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Distribution, abundance and assemblages of decapod crustaceans in waters off Guinea-Bissau (north-west Africa)

ISABEL MUÑOZ[1], EVA GARCÍA-ISARCH[1], IGNACIO SOBRINO[1], CANDELARIA BURGOS[1], RITA FUNNY[2] AND MARCOS GONZÁLEZ-PORTO[3]

[1]Instituto Español de Oceanografía, C.O. de Cádiz, Puerto Pesquero, Muelle de Levante s/n, 11006 Cádiz (Spain), [2]Centro de Investigação Pesqueira Aplicada (CIPA), Avenida Amilcar Cabral, C.P. 102, Bissau, Guinea-Bissau, [3]Laboratorio de Zooloxía Mariña, Departamento de Ecoloxía e Bioloxía Animal, Facultade de Ciencias do Mar, Universidade de Vigo, C.P. 36310 Vigo (Pontevedra-Spain)

This study constitutes a first contribution to the knowledge of the ecology of the decapod crustaceans in waters off Guinea-Bissau. Samples were collected during a survey undertaken between October and November 2008. A total of 122 species of decapod crustaceans were identified. Results showed an increase of decapod biomass and abundance with depth, reaching maxima values in the 200–500 m depth stratum but decreasing at depths over 500 m. Average diversity by strata increased with depth, with maximum over the deep slope. Seven main assemblages were identified: five primarily associated with depth—coastal shelf (<60 m), shelf (60–200 m), upper slope (200–300 m), middle slope (300–500 m), deep slope (500–1000 m)—and two other northern shelf assemblages affected by sediment type—coastal shelf-north (<50 m) and shelf-north (50–100 m). Species of each assemblage are typified. This study provides new information about composition, distribution, abundance and assemblage structure of decapod crustaceans in Guinea-Bissau that may be useful for future assessment of the effect of trawling pressure in the area.

Keywords: decapod crustaceans, species composition, diversity, abundance, bathymetric distribution, faunal assemblages, Guinea-Bissau, central eastern Atlantic, north-west Africa

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INTRODUCTION

Atlantic waters off Guinea-Bissau belong to the tropical West African region, situated between Cape Blanc in Mauritania (20°50′N) and Cape Frio in Northern Namibia (18°30′N) (Le Loeuff & Von Cosel, 1998), which is characterized by a specific marine fauna. The Guinea-Bissau marine ecosystem is strategically situated between two large marine ecosystems (LME): the southern limit of the Canary Current LME and the western limit of the Guinea LME, both being considered as highly productive (Heileman, 2009; Heileman & Tandstad, 2009). In the tropical West African region, the combination of a number of climatic and hydrological factors contributes to the existence of an exceptional environment, even more marked in Guinea-Bissau due to the great extension of its continental shelf, which has encouraged the presence of foreign industrial fleets for decades.

Extensive literature reviewing the effects of fishing on benthic habitats makes the case that essentially all trawling impacts the benthic environment (see reviews of Stevenson *et al.*, 2004; Løkkeborg, 2005). Continuous otter trawling has been shown to have a significant, negative effect on benthic fauna abundance, biomass and species richness. It has also led to changes in community composition of benthic fauna (Thrush *et al.*, 1998; Thrush & Dayton, 2002; Hinz *et al.*, 2009), which may have further implications for the integrity of marine food webs (Hinz *et al.*, 2009). Therefore, studies on macrobenthic communities have been traditionally carried out to evaluate the trawling effects on marine ecosystems, as changes in macrobenthic species composition are good indicators of fishing pressure.

Decapod crustaceans constitute one of the dominant groups of megabenthic invertebrates on the Atlantic continental shelf and slope (Haedrich *et al.*, 1975; Wenner & Boesch, 1979; Macpherson, 1991; Bianchi, 1992a,b; Fariña *et al.*, 1997). Furthermore, interest in their study is greater, considering the fact that they constitute a key taxon linking lower and higher trophic levels (Wenner & Boesch, 1979; Cartes, 1998). Although decapod crustacean assemblages have been intensively studied in Mediterranean waters (Abelló *et al.*, 1988, 2002; Cartes & Sardà, 1993; Maynou *et al.*, 1996; Maynou & Cartes, 2000; Company *et al.*, 2004; Politou *et al.*, 2005; Ungaro *et al.*, 2005; Fanelli *et al.*, 2007; García Muñoz *et al.*, 2008), in proportion fewer studies have been carried out in Atlantic waters, most of them being conducted in the North Atlantic (Haedrich *et al.*, 1975; Wenner & Boesch, 1979; Wenner *et al.*, 1982; Fariña *et al.*, 1997;

Corresponding author:
I. Muñoz
Email: isabel.munoz@cd.ieo.es

Wicksten & Packard, 2005; Cartes *et al.*, 2007). However, most published decapod crustacean studies carried out in West African Atlantic waters have traditionally focused on taxonomic aspects of the species (i.e. Crosnier & Forest, 1973; Kensley, 1980; Anadón, 1981; Macpherson, 1983, 1988). Further information on decapod crustaceans in West African waters can be obtained from more global studies of demersal assemblages developed in waters off Namibia (Lleonart & Roel, 1984), Angola (Bianchi, 1992b), Congo and Gabon (Bianchi, 1992a). Research on macrobenthic communities has been undertaken in shallow waters of the continental shelf of Guinea (Le Loeuff, 1993) and Côte d'Ivoire (Le Loeuff & Intès, 1999). More specific works on different aspects related to the biogeography or community structure of decapod crustaceans have been carried out in waters off Namibia (Macpherson, 1991) or South Africa (Kensley, 2006). However, the decapod crustacean communities on the Guinea-Bissau coast are greatly unknown, in spite of their important ecological role within the megabenthic assemblages.

This study constitutes a first contribution to the knowledge about the ecology of the decapod crustaceans in waters off Guinea-Bissau. Its first aim is the description of the decapod faunal composition on the trawlable bottoms of the continental shelf and slope off the Guinea-Bissau coast. Furthermore, it contributes to the knowledge of the ecology of decapod crustacean communities by describing their bathymetric and geographical distribution, by quantifying their abundance and diversity, and by defining the main decapod assemblages in the area.

MATERIALS AND METHODS

Study area

Guinea-Bissau is located at the southern limit of the Canary Current System and the western limit of the Gulf of Guinea System. The Guinea-Bissauan continental shelf is the largest in Western Africa, with a width of more than 75 miles in the north, 60 miles in the south, and an extension of about 10,800 m^2 (Ramos *et al.*, 1991). In the southern area, the shelf reduces its extension to an effective width of 30 miles due to the presence of the Bijagos Islands. The coasts are deeply cut out by the numerous rivers that open into the sea in this area (Domain, 1980). It contains one of the biggest estuarine areas and one of the most extensive mangrove zones in West African coastal waters (Binet *et al.*, 1995).

Three main zones can be distinguished depending on the sediment's nature and bathymetry. There is a shallow area (20–75 m depth), with soft bottoms (mud and sand) in the northern area (mainly related to the river mouth), and with hard bottoms from Bijagos to the Guinean border in the south, externally associated with coral reefs and crossed by numerous submarine canyons and valleys (McMaster *et al.*, 1971). At bottoms deeper than 200 m, deposits vary from soft (mud and sand) to hard (rubble, gravel and rocks). At depths between 400 and 600 m, sediments are all soft.

The Guinea-Bissau ecosystem is characterized by strong seasonal variations of oceanographic conditions (Berrit & Rebert, 1977), with higher productivity during the dry season (Longhurst, 1983) due to the upwelling events that mainly occur from January to February. Characteristically warm and salty tropical waters dominate from May to June. With the progression of the rainy season, the intrusion of warm, low salinity inner waters tend to dominate. As a result of upwelling events and the input of organic matter from river run-off, primary productivity is relatively high in the area (Berrit & Rebert, 1977). The coastal areas are also under the influence of strong currents and occasional strong winds.

Data collection

The decapod crustaceans examined in this study were collected in a research survey along the Guinea-Bissauan coasts (central-eastern Atlantic), in the context of a scientific collaboration framework between Spain and Guinea-Bissau. The survey 'GUINEA-BISSAU 0810' was carried out on-board the RV 'Vizconde de Eza' during 22 days in October–November 2008 (the transition period between the wet and dry season). The survey area covered 19,847 km^2, from 12°22′N to 10°00′N (Figure 1). A total of 98 valid hauls were carried out during daytime at depths ranging between 20 and 1000 m. A random stratified sampling design based on four bathymetric strata (<50 m, 50–200 m, 200–500 m and 500–1000 m) was used. Hauls of standard 30 minutes' duration were conducted using a 'Conakry' otter bottom trawl ('baka' type).

Decapods taken in each haul were sorted and keyed as specifically as possible to the lowest taxonomic level, then counted and weighed. In order to check and complete the species identification, specimens of all the species caught during the survey were preserved and transported to the laboratory, where they were exhaustively reviewed.

Data analysis

Species abundance (number of individuals/haul) was calculated and species biomass (tonnes) was estimated by the swept area method (Sparre & Venema, 1998). Occurrence (as the frequency of appearance of the species in the valid hauls) and bathymetric ranges were calculated for each species.

Diversity measures, such as species richness and the Shannon–Wiener diversity index were calculated by haul. Average values were estimated by depth strata and total area. Patterns of distribution were analysed for each depth stratum.

To identify species assemblages and its relationship to different factors, cluster analysis was applied to the decapod crustacean abundance-hauls matrix, after performing a fourth-root transformation. Those species appearing with both low frequency (<10% of the hauls) and low abundance (<30 individuals/haul) were removed, as well as those hauls of only one species. Similarity levels between hauls were calculated by means of the Bray–Curtis index (Clifford & Stephenson, 1975). The environmental variables included were depth and bottom type. Regarding the bottom type, the area under study was divided according to the nature of sediment, at the latitude 11°30′N, following the criterion of previous works (Amorim *et al.*, 2002). A two-way crossed analysis of similarities (ANOSIM) was performed to test for statistically significant differences in macrofaunal assemblage structure between samples.

