

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 rôle 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.

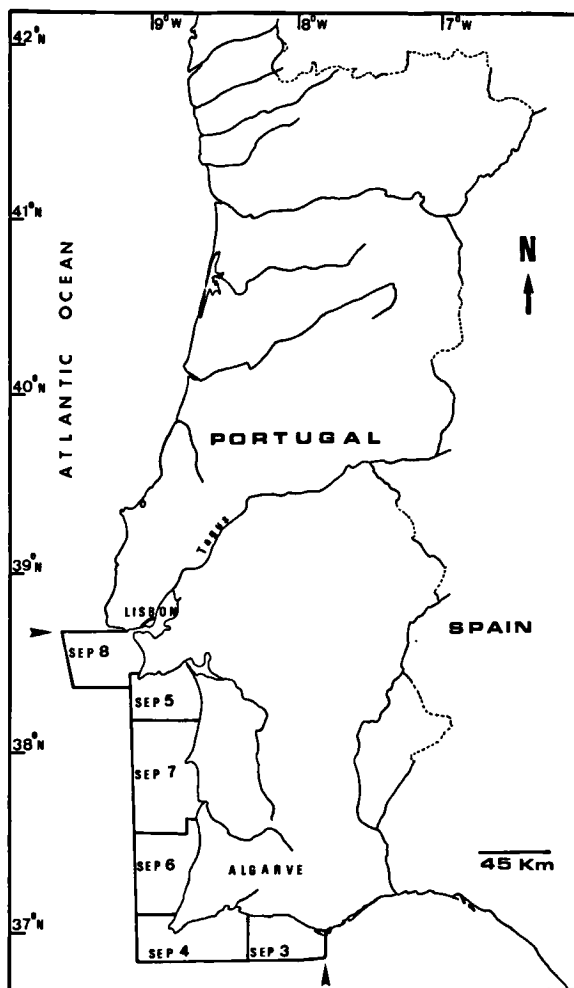


Fig. 1. Area studied. The localisation of each Seplat cruise (SEP) is indicated on the map.

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. 1. (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**
Amphilocheus 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**
Erichthonius 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
Lepidepcreum 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
Periocolodes 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 medio-distally.

