

BIOGEOGRAPHY AND COMMUNITY STRUCTURE OF THE DECAPOD CRUSTACEAN FAUNA OFF NAMIBIA (SOUTHEAST ATLANTIC)

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ABSTRACT

The communities of pelagic and benthic decapod crustaceans off Namibia (Southeast Atlantic) were studied. The samples comprised 97 species differing widely in their geographical and depth distribution. The analyses revealed distinct assemblages, with several well-defined boundaries. However, the barriers were different for pelagic and benthic species. The zonation of the pelagic species presented two clearly differentiated communities, an "inshore association" from the coast to about 70 miles (113 km) offshore, largely coinciding with the shelf, and an "offshore association" more than 70 miles off the coast. Both associations were present in the active (September–October) and quiescent (April) upwelling period, although during the active upwelling period the number of species clearly decreased. These results support the existence of different circulation patterns over the shelf and slope separated by a cross-shelf barrier. A third association seemed to be related to the seasonal intrusion of waters from Angola during the quiescent upwelling period. The communities of benthic species were mainly delimited by the depth, although several latitudinal boundaries exist. The bathymetric boundaries were well defined: the main boundary was located around 400 m, separating the shelf and slope-bathyal species. The latitudinal boundaries seemed to be related to different features of the Benguela upwelling and the circulation pattern in the region.

The waters off Namibia are located between the mouths of the Kunene River (approximately 17°30'S) and the Orange River (approximately 29°30'S). They are characterized by an intense upwelling, originated by the equatorward windstress pattern that exists over the Benguela current (e.g., Shannon, 1985). The upwelling is intense over most of the year, although seasonal differences exist, with a spring maximum and an autumn minimum (Shannon, 1985; Chapman and Shannon, 1985). Upwelling intensity is not uniform in space, being strongest in the perennial Lüderitz upwelling cell (25–28°S) (Chapman and Shannon, 1985). The zone off northern Namibia is also affected by seasonal intrusions of the waters of the Angola system (Boyd *et al.*, 1987). One of the most characteristic features of this system is the existence of large areas of bottom-waters with very low levels of dissolved oxygen (Chapman and Shannon, 1985) (Fig. 1), determining the distribution of many species and the structure of the benthic fish communities in the region (e.g., Abelló and Macpherson, 1989, 1990; Mas-Riera *et al.*, 1990).

The perennial upwelling cell around Lüderitz has been considered as being an environmental barrier which prevents the in-

terchange of species (e.g., pelagic fishes, Crawford *et al.*, 1987; zooplankton, Shannon and Pillar, 1986). Agenbag and Shannon (1988) suggested that this discontinuity is caused by the combined effect of turbulence and stratification of water masses. However, although this upwelling cell has a strong effect on larval fish (Olivar, 1987, 1990) and euphausiid communities (Barangé and Stuart, in press), the structure of the benthic fish communities (Mas-Riera *et al.*, 1990) does not support the existence of this boundary.

Some work on the decapod crustacean fauna in the area (e.g., Macpherson, 1983, 1988) has been carried out in recent years, together with work performed in neighboring areas (e.g., Barnard, 1950; Crosnier and Forest, 1973; Kensley, 1981; Manning and Holthuis, 1981). Despite this, except for some aspects contained in the paper by Kensley (1981), which focused on the area off South Africa, the biogeography and structure of the communities of decapod crustaceans in the region are practically unknown.

Considering the complexity of the Benguela system and the controversy about its effect on the different communities, the study of the decapod communities is of great in-

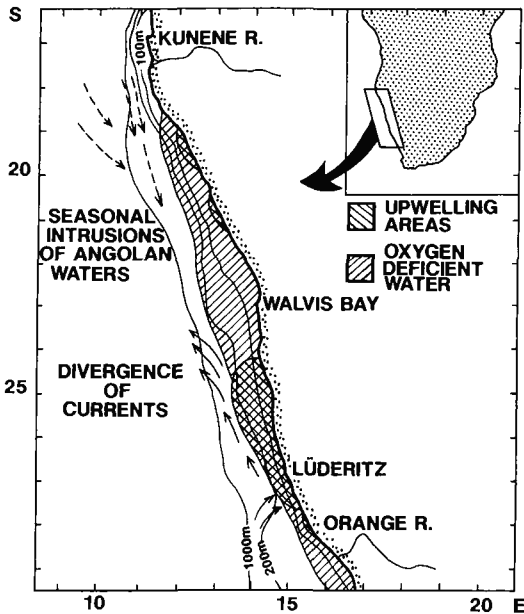


Fig. 1. The study area and a schematic representation of the major environmental features (from Shannon, 1985).

terest. Therefore, the aim of this paper is to contribute to knowledge of the ecology of decapod crustacean communities off Namibia: (1) analyzing the structure and zonation of the communities of pelagic and benthic decapod crustaceans in the area, and (2) discussing the relationships between the distributions of the species and the different assemblages and the particular oceanographic features found in the region.

MATERIALS AND METHODS

The species recorded were grouped according to habitat as either pelagic or benthic species (Table 1). I have considered as pelagic and benthic species those species collected by pelagic and benthic gear, respectively. Those species with a known pelagic habitat caught by benthic gear were not considered in the analyses (marked with an asterisk in Table 1).

Data for pelagic species were collected on 2 research cruises (SNEC I, September–October 1985, and SNEC II, April 1986) corresponding to an active and a quiescent upwelling period, respectively. A total of 66 and 54 stations, respectively, were occupied in the area north of Lüderitz (26°30'S) between the coast and 135 miles (217 km) offshore (bottom depths about 50 and 1,000–4,000 m, respectively) (Fig. 2). Samples were collected using a multiple opening and closing RMT (rectangular midwater trawl) 1 × 6-m net with a mouth area of 1 m² and a mesh size of 200 μm. Only 4 layers, between the surface and 200 m, were sampled. In this study, all the vertical samples taken per station were grouped. Temperature and salinity profiles were taken at each station by means of a sensor for salinity (con-

ductivity), temperature, and depth (CTD) cast (see also Masó and Manriquez, 1986; Masó, 1987; Olivar and Barangé, 1990; Salat *et al.*, in press).

