares.

	Inshore													Offshore														
	1	2	3	4	5	6	7	8	9	10	11	12	13	Total	1	2	3	4	5	6	7	8	9	10	11	12	13	Total
<i>Abyla bicarinata</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	0	3
<i>Abyla haeckeli</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	3	1	1	1	0	0	0	0	0	0	0	0	0	0	3
<i>Abyla ingeborgae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Abyla peruana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Abyla schmidtii</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	3	1	1	0	0	0	0	0	0	0	0	0	0	0	2
<i>Abyla tottoni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
<i>Abyla trigona</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Abylopsis</i> <i>eschscholtzi</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	7	1	1	1	1	1	1	1	1	0	0	0	0	0	8
<i>Abylopsis tetragona</i>	1	1	1	1	1	1	1	0	0	1	1	1	1	11	1	1	1	1	1	1	1	1	1	1	1	1	1	13
<i>Amphicaryon acaule</i>	1	1	1	0	0	1	0	0	0	0	0	0	0	4	1	1	1	0	0	1	1	1	1	1	1	1	1	11
<i>Amphicaryon ernesti</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	2	1	1	1	1	1	1	1	0	0	0	0	0	0	7
<i>Bassia bassensis</i>	1	1	1	1	1	1	1	0	0	0	0	1	1	9	1	1	1	1	1	1	1	1	1	1	1	1	1	13
<i>Ceratocymba dentata</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	2
<i>Ceratocymba</i> <i>leuckarti</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	3
<i>Ceratocymba</i> <i>sagittata</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	2
<i>Chelophyes</i> <i>appendiculata</i>	1	1	1	1	1	1	0	0	0	0	0	1	1	8	1	1	1	1	1	1	1	1	1	1	1	1	1	13
<i>Chelophyes contorta</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	7	1	1	1	1	1	1	1	1	0	0	0	0	0	8
<i>Desmophes annectens</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	2	0	0	0	0	0	1	1	0	0	0	0	0	0	2
<i>Dimophyes arctica</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	2	0	1	0	0	0	1	1	1	1	1	1	1	0	8
<i>Diphyes bojani</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	7	1	1	1	1	1	1	1	0	0	0	0	0	1	8
<i>Diphyes chamissonis</i>	1	1	1	0	0	1	0	0	0	0	0	0	0	4	1	1	1	0	0	0	0	0	0	0	0	0	0	3
<i>Diphyes dispar</i>	1	1	1	1	1	1	1	0	0	0	0	1	1	9	1	1	1	1	1	1	1	1	1	1	0	0	1	11
<i>Enneagonium</i> <i>hyalinum</i>	1	1	1	1	1	1	1	0	0	0	0	0	1	8	1	1	1	1	1	1	1	1	1	1	1	1	1	13
<i>Eudoxoides mitra</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	7	1	1	1	1	1	1	1	1	1	0	0	1	1	11
<i>Eudoxoides spiralis</i>	1	1	1	1	1	1	1	0	0	0	0	0	1	8	1	1	1	1	1	1	1	1	1	1	1	1	1	13
<i>Hippopodius</i> <i>hippopus</i>	1	1	1	0	0	0	0	0	0	0	0	1	1	5	1	1	1	0	0	1	1	0	0	0	0	1	1	7
<i>Lensia campanella</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	7	1	1	1	1	1	1	1	1	1	1	1	1	0	12
<i>Lensia conoidea</i>	1	1	1	1	1	1	1	0	0	1	1	1	1	11	1	0	0	0	0	1	1	1	1	1	1	1	1	8
<i>Lensia cossack</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	3	1	1	1	0	0	0	0	0	0	0	0	0	0	3
<i>Lensia fowleri</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	0	1	1	1	1	0	0	0	0	6
<i>Lensia gnanamuthui</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	2	1	1	1	1	0	0	0	0	0	0	0	0	0	4
<i>Lensia hardy</i>	1	1	0	0	0	1	0	0	0	0	0	0	0	3	1	1	0	0	0	1	1	1	1	1	1	1	1	10
<i>Lensia hotspur</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	7	1	1	1	1	1	1	1	1	1	1	1	1	1	13
<i>Lensia hunter</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2
<i>Lensia meteori</i>	1	1	1	1	1	1	0	0	0	0	0	0	0	6	1	1	1	1	1	1	1	0	0	0	0	0	0	7
<i>Lensia multicristata</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	7	1	1	1	1	1	1	1	0	0	0	0	1	1	10
<i>Lensia panikkari</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lensia subtilis</i>	1	1	1	1	1	1	1	1	0	0	0	0	0	7	1	1	1	1	1	1	1	1	1	1	1	1	0	12
<i>Lensia subtiloides</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	7	1	1	1	1	1	1	1	0	0	0	0	0	0	7
<i>Muggiaea atlantica</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	13	1	1	1	1	1	1	1	1	1	1	1	1	1	13
<i>Muggiaea kochi</i>	0	0	1	1	1	0	0	0	0	0	0	1	1	5	1	1	0	0	0	1	0	0	0	0	0	0	1	4
<i>Praya dubia</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	3	1	1	1	0	0	0	0	0	0	0	0	0	0	3
<i>Praya reticulata</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	3	1	1	1	1	0	0	0	0	0	0	0	0	1	5
<i>Rosacea cymbiformis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	1	1	6
<i>Rosacea plicata</i>	1	1	1	0	0	1	1	0	0	0	0	0	0	5	1	1	1	1	1	1	1	1	1	1	1	1	1	13
<i>Sphaeronectes</i> <i>gracilis</i>	1	1	0	0	0	1	0	0	0	0	0	1	1	5	1	1	1	1	1	1	1	1	1	1	1	1	1	13
<i>Sulculeolaria</i> <i>angusta</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	0	3
<i>Sulculeolaria biloba</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	3	1	1	1	0	0	0	0	0	0	0	0	1	1	5
<i>Sulculeolaria chuni</i>	1	1	1	0	1	1	0	0	0	0	0	1	0	6	1	1	1	1	1	1	0	0	0	0	0	1	1	9
<i>Sulculeolaria</i> <i>monoica</i>	1	1	1	0	0	1	0	0	0	0	0	0	0	4	1	1	1	1	1	1	0	0	0	0	0	0	1	7
<i>Sulculeolaria</i> <i>quadrivalvis</i>	1	1	1	0	1	1	0	0	0	0	0	1	1	7	1	1	1	1	1	1	1	0	0	0	0	1	1	9
<i>Sulculeolaria turgida</i>	1	1	1	1	1	1	0	0	0	0	0	0	1	7	1	1	1	1	1	0	0	0	0	0	0	0	1	6
<i>Vogtia glabra</i>	1	1	1	0	0	0	0	0	0	0	0	1	1	5	0	1	1	0	0	0	0	0	0	0	0	0	1	4
<i>Vogtia spinosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	3
TOTAL	42	41	34	20	22	29	19	2	1	3	3	13	15		41	46	40	27	24	31	29	20	19	15	17	28	31	