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

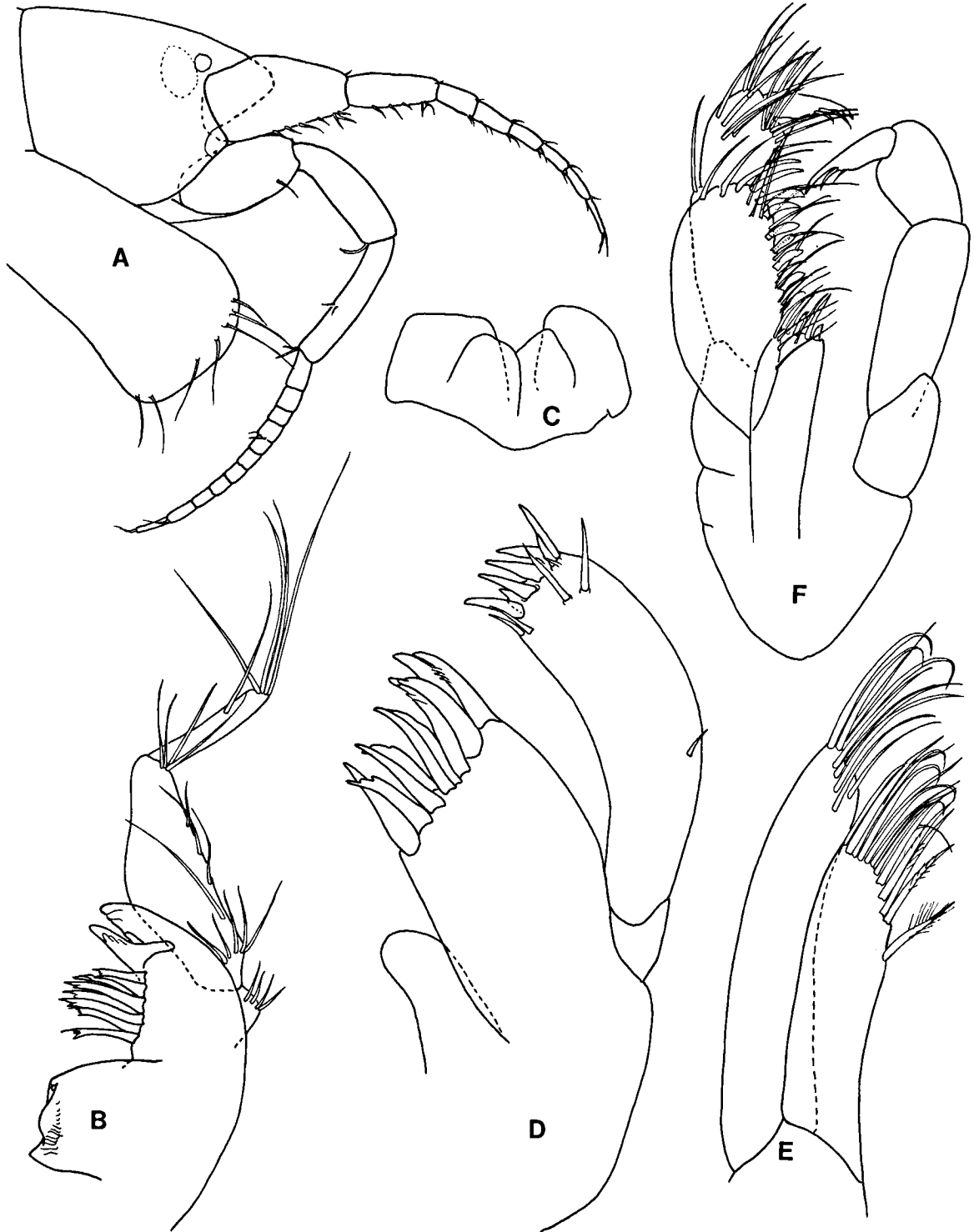


Fig. 2. *Ampelisca heterodactyla*, ♀: A, head; B, mandible; C, labium; D, maxilla 1; E, maxilla 2; F, maxilliped.



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

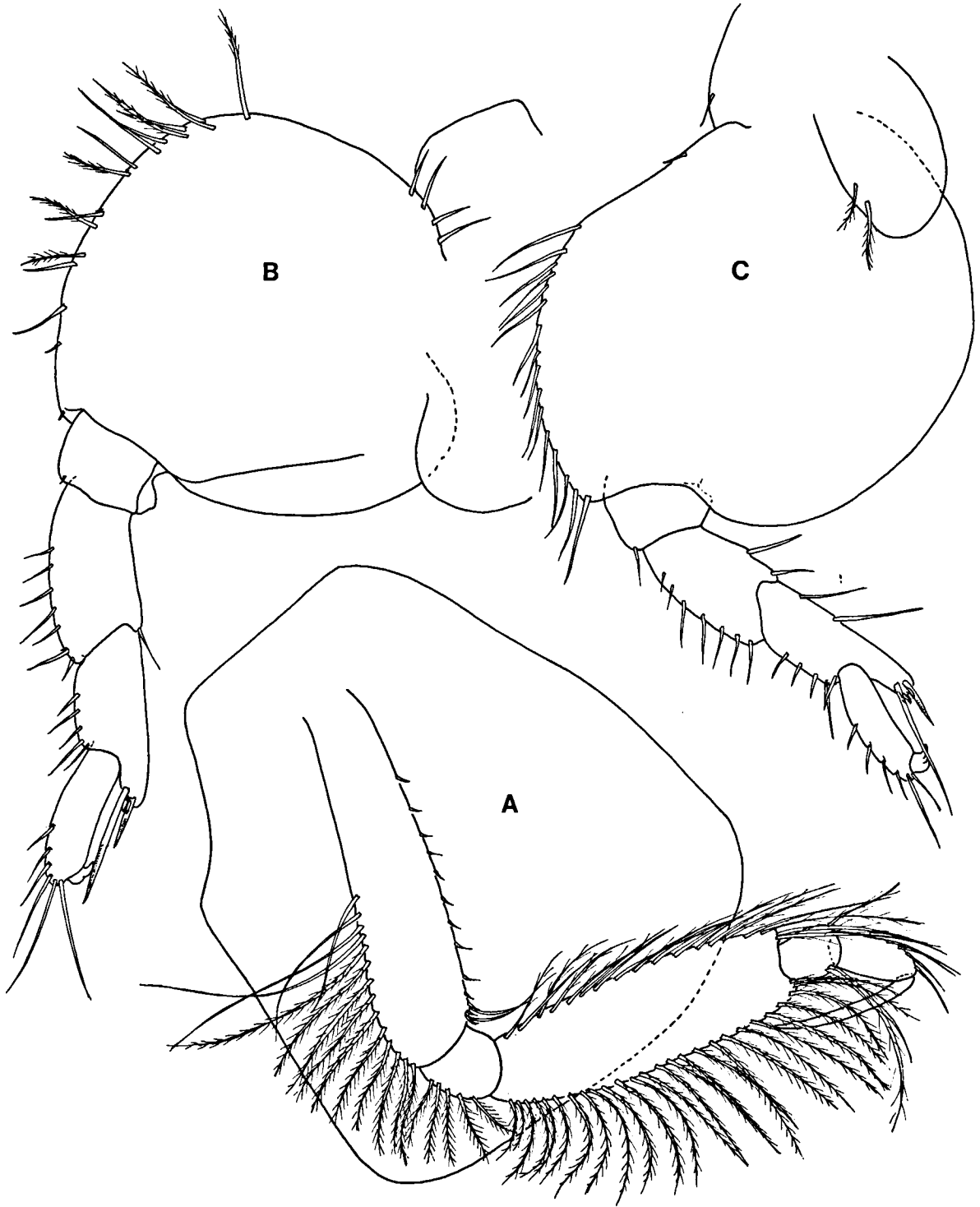


Fig. 4. *Ampelisca heterodactyla*, ♀: A, pereopod 4; B, pereopod 5; C, pereopod 6.