Data for benthic species were collected on 7 research surveys between 1979 and 1989. Three cruises (November 1979, July–September 1980, and March–April 1981), with a total of 216 hauls, were carried out off the northern half of Namibia between Walvis Bay (23°00'S) and the Kunene River (17°30'S), between the 100 and 1,000-m isobaths. Four cruises (September 1987, January 1988, August 1988, and January 1989) with a total of 320 hauls were made in the southern half of Namibia between Walvis Bay (23°00'S) and the Orange River mouth (29°30'S), between the 100 and 1,000-m isobaths (see also Macpherson *et al.*, 1981, 1985, for the methodology used). Data on temperature and salinity profiles were incomplete in each cruise and, therefore, they were not used in this study. The species were caught with a bottom trawl with a 20-mm mesh cod end. To facilitate the analysis, the area was divided into strata of 1° of latitude by 100-m depth interval, with the exception of the northernmost and southernmost zones, where strata of 30' of latitude by 100 m were considered (17°30'S to 17°59'S and 29°00'S to 29°30'S, respectively). Each stratum was sampled on at least 1 cruise, with a minimum of 2 hauls per stratum.

The data for pelagic species were used separately for each cruise, because they covered most of the area and the hydrographic information was adequate. The data for benthic species was pooled, because each cruise encompassed only part of the study area and the hydrographic information was incomplete. In this case, I have used the overall circulation patterns and published oceanographic information to discuss the possible relationships between community structure and oceanographic features.

The composition of the species collected at each station (for pelagic species) and stratum (for benthic species) was used to define faunistic assemblages. Data analysis was based on a presence-absence matrix. Species and stations or strata were classified for cluster analysis, choosing Yule's coefficient as an index of similarity. Jackson *et al.* (1989) stated that this index of association incorporated implicit centering transformations that reduced the size-influence associated with frequency of occurrence. This coefficient, as Jackson *et al.* pointed out, produces artificially tight clusters, with many species pairs having similarities of 1.00 when pairs of species display no mismatches. However, Yule's coefficient was chosen because the aim of this paper is to show only the major groupings of assemblages rather than to delineate the degree of relationships of associated species pairs. The aggregation algorithm was the unweighted pair group method using arithmetic averages (UPGMA) (Sneath and Sokal, 1973).

RESULTS

Table 1 shows the species recorded in the study area (68 benthic and 29 pelagic), including their horizontal and distribution range. Depth cited for pelagic species refers to station depth, and consequently can be considered an estimate of the distance from the coast. Twelve species with a known pe-

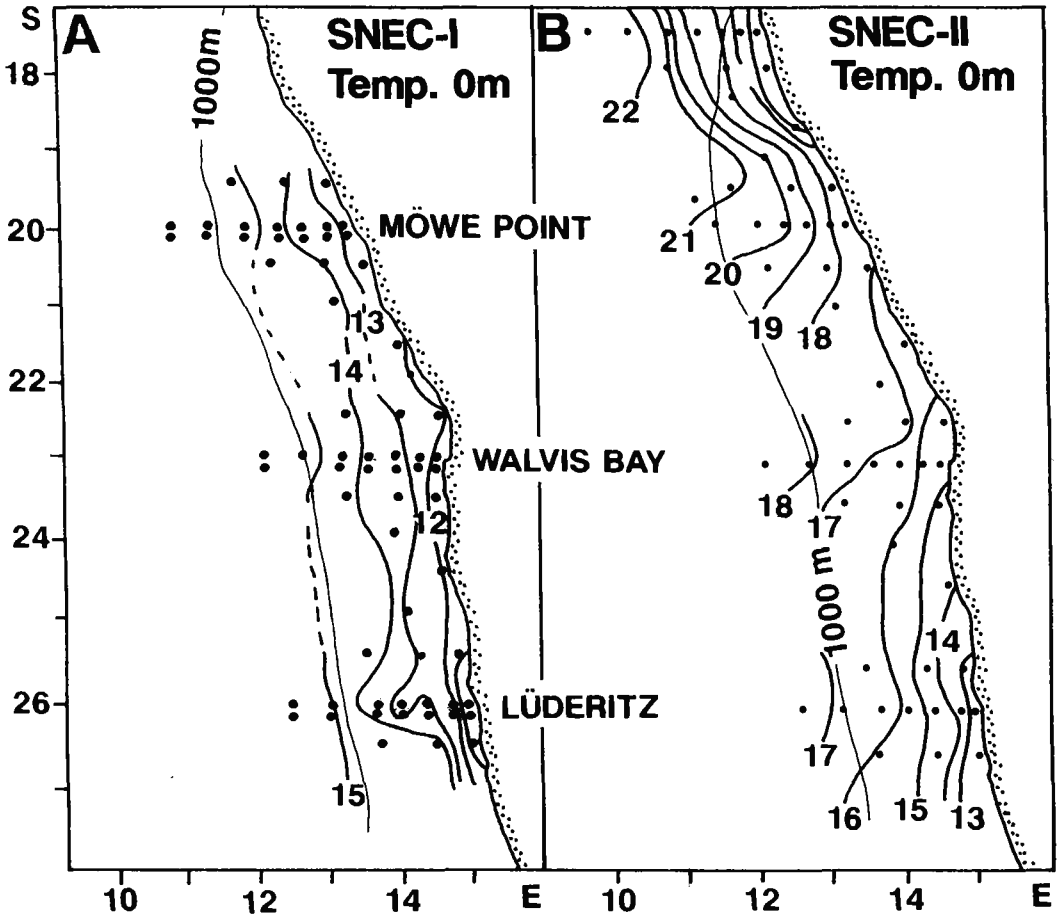


Fig. 2. The study area, surface temperature, and stations occupied on the pelagic cruises: (A) SNEC I (September–October 1985) and (B) SNEC II (April 1986) (from Masó and Manriquez, 1986; Masó, 1987).

lagic habitat, although caught by benthic gear, were not considered in the analyses (marked with an asterisk in Table 1). The geographic distribution corresponds to the northern and southern limits of the species in Namibia. Five species (*Goneplax rhomboides*, *Inachus grillator*, *Solenocera africana*, *Sergestes armatus*, and *S. edwardsi*) presented a discontinuous latitudinal distribution; the other species were caught along its latitudinal range. The depth distribution corresponds to the minimum and maximum depth of occurrence of the species in the area. The depth range of each species was not constant along its latitudinal range.

Pelagic Species

The hydrographic conditions observed during the active upwelling period (SNEC I, September–October 1985) and quiescent

upwelling period (SNEC II, April 1986) were described by Masó and Manriquez (1986), Masó (1987), and Salat *et al.* (in press). During September 1985, surface isotherms ran parallel to the coast, with a narrow belt of cold water observed close to the coast along the whole study area. Upwelling was more intense in the perennial Lüderitz upwelling zone (Fig. 2A). During the quiescent period (April 1986), the area was characterized by a relaxation of the coastal upwelling and the development of the seasonal warming off northern Namibia (see also Shannon, 1985; Boyd *et al.*, 1987) (Fig. 2B). Nevertheless, coastal upwelling was still observed off Lüderitz. More saline waters dominated the northernmost area, as a consequence of the intrusion of Angolan waters, and were separated from the southern water mass by a frontal strip north of 22°S. During the Sep-

Table 1. Species of decapod crustaceans recorded off Namibia, including their geographic and depth distribution in the area. B = benthic species, P = pelagic species. Species marked with an asterisk are pelagic species collected by benthic gear; they are not considered in the analyses (see text for explanations). Depth cited for pelagic species refers to station depths, and consequently can be considered an estimate of the distance from the coast. Geographic distribution corresponds to the northern and southern limits of the species in Namibia. Discontinuous latitudinal distributions are indicated by a slash. The depth distribution corresponds to the minimum and maximum depth of occurrence of the species (in 100-m depth strata). The depth range of each species was not constant along its latitudinal range.

