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Gammaridea and Caprellidea (Crustacea – Amphipoda) of the Portuguese south-western continental shelf: taxonomy and distributional ecology

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Abstract

Amphipods from the Portuguese south and south-western continental shelf were studied with regard to the species inventory, distribution, and ecology. This study allowed the identification of 113 species, belonging to 52 genera; of these species 28 are recorded for the first time along the Portuguese coast. Two species, *Ampelisca heterodactyla* Schellenberg, 1925, and *A. latifrons* Schellenberg, 1925, are redescribed. The latter is different from the *Ampelisca* named *latifrons* by Ledoyer in 1972 and 1982.

The absolute frequencies and abundances of the species, and their distribution in terms of bathymetry and type of substrate are also analysed. The most frequent and abundant species also presented wide ranges of vertical distribution. In addition, these species are preferentially found in medium or fine sand bottoms. The granulometric structure of the habitats might, therefore, be the most important factor conditioning the development of amphipod populations. The group of the most frequent and abundant species was dominated by *Ampelisca*. Thus, at least in the shelf sediments, the species of this genus might have a key role as food for many secondary consumers, especially demersal fishes.

Résumé

L'étude concerne l'inventaire spécifique, la distribution et l'écologie des Amphipodes des côtes sud et sud-ouest du Portugal. Ont été identifiées 113 espèces appartenant à 52 genres; 28 d'entre elles ont été récoltées pour la première fois le long des côtes portugaises. Deux espèces, *Ampelisca heterodactyla* Schellenberg, 1925 et *A. latifrons* Schellenberg, 1925 sont redécrites. La dernière diffère de l'espèce déterminée comme *A. latifrons* par Ledoyer, en 1972 et 1982.

La fréquence absolue et l'abondance des espèces, ainsi que leur distribution du point de vue bathymétrique et du type de substrat sont analysées. Les espèces les plus fréquentes et abondantes présentent aussi de vastes distributions verticales. D'autre part, ces espèces se rencontrent de préférence dans des fonds de sable fin ou moyen. La structure granulométrique des habitats pourrait donc être le facteur le plus important déterminant le développement des populations d'Amphipodes. Le groupe des espèces les plus fréquentes et abondantes est dominé par les *Ampelisca*. Les espèces de ce genre pourraient avoir sur les côtes du Portugal un role clé comme nourriture pour de nombreux prédateurs, et surtout pour les poissons démersaux.

Introduction

Despite their great importance, both qualitative and quantitative, as principal secondary and tertiary producers in the marine macrobenthic communities, the Amphipoda were up to recently very poorly studied along the Portuguese coast. It was mainly in the last decade that benthic surveys have been carried out more systematically, allowing a substantial increase in the knowledge of the amphipod fauna concerning species inventory, distribution, and ecology.

The present paper represents one more contribution to the knowledge of this important group along the Portuguese coast. Two species, *Ampelisca heterodactyla* Schellenberg and *Ampelisca latifrons* Schellenberg are redescribed, because the original descriptions were not sufficiently accurate. In addition, knowledge on species distribution and ecology constitutes reference data that might be effective

for further studies on the function of Amphipoda in the energy flow in the ecosystem of the Portuguese continental margin.

Material and methods

Several Seplat Cruises, organized by the Portuguese Navy Hydrological Institute, took place recently along the coast of Portugal. The goal of these cruises was the cartography of the shelf sediments, but the presence of biologists aboard allowed a large number of biological samples to be obtained. The present paper concerns the results of cruise 3 (cf. Monteiro Marques, 1979), and of cruises 4 to 8 (Fig. 1) that covered, from 1977 to 1983, the south and south-western Portuguese continental shelf, from the Algarve to the latitude of the Tagus estuary.

Samples were carried out essentially, but not always, with Van Veen grabs, which introduced an important bias into the general sampling strategy. Actually, although the sampled area was approximately constant, the amount of sediment collected was not always the same, depending on the bottom compactness and on the depth. In addition, although samples were collected from 12 to 635 m, the sampling efforts were less intensive at deeper levels (150 to 635 m). The available biological data were considered qualitative and therefore, for data analysis, we only took into consideration the absolute frequencies and abundances of the species. Data concerning the type of substrate, according to the classification of Shepard (1954), and depth were provided by the Navy Hydrological Institute.

For the identification of the species we used the following works: Barnard (1969; 1980), Cavedini (1981), Chevreux (1895; 1900; 1902), Chevreux & Fage (1925), Dauvin & Bellan-Santini (1988), Karaman (1972; 1984), Krapp-Schickel (1974; 1975; 1976), Krapp-Schickel & Myers (1979), Ledoyer (1982a), Lincoln (1979), Myers (1972; 1979), Myers & McGrath (1979; 1981; 1982), Ruffo (1985), Ruffo & Schiecke (1977), Ruffo [ed.] et al. (1982; 1989; in press), Sars (1895).

The analysis of the species distribution according to the type of substrate was done by using the Parametric Correlation Coefficient (Pearson's *r*) (*R* mode analysis) and the UPGMA as clustering method (Legendre & Legendre, 1984).

Results

A total of 1535 amphipods was sampled at 460 stations, from 12 to 635 m deep, of which 1298 (84.5%) were identified up to species level. The study of this collection allowed thereby the identification of 113 species, belonging to 52 genera of 24 families. Among 113 species identified, 29 (26%) were recorded for the first time along the Portuguese coast.

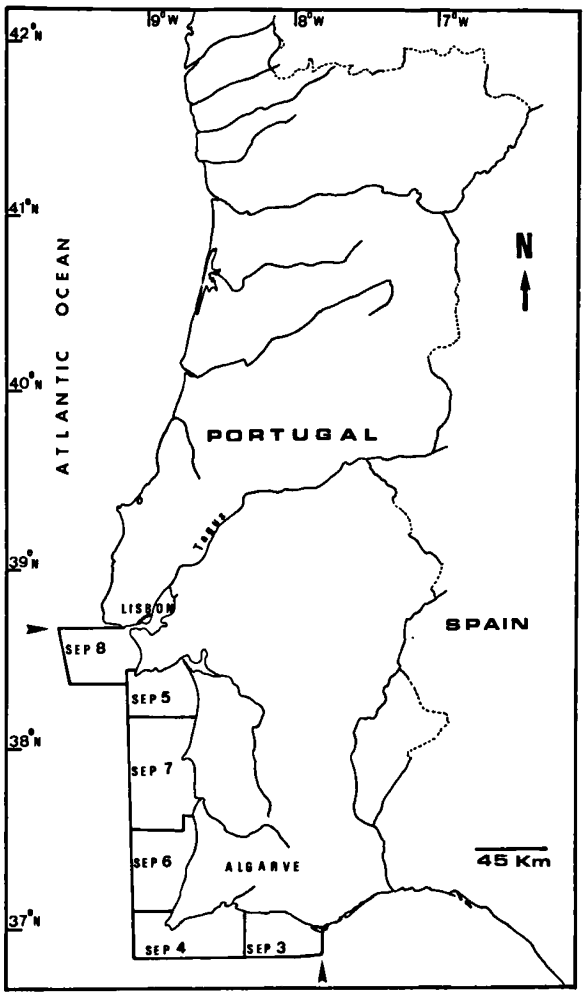

Fig. 1. Area studied. The localisation of each Seplat cruise (SEP) is indicated on the map.

List of species

(* Recorded for the first time off Portugal)

ACANTHONOTOZOMATIDAE

Iphimedia minuta Sars, 1882

AMPELISCIDAE

* *Ampelisca armoricana* Bellan-Santini & Dauvin, 1981

Ampelisca brevicornis s. l. (Costa, 1853)

Ampelisca calypsonis Bellan-Santini & Kaim-Malka, 1977

* *Ampelisca dalmatina* Karaman, 1975

Ampelisca diadema (Costa, 1853)

* *Ampelisca gibba* Sars, 1882

* *Ampelisca heterodactyla* Schellenberg, 1925

* *Ampelisca latifrons* Schellenberg, 1925

Ampelisca massiliensis Bellan-Santini & Kaim-Malka, 1977

Ampelisca pseudosarsi Bellan-Santini & Kaim-Malka, 1977

Ampelisca pseudospinimana Bellan-Santini & Kaim-Malka, 1977
Ampelisca remora Bellan-Santini & Dauvin, 1986
* *Ampelisca ruffoi* Bellan-Santini & Kaim-Malka, 1977
Ampelisca sarsi Chevreux, 1888
Ampelisca serraticaudata Chevreux, 1888
Ampelisca spinifer Reid, 1951
Ampelisca spinimana Chevreux, 1900
Ampelisca spinipes Boeck, 1861
* *Ampelisca spooneri* Dauvin & Bellan-Santini, 1982
Ampelisca tenuicornis Liljeborg, 1855
Ampelisca typica (Bate, 1856)
* *Byblis guernei* Chevreux, 1888
Haploops nirae Kaim-Malka, 1976
* *Haploops proxima* Chevreux, 1919

