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Diversity of epibenthic habitats of gammaridean amphipods in the eastern Weddell Sea

Abstract Gammaridean amphipods appear ubiquitous in the shelf communities of the eastern Weddell Sea where more than 230 species have been recorded. Comparison of catches of the 40 most common species taken by different gears and ethological observations in the aquarium allowed us to distinguish 6 groups: endobenthic, epibenthic, hyperbenthic (or suprabenthic), benthopelagic, pelagic and cryopelagic. Only epibenthic species, which form the bulk of the fauna, are dealt with in the present paper. Aquarium observations indicated three different epibenthic strata occupied by amphipods: the sediment surface, and a lower and upper level on the substrata formed by sessile suspension feeders. In addition, four symbiotic microhabitats were detected in or on sponges, ascidians, hydrozoans and gorgonians.

Introduction

Recent observations by still and video underwater cameras, coupled with analyses of benthos samples, have allowed a precise description of the variety of benthic assemblages from the eastern Weddell Sea shelf (i.e. Galéron et al. 1992; Gutt and Schickan 1998; Gutt and Starmans 1998). The continental shelf, to a depth of more than 600 m, is colonised in many places by species-rich assemblages of abundant, diverse and multistratified suspension feeders, such as sponges, bryozoans, cnidarians, hydrozoans, holothurians and crinoids. However, there is a gradient of species-rich assemblages of suspension feeders, mostly in the Kapp Norvegia region, to extremely poor detritus-feeder assemblages, in the southernmost part of the Weddell Sea. The shelf-bottom cover appears mostly patchy and ranges from a few percent to 100% of the bottom surface. The patchy, diverse and multistratified sessile benthos offers a high diversity of potential microhabitats to small vagile invertebrates.

Gammaridean amphipods, often collected in benthic samples, seem to be ubiquitous in the bottom communities of the eastern Weddell Sea, where they constitute an abundant and diverse group (Voss 1988; De Broyer and Klages 1990; Klages 1991; De Broyer et al. 1997, 1999). Their precise habitats, however, are usually unknown. Some recent "Polarstern" campaigns provided new data on amphipod distribution, which are partly analysed in this paper, in an attempt to document the habitats (and as far as possible the microhabitats) of the 40 most common epibenthic species of the eastern Weddell Sea.

Materials and methods

Sampling

The amphipod material analysed here was collected in the eastern Weddell Sea during the Antarctic summer cruises EPOS 3 (1989), EASIZ I (1996) and EASIZ II (1998) of the RV "Polarstern" (Arntz et al. 1990; Arntz and Gutt 1997, 1999). Benthic samples were taken along different transects, mainly off Kapp Norvegia, southwest of Vestkapp, in Drescher Inlet, and off Halley Bay, at depths from 60 m down to 2,500 m (Fig. 1). In total, 130 catches provided about 80,000 specimens of amphipods belonging to more than 230 species. Collecting gears included Agassiz trawl, bottom trawl, benthopelagic trawl, Rauschert's dredge, epibenthic sledge, TV grab, giant box corer, multibox corer and "autonomous" baited traps. Voucher specimens are kept at the "Antarctic Marine Biodiversity Reference Centre", devoted to amphipods, at the Royal Belgian Institute of Natural Sciences in Brussels, Belgium.

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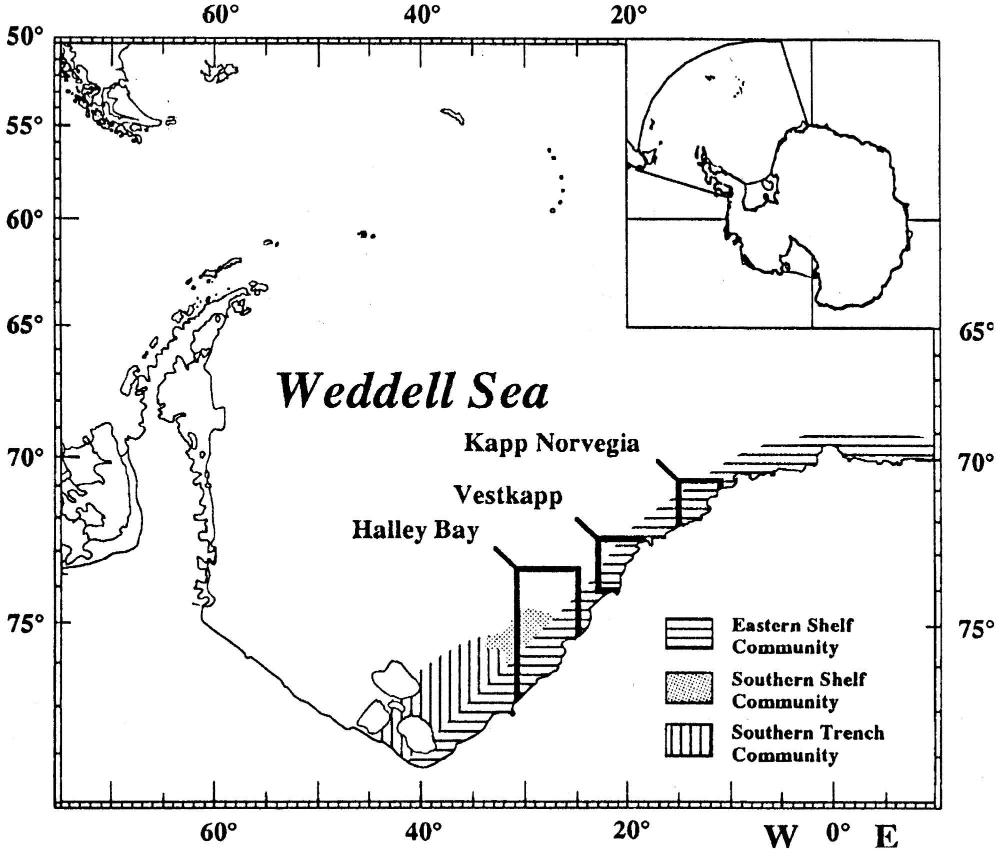