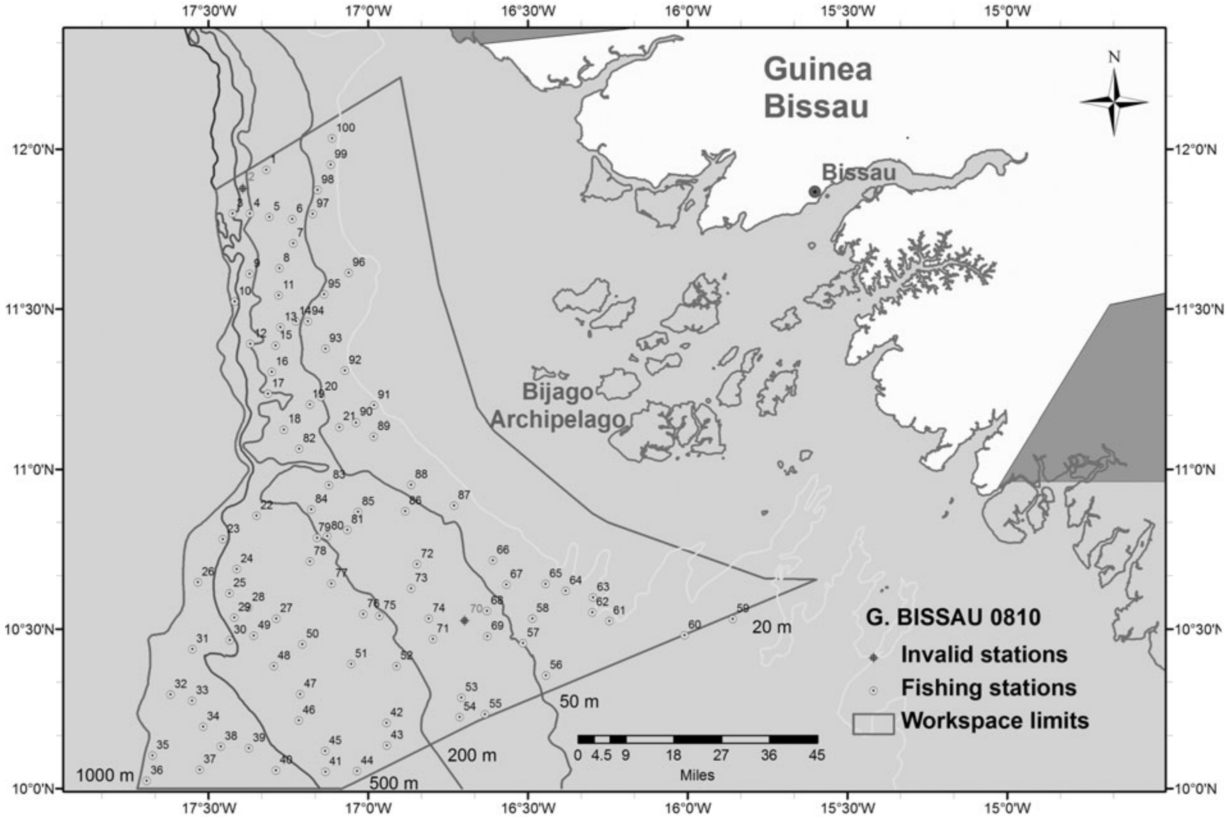

Fig. 1. Map of the study area and positions of trawl stations in the survey 'GUINEA BISSAU 0810'.

Non-metric multidimensional scaling (MDS) was conducted on the same matrix of decapod crustacean abundance-hauls to place the samples (hauls) in a two-dimensional ordination space. The similarity percentages (SIMPER) procedure was used to characterize the species assemblage by calculating the contribution of each species to the similarity (typical species) and dissimilarity (discriminating species) between groups of samples belonging to the same depth stratum (Clarke & Warwick, 2001). The above mentioned analyses were computed with the software package PRIMER (Plymouth Routines In Multivariate Ecological Research) version 6 (Clarke & Warwick, 2001).

RESULTS

Species composition and diversity

A total of 122 decapod species, belonging to 39 families were identified. Table 1 shows the taxonomic list of the species. Regarding their relative location in the water column, species were classified as pelagic, nectobenthic (those swimming or hovering above the sea bottom) and benthic (those that live on or in the sea bottom). Table 3 summarizes the bathymetric range of occurrence of each species. It is worth noting that certain observations made in the current work increase the bathymetric range of some species in Atlantic waters in relation to those cited in the literature for Atlantic waters (García-Isarch, personal communication).

Average values of species richness and diversity (Shannon–Wiener diversity index, H′) by stratum (Table 2) generally increased with depth, the deepest stratum (500–1000 m depth) being the one with the highest number of decapod species (59) and the greatest diversity ($H' = 2.1$). The lowest diversity value ($H' = 0.87$) was found in the 50–200 m depth stratum, possibly due to the presence of one single species in some trawls (always the left-handed hermit crab *Dardanus arrosor*).

The most important families in terms of species richness (Figure 2) were Pandalidae, (with 14 different species), followed by Oplophoridae (with 9 species), Portunidae (8 species), Pasiphaeiade (7 species), Inachidae (6 species) and Scyllaridae (5 species). The rest were families represented in the area by fewer than 5 species. Species families with a high commercial value such as Aristeidae, Penaeidae and Geryonidae were amongst the lowest in specific richness.

Abundance, biomass and frequency of occurrence

Total crustacean biomass estimated in the survey area was near 2609 t, while the abundance was around 100,700 individuals. Table 2 shows the total biomass and total abundance of the decapod species by depth stratum and total area. The shallowest stratum (<50 m) showed the lowest biomass and abundance in the study area. Both biomass and abundance increased with depth, reaching the greatest values at the 200–500 m depth stratum and then decreasing between 500 and 1000 m.

In Table 3 are presented for the decapod species overall depth-range, biomass and abundance within each depth stratum, as well as percentages of occurrence in the total

Table 1. Decapod crustacean species collected by trawling off Guinea-Bissau (north-west Africa). B, benthic species; P, pelagic species; N, nectobenthic species; n.a., not available.

	Species	Habitat
Suborder Dendrobranchiata		
Superfamily Penaeoidea		
Family ARISTEIDAE	*Aristaeopsis edwardsiana* (J. Y. Johnson, 1868)	B
	Aristeus antennatus (Risso, 1816)	N
	Aristeus varidens (Holthius, 1952)	B
Family BENTHESICYMIDAE	*Benthesicymus bartletti* (S.I. Smith, 1882)	B
Family PENAEIDAE	*Farfantepenaeus notialis* (Perez Farfante, 1967)	B
	Parapenaeopsis atlantica (Balss, 1914)	B
	Parapenaeus longirostris (Lucas, 1846)	N
	Penaeopsis sp.	–
Superfamily Sergestoidea		
Family SERGESTIDAE	*Sergia talismani* (Barnard, 1947)	P
	Sergia grandis (Sund, 1920)	P
	Sergia sp.	P
	Sergia robusta (Smith, 1882)	P
Superfamily Penaeoidea		
Family SICYONIDAE	*Sicyonia laevigata* (Stimpson, 1871)	B
	Sicyonia sp.	B
Family SOLENOCERIDAE	*Hymenopenaeus chacei* (Crosnier & Forest, 1969)	B
	Hymenopenaeus laevis (Bate, 1881)	B
	Solenocera africana (Stebbing, 1917)	N
Suborder Pleocyemata		
Infraorder Caridea		
Superfamily Alpheoidea		
Family ALPHEIDAE	*Alpheus* sp. 1	B
	Alpheus sp. 2	B
Superfamily Crangonoidea		
Family CRANGONIDAE	Crangonidae indet.	–
	Metacrangon bellmarleyi (Stebbing, 1914)	B
	Aegaeon lacazei (Gourret, 1887)	B
	Pontophilus sp.	–
Superfamily Nematocarcinoidea		
Family NEMATOCARCINIDAE	*Nematocarcinus africanus* (Gosnier & Forest, 1973)	B
	Nematocarcinus sp.	–
Superfamily Oplophoroidea		
Family OPLOPHORIDAE	*Acantephyra acanthitelsonis* (Bate, 1888)	P
	Acantephyra kingsleyi (Bate, 1888)	P
	Acantephyra pelagica (Risso, 1816)	B
	Acanthephyra acutifrons (Bate, 1888)	n.a.
	Acanthephyra eximia (Smith, 1884)	N
	Acanthephyra purpurea (A. Milne-Edwards, 1881)	n.a.
	Ephyrina ombango (Crosnier & Forest, 1973)	P
	Notostomus crosnieri (Macpherson, 1984)	P
	Systellaspis debilis (A. Milne-Edwards, 1881)	P
Superfamily Pandaloidea		
Family PANDALIDAE	*Heterocarpus ensifer* (A. Milne-Edwards, 1881)	B
	Heterocarpus grimaldii (A. Milne-Edwards, 1900)	B
	Heterocarpus laevigatus (Bate, 1888)	n.a.
	Plesionika narval (Fabricius, 1787)	B
	Plesionika acanthonotus (Smith, 1882)	N
	Plesionika carinata (Holthius, 1951)	P
	Plesionika edwarsii (Brandt, 1851)	N
	Plesionika ensis (A. Milne-Edwards, 1881)	n.a.
	Plesionika giglioli (Senna, 1903)	N
	Plesionika heterocarpus (Costa, 1871)	N
	Plesionika holthuisi (Crosnier & Forest, 1971)	n.a.
	Plesionika martia (A. Milne-Edwards, 1883)	N
	Plesionika sp.	–
	Plesionika williamsi (Forest, 1963)	n.a.
Superfamily Pasiphaeoidea		
Family PASIPHAEIDAE	*Glyphus marsupialis* (Filhol, 1884)	B
	Pasiphaea multidentata (Esmark, 1866)	P
	Pasiphaea semispinosa (Holthius, 1951)	P

Continued

Table 1. Continued

	Species	**Habitat**
	Pasiphaea sivado (Risso, 1816)	P
	Pasiphaea sp.	–
	Pasiphaea tarda (Kroyer, 1845)	P
	Psathyrocaris infirma (Alcock & Anderson, 1894)	P
Infraorder Brachyura		
Superfamily Aethroidea		
Family AETHRIDAE	*Sakaila* sp.	B
	Sakaila africana (Manning & Holthuis, 1981)	B
Superfamily Cancroidea		
Family ATELECYCLIDAE	*Atelecyclus rotundatus* (Olivi, 1792)	B
Superfamily Calappoidea		
Family CALAPPIDAE	*Acanthocarpus brevispinis* (Monod, 1946)	B
	Calappa pelli (Herklots, 1851)	B
	Calappa rubroguttata (Herklots, 1851)	B
	Calappa sp.	–
Superfamily Dorippidea		
Family DORIPPIDAE	*Medorippe lanata* (Linnaeus, 1767)	B
	Ethusa sp.	–
Superfamily Dromioidea		
Family DROMIIDAE	*Sternodromia spinirostris* (Miers, 1881)	B
Superfamily Goneplacoidea		
Family GONEPLACIDAE	*Goneplax barnardi* (Capart, 1951)	B
Superfamily Homolodromioidea		
Family HOMOLIDAE	*Homola barbata* (Fabricius, 1793)	B
	Homolidae indet.	–
	Paromola cuvieri (Risso, 1816)	B
Superfamily Majoidea		
Family EPIALTIDAE	*Rochinia carpentieri* (Wyville Thomson, 1873)	B
	Pisa armata (Latreille, 1803)	B
	Pisa calva (Forest & Guinot, 1966)	B
	Pisa sp.	–
Family INACHIDAE	*Inachus* sp.	–
	Stenorhynchus lanceolatus (Brulle, 1837)	B
	Macropodia doracis (Manning & Holthuis, 1981)	B
	Macropodia rostrata (Linnaeus, 1761)	B
	Macropodia spinulosa (Miers, 1881)	B
	Macropodia sp.	–
Family MAJIDAE	Majidae indet.	–
Superfamily Leucosioidea		
Family LEUCOSIIDAE	*Atlantophila cristata* (Miers, 1881)	B
	Ilia spinosa (Miers, 1881)	n.a.
	Ilia sp.	–
	Merocryptus obsoletus (A. Milne-Edwards & Bouvier, 1898)	n.a.
Superfamily Parthenopoidea		
Family PARTHENOPIDAE		
	Spinolambrus notialis (Manning & Holthuis, 1981)	B
	Parthenope massena var. *rugosa* (Roux, 1830)	B
Superfamily Portunoidea		
Family GERYONIDAE	*Chaceon maritae* (Manning & Holthuis, 1981)	B
Family PORTUNIDAE	*Bathynectes maravigna* (Prestandrea, 1839)	B
	Callinectes marginatus (A. Milne-Edwards, 1861)	B
	Cronius ruber (Lamarck, 1818)	B
	Liocarcinus corrugatus (Pennant, 1777)	B
	Liocarcinus marmoreus (Leach, 1814)	B
	Macropipus rugosus (Doflein, 1904)	B
	Portunidae indet.	–
	Sanquerus validus (Herklots, 1851)	B
Superfamily Raninoidea		
Family RANINIDAE	*Ranilia constricta* (A. Milne-Edwards, 1880)	n.a.
Superfamily Xanthoidea	Xanthoidea indet.	–
Family PILUMNIDAE	*Pilumnus stebbingi* (Capart, 1951)	n.a.
Family XANTHIDAE	*Paraxanthias eriphioides* (A. Milne Edwards, 1867)	B