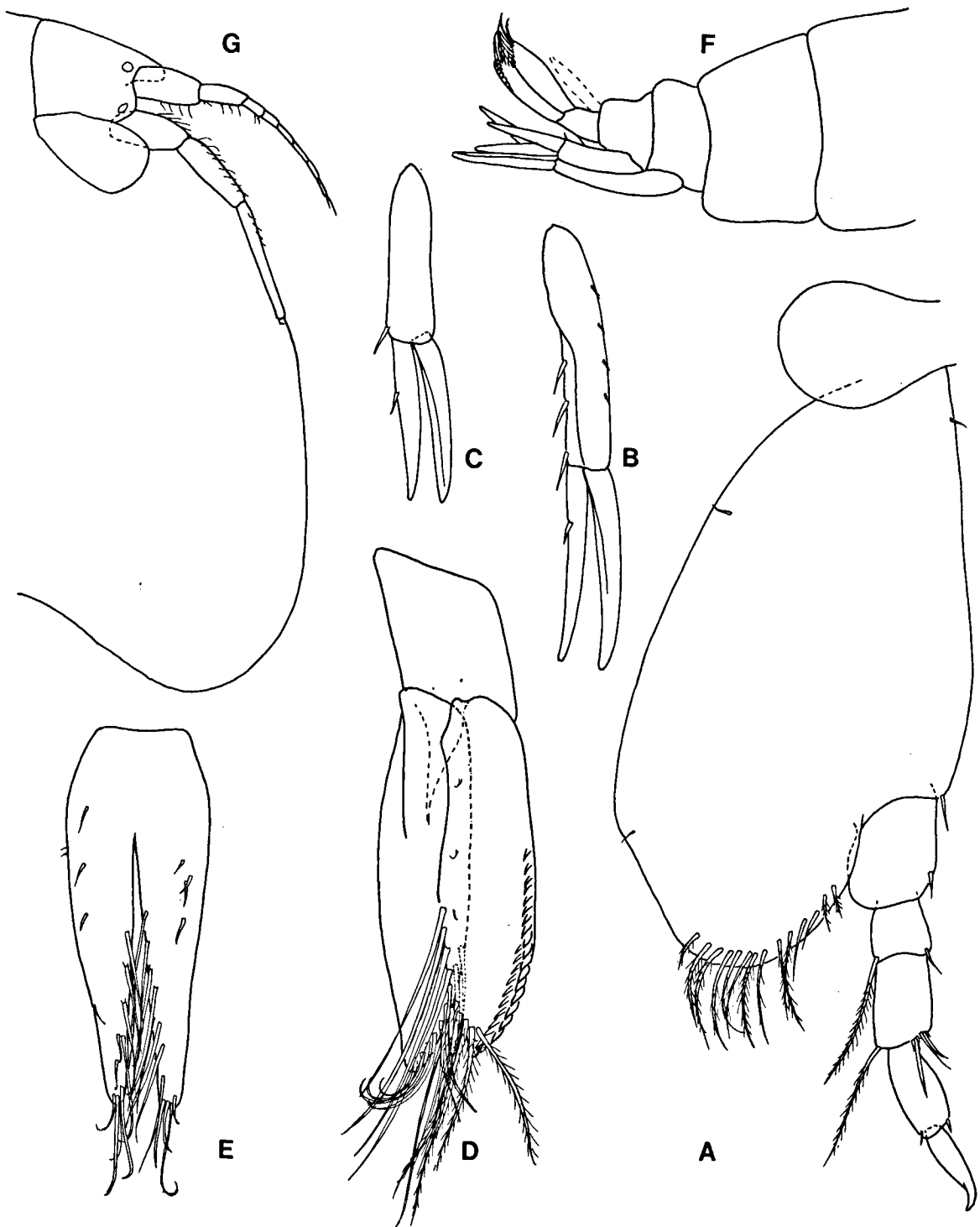


Fig. 5. *Ampelisca heterodactyla* (A–E ♀, F–G ♂): A, pereopod 7; B, uropod 1; C, uropod 2; D, uropod 3; E, telson; F, posterior part; G, head.

(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 spécimens 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 postero-distal 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 rare (only once).