Table 2. *Siphonophora* that have been recorded from around southern Africa, but that were not analysed in the present study.

Species	Depth range	Source
Cystonects (3)		
<i>Physalia physalis</i>	Pleuston	7, 8, 9
<i>Rhizophysa eysenhardti</i>	?	7, 8, 9
<i>Rhizophysa filiformis</i>	?	7, 8, 9
Physonects (16)		
<i>Agalma elegans</i>	0–400	5, 7, 8
<i>Agalma okeni</i>	0–200	5, 6, 7, 8
<i>Apolemia uvaria</i>	?	7, 8
<i>Athorybia rosacea</i>	0–300	8
<i>Bargmannia elongata</i>	500–1000	5
<i>Cordagalma cordiformis</i>	0–200	5, 7, 9
<i>Forskalia edwardsi</i>	0–200	5, 7
<i>Forskalia leuckarti</i>	0–500	7, 8, 9
<i>Forskalia tholoides</i>	?	7
<i>Halistemma rubrum</i>	0–500	5, 7, 8, 9
<i>Marrus antarcticus</i>	700–1400	6
<i>Marrus orthnocannoides</i>	?	5
<i>Melophysa melo</i>	0–200	5
<i>Nanomia bijuga</i>	0–400	7, 8, 9
<i>Physophora hydrostatica</i>	200–500	5, 7, 8
<i>Pyrostephos vanhoeffeni</i>	500–1000	9
Calycophores (18)		
<i>Amphicaryon peltifera</i>	0–100	5
<i>Chuniphyes moserae</i>	>1000	5, 6
<i>Chuniphyes multidentata</i>	300–800	3, 5, 6
<i>Crystalllophyes amygdalina</i>	400–1000	5
<i>Heteropyramis maculata</i>	300–700	5
<i>Lensia achilles</i>	500–900	4, 5
<i>Lensia ajax</i>	200–1000	4, 5
<i>Lensia exeter</i>	400–600	4, 5
<i>Lensia grimaldi</i>	400–600	4, 5
<i>Lensia havock</i>	1200–1600	4, 5
<i>Lensia hostile</i>	500–1500	4, 5
<i>Lensia lelouvetau</i>	600–1000	4, 5
<i>Nectopyramis diomedea</i>	500–1000	5, 6
<i>Nectopyramis natans</i>	400–800	5, 6
<i>Nectopyramis thetis</i>	300–600	5, 6
<i>Thalassophyes crystallina</i>	?	5
<i>Vogtia pentacantha</i>	300–500	5, 6
<i>Vogtia serrata (kuruuae)</i>	400–800	5, 6