Continued

Table 1. Continued

	Species	Habitat
Infraorder Anomura		
Superfamily Galatheoidea		
Family CHIROSTYLIDAE	*Chirostylus* sp.	–
	Uroptychus concolor (A. Milne Edwards & Bouvier, 1894)	B
Family GALATHEIDAE	*Munida speciosa* (von Martens, 1878)	B
	Munida guineae (Miyake & Baba, 1970)	B
Family PORCELLANIDAE	*Pisidia* sp.	–
Superfamily Lithodoidea		
Family LITHODIDAE	*Lithodes ferox* (Filhol 1885)	B
	Paralomis cristulata (Macpherson, 1988)	B
	Paralomis erinacea (Macpherson, 1988)	B
Superfamily Paguroidea		
Family DIOGENIDAE	*Dardanus arrosor* (Herbst, 1796)	B
	Diogenes sp.	–
	Petrochirus pustulatus (H. Milne Edwards, 1848)	B
	Spiropagurus elegans (Miers, 1881)	B
Family PAGURIDAE	Paguridae indet.	–
Family PARAPAGURIDAE	*Parapagurus pilosimanus* (Smith, 1879)	B
	Parapaguridae indet.	–
Infraorder Astacidea		
Superfamily Nephropoidea		
Family NEPHROPIDAE	*Nephropsis atlantica* (Norman, 1882)	B
Infraorder Achelata		
Family SCYLLARIDAE	*Acantharctus posteli* (Forest, 1963)	B
	Scyllarus arctus (Linnaeus, 1758)	B
	Scyllarus caparti (Holthuis, 1952)	B
	Scyllarus sp.	–
	Scyllarus subarctus (Crosnier, 1970)	B
Infraorder Polychelida		
Superfamily Polycheloidea		
Family POLYCHELIDAE	*Stereomastis sculpta* (Smith, 1880)	B
	Polycheles typhlops (Heller, 1862)	B

area. The left-handed hermit crab *D. arrosor* was the most common species in the survey area, present in 48% of the hauls and appearing in a depth-range from 24 to 306 m. The second most frequent species was the squat lobster *Munida speciosa* (occurrence 30.6%), followed by the striped red shrimp *A. varidens* (occurrence 27.6%), the deep-water rose shrimp *Parapenaeus longirostris* (occurrence 24.5%), *Bathynectes maravigna*, one undeterminated species of Diogenes (*Diogenes* sp.), and the sponge crab *Sternodromia spinirostris* (all with occurrence 21.4%). Many species (30% of the total), most of them Brachyura, only appeared in one station.

The species with the highest biomass were the squat lobster *M. speciosa* (478 t), the left-handed hermit crab *D. arrosor* (304 t), the African spider shrimp *Nematocarcinus africanus* (282 t), the crab *B. maravigna* (190 t), the sponge crab *S. spinirostris* (166 t) and *A. brevispinis* (151 t). Other abundant species were: the deep-sea fierce king crab *Lithodes ferox*, the hermit crab *Diogenes* sp. and the deep-water rose shrimp *P. longirostris*, the three species with biomasses between 100 and 120 t.

Table 2. Mean values of total biomass (in tonnes, t), total abundance (in number of individuals, n), species richness and diversity (Shannon–Wiener index, H′) for decapod crustaceans by depth stratum and total area. Strata diversities are average values, while diversity in the whole area (Total) corresponds to a total value.

Stratum	Depth range (m)	Biomass (t)	Abundance (n)	Species richness	Diversity (H′)
A	<50	383	4399	47	1.23
B	50–200	435	13,618	43	0.87
C	200–500	1353	58,569	41	1.44
D	500–1000	437	24,172	59	2.10
Total	<50–100	2609	100,758	122	3.30

The African spider shrimp *N. africanus* was the most abundant species in number (more than 43,000 individuals) followed by the squat lobster *M. speciosa* (near 16,500 individuals) and the pandalid shrimp *P. carinata* (6300 approximately). Other abundant species were: the left-handed hermit crab *D. arrosor* (5705 individuals); the deep-water rose shrimp *P. longirostris* and the golden shrimp *Plesionika martia* (with 4000–5000 individuals); the sponge crab *S. spinirostris* and *Plesionika ensis* (2000–3000 individuals); *S. sculpta*, *Diogenes* sp., *B. maravigna* and the pandalids *Plesionika heterocarpus* and *Plesionika williamsi* (between 1000 and 1700 individuals).

Bathymetric patterns

Figure 3 shows biomass (left) and abundance (right) percentages of the dominant decapod species (accounting for 90% of the total) per bathymetric stratum. The other 10% of the species were grouped in ‘others’. Those species with occurrence percentages higher than 50% by depth strata are

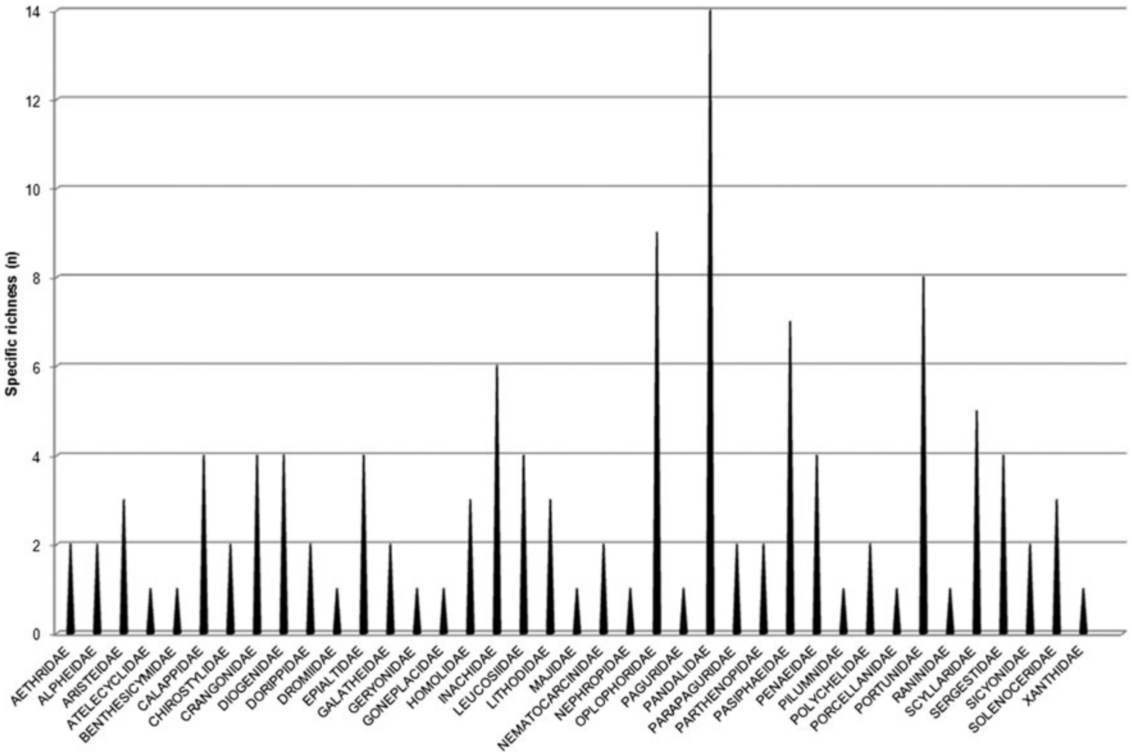

Fig. 2. Specific richness per family in the whole sampled area.

Table 3. Depth-range (m); B, total biomass (t); N, abundance (number of individuals) and occurrence (%) for the different species collected by depth stratum in the survey area (•, ten species of higher biomass; *, ten species of higher abundance).

	Depth strata (m)											
	Depth-range (m)	**<50**		**50–200**		**200–500**		**500–1000**		**Total**		
No. of valid hauls		**27**		**29**		**25**		**17**		**98**		
Scientific name		**B**	**N**	**B**	**N**	**B**	**N**	**B**	**N**	**B**	**N**	**% Occu.**
A. acanthitelsonis	706–809							0.2	15	0.2	15	4.1
A. kingsleyi	735							<0.1	1	<0.1	1	1.0
A. pelagica	735–772							0.1	9	0.1	9	2.1
A. posteli	24–45	0.1	1							0.1	1	2.1
A. acutifrons	149			0.7	12					0.7	12	1.0
A. eximia	869–905							3.8	34	3.8	34	3.1
A. purpurea	518–679							0.1	14	0.1	14	2.1
•*A. brevispinis*	213–517					146.8	623	4.1	17	150.9	640	20.4
A. lacazei	37–488	<0.1	3	<0.1	6	<0.1	11			0.1	20	9.2
Alpheus sp. 1	21	<0.1	1							<0.1	1	1.0
Alpheus sp. 2	21–24	<0.1	2							<0.1	2	2.1
A. edwardsiana	443–905					5.1	36	6.5	62	11.6	98	14.3
A. antennatus	506–905							0.6	8	0.6	8	5.1
A. varidens	246–905					5.8	132	46.4	748	52.2	880	27.6
A. rotundatus	246					0.9	4			0.9	4	1.0
A. cristata	36	<0.1	2							<0.1	2	1.0
•*B. maravigna*	223–629					158.8	856	31.0	233	189.8	1089	21.4
B. bartletti	504–905							1.3	69	1.3	69	4.1
C. pelli	21–104	9.8	21	0.4	12					10.1	33	16.3
C. rubroguttata	21–42	70.2	77							70.2	77	13.3
Calappa sp.	47–84	<0.1	1	4.7	157					4.8	158	4.1
C. marginatus	22–25	0.9	2							0.9	2	2.1
C. maritae	434–809					3.7	3	12.9	9	16.6	12	8.2
Chirostylus sp.	895							<0.1	1	<0.1	1	1.0
Crangonidae indet.	735							<0.1	3	<0.1	3	1.0