Fig. 1 Investigated areas and major macrobenthic assemblages (after Voss 1988; Galeron et al. 1992) on the eastern Weddell Sea shelf

Habitat characterisation

Identification of the amphipod macrohabitats was based on a comparative analysis of catches taken by different collecting gears. Description of particular microhabitats relied on aquarium and incidental catch observations during the cruises, as well as on published records (Kunzmann 1996). Bathymetric distribution (Table 1) refers to collection data from the cited Weddell Sea cruises.

Aquarium observations

Ethological observations (habitat choice and mobility patterns: swimming, crawling, walking, climbing or burrowing) were performed on living specimens kept in a cool container on board (mostly during the "Polarstern" EASIZ II cruise), and afterwards in a cool laboratory at IRScNB, Brussels. The amphipods were maintained at −1°C (±1°C) in aquaria with volumes of 2–30 l. Aquaria were provided with different kind of substrates, according to the known or suspected life-style of studied species. A large aquarium with a "reconstituted natural bottom" (30 cm high) was used to study the species behaviour. The "reconstituted" bottom was composed of a mosaic of mixed (fine/coarse) sediment, sponge spicule mat, stones and different common sessile organisms such as sponges, cnidarians, hemichordates and bryozoans. Observations were qualitative; movements and position of amphipods in aquaria were checked at least twice a day for a period of 10–56 days and typical behaviours were video-recorded.

Results

Comparative analysis of catches allowed to distinguish six major amphipod habitats in the neritic zone (Fig. 2). The *endobenthic* habitat is composed of the first centimetres of the sediment and is occupied by sedentary tube- or "cell"-dwellers of the family Ampeliscidae and by sedentary and temporary burrowers belonging to the Oedicerotidae, Phoxocephalidae and Lysianassoidea. The *epibenthic* habitat with three strata, described hereafter, is colonised by numerous free-living species, the most abundant being the Epimeriidae, Eusiridae s.l., Iphimediidae and Lysianassoidea. Among the epibenthos, several *symbiotic* and *inquilinous* microhabitats are occupied mainly by some Colomastigidae, Dexaminidae, Leucothoidae, Lysianassoidea, Sebidae, Stenothoidae and Stilipedidae. The Benthic Boundary Layer forms the *hyperbenthic* (or suprabenthic) habitat of some swimming Eusiridae s.l. and Lysianassoidea. Few Epimeriidae, Eusiridae s.l., Lysianassoidea and Stegocephalidae occupy the neritic water column, showing either a *benthopelagic* or a purely *pelagic* life-style. In the *cryopelagic* habitat, i.e. the under-surface of the sea ice, three species (one lysianassoid and, surprisingly, two stenothoids) have been incidentally recorded so far. Only the epibenthic level is analysed in detail here; the other compartments will be dealt with elsewhere.

The epibenthic habitats

The epibenthic layer of the eastern Weddell Sea shelf includes all habitats from the sediment surface level up to the top of sessile organisms, which offer secondary

Table 1 Epibenthic habitats and motility patterns of gammaridean amphipods from the eastern Weddell Sea (*according to Kunzmann 1996)