Source key: 1, Moser (1925); 2, Leloup (1934); 3, Leloup & Hentschel (1938); 4, Totton (1941); 5, Totton (1954); 6, Alvarino (1971); 7, Pagès & Gili (1992); 8, Thibault-Botha & Gibbons (unpublished data); 9, Gibbons (unpublished data). Depth range information from Pugh, 1999.

and have a deep, and oceanic, distribution (Alvarino, 1971; Pugh, 1999), so their absence from our fairly shallow samples is no surprise. However, this absence constrains our analyses to epipelagic species, and limits discussion regarding oceanic zoogeography. The total number of species of siphonophore that have now been recorded around southern Africa is 91. Seventy-two belong to the above mentioned Calycophorae, 16 are Physonectae and three are Cystonectae (Tables 1 & 2).

The distribution of species appeared to be more limited spatially inshore than offshore. Over 83% of the species inshore were present in seven (at the most) different areas while offshore almost half (43%) of the species were

present in eight or more areas, with over 15% present in all 13 areas. Seven species of siphonophore were only recovered from offshore waters, whilst one species was only found in coastal waters (Table 1). Although none of these species were widespread (present only in GSs 1 to 3, Table 1), it is unknown whether their restricted, cross-shelf distribution patterns, reflects preferred habitat, or is an artefact of incomplete sampling.

The number of species observed in oceanic waters around southern Africa was generally greater than in coastal waters (data in Table 1). This is in agreement with published observations of siphonophores (Gasca, 1999) and other zooplankton (Gibbons & Hutchings, 1996), and may reflect in part the several complex hydrological/physical conditions (several upwelling areas, mixed region, warm current) encountered along the coast and the more stable temporal nature of offshore ecosystems. According to the inshore/offshore distribution of species, the study area can be divided into two large regions. The first one groups GSs 1–7 and shows that ~70% of the species found offshore were present inshore, while in GSs 8–13 as few as 5% of the species present offshore were found over the shelf. This can be linked, for GSs 1–3, to the narrow edge of the continental shelf, and by the dynamic nature of the prevailing circulation. Indeed, the fast, southward-flowing Agulhas Current moves very close inshore in northern KwaZulu Natal, and regularly introduces oceanic water to the coast there. The region between GSs 5–6 is also characterized by a dynamic oceanography and there is an extensive mixing of shelf and oceanic waters of Agulhas and Benguela Current origins respectively (Shannon, 1985). The strong inshore/offshore gradient in the number of species in the region from GSs 8–11 can be linked to the presence of the Benguela Current and its characteristic cooler upwelled waters.

Muggiaea atlantica was the only species that was recorded around the entire region (Table 1) in coastal waters. A further ten species were noted throughout the entire oceanic realm, or were missing only from (some of) GSs 8–11 (Table 1). Of these, ten (*Abylopsis tetragona*, *Bassia bassensis*, *Chelophyes appendiculata*, *Diphyes dispar*, *Enneagonum hyalinum*, *Eudoxoides spiralis*, *Lensia conoidea*, *Sulculeolaria chumi*, *S. quadrivalvis* and *S. turgida*) were widely distributed in the nearshore region, and were absent only from the Benguela Current region (Table 1). All of these species have a generally circumglobal distribution at these latitudes (Totton, 1965; Pugh, 1999), and have been recorded from a variety of water depths (Pugh, 1999). Some of the widely distributed oceanic species were much more restricted in their nearshore distribution (*Dimophyes arctica*, *Diphyes bojani*, *Eudoxoides mitra*, *Hippopodius hippopus*, *Lensia campanella*, *L. hotspur*, *L. multicristata*, *L. subtilis*, *Muggiaea kochi*, *Rosacea plicata*, *R. cymbiformis*, *Sphaeronectes gracilis* and *Sulculeolaria monoica*). Most of these species are generally considered to have warm temperate affinities. A comparison of the two above lists of species reveals sister taxa in opposite groups (e.g. *M. atlantica* and *M. kochi*, *D. dispar* and *D. bojani*, *Chelophyes contorta* and *C. appendiculata*, *Eudoxoides mitra* and *E. spiralis*). These taxa clearly have slightly different environmental tolerances, and some of them have been used to indicate the movement (inflow) of warm (or cold) water into particular areas (Alvarino, 1971). Thus, *C. contorta* is used to