Continued

Table 3. Continued

	Depth strata (m)											
	Depth-range (m)	**<50**		**50–200**		**200–500**		**500–1000**		**Total**		
No. of valid hauls		**27**		**29**		**25**		**17**		**98**		
Scientific name		**B**	**N**	**B**	**N**	**B**	**N**	**B**	**N**	**B**	**N**	**% Occu.**
C. ruber	36	1.6	5							1.6	5	1.0
* •*D. arrosor*	24–306	5.6	181	172.0	4427	126.8	1097			304.4	5705	48.0
* •*Diogenes* sp.	21–164	113.0	1440	2.5	208					115.5	1648	21.4
E. ombango	869							<0.1	1	<0.1	1	1.0
Ethusa sp.	278					0.1	5			0.1	5	1.0
F. notialis	22–44	21.2	286							21.2	286	5.1
G. marsupialis	679–905							5.3	99	5.3	99	6.1
G. barnardi	257–551	0.2	24			1.0	46	<0.1	1	1.3	71	14.3
H. ensifer	486–603					0.1	4	2.1	134	2.2	138	6.1
H. grimaldii	629–705							0.5	3	0.5	3	2.1
H. laevigatus	629–905							1.1	29	1.1	29	6.1
H. barbata	37–223	0.1	6	1.5	33	0.2	18			1.9	57	9.2
•Homolidae indet.	24–98	<0.1	1	1.0	36					1.0	37	8.2
H. chacei	148–605			86.9	845			0.1	21	87.0	866	7.1
H. laevis	809							<0.1	8	<0.1	8	1.0
Ilia spinosa	46	<0.1	1							<0.1	1	1.0
Ilia sp.	104			<0.1	2					<0.1	2	1.0
Inachus sp.	56–163			1.7	231					1.7	231	10.2
L. corrugatus	22	<0.1	1							<0.1	1	1.0
L. marmoreus	56–103			4.0	105					4.0	105	5.1
•*L. ferox*	517–868							119.1	110	119.1	110	10.2
M. rugosus	57–217			1.7	44	0.3	26			2.0	70	3.1
M. doracis	102			0.3	40					0.3	40	1.0
M. rostrata	76–99			0.2	31					0.2	31	2.1
M. spinulosa	24	<0.1	4							<0.1	4	1.0
Macropodia sp.	24–163	0.1	21	0.7	18					0.9	83	11.2
Majidae indet.	551							0.2	1	0.2	1	1.0
M. lanata	25–52	0.1	2	<0.1	1					0.1	3	3.1
M. obsoletus	68			<0.1	1					<0.1	1	1.0
M. bellmarleyi	460–809			0.1	16			1.3	7	1.4	23	5.1
* •*M. speciosa*	75–809			25.8	3030	450.6	13,285	1.4	97	477.8	16,412	30.6
M. guineae	603–869							0.8	84	0.8	84	5.1
* •*N. africanus*	379–809					203.0	30,012	79.2	13223	282.2	43,235	20.4
Nematocarcinus sp.	551							0.1	6	0.1	6	1.0
N. atlantica	629–905							5.6	184	5.6	184	11.2
N. crosnieri	752–772							<0.1	2	<0.1	2	2.1
P. pustulatus	21–103	56.7	44	1.8	34					58.4	78	16.3
P. cristulata	679							0.4	1	0.4	1	1.0
P. erinacea	809							2.8	4	2.8	4	1.0
Parapaguridae indet.	170			<0.1	1					<0.1	1	1.0
P. pilosimanus	633–905							1.1	101	1.1	101	9.2
P. atlantica	22–25	1.5	181							1.5	181	2.0
* •*P. longirostris*	56–436			46.1	2583	59.9	2013			106.0	4596	24.5
P. eriphioides	67			0.3	27					0.3	27	1.0
P. cuvieri	29–305	0.1	6			2.5	4			2.7	10	4.1
P. massena var. rugosa	24	0.1	7							0.1	7	1.0
P. multidentata	629							<0.1	1	<0.1	1	1.0
P. semispinosa	434					0.1	45			0.1	45	1.0
P. sivado	380–486					0.4	126			0.4	126	4.1
Pasiphaea sp.	246–504					0.1	15	<0.1	3	0.1	18	3.1
P. tarda	869–905							0.2	3	0.2	3	2.1
Penaeopsis sp.	551–752							<0.1	3	<0.1	3	3.1
Pilumnus stebbingi	40–52	<0.1	1	<0.1	2					<0.1	3	2.1
Pisa armata	68–104			0.7	37					0.7	37	3.1
Pisa calva	38	0.2	1							0.2	1	1.0
Pisa sp.	22–163	1.8	99	0.2	7					2.0	106	12.2
Pisidia sp.	38	<0.1	2							<0.1	2	1.0
P. acanthonotus	246–679					3.6	631	<0.1	4	3.6	635	8.2

Continued

Table 3. Continued

	Depth strata (m)											
	Depth-range (m)	**<50**		**50–200**		**200–500**		**500–1000**		**Total**		
No. of valid hauls		**27**		**29**		**25**		**17**		**98**		
Scientific name		**B**	**N**	**B**	**N**	**B**	**N**	**B**	**N**	**B**	**N**	**% Occu.**
*_P. carinata_	246–629					1.2	164	33.7	6194	34.9	6358	7.1
P. edwarsii	103			<0.1	2					<0.1	2	1.0
*_P. ensis_	217–504					37.1	2583	<0.1	3	37.1	2586	11.2
P. giglioli	380					0.1	11			0.1	11	1.0
P. heterocarpus	21–246	<0.1	1	<0.1	11	7.8	1105			7.9	1017	9.2
P. holthuisi	698–752							0.1	12	0.1	12	3.1
*_P. martia_	246–894					55.8	4013	0.2	28	56.0	4041	16.3
P. narval	57			<0.1	2					<0.1	2	1.0
Plesionika sp.	246–505					0.1	22	0.1	25	0.2	47	4.1
P. williamsi	379–505					49.8	842	3.0	165	52.8	1007	10.2
P. typhlops	223–751					24.7	362	3.0	114	27.7	476	17.3
Pontophilus sp.	450					<0.1	2			<0.1	2	1.0
Portunidae indet.	25–42	<0.1	7							<0.1	7	3.1
P. infirma	379–894					0.2	51	1.1	216	1.3	267	6.1
Ranilia constricta	57			<0.1	1					<0.1	1	1.0
R. carpentieri	603							0.1	1	0.1	1	1.0
Sakaila africana	103			<0.1	2					<0.1	2	1.0
Sakaila sp.	71			<0.1	2					<0.1	2	1.0
S. validus	22–217	<0.1	3	<0.1	1	1.7	16			1.7	20	6.1
S. arctus	505							0.3	8	0.3	8	1.0
S. caparti	38–52	<0.1	3	<0.1	2					<0.1	5	3.1
Scyllarus sp.	22–46	0.6	36							0.6	35	10.2
S. subarctus	41	<0.1	5							<0.1	5	1.0
S. grandis	449–905					<0.1	1	<0.1	2	<0.1	3	3.1
Sergia sp.	380–721					<0.1	2	<0.1	1	<0.1	3	2.0
S. robusta	246–603					0.5	178	0.2	59	0.7	237	10.2
S. talismani	246–504					0.1	33	<0.1	2	0.1	35	9.2
S. laevigata	42	<0.1	2							<0.1	2	1.0
Sicyonia sp.	36	<0.1	1							<0.1	1	1.0
S. africana	56–720			<0.1	2	2.0	112	0.1	10	2.1	124	11.2
S. notialis	24–98	0.4	19	0.7	47					1.1	66	11.2
S. elegans	46	0.1	8							0.1	8	1.0
S. lanceolatus	20–71	0.3	20	0.2	66					0.5	86	11.2
*_S. sculpta_	385–905					2.1	98	66.5	1871	68.7	1971	19.4
S. debilis	426–905					0.3	57	0.2	73	0.5	130	13.3
*•_S. spinirostris_	20–67	87.2	1566	78.3	1344					165.5	2910	21.4
U. concolor	679–905							0.1	18	0.1	18	3.1
Xanthoidea indet.	42–720	<0.1	9	0.3	62			<0.1	2	0.3	73	5.1

shown in Table 4. Dominant species clearly differed among depth strata, as well as their biomasses and abundances.

Only 5 species accounted for 90% of the biomass in the shallowest stratum of the coastal shelf (<50 m) (Figure 3). These included *Diogenes* sp. (29%), the sponge crab *S. spinirostris* (23%) (also the most frequent species in this stratum), the box crab *Calappa rubroguttata* (18%) and the big diogenid crab *Petrochirus pustulatus* (15%). The fifth most abundant decapod species (in terms of biomass) on the coastal shelf (21 t) was the southern pink shrimp *Farfantepenaeus notialis*, caught in 5% of the fishing stations, all of them between 22 and 44 m depth (Table 3). The most abundant species in this stratum was *S. spinirostris* (38% in number of individuals) closely followed by *Diogenes* sp. (34%), the southern pink shrimp *F. notialis* (7%), the left-handed hermit crab *D. arrosor* (4%), *Parapenaeopsis atlantica* (4%), Paguridae indet. (3%) and *Pisa* sp. (2%).

Dardanus arrosor, *Hymenopenaeus chacei* and *S. spinirostris* were the most representative species of the 50–200 m stratum, accounting for 75% of the total biomass (Figure 3 left). Only *D. arrosor* accounted for 39% in biomass and 33% in number (Figure 3 right), being the most frequent species in the stratum (76% of occurrence) (Table 4). The following species in biomass were *H. chacei* (20%), *S. spinirostris* (18%), *P. longirostris*, (10%) and *M. speciosa* (6%). This last species was the second in abundance (22%), followed by the deep-water rose shrimp *P. longirostris*, the sponge crab *S. spinirostris* and *H. chacei* with 19%, 10%, and 6%, respectively.

The greatest biomass by stratum (1353 t) was estimated for the upper slope (200–500 m), which was also the stratum with the most abundant species in the whole prospected area (*M. speciosa*, *N. africanus*, *B. maravigna* and *A. brevispinis*). The squat lobster *M. speciosa* was the dominant species in this stratum both in terms of biomass (33%) and occurrence

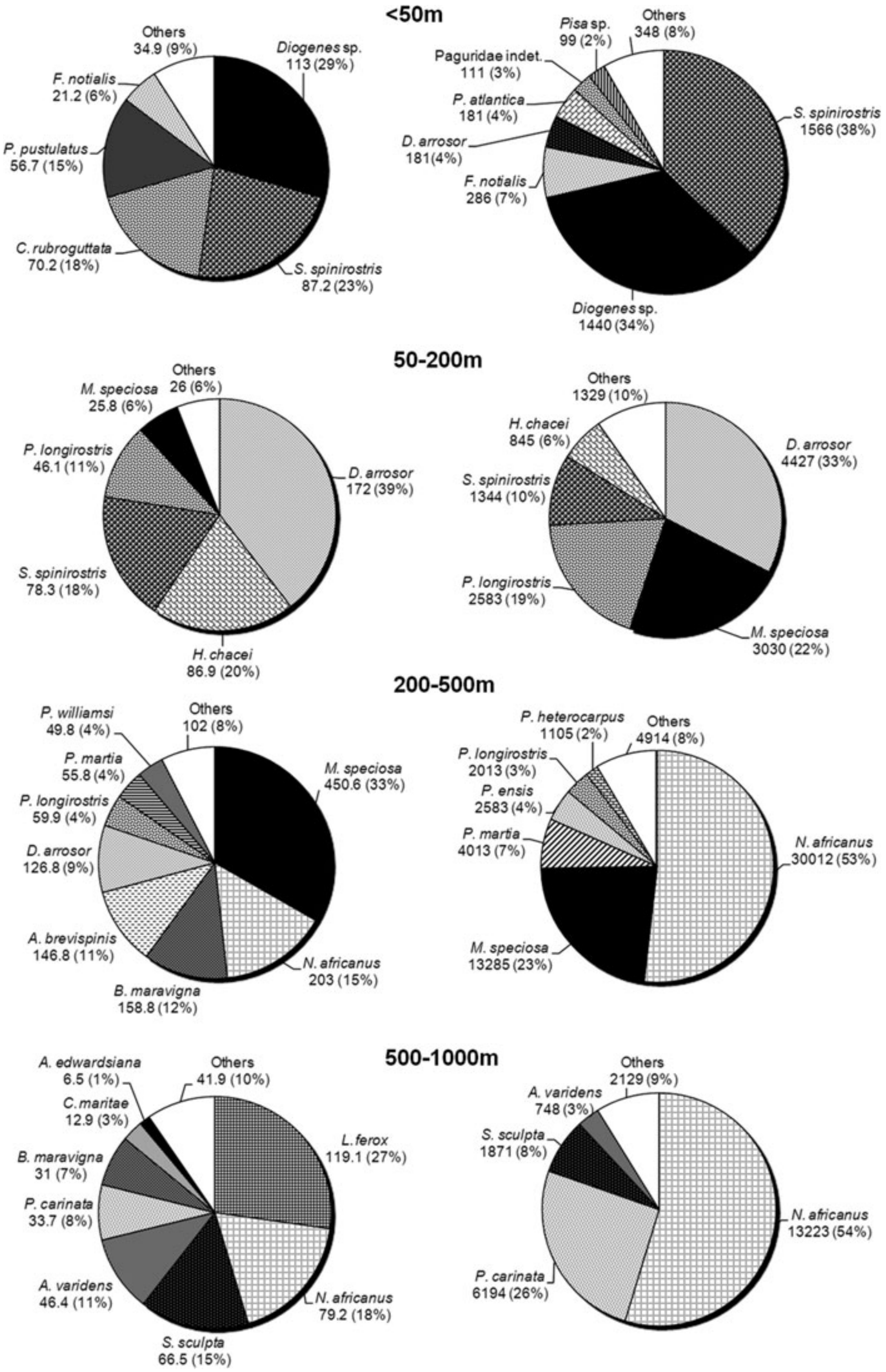

Fig. 3. Relative biomass (left) and abundance (right) of crustacean decapod species per depth stratum in the sampled area.