Species	Epibenthic macrohabitat	Substrate/ microhabitat	E. Weddell Sea depth range (m)	Motility pattern	Aquarium observations		Feeding type (according to Y. Scailteur, unpublished work)
					N (days)	*N* (ind.)	
Melitidae sp. nov.	Surface	Soft	246–836	Weakly motile	45	84	Macrophagous deposit feeder
Melphidippa antarctica	Surface	Soft	232–672	Weakly motile	50	28	Suspension feeder (passive)
Epimeria georgiana	Surface	Soft + mixed	184–928	Weakly motile	10	70	Macrophagous deposit feeder
	Lower level	Sessile benthos			51	52	
Liljeborgia georgiana	Surface	Detritic + mixed	196–1030	Weakly motile	50	28	Macropredator/deposit feeder
Paraceradocus gibber	Surface	Detritic + mixed	118–793	Weakly motile	56	34	Macrophagous deposit feeder
Waldeckia obesa	Surface + ?	Detritic?	80–1030	Highly motile	50	500	Scavenger
Abyssorchomene scotianensis	Surface + ?	Detritic?	600–1500	Highly motile			Scavenger
Orchomenella acanthura	Surface + ?	Detritic?	170–261	Highly motile			Scavenger? Detritivore?
O. pinguides	Surface + ?	Detritic?	234–301	Highly motile			Scavenger
Parschisturella carinata	Surface + ?	Detritic?	219–2081	Highly motile	53	100	Scavenger
Tryphosella murrayi	Surface + ?	Detritic?	80–920	Highly motile	55	71	Scavenger/macro-predator
Uristes adarei	Surface + ?	Detritic?	233–690	Highly motile			Macropredator/deposit feeder
U. gigas	Surface + ?	Detritic?	236–810	Highly motile	40	32	Macrophagous deposit feeder
Echiniphimedia hodgsoni	Lower level	Sponges + bryozoans?	188–1130	Weakly motile	53	40	Micropredatory browser
Echiniphimedia scotti	Lower level	Sponges + bryozoans?	118–571	Weakly motile	50	25	Micropredator
Gnathiphimedia mandibularis	Lower level	Bryozoans + sponges	170–773	Weakly motile	55	55	Micropredatory browser
Iphimediella cyclogena	Lower level	Sessile benthos	178–889	Weakly motile			Micropredator
Maxilliphimedia longipes	Lower level	Sessile benthos	186–617	Weakly motile			Micropredatory browser
Epimeria rubrieques	Lower level	Sessile benthos	352–1030	Weakly motile	46	30	Predator (opportunistic)
Eusirus perdentatus	Surface + lower level	Mixed + sessile benthos	100–928	Moderately motile	55	120	Macropredator
Jassa goniamera	Lower level	Sessile benthos	170–584	Weakly motile	55	20	Suspension feeder (active)
Bathypanoploea schellenbergi	Lower/upper level	Gorgonians?	396–672	Weakly motile			Micropredatory browser
Epimeria macrodonta	Upper level	Sessile benthos	182–1030	Weakly motile	52	62	Predator (opportunistic)
Epimeria robusta	Upper level	Hydrozoans?	233–793	Weakly motile	55	15	Predator (opportunistic)
Epimeria similis	Upper level	Sessile benthos	242–1030	Weakly motile	46	10	Micropredatory browser
Epimeriella walkeri	Upper level	Sessile benthos	184–928	Highly motile	53	28	Macropredator
Hirondellea antarctica	Upper level	Cnidarians?	65–1136	Highly motile			Micropredator
Alexandrella mixta	Upper level	Gorgonians?	242–1543	Highly motile	50	6	Macropredator
*Andaniotes linearis**	Symbiotic	Sponges*	405*	Sedentary?			
*Colomastix simplicicauda**	Symbiotic	Sponges*	228*	Sedentary?			
*Leucothoe spinicarpa**	Symbiotic?	Sponges*	332–771*	Sedentary?			
Scaphodactylus sp. nov. 1	Symbiotic	Sponges	105	Sedentary?			

Table 1 (Contd.)

Species	Epibenthic macrohabitat	Substrate/ microhabitat	E. Weddell Sea depth range (m)	Motility pattern	Aquarium observations N (days)	Aquarium observations N (ind.)	Feeding type (according to Y. Scailteur, unpublished work)
Polycheria antarctica	Symbiotic	Sponges* + ascidians	118–611	Sedentary			Suspension feeder (passive) parasitic predator*
Seba antarctica	Symbiotic	Sponges* + ascidians	253–399	Sedentary			Suspension feeder (passive) parasitic predator*
Leucothoe sp.	Symbiotic	Ascidians	399	Sedentary?			
Orchomenyx sp.	Symbiotic	Ascidians	186	Sedentary?			
Metopoides sp. nov. 2	Symbiotic	Ascidians	600–800	Sedentary?			
Torometopa sp. nov. 1	Symbiotic	Hydrozoans	230	Sedentary?			
Torometopa sp. nov. 6	Symbiotic	Hydrozoans	165	Sedentary?			
Thaumatelson sp. Z	Symbiotic	Hydrozoans?	214	Sedentary?			
Torometopa sp. nov. 5	Symbiotic	Gorgonians	400	Sedentary?			
Polycheria sp.	Symbiotic	Gorgonians?	64–110	Sedentary			

substrates to colonisers. Its thickness can reach about 1 m, as shown by bottom pictures and the size of the largest sessile invertebrates collected. Amphipods appear roughly distributed on the bottom in three different strata: the sediment surface and the lower and upper strata of the sessile epibenthos (Table 1 and Fig. 3).

The sediment surface

Heterogeneous in its composition, structure and thickness, the sediment surface varies from the soft type such as sand and mud to the detritic type such as coarse bryozoan debris or sponge spicule mats. Dropstones from icebergs can be mixed with this soft or coarse sediment. This heterogeneous sediment surface, often with cracks, interstices and holes, offers a great variety of microhabitats to a number of small vagile invertebrates such as amphipods (Fig. 4). Some amphipod species live only temporarily in this biotope, looking for transitory substrate and protection, while others appear sedentary, finding shelter and food there.