AMPHILOCHIDAE
Amphilochus neapolitanus Della Valle, 1893

AORIDAE
Aora typica Krøyer, 1845
Lembos longipes (Liljeborg, 1852)
Leptocheirus hirsutimanus (Bate, 1862)
Leptocheirus pectinatus (Norman, 1869)
Leptocheirus tricristatus (Chevreux, 1887)
Megamphopus cornutus Norman, 1869
Megamphopus longicornis Chevreux, 1911
Microdeutopus versiculatus (Bate, 1856)
Unciola crenatipalma (Bate, 1862)
* *Unciola planipes* Norman, 1867

CALLIOPIIDAE
Apherusa bispinosa (Bate, 1857)

COROPHIIDAE
Siphonoecetes dellavallei Stebbing, 1899
Siphonoecetes kroyeranus Bate, 1856
Siphonoecetes striatus Myers & McGrath, 1979

DEXAMINIDAE
Atylus guttatus (Costa, 1851)
Atylus swammerdami (Milne-Edwards, 1830)
Atylus vedlomensis (Bate & Westwood, 1862)
Tritaeta gibbosa Boeck, 1876

EUSIRIDAE
* *Eusirus longipes* Boeck, 1861

HYALIDAE
* *Parhyale richardi* (Chevreux, 1902)

ISAEIDAE
Gammaropsis maculatus Johnston, 1828
Gammaropsis sophiae (Boeck, 1861)
Photis longicaudata (Bate & Westwood, 1862)
Photis longipes (Della Valle, 1893)

ISCHYROCERIDAE
Ericthonius brasiliensis (Dana, 1852)

LEUCOTHOIDAE
Leucothoe incisa Robertson, 1892
* *Leucothoe lilljeborgi* Boeck, 1861
Leucothoe oboa Karaman, 1972
* *Leucothoe occulta* Krapp-Schickel, 1975
* *Leucothoe procera* Bate, 1857
* *Leucothoe richiardii* Lessona, 1865
Leucothoe spinicarpa (Abildgaard, 1789)

LILJEBORGIIDAE
Idunella longirostris (Chevreux, 1920)
Liljeborgia kinahani (Bate, 1862)
Liljeborgia pallida (Bate, 1857)

LYSIANASSIDAE
Hippomedon denticulatus (Bate, 1857)
* *Hippomedon robustus* Sars, 1895
Ichnopus spinicornis Boeck, 1861
Lepidepecreum longicorne (Bate & Westwood, 1861)
Lysianassa ceratina (Walker, 1889)
* *Lysianassa inesperata* (Lincoln, 1979)
Lysianassa plumosa Boeck, 1871
Socarnes erythrophthalmus Robertson, 1892
* *Tryphosella caecula* Sars, 1891
Tryphosites longipes (Bate & Westwood, 1861)

MELITIDAE
Ceradocus semiserratus (Bate, 1862)
Cheirocratus assimilis (Liljeborg, 1852)
Cheirocratus intermedius Sars, 1894
Cheirocratus sundevalli (Rathke, 1843)
Eriopisa elongata (Bruzelius, 1859)
Eriopisella pusilla Chevreux, 1920
Maera grossimana (Montagu, 1808)
Maera othonis (Milne-Edwards, 1830)
* *Maerella tenuimana* (Bate, 1862) (uncertain family)
Melita hergensis Reid, 1939
Melita obtusata (Montagu, 1813)
* *Psammogammarus caecus* Karaman, 1955

MEGALUROPIIDAE
Megaluropus agilis Hoeck, 1889

OEDICEROTIDAE
Monoculodes borealis Boeck, 1871
Monoculodes carinatus (Bate, 1856)
Monoculodes subnudus Norman, 1889
Perioculodes longimanus (Bate & Westwood, 1869)
Pontocrates altamarinus (Bate & Westwood, 1862)
Pontocrates arenarius (Bate, 1858)
* *Westwoodilla caecula* (Bate, 1856)

PARDALISCIDAE
* *Halicoides anomalus* Walker, 1893
* *Nicippe tumida* Bruzelius, 1859

PHOXOCEPHALIDAE
Harpinia antennaria Meinert, 1890
Harpinia crenulata (Boeck, 1871)
* *Harpinia excavata* Chevreux, 1900
* *Harpinia laevis* Sars, 1891
Harpinia pectinata Sars, 1891

Metaphoxus pectinatus (Walker, 1896)

PONTOPOREIIDAE
Bathyporeia elegans Watkin, 1938
* *Bathyporeia gracilis* Sars, 1891
Bathyporeia guilliamsoniana (Bate, 1856)
Bathyporeia pelagica (Bate, 1856)
Bathyporeia sarsi Watkin, 1938
* *Bathyporeia tenuipes* Meinert, 1877

STENOTHOIDAE
* *Stenothoe richardi* Chevreux, 1895

UROTHOIDAE
Urothoe brevicornis Bate, 1862
Urothoe elegans (Bate, 1856)
Urothoe marina (Bate, 1857)
Urothoe poseidonis Reibish, 1905
Urothoe pulchella (Costa, 1853)

CAPRELLIDAE
Pseudoprotella phasma (Montagu, 1804)

PHTISICIDAE
Phtisica marina Slabber, 1769

Taxonomic section

Ampelisca heterodactyla Schellenberg, 1925 (Figs. 2–5)

A. heterodactyla Schellenberg, 1925: 193; Reid, 1951: 210–211, fig. 16.
A. rubra Chevreux, 1925: 292, figs. 5, 6.

Material examined. – Seplat cruise 8, 4 ♀♀ and 1 ♂.

This rare species was first described from the coast of western Africa by Schellenberg with a single female. Later the same year Chevreux described an *Ampelisca* from the Senegal coast without comparison with Schellenberg's species, probably because he did not know the paper. Reid (1951) recorded this species again from the same area, and established the synonymy.

Redescription. – Female, 4.5 mm long: Head (Fig. 2A) as long as the first three segments of the mesosome, with a distinct rostrum as long as 1/2 of the first segment of antenna 1. Two pairs of ocular spots very difficult to distinguish. Urosome (Fig. 5F) segment 1 with small, round, dorsal hump just in front of segment 2. Coxa 1 expanded distally, distally fringed with plumose setae, part of the surface covered with small setae (Fig. 3A). Coxae 2–3 longer than broad, with parallel margins, distally fringed with short setae; part of the surface of both coxae with small setae (Figs. 3B–C). Coxa 4 broader than coxae 2 and 3, slightly expanded distally (Fig. 4A). Third epimere with margins convex and rounded (Fig. 5F).

First antenna as long as peduncle of second antenna, flagellum with 5 articles; second antenna shorter than half length of body, flagellum with 11 articles (Fig. 2A).

Maxilla 1, inner lobe without setae (Fig. 2D). Other mouthparts as illustrated (Figs. 2B–C, E–F).

Gnathopod 1 (Fig. 3A) basis normal, ischium and merus short, propodus shorter than carpus, dactylus 1/3 length of propodus with 2 setae on the posterior margin. Gnathopod 2 (Fig. 3B) carpus twice length of propodus.

Pereopod 3 (Fig. 3C) basis and merus long, ischium and carpus short, propodus longer than carpus, dactylus longer than propodus but shorter than propodus and carpus together. Pereopod 4 (Fig. 4A) similar to pereopod 3 but dactylus longer than propodus and carpus together; basis, ischium, and merus fringed with plumose setae, merus on both sides, basis and ischium only posteriorly. Pereopod 5 (Fig. 4B) basis dilated, anteriorly fringed with plumose setae; merus and carpus bearing simple setae on anterior margin, carpus distally prolonged in peg-shape, terminated by 2 spines; dactylus small, hook-shaped. Pereopod 6 (Fig. 4C) basis dilated with a large posterior rounded lobe, carpus distally prolonged in peg-shape, terminated by 2 spines; basis, merus, carpus, and propodus anteriorly fringed with simple setae. Pereopod 7 (Fig. 5A) basis reaching distal end of merus, posterior lobe regularly dilated to level of ischium insertion, thereafter evenly rounded, although slightly truncate medially; distal lobe with parallel margins at apex; merus shorter than ischium; dactylus slightly dilated mediodistally.

Uropod 1 (Fig. 5B) peduncle slightly longer than rami; inner ramus with 1 spine, peduncle with 3. Uropod 2 (Fig. 5C) peduncle as long as rami; inner ramus and peduncle with 1 spine. Uropod 3

Fig. 2. Ampelisca heterodactyla, ♀: A, head; B, mandible; C, labium; D, maxilla 1; E, maxilla 2; F, maxilliped.

Fig. 3. Ampelisca heterodactyla, ♀: A, gnathopod 1; B, gnathopod 2; C, pereopod 3.