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

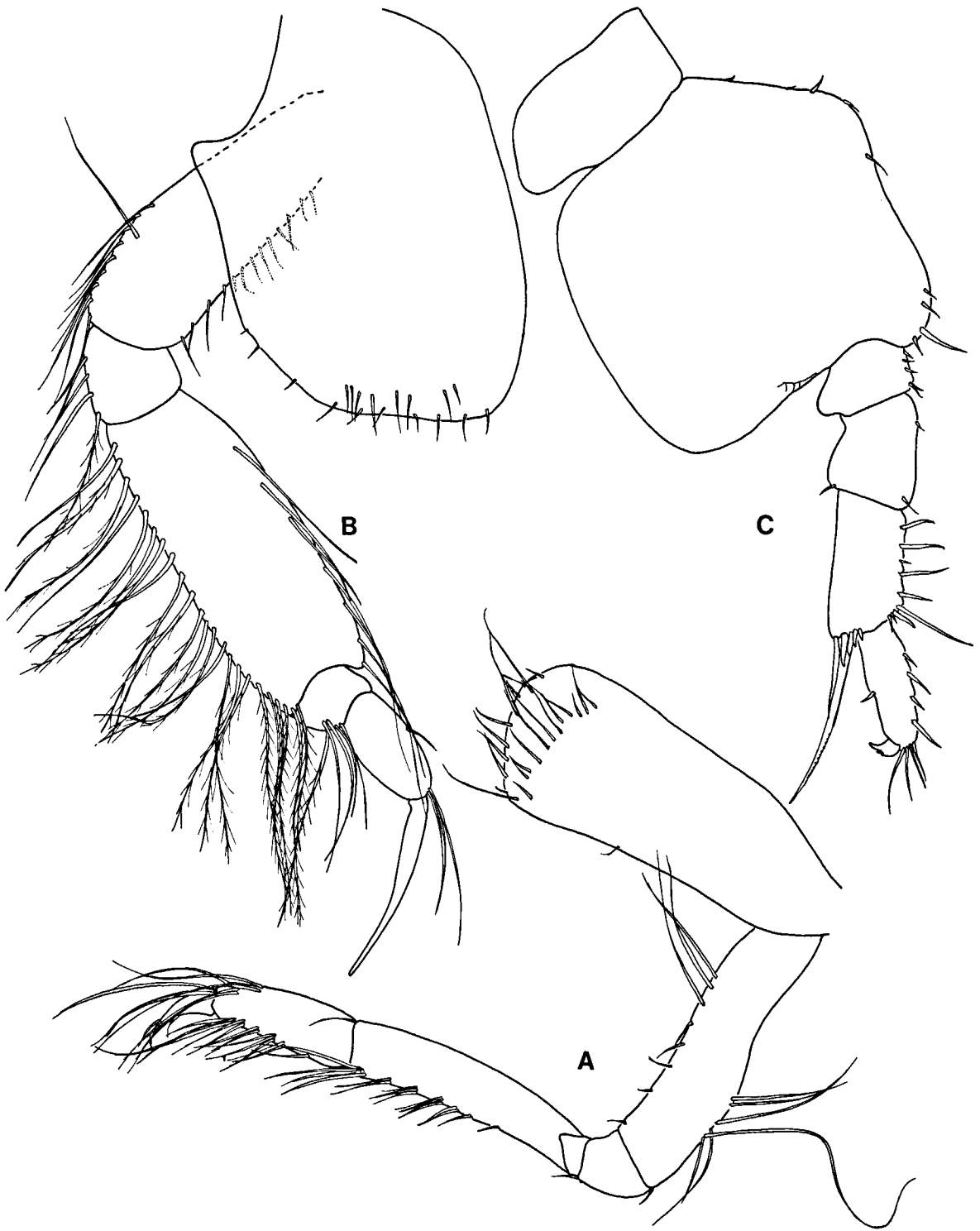


Fig. 7. *Ampelisca latifrons*, ♀: A, gnathopod 2; B, pereopod 4; C, pereopod 6.