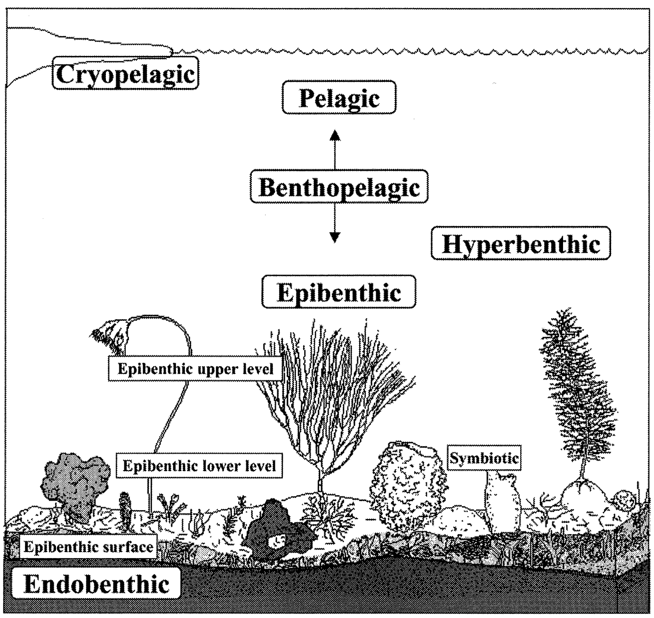

Fig. 2 Scheme of the amphipod macrohabitats in the eastern Weddell Sea neritic zone

Representative species from soft-sediment surface

Melitidae gen nov., sp. nov. Position in aquarium with "reconstituted bottom": stays on the soft-sediment surface, without attempting to burrow or to climb on sessile animals or stones; always keeps contact with the substrate (thigmotropy). Mobility: moderately active; usually walking upright on pereopods; not side-crawling like *Paraceradocus gibber* (Coleman 1989a) despite the similarity of morphology, but can rest on its side; seems unable to swim.

Melphidippa antarctica Schellenberg, 1926 (*Melphidippidae*) Usual position in aquarium is upside down, with dorsum on the bottom resting on the three posterior pereopods with the setose pereopods 3 and 4, as well as antenna 1, directed towards the water column (quite like *Melphidippella macra* Norman, 1869, described by Enequist 1949). Mobility: stays mostly motionless; rarely moving; swimming was not observed; probably sedentary.

Epimeria georgiana Schellenberg, 1931 (*Epimeriidae*) Collected in catches from different kinds of bottoms: bryozoan debris, sponge spicule mats, rich sessile fauna of hydrozoans, sponges, bryozoans and also from soft

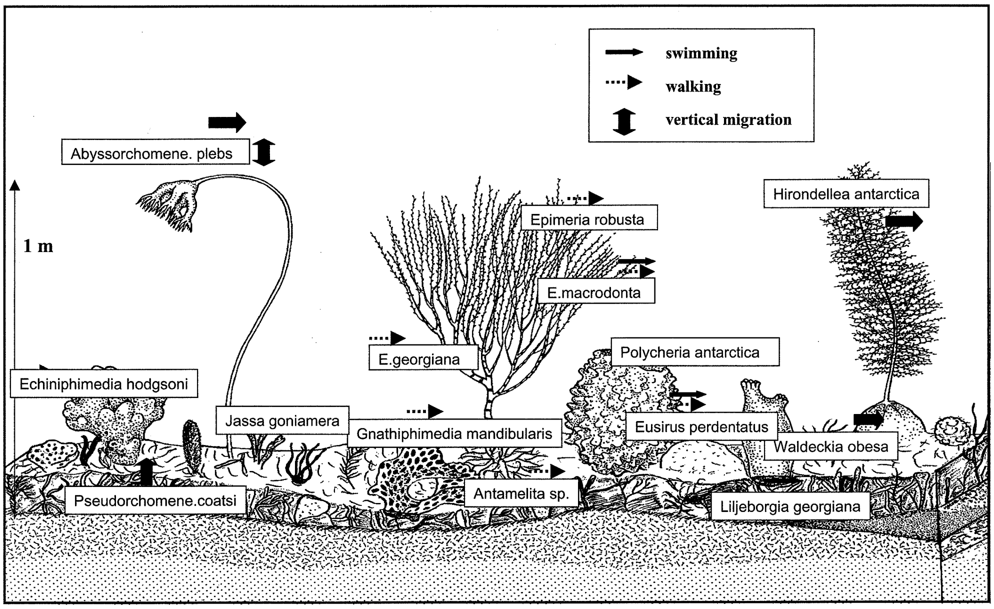

Fig. 3 Scheme of presumed epibenthic habitats of some representative species of gammaridean amphipods on the eastern Weddell Sea shelf

muddy bottom very poor in sessile fauna. Usual position in aquarium: apparently not substrate selective; can stay on the sediment surface, without burrowing, or climb and sit on the lower level of erected sessile invertebrates in the aquarium with "reconstituted natural bottom", e.g. at the base of hydrozoan colonies. Mobility: stays usually motionless on the bottom; never observed swimming spontaneously; when induced by direct stimulation with forceps, swimming is always short and clumsy, the amphipod quickly returning to the substrate.