(84%). The following species in biomass were *N. africanus* (15%), *B. maravigna* (12%), *A. brevispinis* (11%), *D. arrosor* (9%), *P. longirostris* and *P. martia* (both with 4%). In spite of their relative low biomass in this stratum, *P. longirostris*, *A. brevispinis*, *B. maravigna* and *P. martia* appeared with a frequency of occurrence higher than 50% (Table 4). The African spider shrimp *N. africanus* was the most abundant species in number of individuals, accounting for more than 50% of the stratum abundance (Figure 3 right). Other abundant species were the squat lobster *M. speciosa* (23%), the golden shrimp *P. martia* (7%), *P. ensis* (4%), the deep-water rose shrimp *P. longirostris* (3%) and the arrow shrimp *P. heterocarpus* (2%).

Although the biomass decreased at the deepest stratum (500–1000 m), the diversity was maximal at these depths (Table 2). Typical deep water species with high biomass were *L. ferox* (27.2%), *N. africanus* (18%), *S. sculpta* (15%) and *A. varidens* (11%). These four species, which were also very frequent in this stratum, accounted for 75% of the biomass at these depths. The striped red shrimp *A. varidens* (11%) was present in 100% of the stations between 500 and 1000 m depth (Table 4). Other representative species in terms of biomass were *P. carinata* (8%), *B. maravigna* (7%), *Chaceon maritae* (3%) and *Aristaeopsis edwardsiana* (1.5%). The African spider shrimp *N. africanus* was also the most

Table 4. List of the decapod crustacean species with frequency of occurrence (%) higher than 50%, by depth stratum.

Depth strata			
<50 m	**50–200 m**	**200–500 m**	**500–1000 m**
S. spinirostris (52.9%) *D. arrosor* (55.6%) *Diogenes* sp. (51.9%) *P. pustulatus* (51.9%)	*D. arrosor* (76%)	*M. speciosa* (84%) *P. longirostris* (72%) *A. brevispinis* (68%) *B. maravigna* (60%) *P. martia* (52%)	*A. varidens* (100%) *S. sculpta* (88%) *A. edwardsiana* (65%) *N. africanus* (65%) *N. atlantica* (65%) *L. ferox* (59%) *P. pilosimanus* (53%) *S. debilis* (53%)

abundant species in this stratum (54%), followed, in this case, by *P. carinata* (26%), *S. sculpta* (8%) and *A. varidens* (3%).

Clear differences are observed between the depth occurrence patterns among the main groups of decapods (Figure 4). The group of Dendrobranchiata (Figure 4A) was composed of few species with scarce occurrence. Some of them were only present on the continental shelf (as is the case for *F. notialis*, *P. atlantica* and *Sicyonia laevigata*). The deep-water rose shrimp *P. longirostris* has its average depth in the upper slope, although it appeared from 56 to 436 m, both in the continental shelf and the upper slope. *Hymenopenaeus chacei*, *Sergia robusta* and *Sergia talismani* occurred in both the upper and middle slope while *Penaeopsis* sp. and *Sergia* sp. exclusively appeared in the middle slope. Other species such as *A. edwardsiana*, *Aristeus antennatus*, *Benthesicymus bartletti* and *Sergia grandis* occurred in the middle and deep slope. *Hymenopenaeus laevis* only occurred at depths around 800 m, in the deep slope. *Solenocera africana* and the striped red shrimp *A. varidens* were the species of larger bathymetric occurrence within this group, appearing from 56 to 720 m and 249 to 905 m, respectively.

Caridean shrimps (Figure 4B) showed a broad depth of occurrence and clearly were species of the continental slope, both the upper and the middle slope. Only six species occurred exclusively on the continental shelf: *Plesionika edwardsii*, *Plesionika narval*, *Acantephyra acutifrons*, an undetermined Crangonidae and two undetermined species of the genus *Alpheus*. Some species such as *Pasiphaea semispinosa*, *Pasiphaea sivado*, *P. ensis*, *Plesionika giglioli*, *P. williamsi* and *Pontophilus* sp. were mainly distributed in the upper and middle slope (217–500 m), while several species of the genus *Acanthephyra* (*A. kingsleyi*, *A. pelagica* and *A. purpurea*), *Notostomus crosnieri*, *Plesionika holthuisi*; two species of the family Crangonidae; and one of the genus *Nematocarcinus*, exclusively appeared in the deep slope (approximately 500–800 m). The caridean species with deeper distribution were *Acanthephyra eximia*, *Ephyrina ombango*, *Pasiphaea tarda* and several species of the genus *Heterocarpus*. The rest of the species within this group had wider depth-ranges, especially species such as *Aagaeon lacazei*, reported from 37–448 m (shelf and upper slope), *P. martia*, *Psathyrocaris infirma* and *Systellaspis debilis* (upper, middle and deep slope).

Brachyura (Figure 4C) constitute a typical continental shelf group. There were some species that appeared on the shelf and upper slope (*Paromola cuvieri*, *Homola barbata*, *Macropipus rugosus*and *Sanquerus validus*); on the shelf, upper and middle slope (one undetermined xanthoid crab); upper slope (*Atelecyclus rotundatus* and *Ethusa* sp.); upper and middle slope (*A. brevispinis*, *G. barnardi* and *B. maravigna*) and typical deep-sea species such as *C. maritae*, *R. carpentieri* and undetermined *Majidae*, that inhabit the middle–lower slope. The remaining 31 taxa of Brachyura identified were exclusively found on the continental shelf.

Hermit crabs and squat lobsters (Anomura) and scampi (Astacidea) were represented by 15 and 6 species respectively, while only 2 species of deep-sea lobsters (Polychelidae) were found (Figure 4D). The two most abundant and most frequent species in the area (the squat lobster *M. speciosa* and the left-handed hermit crab *D. arrosor*) were anomuran crabs. The group Anomura included coastal species only occurring on the continental shelf, as one undetermined species of Paguridae and the other of Parapaguridae, three species of Diogenidae (*Spiropagurus elegans*, *P. pustulatus* and *Diogenes* sp.), and one species of the genus *Pisidia*; deep water families, such as Lithodidae (the fierce king crab *L. ferox*, *Paralomis cristulata* and *Paralomis erinacea*), *Parapagurus pilosimanus*, *Chirostylus* sp., *Munida guineae* and *Uroptychus concolor*; species with an intermediate distribution between the continental shelf and the upper slope (*D. arrosor*); and species with a wide depth-range such as *M. speciosa* which appeared from the continental shelf (75 m) to the deep slope (809 m). Astacidea were represented by both coastal water and deep water species. Four coastal water species, all belonging to the family Scyllaridae (*Acantharctus posteli*, *Scyllarus subarctus*, *Scyllarus caparti* and an undetermined species of *Scyllarus*) appeared on the continental shelf at depths up to 65 m. One species of Nephropidae (*Nephropsis atlantica*) was the only deep-water species of Astacidea. The infraorder Polychelida was represented by two deep-water species (*Steromastis sculpta* and *Polycheles typhops*).

Assemblage structure

A two-dimensional MDS plot was generated taking into account the pre-defined grouping to depth in order to observe the effect of this variable (Figure 5). The resulting plot demonstrates that the variation in terms of decapod crustacean species composition is strongly influenced by depth. The resulting MDS ordination stress value is 0.1.

The dendrogram of similarities among stations (Figure 6) shows that different faunal groups can be clearly defined along the bathymetric gradient. A first branching of a low similarity level (below 5%) discriminates two main groups: a

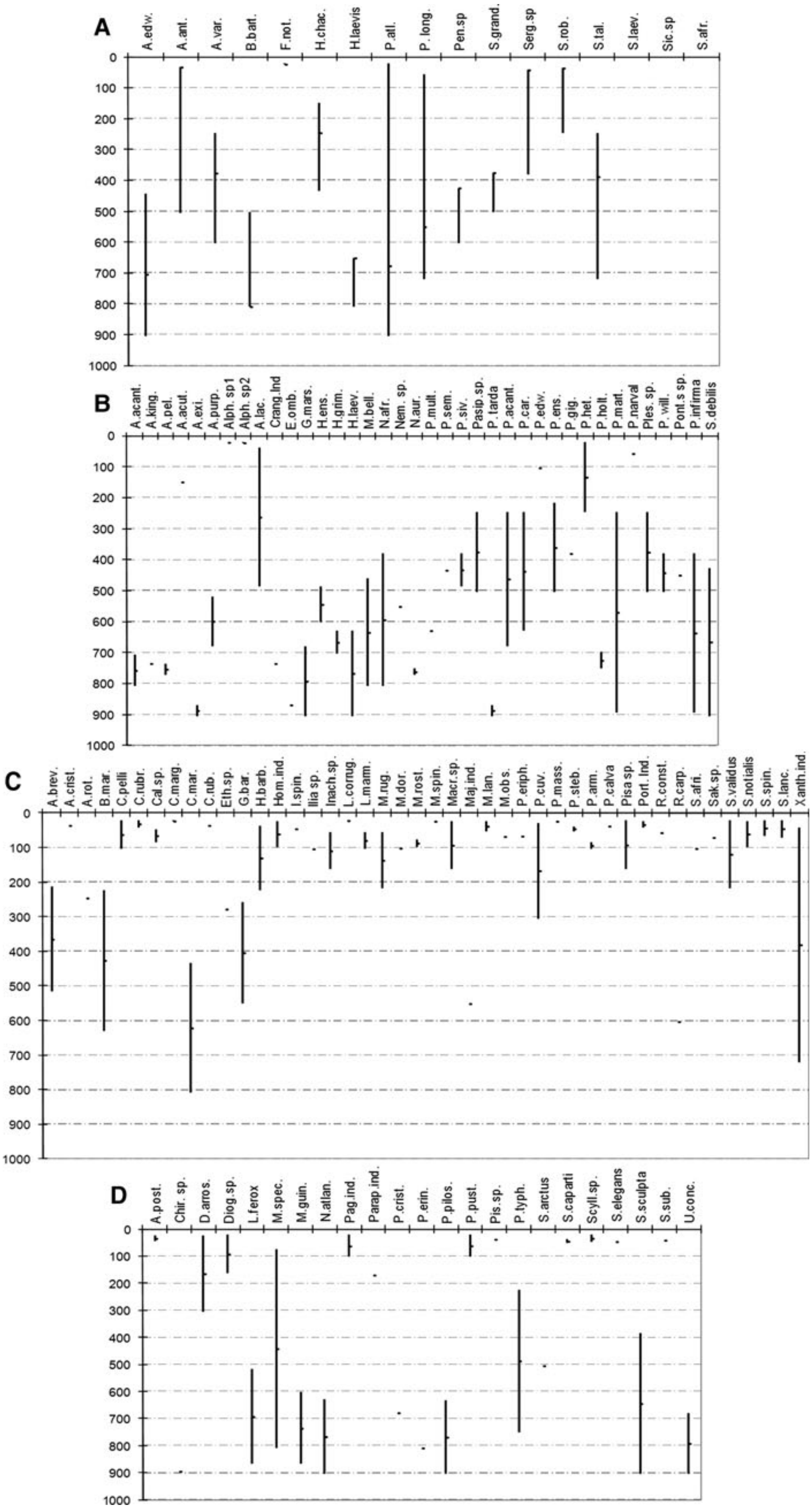

Fig. 4. Bathymetric distribution of the decapod crustaceans collected during the 'GUINEA BISSAU 0810' survey, ranked according to their mean depth of occurrence. (A) Dendrobranchiata; (B) Caridea; (C) Brachyura; (D) Anomura, Astacidea and Polichelida.