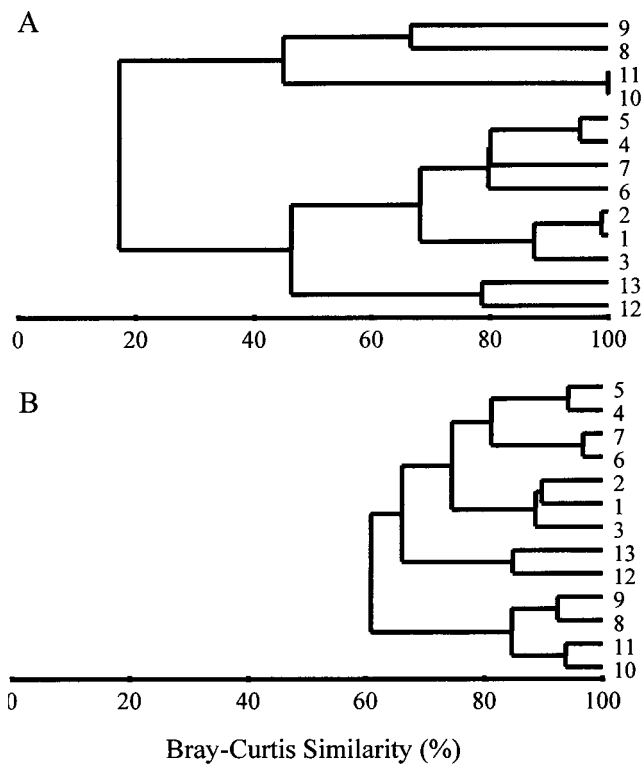


Figure 2. Dendrogram of per cent similarity between the 13 inshore (A) and offshore (B) grid squares around southern Africa. Grid numbers as in Figure 1.

indicate the movement of warm water into the California region (Alvariño, 1971), while *M. kochi* indicates the inflow of warm water around northern Europe (Russell, 1934). It is noteworthy that the distribution ranges of these (generally considered) allopatric species (Alvariño, 1971) are supported by the current, binary analyses, albeit only in the coastal realm. The analyses suggest the existence of other pairs of sister taxa that could prove similarly diagnostic: *E. mitra* and *E. spiralis*, *D. dispar* and *D. bojani*, and the latter of these could be supplemented by *Diphyes chamissonis*.

Zoogeography

Similar patterns of GS groupings were obtained for both the oceanic and coastal data sets, when each was analysed separately (Figure 2). The striking difference between the inshore and offshore sets was the position of GSs 12–13, where inshore communities were more similar to the east and south coast communities than they were to the other west coast ones (GSs 8–11). Although the cluster analysis indicates a low level of similarity between GSs 10–11 and 8–9 inshore, this could reflect the very low number of species present there: the four GSs had only one species out of three in common.

Inshore waters display a pronounced gradient in environmental conditions around the coast, and are subject to the variability induced by proximity to land. Such physical variability is probably not conducive to the prolonged survival and persistence of stenotypic offshore species. It is not surprising to see a better grouping of offshore stations, which reflects both the wide distribution

range of many oceanic siphonophores (Alvariño, 1971), and a broadly similar thermal environment in offshore waters (Shannon, 1985). Furthermore, the width of the continental shelf is not constant around the coast, and this influences the exchange of, and interaction between, nearshore and oceanic waters. The level of similarity and grouping observed on those two clusters (Figure 2A,B), if we do not include the GSs 8–11 inshore are very similar.

Benguela Current assemblages

Both analyses separate those assemblages from along the west coast of southern Africa between ~ 21 – 30° S (GSs 8–11), from the balance of samples to the north and south (Figure 2). These results are broadly similar to those obtained by benthic (Emanuel et al., 1992) and pelagic (Gibbons et al., 1995) biogeographers of the region, who identified a cold-temperate province to extend along the central part of the west coast. This area is characterized by low species richness, specially inshore (data in Table 1). Inshore waters along the west coast of South Africa are characterized by coastal upwelling (Andrews & Hutchings, 1980). This upwelling is perennial in the mid-latitudes (GS 9), but is more seasonal at the northern and southern extremes (Shannon, 1985). It has been suggested that few species of zooplankton have the ability to survive the associated environmental variability, but those that do may be abundant (Gibbons & Hutchings, 1996), owing to the regions' elevated productivity (Brown & Jarman, 1978).