Representative species from coarse or mixed sediment surface

Liljeborgia georgiana Schellenberg, 1931 (*Liljeborgiidae*). Present, always in low number, in mixed-bottom

Fig. 4 Undisturbed sample of detritic bryozoan bottom taken by the multibox corer (ANT XV/3 sta. 02 MG4, northwest of Kapp Norvegia, 174 m)

samples, with bryozoan debris,mud or sand. In aquarium, on "reconstituted bottom", usually stays motionless on the mixed sediment or below the pieces of gauze provided as artificial substrate. Living treelike hemichordates can be used as shelter or substrate. Mobility: able to walk slowly on the substrate in an upright position; the long last pereopods are used for jumping when disturbed by other amphipods or by forceps; swimming, very rarely observed, is jerky and very slow. *Paraceradocus gibber Andres,* 1984 (*Melitidae*) Found in diverse catches often containing a variety of biogenic debris with stones, sand and mud. In a large aquarium with "reconstituted bottom" and in few small aquaria with different bottom types, *P. gibber* shows a strong thigmotropy toward the sediment and does not attempt to climb stones or epibenthic animals. It usually tries to hide the entire body, except the antennae, in any available shelter. On soft sediment, with or without stones, it stays at the surface and was not observed trying to dig. Coleman (1989a), however, observed the species digging a burrow under stones. *P. gibber* seems to be sedentary and able to defend its shelter against other amphipods. Mobility: in all cases, specimens newly introduced into aquarium walk around, mostly crawling on one side. Never observed swimming, which confirms the previous observations by Coleman (1989a) and Klages and Gutt (1990b).

In addition to the two former species probably restricted to this type of bottom, some other species seem to use the sediment surface as a temporary substrate from which they can move, swim and forage in a much larger area, according to their motility patterns. The species of this numerous group all belong to the Lysianassoidea and show common behavioural traits in the aquarium: they usually remain motionless on the substrate and can live close together in high densities; they do not appear to be substrate selective and do not bur-

row in soft sediment. Most are able to swim fast. Representative species include the following.
Waldeckia obesa (*Chevreux,* 1905) From catch observations, they seem to occur on nearly all types of bottoms; always in low numbers in trawl samples but can be collected in thousands in baited traps. In the aquarium, sits at the surface of diverse bottom substrates (except pure soft sediments). Mobility: a sporadic swimmer leaving the bottom substrate to swim sub-vertically to the aquarium surface. Can swim very fast. Also undertakes horizontal swimming trips very close to the bottom. Can walk slowly upright on the substrate. Never seen digging in any kind of sediment.
Uristes gigas Dana, 1949 and *U. adarei* (*Walker*, 1903). On the aquarium bottom, usually seen lying on one side, antennae slowly moving. No observed attempt to dig in the soft sediment or hide in the coarse detritic sediment.
Abyssorchomene scotianensis (*Andres*, 1983), *Lepidecreella* sp A, *Orchomenella acanthura* (*Schellenberg*, 1931), *Orchomenella pinguides* (*Walker*, 1903), *Parschisturella carinata* (*Schellenberg*, 1926), *Tryphosella murrayi* (*Walker*, 1903). All have been observed in the aquarium staying upright (or lying on side: *T. murrayi*) on diverse bottom surfaces. *P. carinata* and *T. murrayi* sometimes hide part of the body in the coarse detritic sediment. Mobility: usually seen motionless but able to swim fast (except *T. murrayi* which swims rather slowly).

The lower level of sessile epibenthos

Covering the bottom in patches or in continuous layers, the diverse assemblages of hexactinellids and demosponges (Barthel and Gutt 1992), the various bryozoans and the multiple cnidarians and hydrozoans form highly heterogeneous structures. Due to its diversity of shapes and structures (including multiple cavities), this sessile epibenthos provides numerous potential substrates for amphipods. According to their feeding type, many amphipods also find food in abundance there (Coleman 1989b, c, 1990; Klages and Gutt 1990b; Dauby et al. 2001).

Aquarium observations showed that some species seem to prefer to occupy the lower part of the erected substrates, whereas others occur on the upper part. But other species show no apparent preference and can occur in both levels and sometimes also on the sediment surface.

Representative species from the lower epibenthic level

The Iphimediidae family is probably the most representative of this level, with at least five common species. All these species are typical walker-climbers, walking on the three last pairs of pereopods and rarely swimming (in the aquarium). Different microhabitats can be distinguished depending on the nature of the "living substrate".

Echiniphimedia hodgsoni Walker, 1906 and *Echiniphimedia scotti K. H. Barnard*, 1930 (*Iphimediidae*). Usually found in trawl samples with abundant stones and sponges. Position in aquarium with "reconstituted bottom": stay at the external surface of sponges, sometimes on bryozoans. Often gathering together. Mobility: usually motionless with only antenna 2 moving in the water, or walking slowly on the substrate. Swimming is very rarely observed; when disturbed *Echiniphimedia hodgsoni* can swim with jerky movements up to the aquarium surface.
Gnathiphimedia mandibularis K.H. Barnard, 1930 (*Iphimediidae*). In the aquarium, often seen sitting on pieces of bryozoan colony or, more rarely, on sponges, with strong antenna 1 erected and more flexible antenna 2 slowly whipping the water. Mobility: walks very slowly on the surface of calcareous bryozoans; swimming very rarely observed. The real habitat of this species (exceptionally recorded in situ) is shown in a bottom picture (Fig. 5).
Iphimediella cyclogena K.H. Barnard, 1930 and *Maxilliphimedia longipes Walker*, 1906 (*Iphimediidae*). Their presence in trawl samples seems to be linked to the abundance of cnidarians. Position in aquarium: observed motionless at the surface of diverse substrates. Mobility very similar to *Gnathiphimedia mandibularis*.
Epimeria rubrieques De Broyer & Klages, 1991 (*Epimeriidae*) Occurrence in catches: very few trawls contained this species, which seems to have a more restricted habitat than the other *Epimeria*. The most important catch during the EASIZ II cruise (sta. ANT XV 206 AGT15) contained 25 specimens among boulders and colonies of cnidarians. Usual position in aquarium: stays on the surface of stones, on diverse colonies of cnidarians and bryozoans. Mobility: walks very slowly. Swimming, which was observed only after stimulation, is jerky, heavy and powerful.