Species	Habitat	Latitude (°S)	Depth (m)
Family Galatheidae			
<i>Munidopsis chuni</i> Doflein and Balss, 1913	B	17–28	400–600
<i>Munidopsis longirostris</i> A. Milne Edwards and Bouvier, 1897	B	23–29	> 900
<i>Munida benguela</i> Saint Laurent and Macpherson, 1988	B	29	400–500
<i>Munida speciosa</i> von Martens, 1878	B	17–19	200–400
Family Chirostylidae			
<i>Eumunida squamifera</i> Saint Laurent and Macpherson, 1990	B	28	300–500
Family Lithodidae			
<i>Neolithodes asperrimus</i> Barnard, 1947	B	17–29	> 500
<i>Lithodes ferox</i> Filhol, 1885	B	17–27	300–800
<i>Paralomis africana</i> Macpherson, 1982	B	20–24	500–700
Family Parapaguridae			
<i>Parapagurus bouvieri</i> Stebbing, 1910	B	17–29	400–800
<i>Sympagurus dimorphus</i> (Studer, 1883)	B	23–29	200–600
<i>Sympagurus macrocerus</i> Forest, 1955	B	17–22	200–300
Family Diogenidae			
<i>Dardanus arrosor</i> (Herbst, 1796)	B	17	100–200
Family Dromidae			
<i>Exodromidia bicornis</i> (Studer, 1882)	B	29	200–300
<i>Exodromidia spinosa</i> (Studer, 1882)	B	20–29	200–600
<i>Pseudodromia inermis</i> Macpherson, 1988	B	28–29	100–300
Family Homolidae			
<i>Paromola cuvieri</i> (Risso, 1816)	B	26	300–400
Family Leucosidae			
<i>Ebalia scandens</i> (Stebbing, 1921)	B	29	200–300
Family Calappidae			
<i>Calappa peli</i> Herklots, 1851	B	17–18	100–200
<i>Acanthocarpus brevispinis</i> Monod, 1946	B	17–20	200–500
<i>Mursia cristimanus</i> de Haan, 1837	B	26–29	100–400
Family Corystidae			
<i>Nautilocorystes ocellatus</i> (Gray, 1831)	B	17–29	100–200
Family Portunidae			
<i>Bathynectes piperitus</i> Manning and Holthuis, 1981	B	17–29	100–500
<i>Macropipus australis</i> Guinot, 1961	B	17–26	100–400
Family Geryonidae			
<i>Chaceon chuni</i> (Macpherson, 1983)	B	26–29	500–700
<i>Chaceon maritae</i> (Manning and Holthuis, 1981)	B	17–26	200–700
Family Xanthidae			
<i>Monodaeus cristulatus</i> Guinot and Macpherson, 1989	B	27–29	100–300
Family Goneplacidae			
<i>Goneplax rhomboides</i> (Linnaeus, 1758)	B	17–18/28–29	100–400
<i>Neopilumnoplax heterochir</i> (Studer, 1882)	B	26–29	300–400
Family Majidae			
<i>Inachus angolensis</i> Capart, 1951	B	17–18	100–200
<i>Inachus grillator</i> Manning and Holthuis, 1981	B	17/28–29	100–200

Table 1. Continued.

Species	Habitat	Latitude (°S)	Depth (m)
<i>Rochinia hertwigi</i> (Doflein, 1900)	B	24–29	300–700
<i>Dorhynchus basi</i> Macpherson, 1983	B	28–29	100–400
<i>Macropodia macrocheles</i> (A. Milne Edwards and Bouvier, 1898)	B	17	100–300
Family Grapsidae			
<i>Miersiograpsus kingsleyi</i> (Miers, 1885)	B	27–29	100–400
<i>Euchirograpsus liguricus</i> H. Milne Edwards, 1853	B	17	100–300
Family Callianassidae			
<i>Callianassa australis</i> Kensley, 1974	B	20–29	100–200
Family Axiidae			
<i>Calocaris barnardi</i> Stebbing, 1914	B	18–29	200–400
<i>Calastacus longispinis</i> (McArdle, 1901)	B	20–29	300–700
Family Nephropidae			
<i>Nephropsis atlantica</i> Norman, 1882	B	17–24	400–700
Family Polychelidae			
<i>Stereomastis suhmi</i> (Bate, 1878)	B	26–29	300–600
<i>Stereomastis grimaldii</i> (Bouvier, 1905)	B	17–29	>800
<i>Stereomastis talismani</i> (Bouvier, 1917)	B	17–29	>700
Family Scyllaridae			
<i>Scyllarus subarctus</i> Crosnier, 1970	B	17	100–300
Family Palinuridae			
<i>Panulirus regius</i> de Brito Capello, 1864	B	17–19	500–600
Family Oplophoridae			
<i>Oplophorus novaezealandiae</i> de Man, 1931	P	17–29	>300
* <i>Notostomus crosnieri</i> Macpherson, 1984	P	17–18	>900
* <i>AcanthePHYra kingsleyi</i> Bate, 1888	P	17–22	>500
* <i>AcanthePHYra pelagica</i> (Risso, 1816)	P	17–29	>500
* <i>AcanthePHYra acanthitelsonis</i> Bate, 1888	P	17–29	>500
* <i>AcanthePHYra quadrispinosa</i> Kemp, 1939	P	26	>900
<i>Systemellaspis cristata</i> (Faxon, 1893)	P	17–25	>900
<i>Systemellaspis debilis</i> (A. Milne Edwards, 1881)	P	17–20	>700
* <i>Ephyrina ombango</i> Crosnier and Forest, 1973	P	17–25	>900
* <i>Meningodora vesca</i> (Smith, 1887)	P	24	>900
Family Nematocarcinidae			
<i>Nematocarcinus africanus</i> Crosnier and Forest, 1973	B	17–19	400–600
<i>Nematocarcinus sigmoideus</i> Macpherson, 1984	B	23–29	>800
Family Pasiphaeidae			
<i>Pasiphaea semispinosa</i> Holthuis, 1951	P	17–29	>100
* <i>Pasiphaea tarda</i> Krøyer, 1845	P	17–23	>700
<i>Glyphus marsupialis</i> Filhol, 1884	B	17–24	400–700
* <i>Psatyrocaris infirma</i> Alcock and Anderson, 1894	P	17–26	>300
Family Hippolytidae			
<i>Merhippolyte agulhasensis</i> Bate, 1888	B	22–29	200–600
<i>Merhippolyte ancistrotota</i> Crosnier and Forest, 1973	P	17–22	50–500
<i>Eualus ctenifer</i> (Barnard, 1950)	B	29	100–300
Family Processidae			
<i>Processa namibiensis</i> Macpherson, 1983	P	17–19	<100
Family Pandalidae			
<i>Chlorotocus crassicornis</i> (Costa, 1871)	B	29	300–400
<i>Heterocarpus grimaldii</i> A. Milne Edwards, 1900	B	17–29	500–800
<i>Pandalina modesta</i> (Bate, 1888)	B	26–29	300–400
<i>Plesionika heterocarpus</i> (Costa, 1871)	B	17–22	200–300
<i>Plesionika acanthonotus</i> (Smith, 1882)	B	17–24	200–600