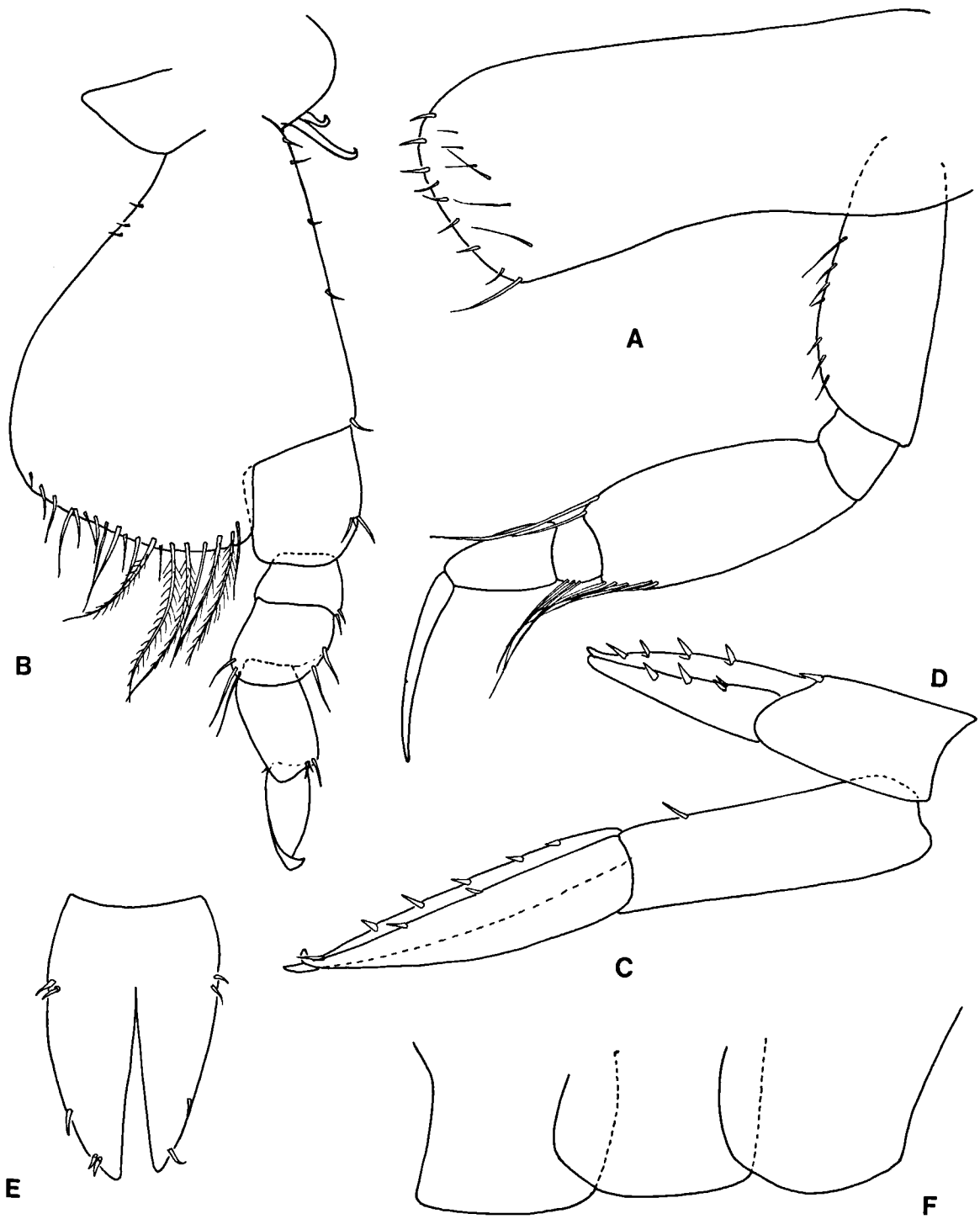


Fig. 8. *Ampelisca latifrons*, ♀: A, pereopod 3; B, pereopod 7; C, uropod 1; D, uropod 2; E, telson; F, epimeral plates 1, 2, 3.