The continental shelf in the area of GS 8 is broader than elsewhere along the west coast, and is bounded in the north by the perennial upwelling cell off Lüderitz (GS 9) (Shannon, 1985). The wide shelf limits mixing of oceanic and coastal waters [which may themselves be influenced by freshwater run-off from the Orange River (Shillington et al., 1992)], and given that the Benguela Current moves in a north-north-west direction, much of the coastal, source water contains few species. The Lüderitz upwelling cell acts as an internal boundary to the Benguela ecosystem and limits latitudinal exchange (Agenbag & Shannon, 1988; Barange et al., 1992). In Emanuel et al. (1992)' study of intertidal biogeography, two distinct, cold-temperate provinces were recognized along the west coast, to the north (Namib) and south (Namaqua) of the Lüderitz upwelling cell. The very low level of species richness reported inshore for siphonophores does not allow us to make any definitive remarks on the importance of the Lüderitz cell. No such internal boundary was also recognized for euphausiid crustaceans (Gibbons et al., 1995), who argued that their holoplanktonic (and opportunistic, eurythermal) nature would prevent effective separation. Interestingly, in the quantitative analysis of euphausiid assemblages in the Benguela ecosystem, Barange et al. (1992) did detect differences in the assemblages either side of the Lüderitz upwelling cell. However, this was due to differential abundance of common species—a feature that would not be detected in the current, binary analysis. Gibbons et al., 1995 also suggested that only those intertidal invertebrates with larvae that display pronounced vertical migration and that are able to survive the requisite prolonged planktonic existence, would be able to cross the

Lüderitz upwelling cell. Although the west coast fauna has no characteristic species of siphonophore (Table 1; Figure 3), nearshore assemblages are nevertheless distinct (Gibbons & Hutchings, 1996), and are typified by low species richness in combination with high densities of *Muggiaea atlantica*. The cosmopolitan *M. atlantica* appears to be a very opportunistic species (Mackie et al., 1987), like many euphausiids (Mauchline & Fisher, 1969) and is mainly found in neritic and cold water (Russell, 1934; Totton, 1965) and can be very abundant in productive coastal waters (Russell, 1934). The impact of run-off from the Orange River does not seem to affect the population of *M. atlantica*.

Angola Current assemblages

The next consistent group to be separated from the cluster analysis corresponds to GSs 12 and 13 (Figure 2). These correspond to those under the influence of the southward-flowing Angola Current (Shannon et al., 1987; Lass et al., 2000), which is thought to penetrate as far south as 19–20°S (Barange et al., 1992). This latitude also marks the point where the north-north-west flow of Benguela surface water tends to move north-west (Shannon, 1985; Lass et al., 2000). That these GSs cluster inshore with those from the south and east coasts reflects the widespread nature of most siphonophores, as well as the presence of some species of subtropical origin (Totton, 1954, 1965; Daniel & Daniel, 1963; Daniel, 1974), that are shared only with GSs 1–3 (such as *Hippopodius hippopus*, *Muggiaea kochi* and *Vogtia glabra*). The results of the offshore cluster analysis showed that the offshore assemblages had a greater number of species in common with the Agulhas current (*Ceratocymba dentata*, *Praya reticulata*, *Sulculeolaria biloba*, *S. turgida*, *Vogtia glabra*, and *V. spinosa*). These species might have a lower thermal preference range and could possibly be used in tracing the core of warm currents (Totton, 1954, 1965).

Grid squares 12 and 13 are characterized by the presence of species of *Ceratocymba*, and by *Abyla ingeborgae* and *A. tottoni* (Table 1; Figure 3), which can be thought of here as Angola Current species. These taxa are all tropical or warm temperate species (Sears, 1953; Daniel, 1974; Pagès & Gili, 1992), and *C. sagittata* may be more common in the Atlantic Ocean than elsewhere (Pagès & Gili, 1992, van der Land, unpublished data).