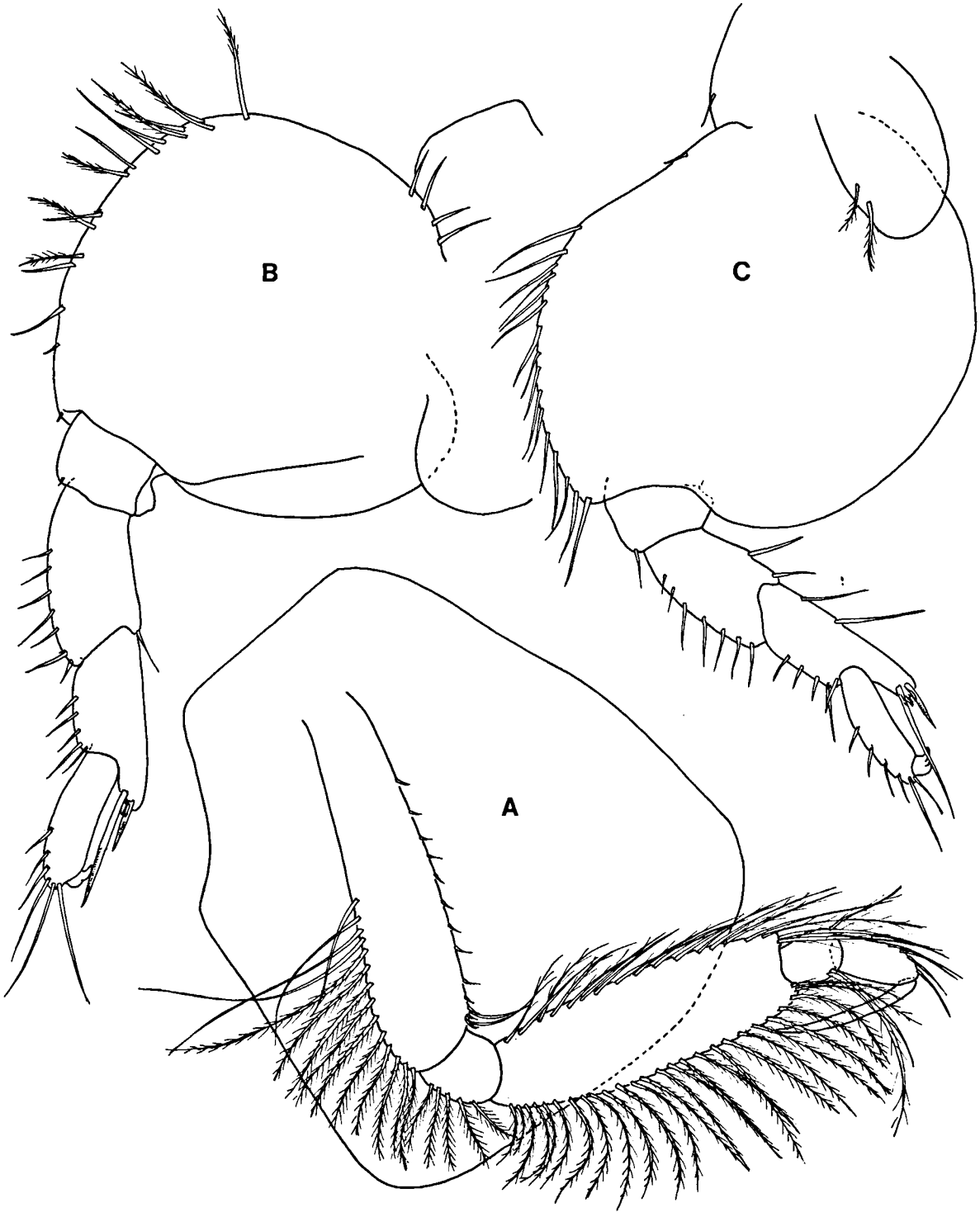

Fig. 4. Ampelisca heterodactyla, ♀: A, pereopod 4; B, pereopod 5; C, pereopod 6.

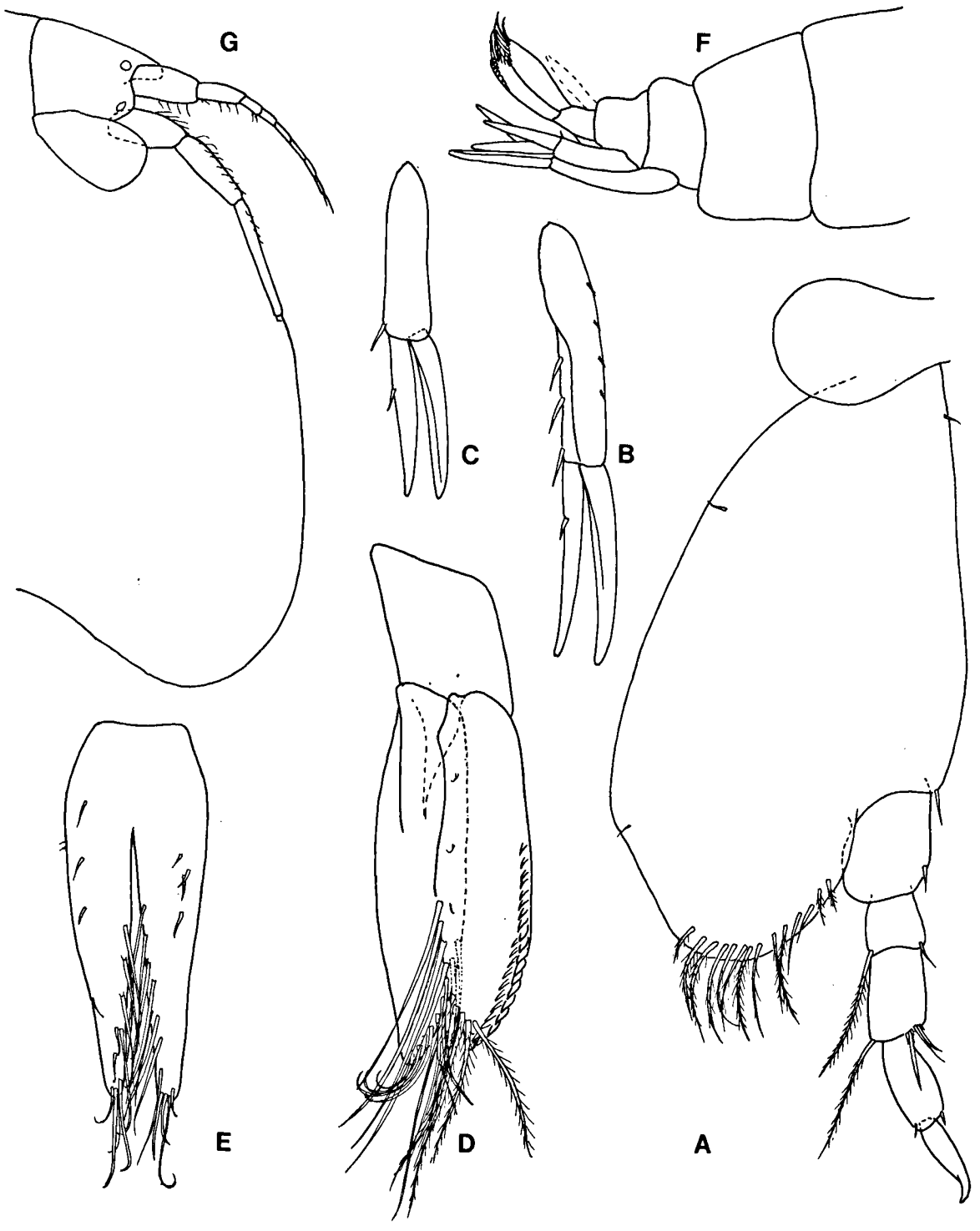

Fig. 5. Ampelisca heterodactyla (A–E ♀, F–G ♂): A, pereopod 7; B, uropod 1; C, uropod 2; D, uropod 3; E, telson; F, posterior part; G, head.

(Fig. 5D) rami foliaceous; outer ramus slightly shorter than inner, fringed laterally with 2 rows of short spines, and medially with long setae; inner ramus with long setae laterally.

Telson (Fig. 5E) long and tapering, deeply cleft, inner margins fringed with long setae; 3–4 pairs of short setae on the surface of the lobes.

Male: Antenna 2 longer than 1/2 body length (Fig. 5G). Urosome with dorsal hump higher than in female (Fig. 5F).

Ampelisca latifrons Schellenberg, 1925
(Figs. 6–9)

A. latifrons Schellenberg, 1925: 121–122; Reid, 1951: 199, fig. 3.
Non Ledoyer, 1972: 174–175; 1982b: 60–62, fig. 14.

Material examined. – Seplat cruises 6 and 7, 1 ♀ and 1 ♂.

Redescription. – Female 5 mm long: Head (Fig. 6A) broad, anteriorly truncate, not as long as the first three segments of the mesosome. Two pairs of ocular lenses. Urosome (Fig. 6B) segment 1 with rounded carina. Coxa 1 (Fig. 6G) distally expanded, bearing three rows of long setae. Coxae 2–3 (Figs. 7A and 8A) subrectangular, distally fringed with setae; only coxa 2 with additional small row of setae distally. Coxa 4 (Fig. 7B) sub-quadrangular, with two rows of small setae. Epimere 3 (Fig. 8F) quadrate.

First antenna shorter than peduncle of second, with 7-articulate flagellum. Second antenna as long as body, flagellum with about 25 articles. Maxilla 1 (Fig. 6D) inner lobe without setae. Other mouthparts as illustrated (Figs. 6C, E–F).