Table 1. Continued.

Species	Habitat	Latitude (°S)	Depth (m)
<i>Plesionika carinata</i> (Holthuis, 1951)	P	17–29	> 300
<i>Plesionika martia</i> (A. Milne Edwards, 1883)	B	28–29	400–600
<i>Stylopandalus richardi</i> (Coutière, 1905)	P	17–20	> 500
Family Alpheidae			
<i>Alpheopsis africana</i> Holthuis, 1952	B	29	100–200
<i>Alpheus macrocheles</i> (Hailstone, 1835)	B	17	100–200
Family Crangonidae			
<i>Pontocaris lacazei</i> (Gourret, 1887)	B	19–21	300–400
<i>Pontophilus gracilis</i> Smith, 1882	B	24–29	300–700
<i>Metacrangon jacqueti bellmarleyi</i> (Stebbing, 1914)	B	17–25	600–800
Family Glyphocrangonidae			
<i>Glyphocrangon longirostris</i> (Smith, 1882)	B	17–29	> 900
Family Palaemonidae			
<i>Periclimenes andresi</i> Macpherson, 1988	B	17	100–200
Family Aristeidae			
<i>Aristeus varidens</i> Holthuis, 1952	B	17–24	300–700
<i>Aristeomorpha foliacea</i> (Risso, 1827)	B	28	300–500
<i>Plesiopenaeus edwardsianus</i> (Johnson, 1868)	B	17–29	400–700
<i>Gennadas brevirostris</i> Bouvier, 1905	P	17–29	> 700
* <i>Gennadas clavicarpus</i> de Man, 1907	P	26	> 900
Family Solenoceridae			
<i>Solenocera africana</i> Stebbing, 1917	B	17/28	200–400
<i>Hymenopenaeus chacei</i> Crosnier and Forest, 1969	B	17–18	400–600
Family Penaeidae			
* <i>Funchalia woodwardi</i> Johnson, 1868	P	22–29	> 500
<i>Parapenaeus longirostris</i> (Lucas, 1849)	B	17	100–300
Family Sergestidae			
<i>Sergia robusta</i> (Smith, 1882)	P	17–29	> 500
* <i>Sergia potens</i> (Burkenroad, 1940)	P	22–29	> 700
<i>Sergia grandis</i> (Sund, 1920)	P	17	> 900
<i>Sergestes diapontius</i> Bate, 1881	P	17–25	> 500
<i>Sergestes pediformis</i> Crosnier and Forest, 1973	P	17–19	> 900
<i>Sergestes arcticus</i> Krøyer, 1859	P	23–29	> 900
<i>Sergestes armatus</i> Krøyer, 1855	P	17–18/26	> 900
<i>Sergestes edwardsi</i> Krøyer, 1855	P	17–18/28	> 900
Family Luciferidae			
<i>Lucifer faxoni</i> Borradaile, 1915	P	17–20	> 100

tember–October cruise two different water types, as defined by O'Toole (1980), were detected: South Atlantic Central waters and oceanic waters, reflecting the hydrographic complexity of the area. These two water types were also observed during the April survey together with a third water type, the Angolan waters, in the north.

Analysis of the pelagic species by station (Fig. 3) showed two clearly distinguishable geographic associations: (1) "inshore association" from the coast to about 70 miles offshore, over bottom depths of between 50

and 900–1,000 m (near the Kunene River deeper than 4,000 m) and (2) "offshore association" more than 70 miles off the coast, over bottom depths greater than 1,000 m. Both associations were present in the active (September–October) (Figs. 3A, 4A) and quiescent (April) upwelling period (Figs. 3B, 4B). The cophenetic correlation coefficient was high (1.0 and 0.78 for September–October and April cruises, respectively), as was the measure of enchaining (1.0 and 0.43, respectively) (see Sneath and Sokal, 1973, for the range values of these coefficients).