Agulhas Current assemblages

The remaining three clusters in Figure 2 correspond to the east (GSs 1–3), south (GSs 4 and 5) and south-west (GSs 6 and 7) coasts, all of which are influenced to some extent by the Agulhas Current. As noted previously, the Agulhas Current flows southward along the KwaZulu Natal coastline, before moving offshore in the region of East London (GS 3) to track the edge of the Agulhas Bank (GSs 4–5). It retroflects eastwards, south of Cape Agulhas (Gordon et al., 1987). The Agulhas Current is composed of subtropical Indian Ocean water (Pearce, 1977; Harris & van Forstest, 1978; Gründlingh & Lutjeharms, 1979; Lutjeharms & de Ruijter, 1996), and has a typically diverse zooplankton assemblage (as Gibbons & Hutchings,

1996). It clearly has a direct influence on the assemblages in GSs 1–3, and interacts with the shelf waters over the Agulhas Bank through eddies and filaments and with the Benguela Current through rings and entrainment in the frontal jet (Schouten et al., 2000 and references therein; Penven et al., 2001).

The results presented here for siphonophores agree in almost all details with previous biogeographic studies of pelagic (Gibbons et al., 1995) and benthic (Emanuel et al., 1992) taxa, and suggest that there is a very tight agreement between oceanography and biogeography. Although analyses of benthic taxa have tended to include GS 7 amongst cold- and not warm-temperate fauna (Emanuel et al., 1992), this difference reflects the greater influence of water mass movement on the distribution of pelagic, than benthic, taxa.

In their study of regional euphausiid biogeography, Gibbons et al. (1995) noted that nearshore assemblages in northern KwaZulu Natal (GSs 1–2) lacked coastal species from further south. These authors attributed this to an inability by those species (*Nyctiphanes capensis* and *Euphausia lucens*) to penetrate northwards in the face of the fast flowing Agulhas Current. Although similar observations are not made here with regard to *Muggiaea atlantica* (which occupies a similar environment to both foregoing krill species), it is likely that populations of this calycophoran are replenished from the St Lucia upwelling cell to the north (D. Thibault-Botha, unpublished data). By contrast, *Lensia conoidea* failed to be found in the oceanic waters along the east coast, but was noted in coastal waters there and around the rest of the region. This is a cold-water species (Totton, 1965; Daniel, 1974), and its absence from offshore water along the east coast could reflect the generally warm water there, or its deeper distribution and its capacity to display vertical diel migrations (Pugh, 1999). Its presence in coastal waters could be the result of the southward advection of cool water from the St Lucia upwelling cell. The other species that failed (except in one instance: October off Mbashe) to penetrate the east coast, either in- or off-shore, was *Dimophyes arctica*. This is an unusual observation, given its generally cosmopolitan distribution (Margulis, 1976 in Mackie et al., 1987), although it may be an uncommon epipelagic species in tropical waters, owing to tropical submergence.

Subtropical water of Agulhas Current origin can be identified by the presence of some 11 species of siphonophore (Table 1; Figure 3). These include five species of *Abyla* (different from those in the Angola Current), four species of *Lensia* (*L. cossack*, *L. gnanamuthui*, *L. hunter* and *L. panikkari*), *Praya dubia*, as well as *Sulculeolaria angusta* (which has been recognized by Carré (1979) as a synonym of *S. turgida*). Two of the species (*L. gnanamuthui* and *L. panikkari*) have only been described from the Indian Ocean (Daniel, 1974), whilst *S. angusta* has only been recorded from subtropical waters (Alvariano, 1971). And as noted previously, species of *Abyla* tend to be tropical and warm temperate.

A further 15 species display a spatial distribution strongly influenced by the upwelling present on the west coast being only present on the east and south coasts. These species include *Abylopsis eschscholtzi*, *Ceratocymba leuckarti*, *Diphyes chamissonis*, and *Chelophyes contorta*, all of which can be considered to have warm-water affinities