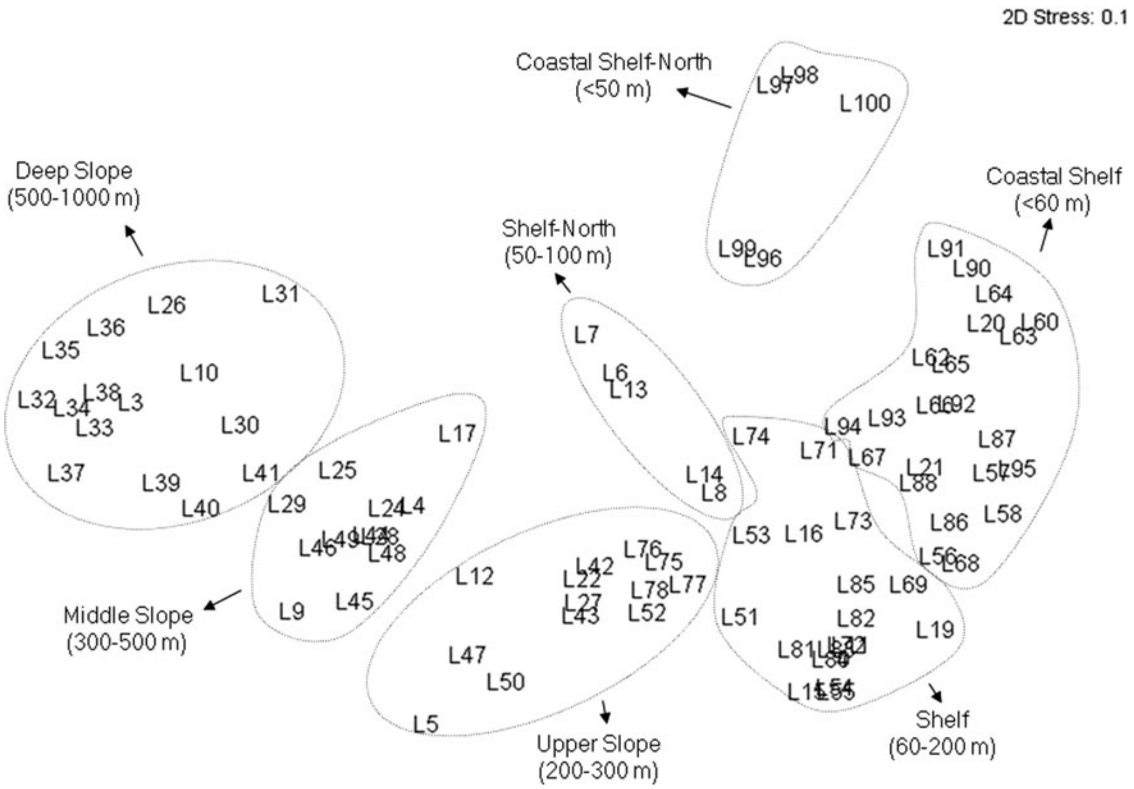

Fig. 5. Two-dimensional multidimensional scaling ordination plot of average abundance data of decapod crustaceans obtained during the 'GUINEA BISSAU 0810' survey.

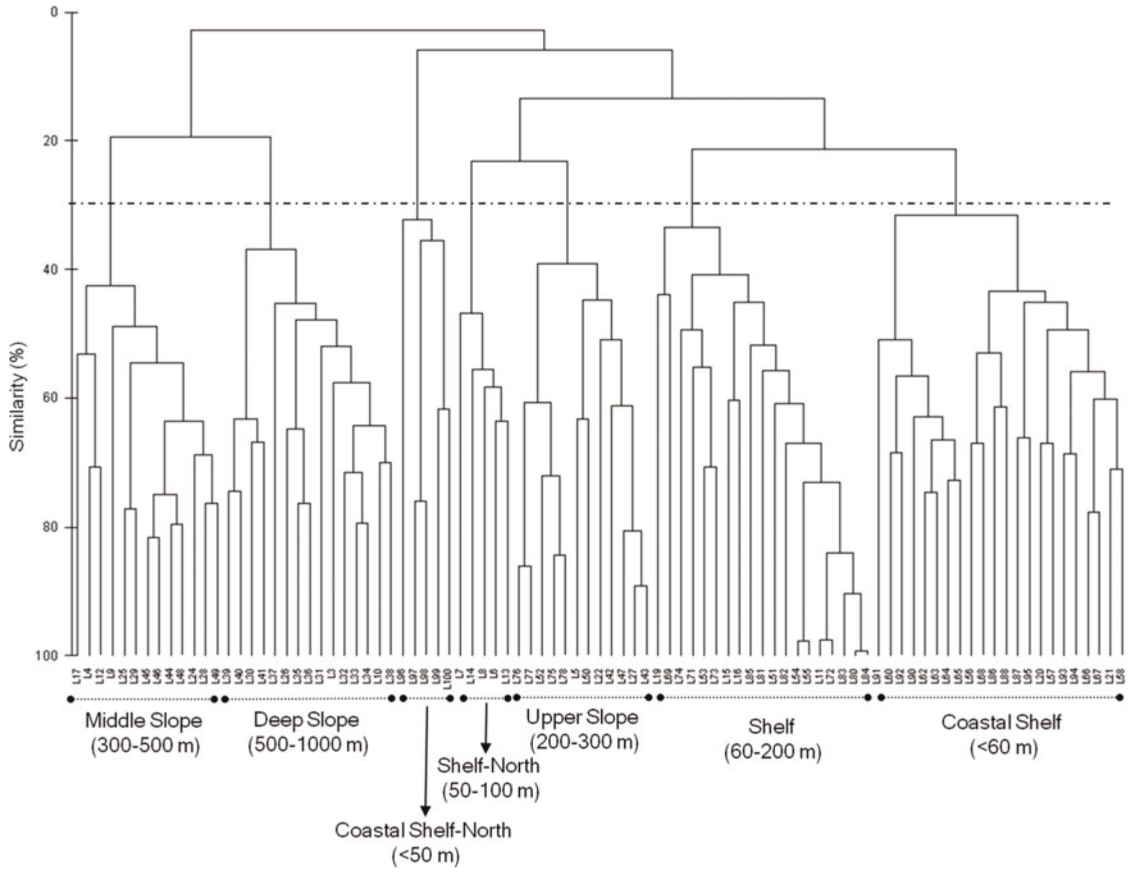

Fig. 6. Dendrogram of trawl stations using group-average clustering from Bray–Curtis similarity measures on average abundance of decapod crustaceans obtained during the 'GUINEA BISSAU 0810' survey. L, station.

shelf–upper slope group and a middle–deep slope group. At a level of similarity of about 30% the similarity tree clearly discriminates between seven groups: (1) a group composed of 22 strictly coastal hauls down to 60 m depth ('coastal shelf'); (2) a group made up of 19 hauls essentially ranging between 60 and 200 m depth, corresponding to most of the hauls on the middle shelf ('shelf'); and (3) the 'upper-slope' group, made up of 12 hauls between 200 and 300 m. Furthermore, there are two shelf groups restricted to the northern area: (4) a group of 5 coastal stations (<50 m) ('coastal shelf-north'); and (5) another shelf group of hauls at depths between 50 and 100 m ('shelf-north'). These five groups (1 to 5) are included in the 'shelf–upper slope' main branch. The two remaining groups (6 and 7) belong to the slope: (6) a group of 13 stations between 300 and 500 m ('middle slope'); and (7) another group of 14 stations between 500 and 1000 m ('deep slope').

The SIMPER analysis showed that the average dissimilarity between the seven assemblages ranged from 88.24% to 99.99%. These differences were due to the different contribution of species in each group. Table 5 shows those species responsible for the intergroup dissimilarities.

Although many species occurred in more than one group, each faunal assemblage was characterized by its own distinctive species composition. The pair-wise comparisons between groups (Table 6) defined by the ANOSIM showed high separation between the seven groups, with a global R value of 0.91.

The mean abundance, similarity percentage of contribution and cumulative percentage of each species in the seven assemblages are shown in Table 7, recapitulating the differences in the dominant species between the seven aforementioned main assemblages (SIMPER analysis).

The coastal shelf assemblage is mostly characterized by *S. spinirostris*, *Diogenes* sp., *D. arrosor* and *C. rubroguttata* with decreasing abundance, while *F. notialis* and *P. atlantica* typify the coastal shelf–north assemblage.

The hermit crab *D. arrosor* is the discriminating species of the shelf assemblage, with a contribution higher than 97% within the group. However, the shelf–north assemblage is characterized by the deep-water rose shrimp *P. longirostris*, with a small contribution of *Inachus* sp.

Three species, *M. speciosa*, *P. longirostris* and *P. heterocarpus* typified the group corresponding to the upper slope, *M. speciosa* being the most abundant and the main contributor species within this group. The middle slope assemblage is characterized by six species, being in order of abundance: *N. africanus*, *M. speciosa*, *P. martia*, *B. maravigna*, *P. longirostris* and *S. robusta*. The deepest assemblage (deep slope), is typified by five species: *N. africanus*, *S. sculpta*, *A. varidens*, *N. atlantica* and *L. ferox* in order of decreasing abundance.

DISCUSSION

This study provides valuable information on the faunal composition of decapod crustaceans in waters off Guinea-Bissau. Several observations have extended the bathymetric and geographical distribution-ranges cited in the literature for certain species in Atlantic waters (García-Isarch, personal communication). In addition, our results show clear patterns in diversity, abundance and biomass of decapod crustaceans on the continental shelf and slope waters of the Guinea-Bissau EEZ, highly related to depth. Different depth-ranges, occurrences, biomasses and abundances among depth strata demonstrate the differences in the crustacean distribution due to bathymetry. Decapod biomass and abundance increased with depth, reaching maxima values in the upper slope (200–500 m depth) and minimum ones in the shallowest stratum. Over 500 m, the decapod abundance and biomass exhibited the typical decrease with depth observed in the deep-sea environment (Cartes & Sardà, 1992; Company *et al.*, 2004; Politou *et al.*, 2005; Cartes *et al.*, 2007). As the environmental conditions are relatively constant in deep

Table 5. Most important species, in terms of percentage contribution to the group dissimilarity (similarity percentage analysis), listed for each group resulting from the cluster analysis.