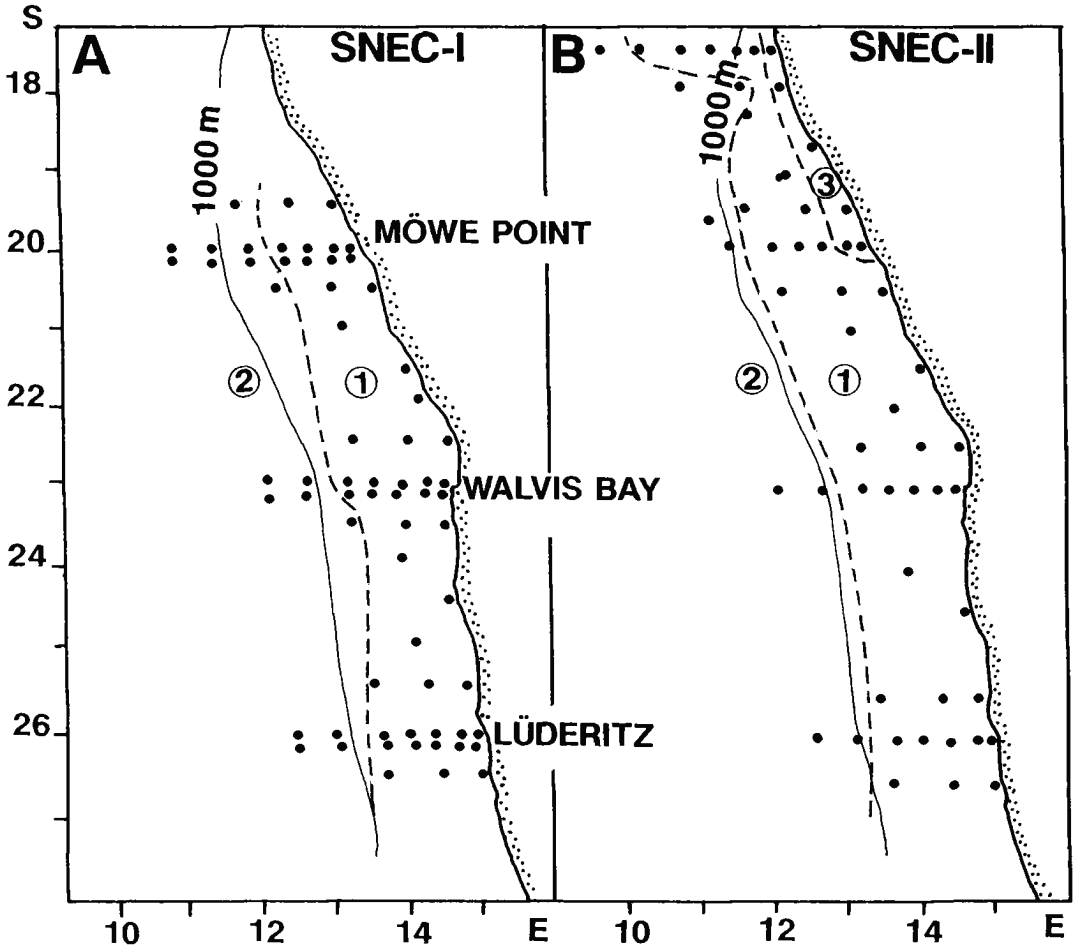
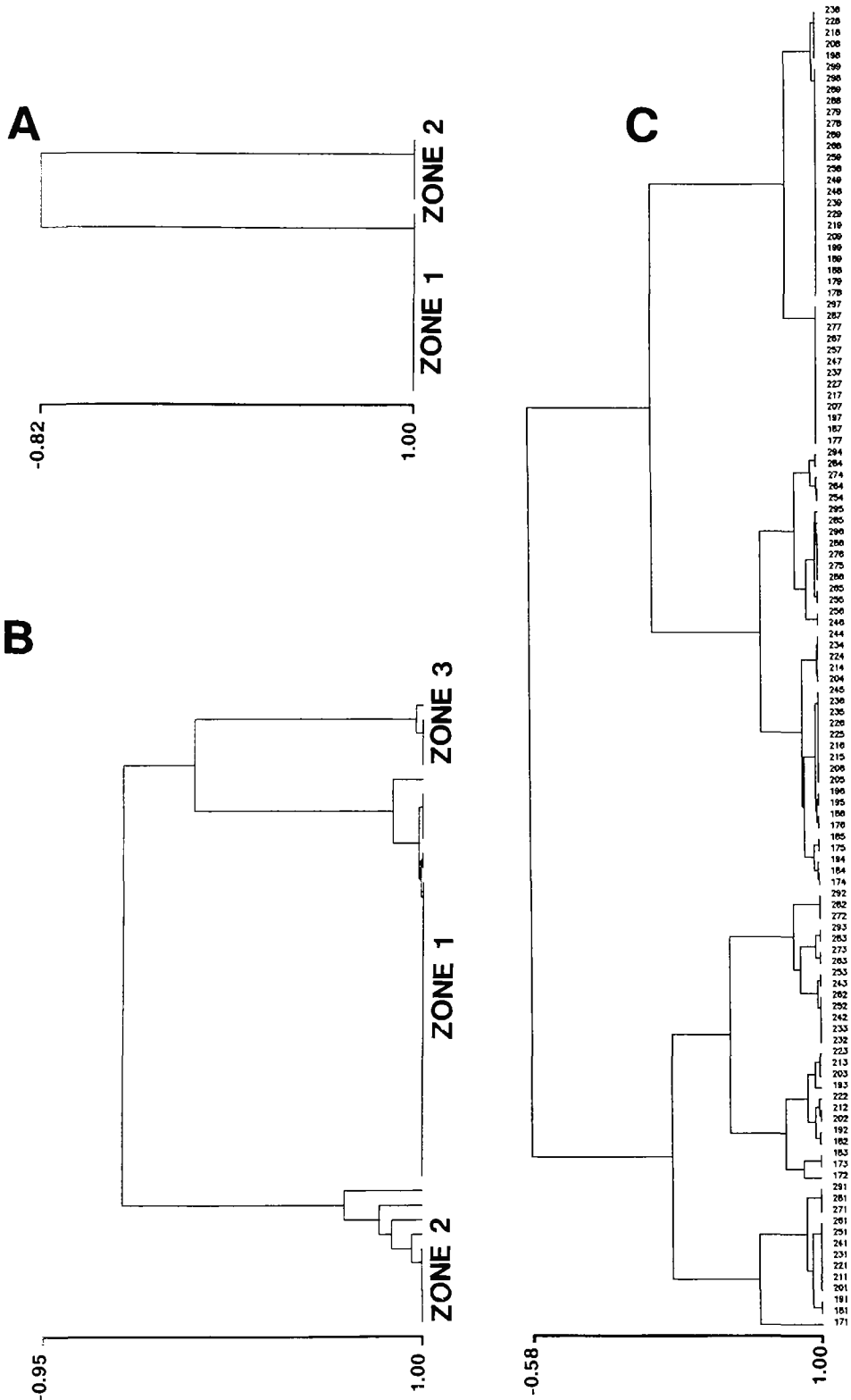


Fig. 3. Location of different pelagic station groups discriminated by cluster analysis in: (A) SNEC I (September–October 1985) and (B) SNEC II (April 1986) cruises. (1) inshore association, (2) offshore association, and (3) northern coastal association. (See Fig. 4 for similarities between stations.)

Another inshore association from the April cruise was observed north of 20°00'S between the coast and 15 miles (24 km) offshore (bottom depth shallower than 110 m) (number 3 in Fig. 3B).