Gnathopod 1 (Fig. 6G) propodus and carpus equal in length. Gnathopod 2 (Fig. 7A) longer and more slender than gnathopod 1; propodus less than 2/3 of carpus length; dactylus with internal setae.

Pereopods 3 and 4 (Figs. 8A and 7B) with dactylus longer than carpus and propodus together. Pereopods 5 and 6 (Figs. 9A and 7C) classical, weakly setose. Pereopod 7 (Fig. 8B) basis short, not reaching end of ischium, about as broad as long, fringed with plumose and short setae; ischium as long as merus and carpus together; dactylus oval, slightly curved.

Uropod 1 (Fig. 8C) rami longer than peduncle, fringed with few spines. Uropod 2 (Fig. 8D) rami longer than peduncle, also fringed with few spines. Uropod 3 (Fig. 9B) lanceolate, outer ramus slightly shorter than inner, with two short spines laterally and a row of simple setae medially; outer ramus with a few lateral setae distally.

Telson (Fig. 8E) twice as long as broad, distally tapering, bearing 1 pair of setae and 1 pair of spines distally, and 1 pair of setae both subdistally and laterally.

Male: Posterior part illustrated (Fig. 9C).

Remarks. – Schellenberg's and Reid's descriptions cover the Portuguese specimens very closely, but some differences were found with Ledoyer's description. Ledoyer's specimens from the Indian Ocean differ essentially by: P7, being long, and the basis nearly twice as long as broad, posterior lobe rounded and not especially enlarged; telson wider than in *A. latifrons*; dactylus of pereopod 3 as long as carpus and propodus together. Actually, according to Ledoyer's first citation (1972: 175) "les bords latéraux céphaliques des specimens de Tuléar apparaissent moins transverses que celui figuré par Schellenberg". The second specimen from the same station represented by Ledoyer (1982b) has the same characteristics. In addition, he specifies that the dactyli of pereopods 3 and 4 are equal to the carpus and the propodus together, and the posterodistal corner of epimere 3 is rounded and not quadrate, as in *A. latifrons*. Therefore, we think that the species from Tuléar is different from *A. latifrons*.

Analysis of absolute frequencies and abundances of the species

The absolute frequencies of the species recorded showed strong differences (Table I). Six categories have therefore been considered, according to the number of times the species was sampled in the total of 460 samples, viz.: 1, very common (more than 50 times); 2, quite common (21 to 50 times); 3, common (11 to 20 times); 4, uncommon (5 to 10 times); 5, rare (2 to 4 times), and 6, quite rate (only once).

Fig. 6. Ampelisca latifrons, ♀: A, head; B, urosome; C, mandible; D, maxilla 1; E, maxilla 2; F, maxilliped; G, gnathopod 1.

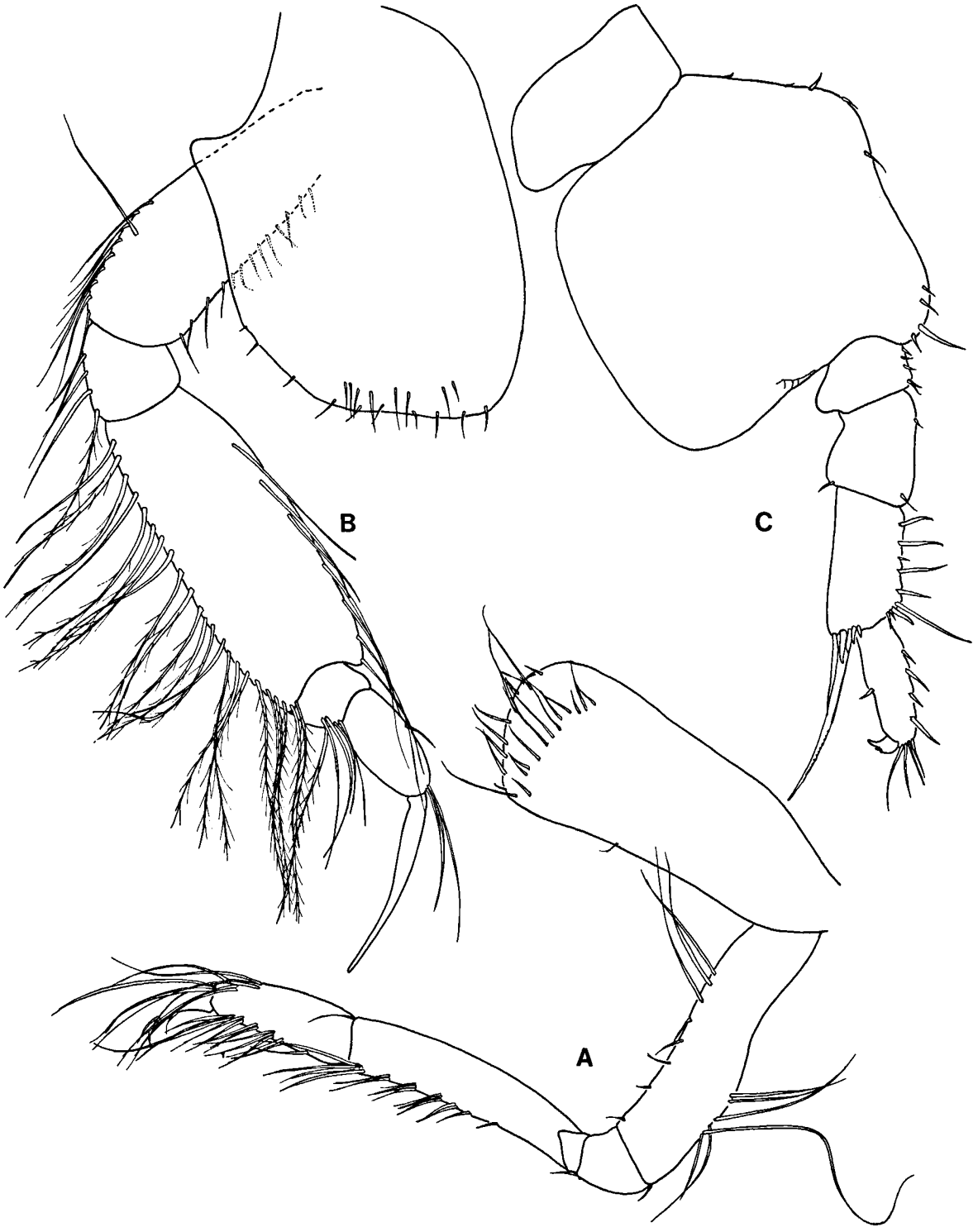

Fig. 7. Ampelisca latifrons, ♀: A, gnathopod 2; B, pereopod 4; C, pereopod 6.