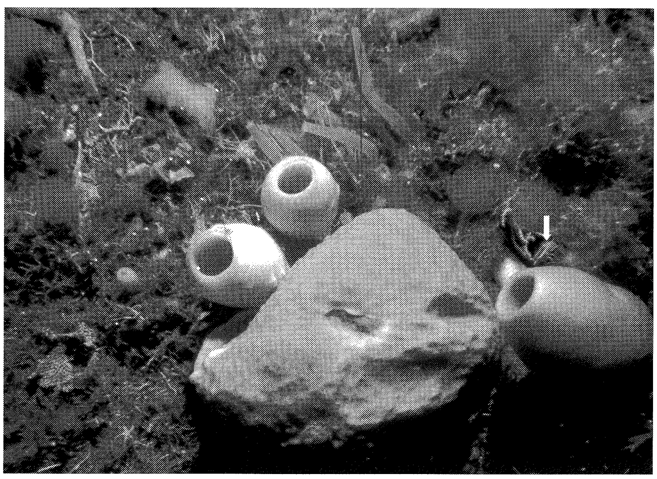

Fig. 5 Habitat of *Gnathiphimedia mandibularis* (*arrow*): bryozoan colonies and sponges (ANT VII/4 frame 262). Picture courtesy of J. Gutt, A.W.I.

Eusirus perdentatus Chevreux, 1912 (*Eusiridae*) In the aquarium, usually observed staying motionless on the substrate surface or on stones. Mobility: seems influenced by the nature of the substrate and by the aquarium population density. On a "reconstituted bottom" and with few (two or three) specimens in a 30-l aquarium, *Eusirus perdentatus* stays mostly motionless but can be seen walking slowly on the bottom; swimming is very rarely observed. With higher density conditions (unlikely in nature for this predator) and on artificial substrate, *Eusirus perdentatus* was observed swimming upwards, especially at night. Swimming is jerky and always short.
Jassa goniamera Walker, 1903 (*Ischyroceridae*) Position in aquarium: usually fixed by pereopods 5–7 on substrates like bryozoans, hydrozoans or sponges. The powerful first gnathopods can be used to grip substrate. Pereopodal glands produce secretion, building a kind of translucent, protecting cocoon. Mobility: usually motionless; can very briefly swim vertically with jerky movements. Probably sedentary.

The upper level of sessile epibenthos

ROV video records of the sessile suspension-feeder community showed a succession of ball-like, urn- or finger- shaped sponges, tree-like hydrozoans or flower-shaped gorgonians or bryozoans. The "canopy" of these assemblages, composed of a mixture of delicate and strong organisms, constitutes a secondary bottom colonised by other invertebrates, the most obvious being echinoderms (e.g. the crinoid *Promachocrinus kerguelensis* Carpenter, 1888, several *Ophiurolepis*), and by fish (*Artedidraco skottsbergi* Lönnberg, 1905, *Trematomus scotti* Boulenger, 1907. Amphipods are suspected of being also present in this layer but, due to their size, are usually not visible on pictures.

Representative species from the upper epibenthic level

The family Epimeriidae comprises typical representatives of this habitat with at least four common species: *Epimeria macrodonta* Walker, 1906, *Epimeria robusta* K.H. Barnard, 1930, *Epimeria similis* Chevreux, 1912 and *Epimeriella walkeri* K.H. Barnard, 1930. Some differences in usual position and motility were noticed.
Epimeria macrodonta In the aquarium, stays at different levels; it was observed walking slowly or sitting on the sediment surface, on sponges or, more frequently, on cnidarian colonies (*Primnoisis formosa* Gravier, 1913, *Dasystanella* sp., *Thorella* sp.). Mobility: swimming is rarely observed but can be spontaneous and fast; swims in an upright position, usually turns two or three times around the aquarium and returns to the bottom.
Epimeria robusta Occurs in trawl catches with coarse detritic sediment (bryozoan fragments, sponges and gorgonians), stones and diverse sessile benthos. In the aquarium with "reconstituted bottom", does not select a particular substrate but never seen on bare sediment surface; usually sits near the top of hydrozoan colonies. Mobility: usually motionless for long periods; can swim actively and fast when disturbed.
Epimeria similis This species has very similar habits to *Epimeria macrodonta*.
Epimeriella walkeri In aquarium with "reconstituted bottom", usually stays motionless at the sediment surface or more frequently on the top of gorgonian or hydrozoan colonies. Mobility: swims very fast when disturbed.
Hirondellea antarctica (*Schellenberg*, 1926) (*Lysianassoidea*) Frequently collected in low numbers by trawls; also caught in baited traps. In the aquarium, stays motionless at the sediment surface or more frequently on the top of gorgonian colonies. Mobility: although usually very quiet, can spontaneously swim upwards very fast.
Alexandrella mixta (*Nicholls*, 1938) (*Stilipedidae*) In the aquarium, usually stays on sessile animals like gorgonians. Mobility: like *Hirondellea*, usually motionless, but able to swim fast.