The pelagic species for the September–October cruise constituted two well-defined species associations (Fig. 5A) with a high cophenetic correlation coefficient (1.0) and a high measure of enchainment (1.0). The first association (1) was composed solely of species dwelling mainly over the shelf (*Pasiphaea semispinosa*). The second association (2) consisted of oceanic species (e.g., mainly species of the families Oplophoridae and Sergestidae). The pelagic species for the April cruise constituted three well-defined species

associations (Fig. 5B) with a high cophenetic correlation coefficient (0.87) and a high measure of enchainment (0.57). The first association was composed solely of *Processa namibiensis*, the most inshore species caught along the water column and a species living exclusively in the northern part off Namibia. The second group of species can be subdivided into two groups, similar to those found in the September–October cruise: an association composed solely of species dwelling mainly over the shelf (*Pasiphaea semispinosa* and *Merhippolyte ancistrota*) and a second association consisting of oceanic species (mainly species of the families Oplophoridae and Sergestidae). The number of species occurring in the quiescent up-



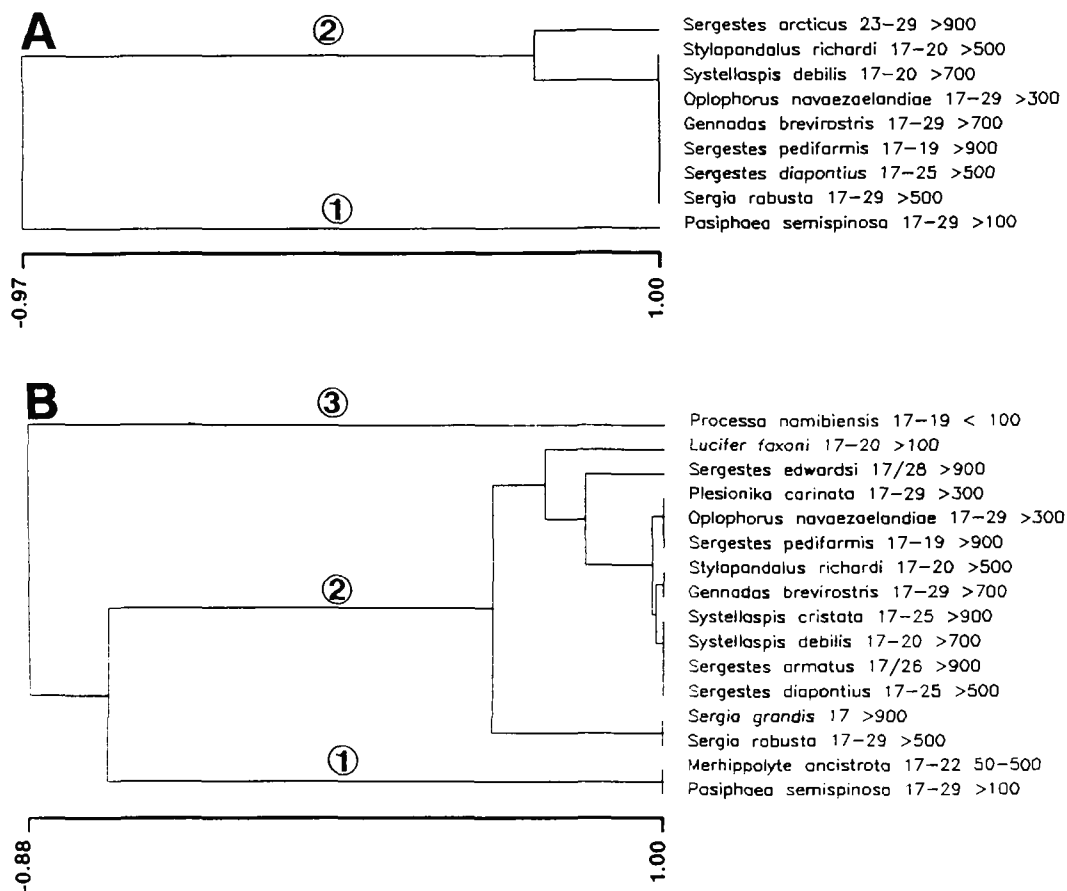


Fig. 5. Classification from pelagic species-cluster analysis. Ordinate shows similarity. (A) SNEC I (September–October 1985) cruise and (B) SNEC II (April 1986) cruise. (1) inshore species association, (2) offshore species association, and (3) northern coastal association. Each species includes its latitude and station depth range distribution. (See also Table 1 and text for explanations.)

welling period (April) was higher than in the active upwelling period (September–October).

Benthic Species

Analysis of the benthic species by strata indicated that the first branching of the similarity tree clearly discriminated between shelf (100–399 m) and slope-bathyal zone (deeper than 400 m) (Figs. 4C, 6) (see Shannon, 1985, for the topography of the zone and situation of the shelf break). The first group can be further divided into shallow-shelf (100–199 m) and deep-shelf (200–399

m). The second cluster can also be separated into slope (400–699 m) and bathyal (deeper than 700 m) groups. The cophenetic coefficient was low (0.74), as was the measure of enchainment (0.08). A latitudinal boundary was also observed in the shallow-shelf association (100–199 m) between 17°S and 18°S. Another latitudinal boundary was located in the deep-shelf assemblage (200–399 m) between 22°S and 23°S. Finally, a third latitudinal separation was observed in the slope (400–699 m) between 24°S and 25°S, but there was no distinct latitudinal boundary beyond the 700-m isobath.

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Fig. 4. Similarities between stations and strata. (A) SNEC I (September–October 1985) cruise stations, (B) SNEC II (April 1986) cruise stations, and (C) strata considered for benthic species analysis. Each stratum is numbered according to its latitude and depth interval (e.g., 231 is the stratum from 23°00'S to 23°59'S, between 100 and 199-m depth). The stations from SNEC I and II are grouped according to the zones given in Fig. 3.

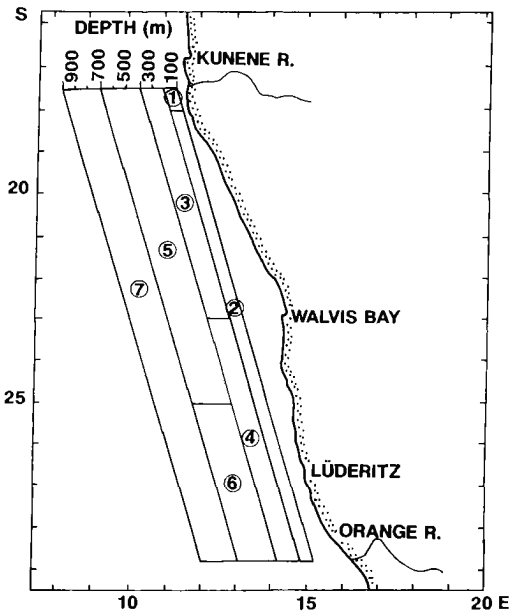


Fig. 6. Location of different benthic strata groups discriminated by cluster analysis: (1) northern shallow-shelf assemblage, (2) central and southern shallow-shelf assemblage, (3) northern deep-shelf assemblage, (4) southern deep-shelf assemblage, (5) northern slope assemblage, (6) southern slope assemblage, and (7) bathyal assemblage. (See Fig. 4 for similarities between strata.)