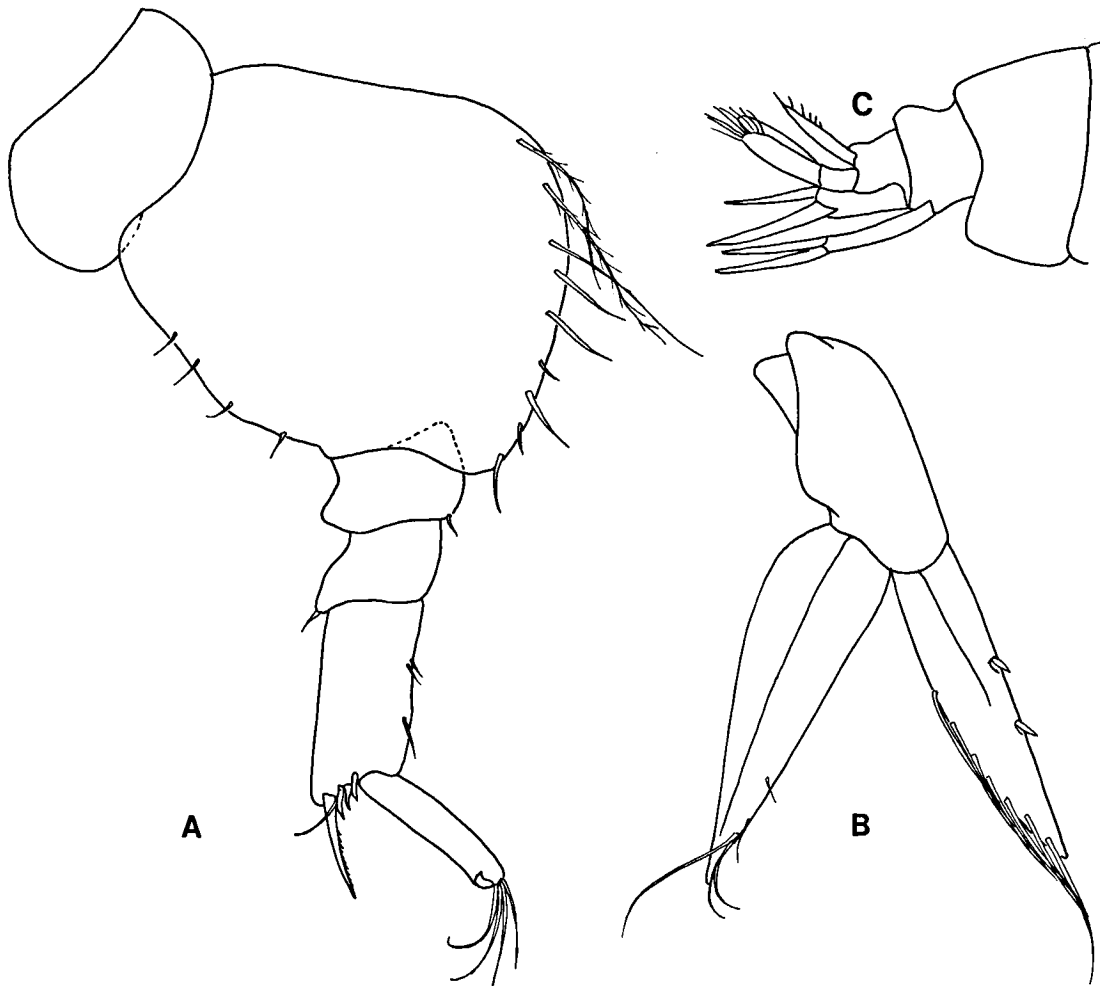


Fig. 9. *Ampelisca latifrons* (A–B ♀, C ♂): A, pereopod 5; B, uropod 3; C, posterior part.

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 abun-

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

Table I. Continuation.

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

Table I. Continuation.

Species	Absolute frequency	Absolute abundance	Occurrence (Sep. cruise)
<i>Idunella longirostris</i>	1	1	4
<i>Lembos longipes</i>	1	1	5
<i>Leptocheirus tricristatus</i>	1	2	4
<i>Leucothoe incisa</i>	1	1	5
<i>Leucothoe oboa</i>	1	1	6
<i>Leucothoe procera</i>	1	1	6
<i>Leucothoe richiardii</i>	1	1	6
<i>Liljeborgia kinahani</i>	1	1	6
<i>Lysianassa ceratina</i>	1	1	7
<i>Megamphopus cornutus</i>	1	1	4
<i>Megamphopus longicornis</i>	1	1	6
<i>Melita hergensis</i>	1	2	4
<i>Megaluropus agilis</i>	1	1	7
<i>Metaphoxus pectinatus</i>	1	1	4
<i>Monoculodes borealis</i>	1	1	4
<i>Nicippe tumida</i>	1	1	6
<i>Parhyale richardi</i>	1	2	7
<i>Pontocrates arenarius</i>	1	12	5
<i>Siphonocetes striatus</i>	1	1	8
<i>Stenothoe richardi</i>	1	1	5
<i>Tritaeta gibbosa</i>	1	1	7
<i>Unciola crenatipalma</i>	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)
<i>Atylus swammerdami</i>	12
<i>Pontocrates arenarius</i>	12
<i>Siphonocetes striatus</i>	19
<i>Parhyale richardi</i>	20
<i>Ampelisca serraticaudata</i>	25
<i>Lysianassa ceratina</i>	25
<i>Bathyporeia pelagica</i>	25
<i>Bathyporeia tenuipes</i>	19–27
<i>Megaluropus agilis</i>	30
<i>Tritaeta gibbosa</i>	33
<i>Bathyporeia guilliamsoniana</i>	19–36
<i>Urothoe pulchella</i>	19–37
<i>Atylus guttatus</i>	39
<i>Iphimedia minuta</i>	40
<i>Lepidepecreum longicorne</i>	12–47
<i>Urothoe brevicornis</i>	20–47
<i>Bathyporeia elegans</i>	47
<i>Maerella tenuimana</i>	47
<i>Bathyporeia sarsi</i>	48
<i>Siphonocetes kroyeranus</i>	12–50
<i>Ampelisca heterodactyla</i>	25–50
<i>Lysianassa inesperata</i>	22–51
<i>Lysianassa spinicarpa</i>	33–52
<i>Leucothoe oboa</i>	52
<i>Leptocheirus tricristatus</i>	54
<i>Melita hergensis</i>	54
<i>Microdeutopus versiculatus</i>	26–57
<i>Megamphopus longicornis</i>	61
<i>Amphilochus neapolitanus</i>	37–64
<i>Leucothoe incisa</i>	68
<i>Leucothoe richiardii</i>	70
<i>Monoculodes borealis</i>	70
<i>Idunella longirostris</i>	71
<i>Metaphoxus pectinatus</i>	71
<i>Ampelisca remora</i>	26–74
<i>Erichthonius brasiliensis</i>	74
<i>Lembos longipes</i>	83
<i>Bathyporeia gracilis</i>	85
<i>Ampelisca latifrons</i>	30–93
<i>Ceradocus semiserratus</i>	39–105
<i>Eriopisella pusilla</i>	105
<i>Urothoe poseidonis</i>	19–108
<i>Ampelisca spinimana</i>	22–108
<i>Ampelisca massiliensis</i>	110
<i>Photis longipes</i>	12–113
<i>Pontocrates altamarinus</i>	20–113
<i>Monoculodes subnudus</i>	22–113
<i>Leptocheirus pectinatus</i>	12–115
<i>Ampelisca armoricana</i>	18–118
<i>Gammaropsis sophiae</i>	33–118
<i>Harpinia laevis</i>	121
<i>Stenothoe richardi</i>	121