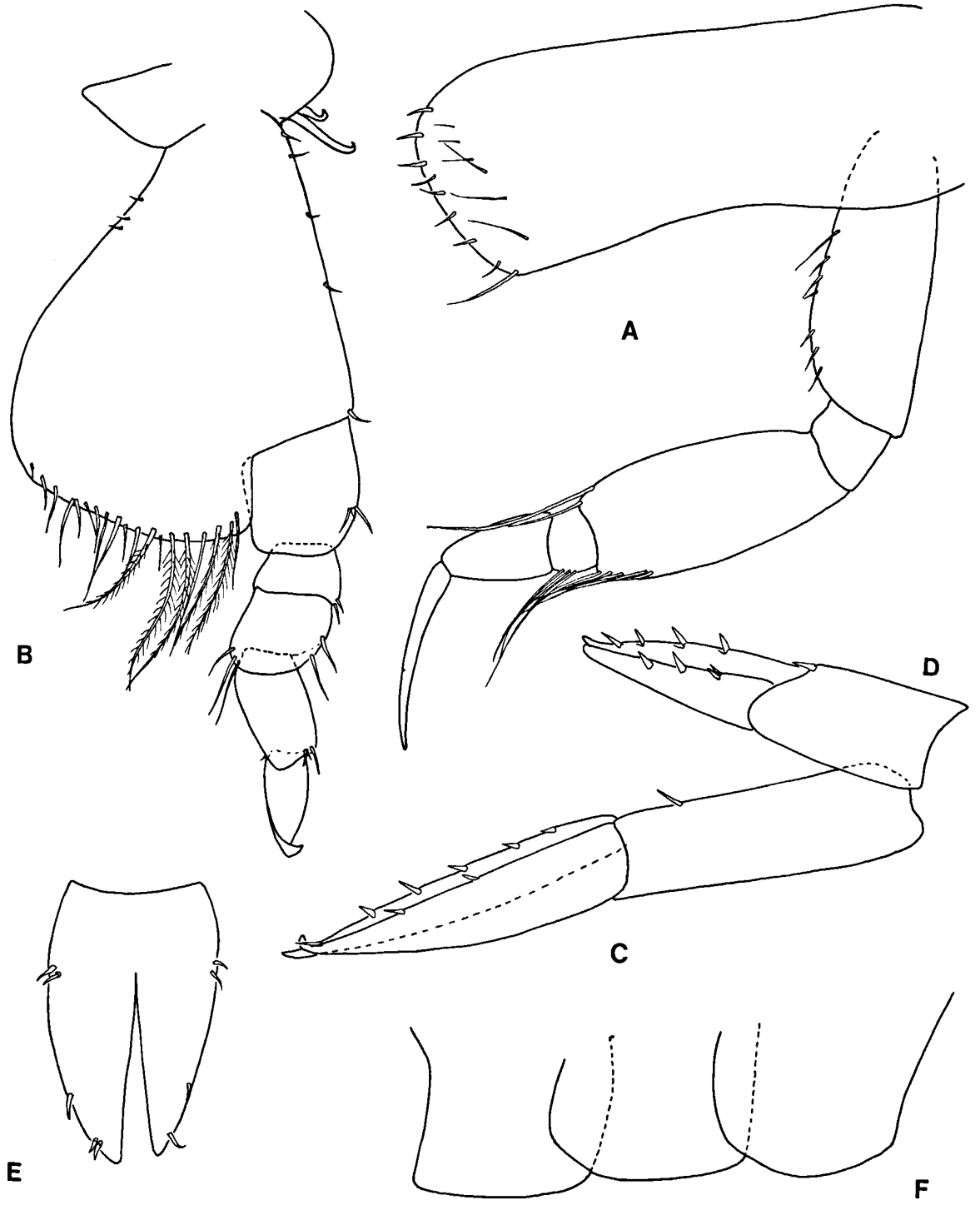

Fig. 8. Ampelisca latifrons, ♀: A, pereopod 3; B, pereopod 7; C, uropod 1; D, uropod 2; E, telson; F, epimeral plates 1, 2, 3.

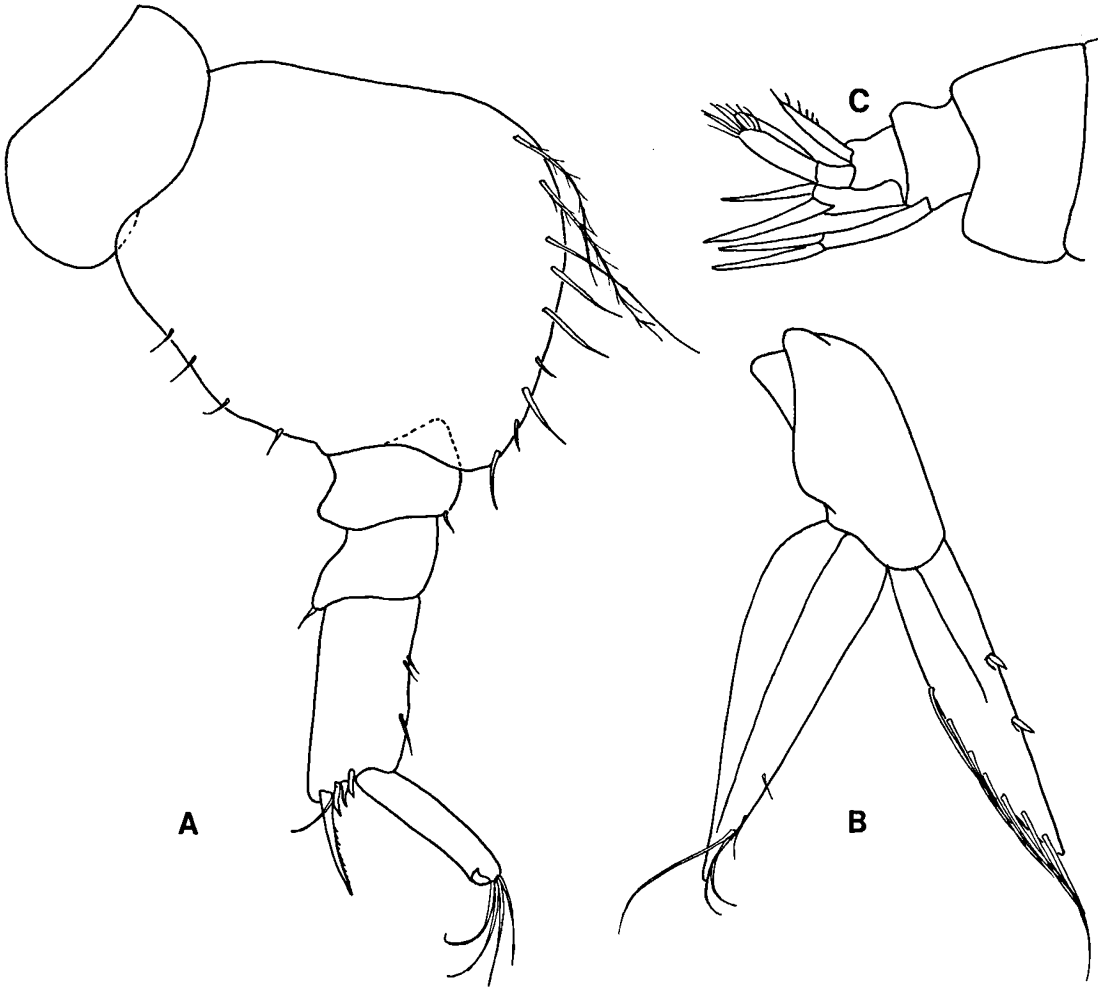

Fig. 9. Ampelisca latifrons (A–B ♀, C ♂): A, pereopod 5; B, uropod 3; C, posterior part.

Most of the species (65.5%) were found to be rare or quite rare (37 rare and 37 quite rare). One species was very common (*Ampelisca brevicornis* s. l.), 9 were quite common, 9 were common, and 20 were uncommon. Actually, the 10 most frequent species (8.8%) (*Ampelisca brevicornis, A. diadema, A. pseudospinimana, A. sarsi, A. spooneri, A. spinipes, A. typica, Hippomedon denticulatus, Maera othonis*, and *Harpinia antennaria*) represented 35% of the entire amphipod collections. With a few exceptions (*Ampelisca armoricana, A. spinimana, Photis longipes, Atylus vedlomensis, Harpinia excavata, Bathyporeia elegans*, and *Urothoe pulchella*), this group included also the most abundant species. Therefore, although data concerning abundances must be considered qualitative, the genus *Ampelisca* (21 species and 70% of the individuals) dominated the group of the most frequent and abundant species.

Vertical distribution of species

Although sampling took place from 12 to 635 m deep, most of the samples (75%) were obtained over the isobath of 150 m, which might have introduced a bias into the present results.

Thirty-nine species (34.5% of the total) were limited to the first 100 m. The dominant families within this group, with 61.5% of the species, were

Table I. Absolute frequencies and abundances of the species. The Seplat cruises in which the species were found are indicated.

Species	Absolute frequency	Absolute abundance	Occurrence (Sep. cruise)
Ampelisca brevicornis s.l.	74	185	4,5,6,7,8
Maera othonis	39	55	3,4,5,6,7,8
Ampelisca diadema	35	56	4,5,6,7,8
Harpinia antennaria	31	36	5,6,7,8
Ampelisca sarsi	30	38	4,5,6,7,8
Ampelisca spooneri	27	44	5,6,7,8
Ampelisca typica	24	35	4,5,6,7,8
Ampelisca pseudospinimana	21	34	4,5,7,8
Ampelisca spinipes	21	29	3,4,5,6,7,8
Hippomedon denticulatus	21	27	4,5,6,7
Atylus vedlomensis	20	30	4,5,6,7
Perioculodes longimanus	18	18	5,6,7,8
Ampelisca tenuicornis	15	19	4,5,7,8
Harpinia excavata	13	44	5,8
Hippomedon robustus	13	14	5,6,7,8
Melita obtusata	12	22	5,6,7
Ampelisca armoricana	11	29	5,6,7,8
Psammogammarus caecus	11	14	5,8
Tryphosites longipes	11	14	5,6,8
Ampelisca spinimana	10	32	5,7,8
Phtisica marina	10	12	4,6,7,8
Urothoe pulchella	10	40	5,6,7,8
Ampelisca calypsonis	9	11	3,4,5,6,7
Leptocheirus pectinatus	9	10	4,5
Gammaropsis maculatus	8	10	3,4,5,6,7
Lysianassa plumosa	8	9	4,5,6,7
Eriopisa elongata	7	9	4,5,7,8
Ceradocus semiserratus	6	16	4,7
Lepidepecreum longicorne	6	23	4,5,7
Photis longicaudata	6	12	5,7,8
Urothoe poseidonis	6	20	6,7,8
Westwoodilla caecula	6	8	5,8
Bathyporeia elegans	5	35	6,8
Bathyporeia guilliamsoniana	5	25	5,8
Bathyporeia tenuipes	5	10	5,8
Cheirocratus assimilis	5	6	4,5,7
Gammaropsis sophiae	5	9	6,8
Siphonoecetes dellavallei	5	7	4,5,6,8
Urothoe marina	5	5	5,7
Ampelisca spinifer	4	4	4,5,8
Ichnopus spinicornis	4	4	4,6,7
Monoculodes carinatus	4	4	4,5,6
Urothoe brevicornis	4	4	5,8
Urothoe elegans	4	5	5,7
Ampelisca heterodactyla	3	5	8

Table I. Continuation.