The symbiotic and inquilinous habitats

Among the amphipods living on the sessile invertebrates, some species, usually sedentary, have established different symbiotic relationships with their hosts. Hereafter are recorded the amphipod-benthos associations observed or suspected among the eastern Weddell Sea bottom communities.

Species associated with sponges

No less than 16 species of amphipods were recorded on common hexactinellids and demosponges by Kunzmann (1996). On the walls or at the bottom of the central cavity of some hexactinellids (*Rossella antarctica* Cater, 1872, *R. nuda* Topsent, 1901, *R. racovitzae* Topsent, 1901, *Scolymastra joubini* Topsent, 1910), she found, in order of frequency, *Leucothoe spinicarpa* Abildgaard, 1789 s.l., *Eusirus microps* Walker, 1906, *Eusirus* cf *antarcticus* Thomson, 1880, *Seba antarctica* Walker, 1906, *Alexandrella* sp. and *A. mixta*. In addition, *Polycheria antarctica* Stebbing, 1875 s.l. was found on the external surface of *Rossella* spp. and among their basal scleres, and *Seba antarctica*, as well as some unidentified Lysianassoidea, on the external surface and in the surface tissue lesions of *Rossella nuda* and *Scolymastra joubini*.

The internal cavities of eight common demosponges (mostly *Mycale acerata* and *Tedania trirhapis*) examined by Kunzmann (1996) hosted *Seba antarctica*, *Andaniotes linearis* K.H. Barnard, 1932, *Leucothoe spinicarpa*, *Ampelisca* sp., *Euandania gigantea* Stebbing, 1883 and some unidentified Stegocephalidae and Stenothoidae (Kunzmann's identification of *Euandania gigantea* appears doubtful; the species is known as a purely pelagic one, usually recorded in the bathypelagic zone). *L. spinicarpa*, *Eusirus* cf *antarcticus*, and some Lysianassoidea were found on the external surface, in addition to *Polycheria antarctica*, which live – mostly lying on the back – in self-excavated oval pits in the host tissues, and *Colomastix simplicicauda* Nicholls, 1938, which form ball-shaped groups at the sponge surface.

Kunzmann (1996) established no host-specific relationships. Among her material, 4 species appear frequently and in relatively high numbers in some sponges (48–898 individuals per sponge): *Seba antarctica*, *Polycheria antarctica* s.l., *Colomastix simplicicauda* and *Andaniotes linearis*. They can be considered preferential spongicolous species, but not exclusive, as *S. antarctica* and *P. antarctica* s.l. have also been recorded on ascidians (see below). According to Kunzmann (1996), *S. antarctica* and *P. antarctica* s.l are ectoparasites eating the host tissues and using the sponge as a shelter from predators.

The following additions are made to Kunzmann's records.

Polycheria antarctica s.s.(Dexaminidae). Occurrence/habitat: 15 specimens (sta. ANT VII/4 259 BPN 4) were found in holes in the surface tissues of the demosponge *Crella crassa* Hentschel, 1914 (det. O. Tendal, Copenhagen). Stomach content analysis (12 ind.) revealed no sponge spicules but only small particles (less than 100 μm) of unidentifiable organic matter, diatom fragments and mineral grains (Dauby et al. 2001), which does not confirm Kunzmann's observation of ectoparasitism.

Scaphodactylus sp. nov. 1 (Stenothoidae) was found on an unidentified demosponge at sta. ANT XV/3 37 D, 105 m.

Species associated with ascidians

Species of the families Leucothoidae, Lysianassoidea, Stegocephalidae or Stenothoidae (still in process of identification) have been found in the branchial cavity of different ascidians. *Leucothoe* sp. was found in *Corella eumyota* Traustedt, 1882 (sta. ANT VII/4 AGT 15). The lysianassoid, *Orchomenyx* sp., was found in *Ascidia challengeri* Herdman, 1842 (sta. ANT VII/4 224 GSN4) and an unidentified species in a "large red ascidian" (sta. ANT XV/3 49 AGT). Stegocephalids have been found in *Ascidia challengeri* at sta. ANT XV/3 120 GSN and in *Eugyrioides polyducta* Monniot & Monniot, 1983 (sta. ANT VII/4 AGT 8). *Metopoides* sp. nov. 2 (Stenothoidae) was recorded in *Ascidia challengeri* at depths of 600 m (sta. ANT XV/3 120 GSN) and 710 m (sta. ANT XV/3 150 GSN). Preliminary examination indicated no apparent host specificity.

Species associated with hydrozoans

Two new stenothoid species of the genus *Torometopa* were found on *Oswaldella billardi* Briggs,1938: *Torometopa* sp. nov. 1 (sta. ANT XV/3 62 AGT) and *Torometopa* sp. nov. 6 (sta. ANT XV/3 5 TVG). *Thaumatelson* sp. Z (Stenothoidae) was found on a unidentified hydrozoan (sta. ANT XV/3 62 AGT). The stolons produced by *Tubularia ralphii* Bale, 1884 and *Oswaldella antarctica* on several stones from the underwater hilltop of Four Seasons Inlet (northeast of Kapp Norwegia; sta. ANT XV/3 212) host a few hundreds of stenothoids from two spp, which could not, however, be associated with the hydrozoans but simply shelter in this tri-dimensional substrate (De Broyer et al. 1999; Gili et al. 1999).