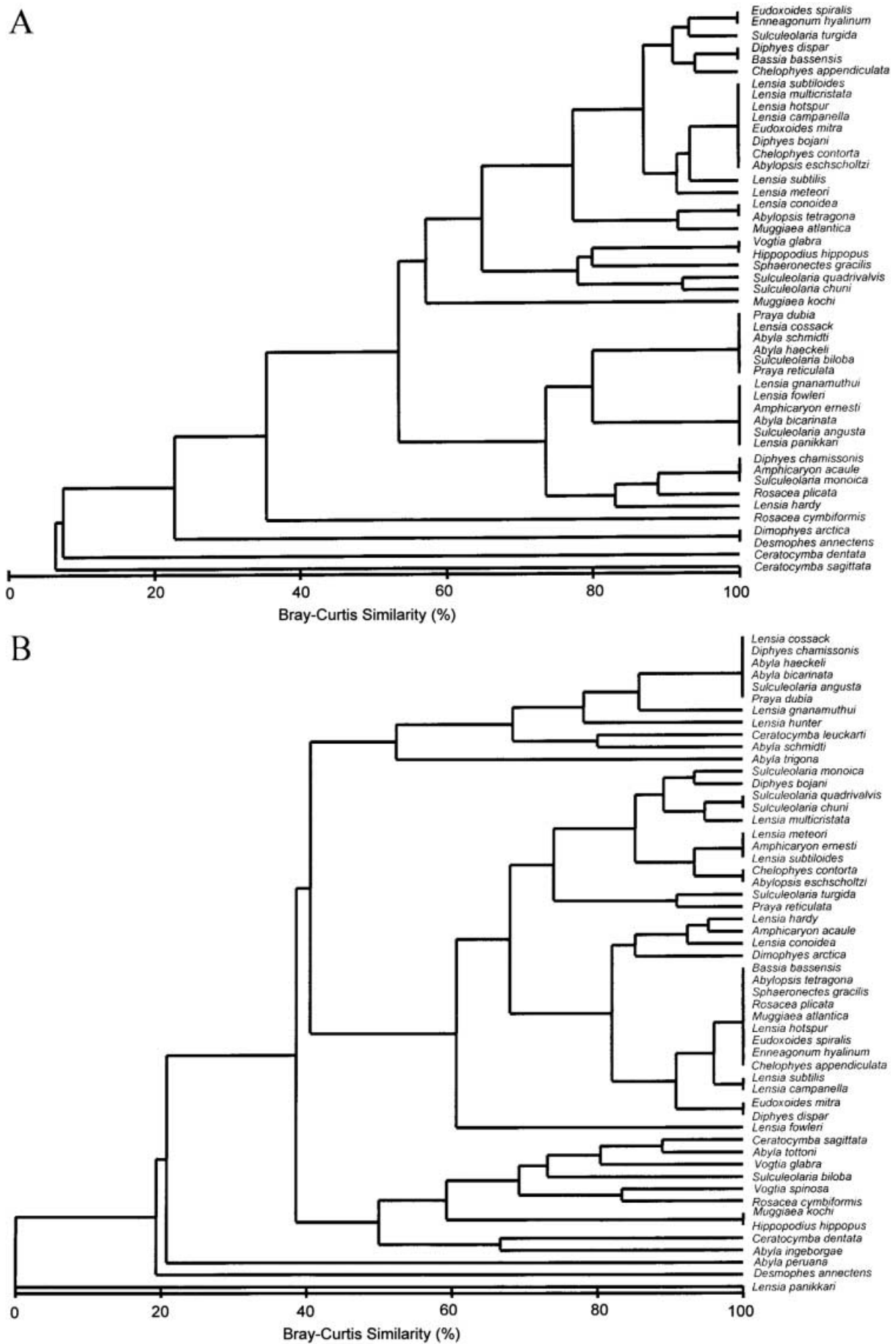


Figure 3. Dendrogram of per cent similarity amongst the siphonophores found in the 13 inshore (A) and offshore (B) grid squares around southern Africa.