Species	Absolute frequency	Absolute abundance	Occurrence (Sep. cruise)
Ampelisca remora	3	4	5,8
Eusirus longipes	3	3	6,7,8
Harpinia pectinata	3	10	4,7
Leptocheirus hirsutimanus	3	3	4,6
Liljeborgia pallida	3	3	7,8
Lysianassa inesperata	3	3	5
Pontocrates altamarinus	3	3	5
Socarnes erythrophthalmus	3	11	6,8
Ampelisca latifrons	2	2	6,7
Ampelisca pseudosarsi	2	4	4,5
Amphilochus neapolitanus	2	2	4,6
Aora typica	2	5	5
Apherusa bispinosa	2	3	5,7
Biblys guernei	2	2	6,8
Cheirocratus intermedius	2	2	7,8
Cheirocratus sundevalli	2	2	4,5
Halicoides anomalus	2	2	6,7
Haploops nirae	2	3	3,8
Haploops proxima	2	2	6
Leucothoe lilljeborgi	2	2	6,7
Leucothoe occulta	2	2	5,8
Leucothoe spinicarpa	2	5	6,7
Maera grossimana	2	2	3,7
Maerella tenuimana	2	3	5
Microdeutopus versiculatus	2	9	4,5
Monoculodes subnudus	2	2	5
Photis longipes	2	58	5
Pseudoprotella phasma	2	3	6,8
Siphonoecetes kroyeranus	2	2	5,8
Tryphosella caecula	2	2	5,8
Unciola planipes	2	4	5,7
Ampelisca dalmatina	1	1	8
Ampelisca gibba	1	3	5
Ampelisca massiliensis	1	1	4
Ampelisca ruffoi	1	2	7
Ampelisca serraticaudata	1	1	7
Atylus guttatus	1	1	5
Atylus swammerdami	1	1	5
Bathyporeia gracilis	1	1	6
Bathyporeia pelagica	1	2	4
Bathyporeia sarsi	1	1	6
Ericthonius brasiliensis	1	1	8
Eriopisella pusilla	1	4	4
Harpinia crenulata	1	1	8
Harpinia laevis	1	1	5
Iphimedia minuta	1	1	7

Table I. Continuation.

Species	Absolute frequency	Absolute abundance	Occurrence (Sep. cruise)
Idunella longirostris	1	1	4
Lembos longipes	1	1	5
Leptocheirus tricristatus	1	2	4
Leucothoe incisa	1	1	5
Leucothoe oboa	1	1	6
Leucothoe procera	1	1	6
Leucothoe richiardii	1	1	6
Liljeborgia kinahani	1	1	6
Lysianassa ceratina	1	1	7
Megamphopus cornutus	1	1	4
Megamphopus longicornis	1	1	6
Melita hergensis	1	2	4
Megaluropus agilis	1	1	7
Metaphoxus pectinatus	1	1	4
Monoculodes borealis	1	1	4
Nicippe tumida	1	1	6
Parhyale richardi	1	2	7
Pontocrates arenarius	1	12	5
Siphonoecetes striatus	1	1	8
Stenothoe richardi	1	1	5
Tritaeta gibbosa	1	1	7
Unciola crenatipalma	1	1	7

the Pontoporeiidae (6/6 species), Ampeliscidae (5/24 species), and Leucothoidae (4/7 species), followed by the Dexaminidae, Aoridae, and Lysianassidae (3/4 species for the first, and 3/10 species for the other two) (Table II). The single species of Acanthonotozomatidae, Amphilochidae, Hyalidae, and Ischyroceridae found in this study were sampled also shallower than 100 m.

All families were found from 0 to 150 m, but the most widely represented ones were the Ampeliscidae (23/24 species), Melitidae (11/12 species), Lysianassidae (10/10 species), Aoridae (8/10 species), Pontoporeiidae (6/6 species), and Leucothoidae (6/7 species). Forty-six species were found deeper than 150 m. The most important specific representation of the different families was found from 0 to 350 m. Only six families (Ampeliscidae, Corophiidae, Leucothoidae, Melitidae, Oedicerotidae, and Phoxocephalidae) were represented at deeper levels, and only two species were sampled at more than 500 m (*Leucothoe occulta* and *Harpinia excavata*) (Fig. 10).

Table II. Vertical distribution of the species.

Species	Depth (m)
Atylus swammerdami	12
Pontocrates arenarius	12
Siphonoecetes striatus	19
Parhyale richardi	20
Ampelisca serraticaudata	25
Lysianassa ceratina	25
Bathyporeia pelagica	25
Bathyporeia tenuipes	19–27
Megaluropus agilis	30
Tritaeta gibbosa	33
Bathyporeia guilliamsoniana	19–36
Urothoe pulchella	19–37
Atylus guttatus	39
Iphimedia minuta	40
Lepidepecreum longicorne	12–47
Urothoe brevicornis	20–47
Bathyporeia elegans	47
Maerella tenuimana	47
Bathyporeia sarsi	48
Siphonoecetes kroyeranus	12–50
Ampelisca heterodactyla	25–50
Lysianassa inesperata	22–51
Lysianassa spinicarpa	33–52
Leucothoe oboa	52
Leptocheirus tricristatus	54
Melita hergensis	54
Microdeutopus versiculatus	26–57
Megamphopus longicornis	61
Amphilochus neapolitanus	37–64
Leucothoe incisa	68
Leucothoe richiardii	70
Monoculodes borealis	70
Idunella longirostris	71
Metaphoxus pectinatus	71
Ampelisca remora	26–74
Ericthonius brasiliensis	74
Lembos longipes	83
Bathyporeia gracilis	85
Ampelisca latifrons	30–93
Ceradocus semiserratus	39–105
Eriopisella pusilla	105
Urothoe poseidonis	19–108
Ampelisca spinimana	22–108
Ampelisca massiliensis	110
Photis longipes	12–113
Pontocrates altamarinus	20–113
Monoculodes subnudus	22–113
Leptocheirus pectinatus	12–115
Ampelisca armoricana	18–118
Gammaropsis sophiae	33–118
Harpinia laevis	121
Stenothoe richardi	121

Table II. Continuation.

Species	Depth (m)
Leptocheirus hirsutimanus	50–124
Leucothoe procera	124
Monoculodes carinatus	68–126
Phtisica marina	27–134
Photis longicaudata	19–135
Pseudoprotella phasma	60–135
Ampelisca pseudosarsi	122–139
Ampelisca tenuicornis	33–140
Tryphosella caecula	117–140
Harpinia crenulata	140
Nicippe tumida	140
Hippomedon robustus	84–145
Cheirocratus intermedius	138–145
Ampelisca ruffoi	147
Unciola crenatipalma	150
Ampelisca typica	20–155
Urothoe marina	22–155
Ampelisca sarsi	18–160
Liljeborgia pallida	33–165
Gammaropsis maculatus	52–170
Ampelisca spinifer	43–177
Cheirocratus sundevalli	68–184
Tryphosites longipes	12–185
Haploops nirae	45–185
Socarnes erythrophthalmus	100–185
Liljeborgia kinahani	190
Cheirocratus assimilis	58–205
Lysianassa plumosa	22–218
Perioculodes longimanus	19–222
Aora typica	223
Halicoides anomalus	205–228
Unciola planipes	190–235
Atylus vedlomensis	12–242
Harpinia pectinata	78–242
Ampelisca diadema	26–253
Hippomedon denticulatus	31–253
Ampelisca gibba	253
Maera othonis	20–282
Leucothoe lilljeborgi	256–290
Ampelisca brevicornis s.l.	12–300
Harpinia antennaria	54–300
Megamphopus cornutus	20–304
Apherusa bispinosa	39–310
Eusirus longipes	113–310
Urothoe elegans	94–320
Maera grossimana	65–325
Ichnopus spinicornis	105–325
Byblis guernei	310–350
Ampelisca spooneri	22–355
Siphonoecetes dellavallei	23–355
Melita obtusata	37–355
Ampelisca spinipes	45–355

Table II. Continuation.

Species	Depth (m)
Ampelisca pseudospinimana	49–370
Ampelisca dalmatina	277–383
Ampelisca calypsonis	45–395
Haploops proxima	130–402
Eriopisa elongata	265–410
Westwoodilla caecula	19–433
Psammogammarus caecus	74–433
Leucothoe occulta	50–635
Harpinia excavata	107–635

Several species (e.g. *Ampelisca brevicornis* s.l., *A. diadema, A. spooneri, Megamphopus cornutus, Siphonoecetes dellavallei, Maera othonis,* and *Westwoodilla caecula*) were found from less than 30 m to more than 250 m, exhibiting therefore apparent eurybathic characteristics.

Species distribution according to the type of substrate

Fifty-four species (48%) were found exclusively in a particular type of substrate, viz. 7 (6.2%) on rock, 5 (4.4%) in gravel or gravelly sand, 2 (1.8%) in coarse sand, 33 (29.2%) in medium or fine sand, 4 (3.5%) in muddy sand, 1 (0.9%) in sandy mud, and 2 (1.8%) in mud (Table III). Thirty-six (67%) of these species were sampled only once (quite rare), and consequently their preferences to the type of substrate cannot be considered significant. The remaining 60 species (53%) were found in different substrates, of which 11 (18%) occurred both in rocky and soft bottoms (Table III).