Species associated with gorgonians

One stenothoid species of the genus *Torometopa* (sp. nov. 5) was found on *Primnoella* sp. at 400 m (sta. ANT XV/3 62 AGT). *Polycheria* sp (Dexaminidae) occurred on an unidentified gorgonian host at sta. ANT XV/3 214 D, 110–64 m.

Discussion

About the methods

Contrary to the coastal zone where detailed investigations of amphipod habitats have been done successfully by scuba-diving (e.g. Bregazzi 1972; Richardson and Whitaker 1979), shelf habitat determination has to rely on indirect approaches. Bottom pictures and video records have been particularly useful for characterising the habitats of fishes (Ekau and Gutt 1991) or conspicuous macrobenthos (e.g. holothurians, Gutt 1991; shrimps, Gutt et al. 1991; sponges, Barthel and Gutt 1992) but are of little help for the small and often hidden amphipods. Analysis of trawl-catch contents is of limited or no value for indicating the potential habitat of collected amphipods because of the usually disturbed state of the catch (e.g. a mixture of sediments, stones and diverse fauna), and also the usual high patchiness of sampled assemblages (see, for example, Gutt and Koltun 1995). They can, however, be informative in the case of homogeneous bottom catches or symbiosis on well-preserved hosts, for instance. However, undisturbed bottom samples from corers and large grabs (which should be more systematically checked) can provide useful epibenthic habitat indications (Fig. 3). Aquarium observations can provide information on general behaviour (see, for example, Enequist 1949; Klages and Gutt 1990a, b) and on the species' ability to select a particular habitat (e.g. Coleman 1989a). However, extrapolations on the basis of similar morphologies to infer similar habitats can be hazardous, as shown for instance by the *Eusirus* case: *Eusirus perdentatus* is a typically epibenthic animal, walker and poor swimmer (see Klages 1993) although its sister species *Eusirus propeperdentatus* Andres, 1979 is a purely pelagic animal (Andres 1979; De Broyer and Jazdzewski 1993).

The habitat diversity

From a preliminary comparison with the other amphipod macrohabitats in the eastern Weddell Sea, the epibenthic zone, here subdivided into three different levels, appears the most heterogeneous and the richest in species. The presumed habitats of some representative epibenthic species are presented schematically in Fig. 5. Each epibenthic stratum from the heterogeneous sediment surface to the top of the erect sessile benthos offers to amphipods different habitats, characterised by some physical parameters and by nature and availability of food. Some species find there a temporary substrate or a shelter; others forage in this habitat, in some cases on the living substrate itself. The comparatively high number of "walker-climber" species (mainly belonging to the Iphimedioidea, with more than 50 species), mostly found on the different levels of the rich suspension-feeder assemblages, seems unique to the eastern Weddell Sea. It is most probably linked to the diversity of microhabitats and the abundance of food offered by the rich epibenthos to these specialised micropredatory grazers or unspecialised predators (feeding types according to Coleman 1989b, c; Klages and Gutt 1990b; Dauby et al., 2001).

Aquarium observations have indicated two possible levels of amphipod distribution on the sessile epibenthos substrates, which require confirmation. It seems, nevertheless, possible to differentiate the environmental conditions of the two levels. At the top of the epibenthic substrates, the upper level stratum can be more exposed to strong currents (a current of 40 cm/s was recorded in Kapp Norvegia at 5 m above the bottom at a depth of 676 m; Fahrbach et al. 1992). This seems a priori a favourable position for the free-living suspension-feeders (Ischyroceriidae) to collect the organic rain from the water column above and from lateral advection. Currents can also carry carrion smell and this area could be advantageous for scavengers such as Lysianassoidea (see Ingram and Hessler 1983). These trophic advantages are balanced, however, by a greater exposure to predators. Demersal fish stomach contents (*Trematomus* spp., *Pogonophryne* spp., *Artedidraco orianae*), for instance, frequently revealed *Epimeria* species supposed to stay at this level (Olaso 1999; Olaso et al. 2000).

Are the results representative of all habitats in this taxocoenosis?

The selected species undoubtedly represent the most conspicuous and most common ones in the epibenthic catches so far analysed. But the majority of specimens have been caught by trawls with a 15-mm mesh size, which do not always allow adequate collection of small species, which can be numerous judging from the preliminary analysis of material from small-mesh-sized dredge (M. Rauschert, unpublished work). The diversity of symbiotic and inquilinous habitats is probably highly underestimated. Only sponge habitats have been systematically investigated (Kunzmann 1996) so far. Ascidians remain to be more systematically checked for their inquilinous fauna. Potential associations with cnidarians and hydrozoans should attract more attention. A number of small species, among them the numerous Stenothoidae detected by M. Rauschert, might have developed preferential relationships with some hosts. They could represent an important part of the specific diversity of eastern Weddell Sea amphipods.

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