Groups	Average dissimilarity	Most discriminator species	Contribution %
Coastal shelf versus coastal shelf-north	97.38	*Diogenes* sp.	22.35
Shelf versus coastal shelf-north	99.02	*Dardanus arrosor*	49.32
Shelf-north versus coastal shelf-north	99.68	*Papapenaeus longirostris*	54.37
Upper slope versus coastal shelf-north	99.99	*Munida speciosa*	48.43
Middle slope versus coastal shelf-north	99.88	*Nematocarcinus africanus*	38.79
Deep slope versus coastal shelf-north	99.99	*Stereomastis sculpta*	21.22
Shelf versus coastal shelf	89.64	*Dardanus arrosor*	45.20
Shelf-north versus coastal shelf	97.38	*Papapenaeus longirostris*	52.06
Upper slope versus coastal shelf	98.68	*Munida speciosa*	47.98
Middle slope versus coastal shelf	99.99	*Nematocarcinus africanus*	37.95
Deep slope versus coastal shelf	99.99	*Nematocarcinus africanus*	20.44
Shelf-north versus shelf	90.06	*Papapenaeus longirostris*	50.93
Upper slope versus shelf	93.34	*Munida speciosa*	48.30
Middle slope versus shelf	99.81	*Nematocarcinus africanus*	37.25
Deep slope versus shelf	99.99	*Dardanus arrosor*	28.76
Upper slope versus shelf-north	88.24	*Munida speciosa*	39.55
Middle slope versus shelf-north	95.87	*Nematocarcinus africanus*	36.17
Deep slope versus shelf-north	99.98	*Papapenaeus longirostris*	38.17
Middle slope versus upper slope	89.62	*Nematocarcinus africanus*	32.75
Deep slope versus upper slope	99.93	*Munida speciosa*	39.82
Deep slope versus middle slope	90.80	*Nematocarcinus africanus*	44.37

Table 6. Analysis of similarities performed on the seven assemblages identified by the cluster analysis. Sample statistic (Global R), 0.911; significance level of sample statistic, 0.1%; number of permutations, 999 (random sample from a large number); number of permuted statistics greater than or equal to Global R, 0.

Groups	R statistic	Significance level %
Deep slope (500–1000 m), middle slope (300–500 m)	0.84	0.1
Deep slope (500–1000 m), upper slope (200–300 m)	0.99	0.1
Deep slope (500–1000 m), shelf-north (50–100 m)	1	0.1
Deep slope (500–1000 m), shelf (60–200 m)	1	0.1
Deep slope (500–1000 m), coastal shelf (<60 m)	0.98	0.1
Deep slope (500–1000 m), coastal shelf-north (<50 m)	1	0.1
Middle slope (300–500 m), upper slope (200–300 m)	0.84	0.1
Middle slope (300–500 m), shelf-north (50–100 m)	0.99	0.2
Middle slope (300–500 m), shelf (60–200 m)	1	0.1
Middle slope (300–500 m), coastal shelf (<60 m)	0.97	0.1
Middle slope (300–500 m), coastal shelf-north (<50 m)	1	0.1
Upper slope (200–300 m), shelf-north (50–100 m)	0.83	0.1
Upper slope (200–300 m), shelf (60–200 m)	0.85	0.1
Upper slope (200–300 m), coastal shelf (<60 m)	0.92	0.1
Upper slope (200–300 m), coastal shelf-north (<50 m)	0.98	0.1
Shelf-north (50–100 m), shelf (60–200 m)	0.84	0.1
Shelf-north (50–100 m), coastal shelf (<60 m)	0.88	0.1
Shelf-north (50–100 m), coastal shelf-north (<50 m)	1	0.8
Shelf (60–200 m), coastal shelf (<60 m)	0.72	0.1
Shelf (60–200 m), coastal shelf-north (<50 m)	0.98	0.1
Coastal shelf (<60 m), coastal shelf-north (<50 m)	0.83	0.1

waters, this reduction in waters deeper than 500 m may be due to low trophic resource availability. The increase of decapod biomass with increasing depth has been described in North Atlantic waters (Fariña *et al.*, 1997; Cartes *et al.*, 2007), and Amorim *et al.* (2002) found similar results with demersal fish in Guinea-Bissau. In tropical waters, however, the general assumption is that higher biomasses are found in shallow and suprathermocline waters (Longhurst & Pauly, 1987). The explanation for lower biomass in coastal areas may be that Guinea-Bissau waters do not belong to the typical tropical type, as its environment is characterized by strong seasonal variations of oceanographic conditions (Berrit & Rebert, 1977), mainly due to seasonal upwelling events. Thus, seasonal variations are probably responsible for the deviations in the distribution of demersal biomass, as observed in waters off Gabon and Congo (Bianchi, 1992a).

A total of 122 species of decapod crustaceans were identified from coastal waters to depths up to 1000 m off Guinea-Bissau. This species richness is very high in comparison to those recorded in similar bathymetric ranges of other Atlantic (Macpherson, 1991; Serrano *et al.*, 2006) or Mediterranean waters (e.g. Abelló *et al.*, 1988, 2002; Cartes & Sardà, 1992; Maynou *et al.*, 1996; Biagi *et al.*, 2002; Massutí & Reñones, 2005; Ungaro *et al.*, 2005; Abad *et al.*, 2007; Fanelli *et al.*, 2007). In decapod crustaceans, species richness is affected by latitude, being highest in tropical and subtropical regions compared to temperate and cold ones, where a significant decrease of species richness is observed (Abele, 1982). In this study, the average diversity increased with depth, reaching a maximum over the deep slope strata. This tendency of increasing decapod diversity with depth, reaching maxima values between 1000 and 2000 m, has already been described for other areas (Haedrich *et al.*, 1980; Abelló, *et al.*, 1988; Cartes & Sardà, 1992; Fariña *et al.*, 1997; Politou *et al.*, 2005; Cartes *et al.*, 2007; Fanelli *et al.*, 2007). Diversity in benthic marine communities may be linked to many factors such as productivity, trophic relationships and biological interactions, which vary in importance according to depth (Rex *et al.*, 1997). The increasing diversity with depth can be explained by the greater environmental stability of the slope zone, which allows a more mature and thus, a more diverse community to develop (Haedrich *et al.*, 1980; Abelló *et al.*, 1988). The presence of steep bottoms favours the coexistence of pelagic and nectobenthic species with the strictly benthic species, resulting in an increased diversity (Abelló *et al.*, 1988). In addition, a very low oxygen zone (<1 ml O_2/l) was detected in the Guinea-Bissau continental slope (Sánchez-Leal, personal communication), a factor that has been also related to higher occurrence of crustacean species (Mincks *et al.*, 2000; Hendricks, 2001).

The dendrogram of similarities among hauls has shown the existence of seven main groups that may correspond to seven different faunal assemblages: coastal or shallower shelf (<60 m), shelf (60–200 m), upper slope (200–300 m), middle slope (300–500 m), deep slope (500–1000 m), coastal shelf–north (<50 m at the northern area) and shelf–north (50–100 m, in the northern area). These assemblages are mainly sorted by depth, although type of sediment (as a function of latitude) also affected the subdivision in the coastal shelf and shelf assemblages in the northern shallow area, characterized by soft bottoms (mud and sand) mainly related to the river mouth (McMaster *et al.*, 1971; Domain, 1980).

In the cluster analysis, some species serve as indicators of the assemblages when they are more frequent and abundant in a series of samples than in others. Thus, benthic species such as brachyurans (*Sternodromia spinirostris* and *Calappa rubroguttata*) and left-handed hermit crabs (*Diogenes* sp. and *D. arrosor*) are indicators in the shallowest assemblage (coastal shelf) located at depths below 60 m. Coastal strata were very favourable habitats for the pagurid crabs (Le Danois, 1948; Serrano *et al.*, 2006). The most abundant species in the coastal assemblage was the sponge crab

Table 7. Most important species, in terms of percentage contribution to the group similarity (similarity percentage analysis) listed for each group resulting from the cluster analysis (cut-off for low contribution, 90.00%).

	Average abundance	Average similarity	Contribution %	Cumulated %
Group coastal shelf-north		Depth-range: <50 m		
Average similarity: 18.76				
Farfantepenaeus notialis	57.20	11.97	63.79	63.79
Parapenaeopsis atlantica	36.20	4.97	26.48	90.27
Group coastal shelf		Depth-range: <60 m		
Average similarity: 19.94				
Diogenidae indet.	74.77	7.33	36.77	36.77
Sternodromia spinirostris	131.05	6.52	32.68	69.45
Dardanus arrosor	9.59	3.52	17.62	87.08
Calappa rubroguttata	3.05	0.77	3.84	90.92
Group shelf		Depth-range: 60–200 m		
Average similarity: 34.32				
Dardanus arrosor	241.11	33.46	97.50	97.50
Group shelf-north		Depth-range: 50–100 m		
Average similarity: 36.33				
Parapenaeus longirostris	515.40	29.52	81.27	81.27
Inachus sp.	41.40	3.50	9.63	90.90
Group upper slope		Depth-range: 200–300 m		
Average similarity: 31.57				
Munida speciosa	1142.75	22.75	72.06	72.06
Plesionika heterocarpus	83.50	2.88	9.12	81.18
Parapenaeus longirostris	85.42	2.84	9.00	90.18
Group middle slope		Depth-range: 300–500 m		
Average similarity: 23.75				
Nematocarcinus africanus	2347.08	10.73	45.20	45.20
Plesionika martia	171.62	5.06	21.30	66.50
Munida speciosa	204.46	3.02	12.73	79.23
Bathynectes maravigna	70.15	1.52	6.40	85.63
Parapenaeus longirostris	67.69	0.54	2.26	87.89
Sergia robusta	18.00	0.52	2.21	90.09
Group deep slope		Depth-range: 500–1000 m		
Average similarity: 28.75				
Stereomastis sculpta	129.40	12.62	43.92	43.92
Aristeus varidens	44.20	7.56	26.29	70.20
Nephropsis atlantica	12.27	2.71	9.42	79.63
Nematocarcinus africanus	847.00	2.61	9.08	88.71
Lithodes ferox	7.27	0.79	2.75	91.46

S. spinirostris, which has also been cited as one of the characterizing species of the macrobenthic community in the same bathymetric range off Guinea (Le Loeuff, 1993). It has also been described in the coastal waters of Côte d'Ivoire (Le Loeuff & Intès, 1999). *Diogenes* sp., which always appeared associated with a zoanthid was the main contributor to the similarity within the group. The typifying species varies if we consider the coastal shelf faunal subgroup assemblage in the northern area. Two penaeid species (*Farfantepenaeus notialis* and *Penaeopsis atlantica*) characterized this subgroup, located in the northernmost eastern area of the prospected zone, at depths below 50 m, with the southern pink shrimp *F. notialis* being the main species of this assemblage. It is worth mentioning the commercial value of the southern pink shrimp in this area, which is one of the target species for both artisanal and industrial fleets (Sobrino & García, 1992). This species has been described as belonging to other shallow water assemblages in West African waters of Guinea (Le Loeuff, 1993), Congo and southern Gabon, with an average depth of 21 m (Bianchi, 1992a) and another from northern Angola to Benguela, with an average depth of 24 m (Bianchi, 1992b). *Penaeopsis atlantica* has been described together with *F. notialis* in the same shallow water assemblages of Guinea (Le Loeuff, 1993), Congo and Gabon, (Bianchi, 1992a). Furthermore, the species has been cited in shallow coastal waters of Guinea (Le Loeuff, 1993), Côte d'Ivoire (Le Loeuff & Intes, 1999) and Angola (Bianchi, 1992b).

The typifying species of the shelf assemblage (60–200 m) is *D. arrosor*. This left-hand hermit crab, very well known in European waters, is also very common on continental shelf bottoms of West Africa, having been sighted in waters off Morocco (Maurin, 1968; García Raso, 1996), Mauritania (Maurin, 1968), Guinea (Le Loeuff, 1993), Côte d'Ivoire (Le Loeuff & Intès, 1999) and Namibia (Macpherson, 1991).