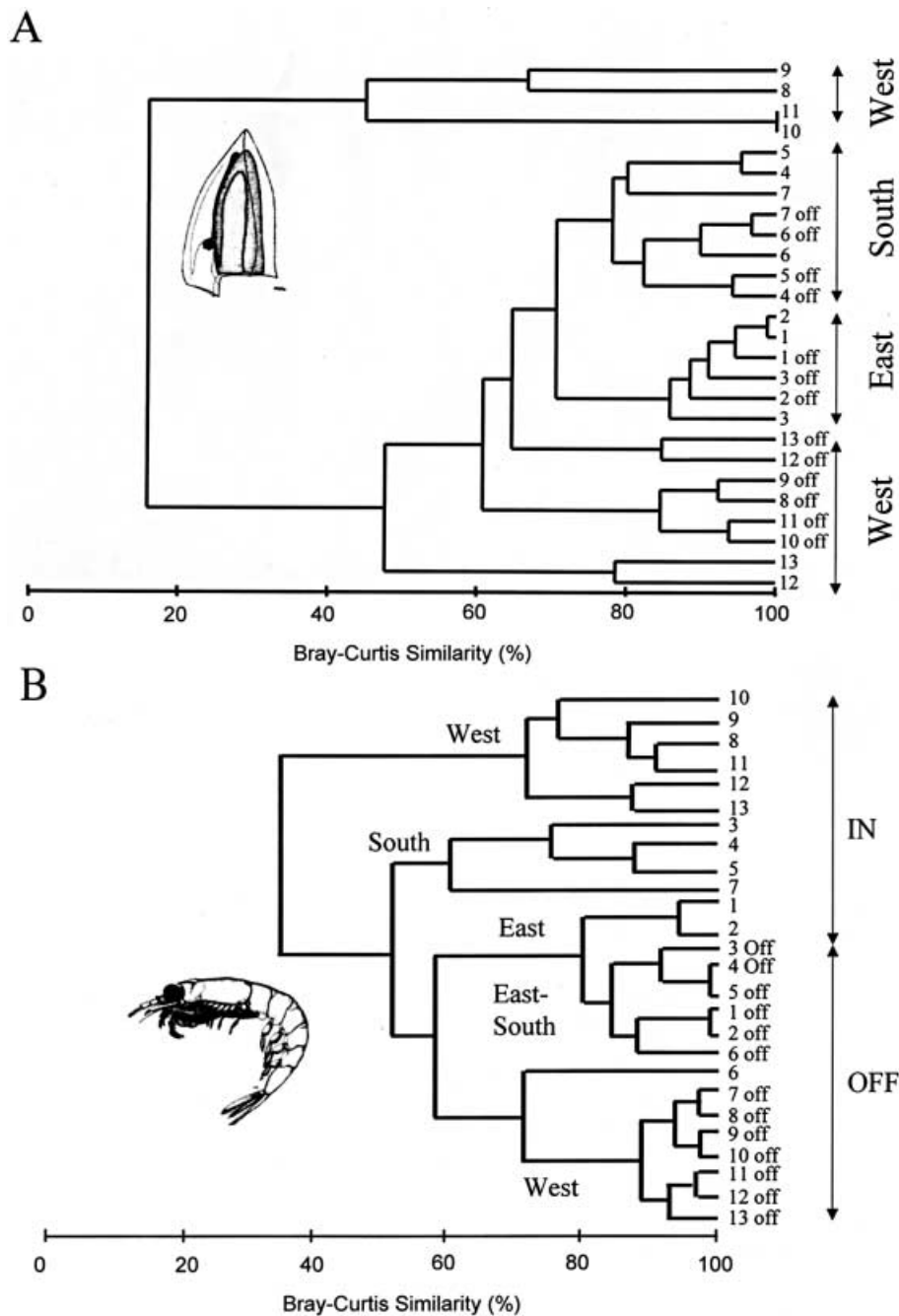


Figure 4. Dendrogram of per cent similarity between the 26 combined inshore and offshore grid squares around southern Africa, for epipelagic siphonophores (A) and euphausiids (B). Grid numbers as in Figure 1 (euphausiid data modified from Gibbons et al., 1995).

(Daniel, 1974). *Amphicaryon ernesti* and *Lensia fowleri* are the exceptions, because these have much more widespread distributions. Only two species (*Lensia subtiloides* and *L. meteori*) do not penetrate further west offshore. Another four were absent over the Agulhas Bank but make an appearance in the dynamic mixing area between GSs 5–7 (Table 1; Figure 3). Interestingly, the south coast itself was characterized by the presence of only one species (Table 1; Figure 3), *Desmophyes annectens*.

CONCLUSIONS

The dendrogram showing relations amongst all (oceanic and neritic) GSs is shown in Figure 4A, and is broadly similar to that for euphausiids (Figure 4B).

Distinct subtropical (east and west), and warm- and cold-temperate provinces are visible. The boundaries between the different provinces are similar in both instances, and we are generally justified in separating oceanic from neritic regions. However, there are differences between the two data sets. Firstly, siphonophore assemblages along the central regions of the Benguela ecosystem are much more distinct from other assemblages than in the case of euphausiids. This is probably because unlike siphonophores, euphausiids are omnivorous and have the ability to survive off lipids when food is in short supply (Mauchline & Fisher, 1969)—a factor that must give them some advantage in such a variable environment. The level of similarity amongst the distinct euphausiid assemblages in the different areas is less than is observed

for siphonophores. This is probably due to the fact that some species of euphausiid show localized areas of endemism in the region (*Euphausia hanseni*, *E. americana*, *E. diomediae*, *Nematoscelis gracilis*, *Stylocheiron microphthalmum*), whereas the siphonophores are much more widely distributed. Thirdly, neritic assemblages of euphausiids are consistently different from oceanic assemblages, unlike the situation with siphonophores. This can probably be attributed to the greater control that euphausiids have over their horizontal position than do siphonophores, and so neritic species (such as *Nyctiphanes capensis*) are rarely found in oceanic waters. In conclusion then, although there are similarities between the zoogeography of siphonophores and euphausiids, there are also differences—differences that reflect the interaction of oceanography and biology.

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