The clusters of benthic species (Fig. 7) revealed the combined shelf and slope species (association 1) to be clearly distinguishable from the bathyal species (association 2). The cophenetic correlation coefficient was low (0.70), as was the measure of enchainment (0.09). The association 1 (shelf and slope species) could in turn be subdivided into several distinctly separate associations. The first broad association (1A) grouped species more common on the shelf and slope off southern Namibia and a group of species more common along the slope-bathyal zone off Namibia (generally living between 400 and 800 m). The southern shelf species were present between 100 and 400 m and usually south of 26°S. The southern slope species included species living between 200 and 700 m and not usually north of 22°S, although several exceptions were observed (e.g., *Calocaris barnardi*, *Calastacus longispinis*, *Exodromidia spinosa*, *Bathynectes piperi-*

tus). The group of species from the slope-bathyal zone included species living either along the slope off Namibia (e.g., *Plesionopaeus edwardsianus*, *Parapagurus bouvieri*, *Heterocarpus grimaldii*), in the northern part (e.g., *Nephropsis atlantica*, *Glyphus marsupialis*, *Nematocarcinus africanus*) or in the southern part off Namibia (e.g., *Chaceon chuni*).

The second broad association (1B) comprised the shelf and slope species off northern Namibia, which were not usually present south of 26°S. The shelf species were observed between 100 and 400 m and most of them were not present south of 18°S. However, several exceptions were observed: *Nautilocorystes ocellatus* and *Callianassa australis* caught along the shelf off Namibia and *Goneplax rhomboides* and *Inachus grillator* present off both northern and southern Namibia but not off central Namibia. The northern slope species generally were living between 200 and 700 m and not usually south of 26°S.

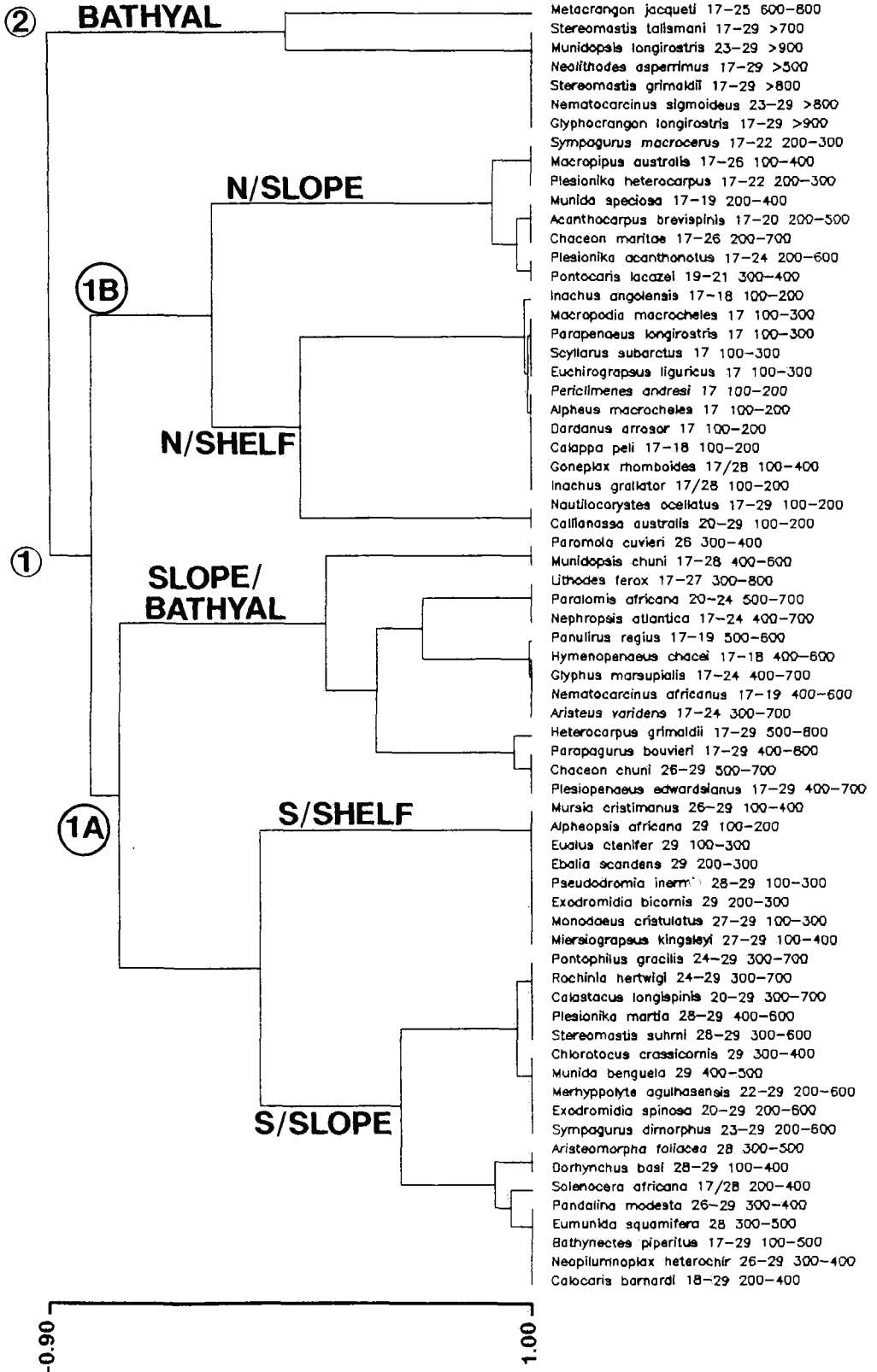
The bathyal species association (2) consisted of species dwelling exclusively at depths greater than 500 m, species which ranged along practically the entire coast (e.g., *Neolithodes asperrimus*, *Stereomastis talismani*, and *Glyphocrangon longirostris*).

DISCUSSION

The decapod crustacean fauna off Namibia presented a clear zonation effect, with a series of well-defined bathymetric and latitudinal boundaries. The boundaries were, nonetheless, different for the benthic species than for the pelagic species, and their existence seemed to be connected with a variety of factors, all related to depth, the intense coastal upwelling, and the circulation pattern of the region. However, the limitations caused by the sampling strategy, especially for the benthic species, recommend the consideration of the different boundaries as approximate and subject to certain seasonal and/or annual changes.