Bottom grabs appeared to be inadequate for quantitative sampling. Therefore, the available biological data were considered qualitative and, for the analysis of these data, we only took into consideration the absolute frequencies of the species. The statistical approach (taking only into consideration the links with a correlation equal or superior to 0.50) allowed the identification of the following groups of species (Fig. 11):

Group 1: Fifty-six species found exclusively or predominantly in medium to fine sand bottoms. Nevertheless, a clear gradient of distribution is re-

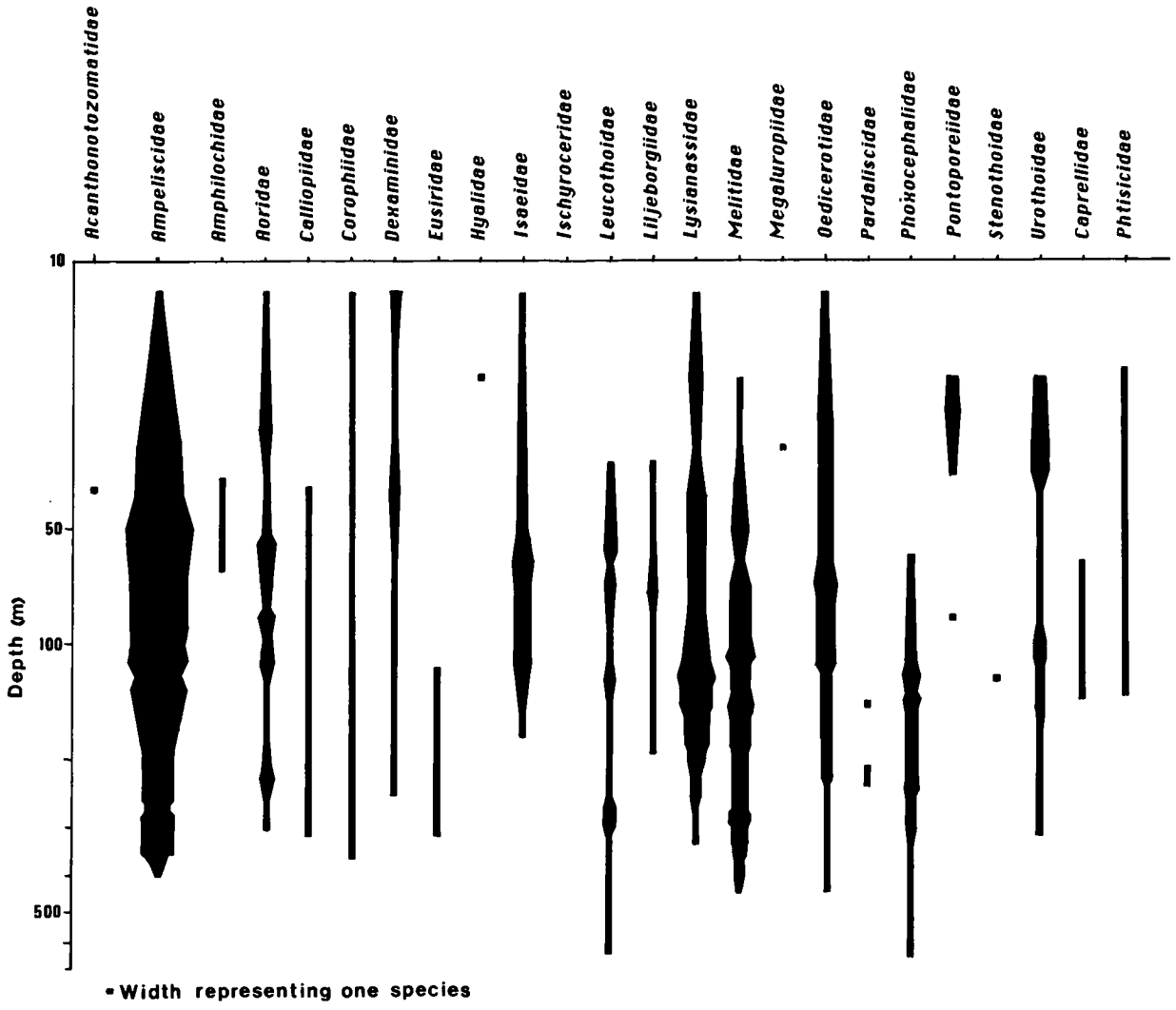

Fig. 10. Relative importance of the families according to depth. The width of the columns represents the number of species.

Table III. Species distribution according to the type of substrate. Numbers indicate the absolute frequencies of the species in each type of substrate. R = rock; G–GS = gravel or gravelly sand; CS = coarse sand; MFS = medium or fine sand; MS = muddy sand; SM = sandy mud; M = mud.

Species	Type of substrate						
	R	G–GS	CS	MFS	MS	SM	M
Ampelisca serraticaudata	1						
Iphimedia minuta	1						
Leucothoe richiardii	1						
Liljeborgia kinahani	1						
Lysianassa ceratina	1						
Melita hergensis	1						
Parhyale richardi	1						
Leucothoe spinicarpa	1	1					
Liljeborgia pallida	1	2					

Table III. Continuation.

Species	Type of substrate						
	R	G–GS	CS	MFS	MS	SM	M
Ceradocus semiserratus	1	2	2				
Lepidepecreum longicorne	1	1	1	3			
Pseudoprotella phasma	1			1			
Urothoe poseidonis	1			5			
Ampelisca spooneri	1	3		22	1		
Amphilochus neapolitanus	1				1		
Maera othonis	2	8	5	14	8	1	
Phtisica marina	2	1		5	1		1
Gammaropsis maculatus	1	1	1	2	1	1	1
Atylus guttatus		1					
Harpinia laevis		1					
Leucothoe incisa		1					
Megaluropus agilis		1					
Tritaeta gibbosa		1					
Leptocheirus hirsutimanus		2	1				
Ampelisca latifrons		1		1			
Aora typica		1		1			
Gammaropsis sophiae		1		4			
Hippomedon robustus		2		11			
Lysianassa inesperata		2		1			
Maerella tenuimana		1		1			
Perioculodes longimanus		1		17			
Tryphosites longipes		3		8			
Unciola planipes		1		1			
Urothoe marina		2		3			
Ampelisca brevicornis s.l.		6	7	52	9		
Ampelisca pseudospinimana		6	1	10	4		
Ampelisca sarsi		3		26	1		
Atylus vedlomensis		6		11	3		
Cheirocratus assimilis		3			2		
Cheirocratus sundevalli		1			1		
Harpinia pectinata		1		1	1		
Ichnopus spinicornis		1		2	1		
Leptocheirus pectinatus		4		4	1		
Hippomedon denticulatus		4	1	15	1		
Lysianassa plumosa		2	1	3	2		
Melita obtusata		1		10	1		
Monoculodes carinatus		2		1	1		
Ampelisca calypsonis		1		3	3	2	
Ampelisca tenuicornis		4		8	2	1	
Ampelisca diadema		5	1	14	6	2	7
Ampelisca spinipes		2		14	2	1	2
Ampelisca typica		11	1	8	1		3
Apherusa bispinosa		1					1
Photis longicaudata		1		4			1
Socarnes erythrophthalmus		1		1			1
Idunella longirostris			1				
Monoculodes borealis			1				
Haploops proxima			1	1			
Microdeutopus versiculatus			1	1			
Harpinia antennaria			1	28	2		
Ampelisca gibba				1			

Table III. Continuation.

Species	Type of substrate						
	R	G–GS	CS	MFS	MS	SM	M
Ampelisca remora				3			
Ampelisca ruffoi				1			
Atylus swammerdami				1			
Bathyporeia elegans				5			
Bathyporeia gracilis				1			
Bathyporeia guilliamsoniana				5			
Bathyporeia pelagica				1			
Bathyporeia sarsi				1			
Bathyporeia tenuipes				5			
Byblis guernei				2			
Cheirocratus intermedius				2			
Ericthonius brasiliensis				1			
Eusirus longipes				3			
Halicoides anomalus				2			
Harpinia crenulata				1			
Lembos longipes				1			
Leptocheirus tricristatus				1			
Leucothoe lilljeborgi				2			
Leucothoe oboa				1			
Leucothoe occulta				2			
Leucothoe procera				1			
Monoculodes subnudus				2			
Nicippe tumida				1			
Photis longipes				2			
Pontocrates altamarinus				3			
Pontocrates arenarius				1			
Siphonoecetes kroyeranus				2			
Siphonoecetes striatus				1			
Unciola crenatipalma				1			
Urothoe brevicornis				4			
Urothoe elegans				4			
Urothoe pulchella				10			
Ampelisca armoricana				10	1		
Ampelisca heterodactyla				2	1		
Ampelisca pseudosarsi				1	1		
Ampelisca spinifer				3	1		
Ampelisca spinimana				8	2		
Siphonoecetes dellavallei				4	1		
Psammogammarus caecus				3	1		7
Westwoodilla caecula				5	1		
Maera grossimana				1		1	
Eriopisa elongata				1	2	1	3
Ampelisca massiliensis					1		
Megamphopus cornutus					1		
Megamphopus longicornis					1		
Metaphoxus pectinatus					1		
Harpinia excavata					1	2	10
Tryphosella caecula					1		1
Eriopisella pusilla						1	
Haploops nirae						1	1
Ampelisca dalmatina							1
Stenothoe richardi							1

vealed inside of it. Actually, 4 subgroups were considered, viz.: A (43 species), B (4 species), C (6 species), and D (3 species). From A to D the specificity concerning this substrate decreased gradually, although the preferences for it still remained high.