Like other invertebrates, this species shows a tropical submergence phenomenon and lives at greater bathymetric levels in West African waters than in Europe, in order to avoid warmer waters (Le Loeuff, 1993). There is a clearly different shelf assemblage in the northern area, characterized by the deep-water rose shrimp *Parapenaeus longirostris*. This assemblage is composed of muddy bottom stations between 50 and 100 m depth in the northern zone of the survey area (Domain, 1980), located below the thermocline (Sánchez-Leal, personal communication). The small size of the shrimps caught (García-Isarch, personal communication) may indicate a recruitment zone for the species in the area.

The indicator species of the upper slope assemblage (from 200–300 m depth), are, in order of decreasing abundance, the squat lobster *Munida speciosa*, the deep-water rose shrimp *P. longirostris* and the arrow shrimp *P. heterocarpus. Munida speciosa* is the discriminator species of the assemblage, accounting for 72% of the sample similarity. It has also been the most abundant species (in number and biomass) in the survey. This species has been found at similar depths in slope assemblages of northern Namibia (Macpherson, 1991) and in waters off River Congo, Equatorial Guinea and Senegal (Miyake & Baba, 1970). *Parapenaeus longirostris* and *Plesionika heterocarpus* contribute to the similarity of the assemblage with similar percentages (around 9% in each case). The deep-water rose shrimp is a typical deep shelf–upper slope species, which has also been described as belonging to shelf–upper slope assemblages in Atlantic waters of northern Namibia (Macpherson, 1991), Angola (Bianchi, 1992b), Congo and Gabon (Bianchi, 1992a), Morocco, Mauritania and Senegal (Maurin, 1968) and in the Mediterranean Sea (Abelló *et al.*, 1988, 2002; Maynou & Cartes, 2000; Biagi *et al.*, 2002; Company *et al.*, 2004; Massutí & Reñones, 2005; Politou *et al.*, 2005; Abad *et al.*, 2007; Fanelli *et al.*, 2007). This species characterized two assemblages in waters off Guinea-Bissau. On one hand, as explained above, it was the typifying species of the coastal shelf assemblage located in the northern muddy bottoms below the thermocline, and mainly constituted by recruits. On the other hand, it is the second species in abundance in the upper slope assemblage. Similarly, *P. longirostris* has also been described in two different assemblages, one coastal and another in the upper slope in waters off Congo, Gabon and Angola (Bianchi, 1992a,b). In all cases the coastal faunal groups were subthermocline assemblages over soft bottoms of mud, and mud–sand (at average depths of 79 m in Congo, 70–140 m in northern Angola and 50–100 in Guinea-Bissau) almost identical in species composition, with deep-water rose shrimps not very abundant but quite frequent. In the upper slope assemblages, *P. longirostris* was more abundant and found at average depths of 219, 256 and 200–300 m in Congo–Gabon, Angola and Guinea-Bissau, respectively. The deep-water rose shrimp is the target species of industrial shrimper fleets fishing in Guinea-Bissau waters, such as the Spanish fleet, for which it makes around 75% of the landings (Sobrino & García, 1992). The arrow shrimp *P. heterocarpus* is a typifying species of other slope communities in African waters (Macpherson, 1991). It has been found at similar depths (150–300 m) in north-west African waters (Maurin, 1968; Anadón, 1981) and North Atlantic waters (Fariña *et al.*, 1997), while its presence in the Mediterranean covers a wider depth-range between 45 and 468 m (Abelló *et al.*, 2002).

The middle slope assemblage (between 300 and 500 m) was dominated by benthic or nectobenthic species such as *Nematocarcinus africanus*, *M. speciosa*, *Plesionika martia*, *Bathynectes maravigna*, *P. longirostris* and *Sergia robusta*. The typifying species of this community were *N. africanus*, *M. rutllanti* and *P. martia* accounting together for almost 80% of the similarity within the group. The African spider shrimp *N. africanus* was the most characteristic species of the slope community, being the most abundant and the one with the highest contribution in the group. Furthermore, as described below, this species also typifies the deep slope assemblage. *Nematocarcinus africanus* has been described in slope communities of other areas of West African coasts (Macpherson, 1991; Bianchi, 1992a). It is, together with the black hake *Merluccius polli*, the indicator species of the slope assemblage of quite similar depths in waters off Congo, Gabon and Angola (Bianchi, 1992a, b). The golden shrimp *P. martia*, which is the third species in abundance in the middle slope community, has a worldwide distribution in tropical and temperate ocean waters and has been described as a typical deep Mediterranean decapod, being one of the most frequent or abundant species at depths of over 350–400 m (Abelló *et al.*, 1988, 2002; Maynou *et al.*, 1996; Maynou & Cartes, 2000; Biagi *et al.*, 2002; Maiorano *et al.*, 2002; Company *et al.*, 2004; Massutí & Reñones, 2005; Politou *et al.*, 2005; Abad *et al.*, 2007; Fanelli *et al.*, 2007; Moranta *et al.*, 2008). Its presence has also been referenced in slope communities of South Atlantic waters (Macpherson, 1991) and in the North Atlantic (Maurin, 1968; García Raso, 1996; Fariña, 1997; Cartes *et al.*, 2007), where it is much less frequent. Another typical species of the middle slope community was the crab *B. maravigna*, usually recorded on the upper continental slope deeper than 250 m (Abelló *et al.*, 2001), and very abundant in deep water decapod assemblages of the North Atlantic (Fariña *et al.*, 1997; Cartes *et al.*, 2007) and the Mediterranean (see review in Abelló *et al.*, 2001). Even though Morocco and the Canary Islands were the southern distribution zone limit of the species (Abelló *et al.*, 2001), this study demonstrated its presence at southern latitudes, in waters off Guinea-Bissau. The sergestid shrimp *S. robusta* has been described in depth assemblages at 400–500 m, 500–800 and below 600 m in Mediterranean waters (Abelló *et al.*, 1988; Maynou & Cartes, 2000), where it has been recorded in a depth-range from 300 to more than 1500 m (Abelló *et al.*, 1998, 2002; Company *et al.*, 2004). In North Atlantic waters, *S. robusta* is a typifying species of deep slope assemblages around 600–1000 m (Cartes *et al.*, 2007).

Nematocarcinus africanus, *Stereomastis sculpta* and *Aristeus varidens* typified the deep slope-assemblage (500–1000 m), accounting together for around 80% of similarity within the group. *Nematocarcinus africanus* is the most abundant in this assemblage and, as described above, it is a typical slope species in African waters (Macpherson, 1991; Bianchi, 1992a). However, *S. sculpta* and *A. varidens* provide more similarity to the group, being the discriminating species of the deep slope assemblage. *Stereomastis sculpta* is a typical deep water species, described in the Mediterranean Sea at depths between 800 and 2800 m (Company *et al.*, 2004). The striped red shrimp *A. varidens* is one of the target species of the crustacean industrial fleet in waters off Guinea-Bissau (Sobrino & García, 1992). This species has been described as belonging to deeper continental slope assemblages in waters off Congo, Gabon and Angola (Bianchi, 1992a, b), Mauritania (Maurin, 1968) and to a slope/bathyal assemblage in Namibian waters (Macpherson, 1991). The scarlet lobsterette *Nephropsis atlantica* and the fierce king crab *Lithodes ferox* are other species characterizing this assemblage, as it occurs in slope/bathyal assemblages of Namibia (Macpherson, 1991).

Although similarities can be found with other decapod assemblages, especially with those of Western African coasts or with deeper assemblages of other seas (like the Mediterranean), any assemblage significance is strictly local and related to the taxocenosis studied (Haedrich & Merret, 1990; Maynou & Cartes, 2000). However, within an environmentally homogeneous area the composition of crustacean decapod assemblages scarcely varies (Maynou & Cartes, 2000). Numerous decapod species appearing in waters off Guinea-Bissau are common in Mediterranean and European Atlantic waters, a fact also underlined in benthic faunal studies of other African areas. Palaeogeographical studies have shown that there is a strong similarity between the present West African fauna and the Pliocene fauna of Southern Europe (Le Loeuff & Zabi, 2002).

In our study, the dominant species differed among depth strata, confirming the importance of depth in structuring crustacean decapod communities, as it has been described in other areas of the South Atlantic (Lleonart & Roel, 1984; Macpherson, 1991; Bianchi, 1992a,b); North Atlantic (Fariña, 1997; Serrano *et al.*, 2006) and Mediterranean (Abelló *et al.*, 1988, 2002; Maynou & Cartes, 2000; Fanelli *et al.*, 2007). The structure of decapod crustacean assemblages on the continental margins in different geographical areas is largely determined by spatial differences in environmental and oceanographic conditions, and in particular: depth; nature of the substrate; and characteristics of the water masses (e.g. Haedrich *et al.*, 1975, 1980; Abelló *et al.*, 1988; Macpherson, 1991; Bianchi, 1992a, b; Cartes & Sardà 1993; Fariña *et al.*; 1997; Cartes *et al.*, 2007). Food supply (Maynou & Cartes, 2000; Massutí & Reñones, 2005) and climatic seasonal variations (Le Loeuf & Intes, 1999; Soto *et al.*, 1999) have also been identified as contributing factors in the variations of benthic communities. Therefore, it can be concluded that demersal faunal associations are probably determined by a combination of both abiotic (in particular bottom structure and type, and dynamic of the water masses) and biotic (competition, resource availability and food web structure) factors (Moranta *et al.*, 2008).

In this study having not analysed other possible contributing factors, depth was the main factor influencing the structure of decapod crustacean assemblages. The decapod crustacean community in shelf and slope waters off Guinea-Bissau presented a zonation effect, with clear bathymetric boundaries. Main faunal discontinuities were located at depths of 60, 200 and 500 m. The 60 m boundary could be attributed to the position of the thermocline as thermal stratification has been related to demersal groupings in shallow West African waters (Bianchi, 1992a, b). The faunal discontinuity found at 200 m may be located where the continental shelf ends and begins the slope zone (shelf break), as described for fish assemblages in the same area (Amorim *et al.*, 2002). The 500 m boundary may correspond to the transition between a middle-slope fauna and a strictly bathyal fauna, which is in general accordance with faunal studies in other areas, where this transition depth has been located around 400–500 m (Abelló *et al.*, 1988; Macpherson, 1991; Fanelli *et al.*, 2007).

This work has contributed to obtaining the first decapod crustacean faunal list in Guinean-Bissauan waters, as well as to determining inter-specific relationships between these organisms. Knowledge about the crustacean communities inhabiting Guinea-Bissauan waters is of great importance both for assessing possible changes in the structure of the ecosystem as a consequence of strong trawling pressure in the area, and for the establishment of ecosystem-based-management strategies. For the first, our study may constitute a reference point for further research focused on the possible changes in the Guinea-Bissau decapod assemblages, biomass or densities, as a result of fishing pressure. For the second, this study could contribute to the establishment of an ecosystem-based management approach to fisheries, which takes into account all living organisms and the environment, with special emphasis on habitats, communities and the effect of inter-specific relationships on the species abundance and distribution (Garcia *et al.*, 2003; Pikitch *et al.*, 2004). For ecosystem-based fishing management purposes, we recommend the implementation of long term monitoring programmes that could detect possible changes in the structure, biomass and diversity of benthic assemblages resulting from trawling. In conclusion, this study provides new information about composition, distribution, abundance and structure of decapod assemblages in Guinea-Bissau that may be useful for future studies aiming to quantify the effect of the trawling pressure in the area.

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Correspondence should be addressed to:

I. Muñoz
Instituto Español de Oceanografía
C.O. de Cádiz, Puerto Pesquero
Muelle de Levante s/n, 11006 Cádiz (Spain)
email: isabel.munoz@cd.ieo.es