The zonation of the pelagic species presented two clearly differentiated communities, an "inshore association" from the coast to about 70 miles offshore, largely co-

Fig. 7. Classification from benthic species-cluster analysis. Ordinate shows similarity. Each species includes its latitude and depth range distribution. (See also Table 1 and text for explanations.)



inciding with the shelf, and an "offshore association" more than 70 miles off the coast. Both associations are present in the active (September–October) and quiescent (April) upwelling period. Therefore, the upwelling intensity does not greatly affect the zonation of the pelagic species assemblages, although during the active upwelling period the number of species clearly decreases. In a discussion of the maintenance mechanisms of coastal and oceanic euphausiid species, Barangé and Pillar (in press) postulated a cross-shelf circulation pattern off Namibia characterized by a two-celled circulation. The authors suggest that different circulation patterns over the shelf and slope, separated by a cross-shelf barrier over the shelf-break, exist in areas of broad shelf and steep slope. The results presented here, as well as those reported in relation to myctophids (Hulley and Lutjeharms, 1989), support the existence of different circulation patterns over the shelf and slope, and suggest that this pattern is maintained for most zooplankton species.

The inshore pelagic community was closely associated with the most active upwelling areas and consisted of three species: *Pasiphaea semispinosa*, *Processa namibien-sis*, and *Merhippolyte ancistrota*. The first species is the most common and abundant pelagic species in the area (unpublished data). The last two species seem to be associated with the seasonal intrusion of waters from Angola during the quiescent upwelling period (Boyd *et al.*, 1987). The small number of species in this association was consistent with the instability of the system, as would be expected in an area in which intense coastal upwelling activity is the rule (e.g., Margalef, 1974). The number of pelagic species was larger for the community of offshore species in the region. Neither the inshore nor the offshore communities presented a strong latitudinal boundary, with the exception of the species associated with the seasonal intrusion of Angolan waters. These findings do not agree with the discontinuity found in other planktonic groups, e.g., euphausiids (Barangé and Stuart, in press) and chaetognaths (Shannon and Pillar, 1986), suggesting that the environmental boundary described by Agenbag and Shannon (1988) does not affect drastically the population of pelagic decapods.

The communities of benthic species are mainly delimited by depth, although several latitudinal boundaries exist. The bathymetric boundaries are well defined: the main boundary was located at approximately 400 m, separating the shelf and the slope-bathyal species; the secondary boundaries separated the shallow-shelf and the deep-shelf species and the slope and the bathyal species. These results agree with the findings of other workers (Roel, 1987; Mas-Riera *et al.*, 1990) for the fish communities on the continental shelf off South Africa and Namibia. The presence of these depth boundaries substantiates the results reported by other researchers for various groups of organisms and geographic regions, and they appear to be associated with generalized oceanographic features differentiating the continental shelf, slope, and bathyal zone (e.g., Menzies *et al.*, 1973; Haedrich *et al.*, 1980; Wenner and Read, 1982; Carney *et al.*, 1983; Wenner and Wenner, 1988; Abelló *et al.*, 1988).

There are several latitudinal boundaries, the first at approximately 18°S between the 100 and 200-m isobaths, a second at approximately 23°S between 200 and 400-m isobaths, and a third at approximately 25°S between 400 and 700-m isobaths. The existence of the first boundary would appear to be related to the presence of areas in which anoxic conditions prevail on the bottom. As several workers (e.g., Chapman and Shannon, 1985) have pointed out, one of the characteristic features of the Benguela upwelling is the presence of areas of extremely low levels of dissolved oxygen, caused by the high rate of sedimentation of organic matter and poleward transport of anoxic water over the shelf and slope. The location of such areas exerts an effect on the distribution of many organisms, which tend to avoid these anoxic bottoms (e.g., Bailey *et al.*, 1985; Macpherson and Mas-Riera, 1987; Abelló and Macpherson, 1989, 1990; Mas-Riera *et al.*, 1990). The region of oxygen-deficient water runs from 19–27°S from the coast out to the 200–400-m isobaths (Chapman and Shannon, 1985). Another small area, where anoxic conditions can also arise, exists off the mouth of the Orange River (28°30'S), though it does not usually extend out beyond the 150-m isobath (Chapman and Shannon, 1985; Mas-Riera *et al.*, 1990).

The northern limit to the area of oxygen-deficient waters constitutes an effective barrier that is normally not crossed by species of tropical origin (e.g., *Calappa peli*, *Periclimenes andresi*, *Alpheus macrocheles*, *Inachus angolensis*). In contrast, the southern limit does not form such a clear-cut barrier. This would seem to be because, although various species from the shelf of the southern Benguela system do not extend further north than 26°S (e.g., *Miersiograpsus king-sleyi*, *Eualus ctenifer*, *Monodaeus cristulatus*, *Mursia cristimanus*), a certain number of species range northwards to 19°S and 20°S (*Exodromidia spinosa*, *Calocaris barnardi*, and *Callianassa australis*). These last species, together with *Macropipus australis* and *Nautilocorystes ocellatus*, are the only ones that consistently inhabit oxygen-deficient areas.

The other latitudinal boundaries, located around 23°S and 25°S between 200 and 700 m, would appear to be caused by different factors than those that gave rise to the preceding boundary. The oxygen-deficient water extends out to the 200–400-m isobaths and its maximum extent reaches down to approximately 23°S (Chapman and Shannon, 1985). The seasonal variations in the area affected by these anoxic conditions have been correlated with migrations carried out by demersal fish communities (Mas-Riera *et al.*, 1990). This suggests that, at least out to 400 m, the low oxygen levels on the bottom might play a role in determining the zonation of decapod crustacean communities. On the other hand, the fact that the boundary encompasses depths out to 700 m means that there are probably other mechanisms that make a lesser contribution to the formation of the boundary mentioned.

These boundaries between communities are situated just north of the area of maximum upwelling activity as well as with the pronounced divergence of currents that occurs from 27°S (Nelson and Hutchings, 1983; Shannon, 1985; Lutjeharms and Stockton, 1987; Nelson, 1989). Maximum upwelling activity is concentrated between 25°30'S and 27°30'S, where upwelled water may extend out to beyond 100 miles (161 km) offshore (bottom depths greater than 900 m). This level of upwelling activity is nearly perennial over most of the year. Changes in the

circulation pattern and in the turbulence/stratification of the water column in this area could, as suggested by Agenbag and Shannon (1988), influence the developmental success of the larval stages of a large number of species, thereby affecting their distribution. Although no information is available concerning the distribution of decapod crustacean larvae in the area, the results of surveys on fish larvae indicate a sharp drop in larval diversity in the area of greatest upwelling intensity, as well as alterations in the structure and composition of the larval fish communities there (Olivar, 1990).

The differing responses exhibited by the benthic and pelagic species raise interesting questions about the effect of hydrographic features on these species. Nevertheless, more data are needed to adequately explain these differences. In particular, more information on the vertical and horizontal distribution of both larvae and adults is required before such an explanation will become feasible.

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