Group 2: Nineteen species found in different types of substrate, from rock to mud, although still preferentially in medium to fine sand. It was also possible to consider 2 major subgroups, viz.: A (8 species), and B (6 species). The subgroup A included species found more frequently in gravel or gravelly sand up to medium or fine sand bottoms. The subgroup B included species well represented in these substrates but also frequently recorded in muddy sand and sandy mud bottoms. *Monoculodes carinatus, Harpinia pectinata, Ampelisca calypsonis, A. pseudosarsi,* and *Maera grossimana*, all uncommon to rare species, although included in the group, showed less clear substrate preferences.

Group 3: Four species, all rare to quite rare, found from coarse sand to medium or fine sand.

Group 4: Eleven uncommon to quite rare species, recorded exclusively or predominantly from gravel or gravelly sand bottoms.

Group 5: Six species found exclusively or preferentially in muddy bottoms.

Group 6: Two rare species with very indefinite substrate preferences.

Group 7: Two rare or quite rare species, confined to sandy mud or mud bottoms.

Group 8: Five species exclusively or preferentially found in sandy mud bottoms. The presence of *Amphilochus neapolitanus* in this group was probably accidental, due to a small hard substrate or to a wreck at the bottom. Actually this species normally occurs in rocky bottoms.

Group 9: Eight species found exclusively or preferentially on rock.

Data analysis clearly showed a distributional gradient of the soft bottom species from the sandy to the muddy pole (groups 1 to 8), while rocky species appeared obviously separated (group 9). Although groups 1 to 8 tend to express a gradient, it was possible to identify clear substrate affinities. Actually, all *Bathyporeia* (Pontoporeiidae) and *Urothoe* (Urothoidae), 6 of 7 Oedicerotidae species, and 18 of 21 *Ampelisca* species (including the most abundant ones) belong to groups 1 and 2, showing therefore a very strong preference to medium up to fine sand bottoms. Other families and genera showed less clear preferences to a particular type of substrate, or they were too scarce to have any significance.

Although the area sampled was approximately constant, the amount of sediment collected was not always the same, depending on the bottom compactness and on the depth. In addition, the number of samples was not the same in each type of substrate. Despite this important bias, these results indicate that medium or fine sand bottoms are the richest ones in number of species. In addition, 90% of the most frequent and abundant species (*Ampelisca brevicornis* s.l., *A. diadema, A. pseudospinimana, A. sarsi, A. spinipes, A. spooneri, Harpinia antennaria, Hippomedon denticulatus*, and *Maera othonis*) occurred preferentially in this type of substrate. Therefore, this indicates that medium or fine sand bottoms might offer favoured environmental conditions for the development of amphipod populations in the area studied.

Discussion and conclusions

Among 113 species identified, 29 were recorded for the first time along the Portuguese coast, which reflects clearly the incomplete knowledge of the composition of the amphipod fauna in this area. Actually, despite recent studies concerning species inventory and ecology (Marques & Bellan-Santini, 1985; Marques, 1989), the available data cannot yet be considered exhaustive, particularly for hard substrates and deeper levels. Further studies, especially at deeper levels, are therefore necessary, as well as the accomplishment of the ongoing programmes.

Along the Portuguese coast, despite the bias introduced by the concentration of the sampling efforts at the most superficial levels (excluding the intertidal zone), results showed that the most frequent and abundant species presented also wide ranges of vertical distribution. In addition, these species were found preferentially in medium or fine sand bottoms. Thus, the geometrical configuration of the habitats might be the most important factor

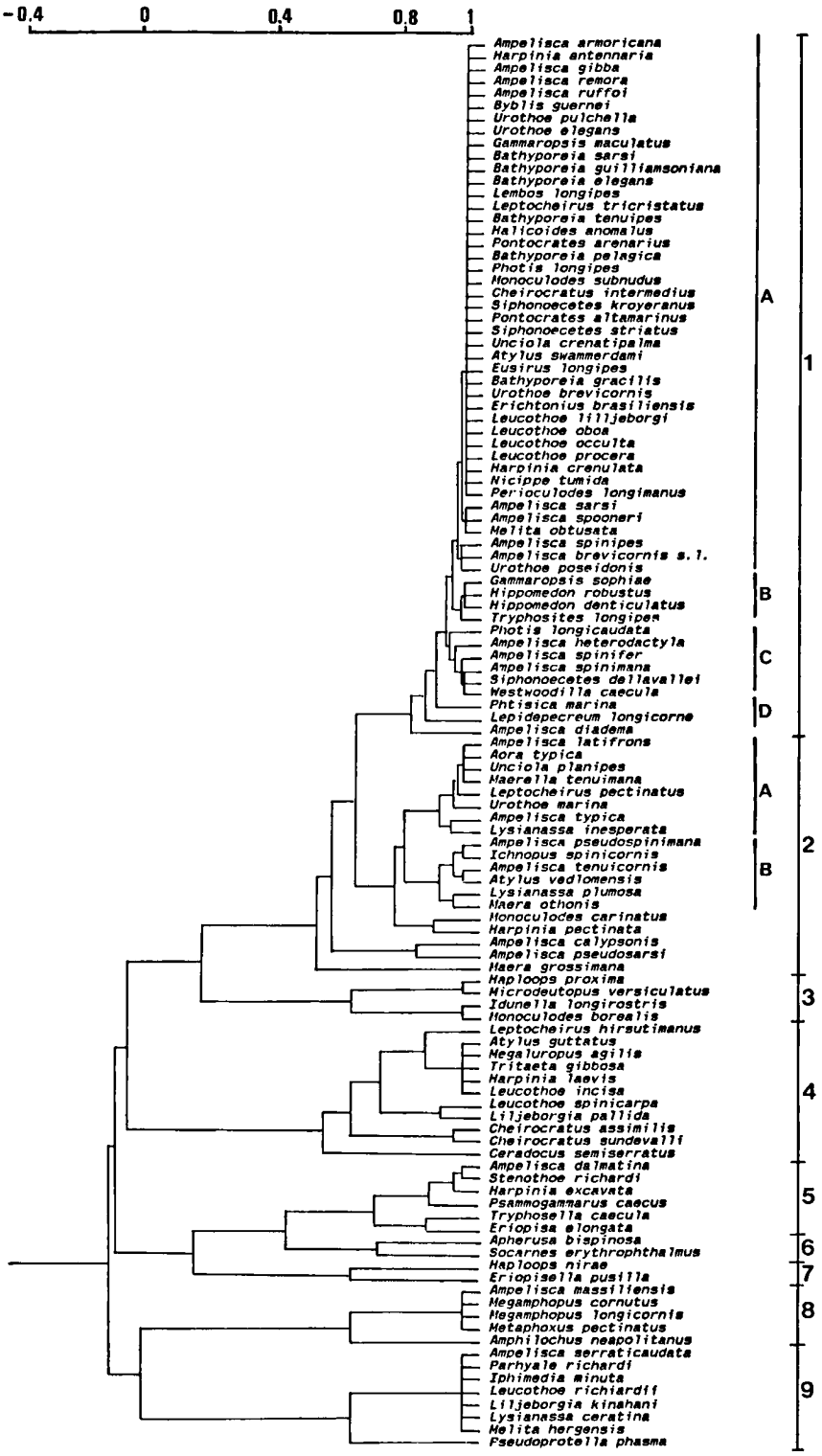

Fig. 11. Statistical analysis of species distribution according to the type of substrate (*R* analysis). Correlation coefficient of Pearson, UPGMA $r = 0.90702$. Groups and subgroups discussed in the text are indicated.

conditioning the development of amphipod populations. Actually, this factor conditions the oxygenation levels, the rate of water renovation and the number of shelters. In addition, it might also condition the quantity of nutritional resources suitable for amphipods.

The group of the most frequent and abundant species (common or very common species) was dominated by *Ampelisca*, probably due to the great number of samples in fine soft bottoms. These results are coincident with the composition of the amphipod fauna found, for example, in the West-Manche, before the Amoco Cadiz oil spill (Dauvin, 1988). Although demersal fishes adapt their food items to the available prey, it has been observed that they feed on the macrobenthic fauna, especially amphipod crustaceans, while polychaetes and bivalves appear only as secondary prey animals (Dauvin, 1988). Thus, at least in the shelf sediments, *Ampelisca* species might have a key role as food for many secondary consumers. The nutritional resource represented by amphipods, that was pointed out by other authors (Bellan-Santini & Dauvin, 1988), is due to the secondary production of several co-inhabitant species, and consequently it seems that interspecific interactions should be relatively limited.

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