Table II. Continuation.

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

Table II. Continuation.

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

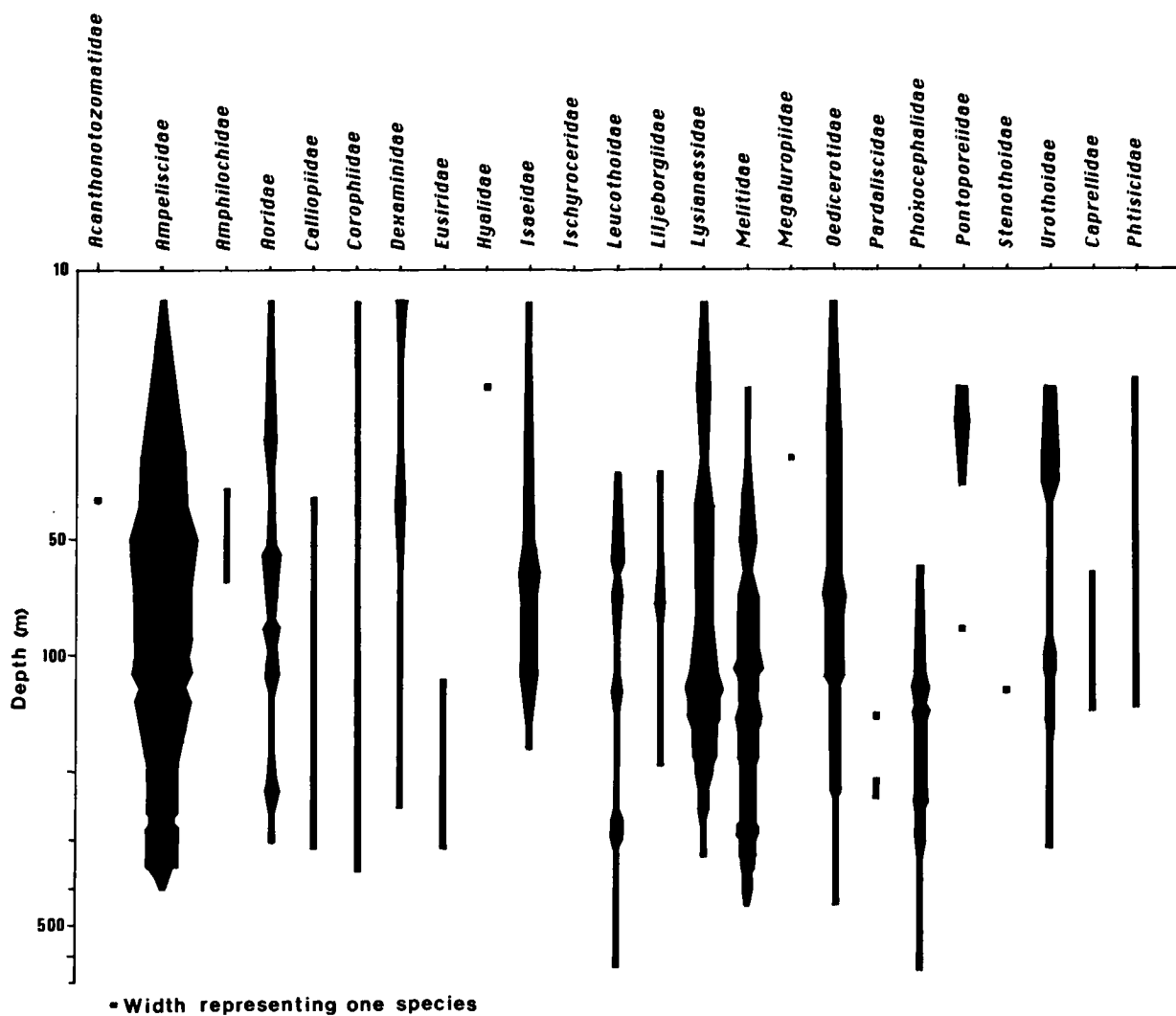


Fig. 10. Relative importance of the families according to depth. The width of the columns represents the number of species.

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
<i>Ampelisca serraticaudata</i>	1						
<i>Iphimedia minuta</i>	1						
<i>Leucothoe richardii</i>	1						
<i>Liljeborgia kinahani</i>	1						
<i>Lysianassa ceratina</i>	1						
<i>Melita hergensis</i>	1						
<i>Parhyale richardi</i>	1						
<i>Leucothoe spincarpa</i>	1	1					
<i>Liljeborgia pallida</i>	1	2					

Table III. Continuation.

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

Table III. Continuation.

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

dant 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

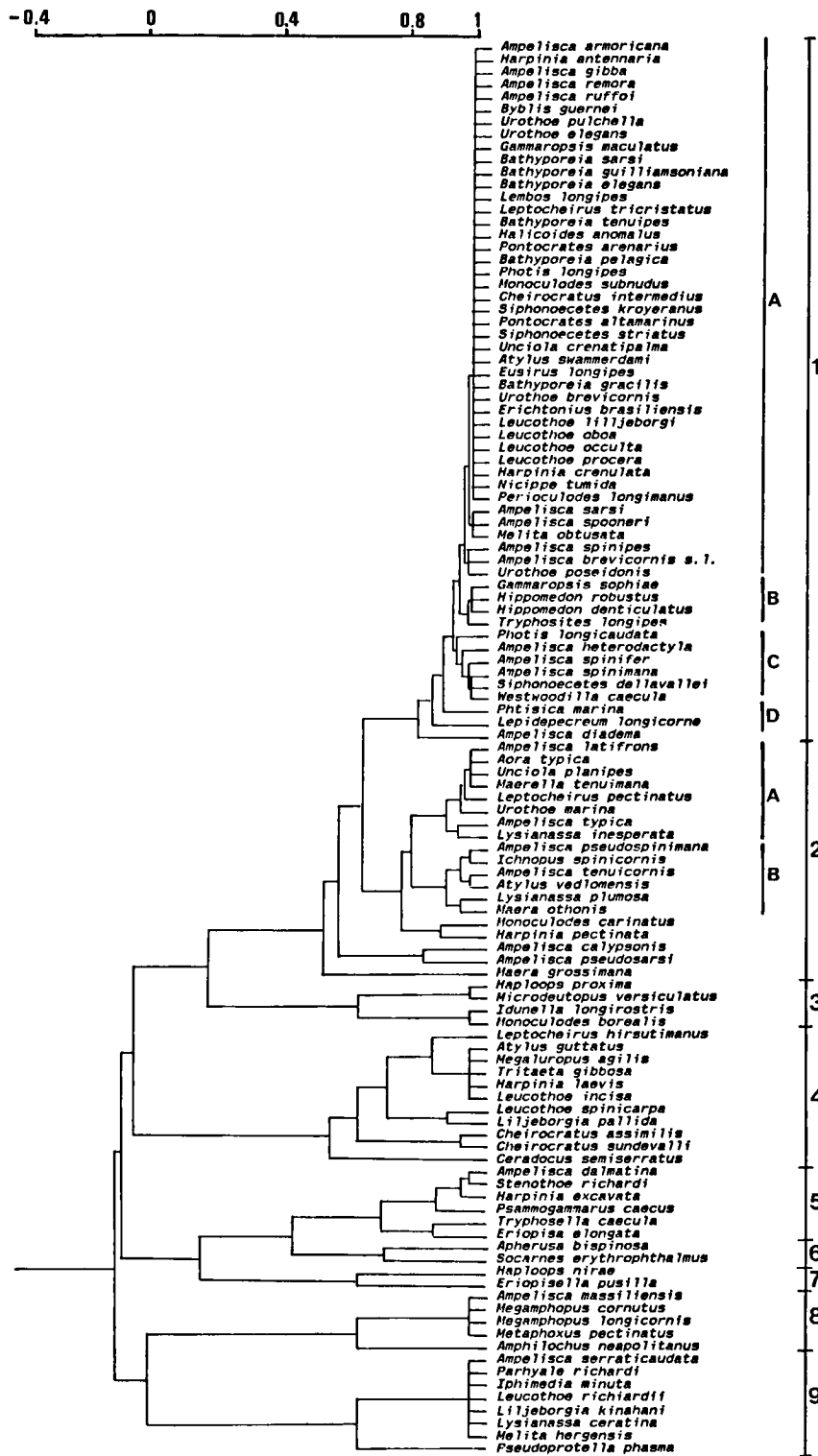


Fig. 11. Statistical analysis of species distribution according to the type of substrate (*R* analysis). Correlation coefficient of Pearson, UPGMA $r = 0.90702$. Groups and subgroups discussed in the text are indicated.

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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