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BIODIVERSITY OF THE SOUTHERN OCEAN: TOWARDS A NEW SYNTHESIS FOR THE AMPHIPODA (CRUSTACEA)

ABSTRACT. On the basis of a recent inventory of the whole Southern Ocean amphipod fauna, the authors briefly review some aspects of the present state of knowledge of the species and taxonomical diversity, of the geographical and bathymetrical distribution and of the eco-functional diversity of the amphipods in the Antarctic benthic communities in particular. They point out some gaps in taxonomic knowledge and the faunal survey of amphipods in the Antarctic and Subantarctic regions. With more than one thousand strictly Antarctic species, the peracarid Crustacea are the most speciose group in the Southern Ocean, and, among them, the amphipods, with 531 Antarctic species and 821 spp. in the whole Southern Ocean, are obviously the most diverse. Some potential causes of this high amphipod diversity are discussed.

Key words: biodiversity, Amphipoda, benthos, Southern Ocean, Antarctica.

RIASSUNTO. Sulla base di recenti inventari dell'intera fauna ad anfipodi dell'Oceano Meridionale, gli autori riesaminano alcuni aspetti dell'attuale stato delle conoscenze sulle specie e sulle differenze tassonomiche, sulla distribuzione geografica e batimetrica e sulla diversità ecofunzionale degli anfipodi appartenenti in particolare alle comunità bentiche dell'Antartide. Vengono quindi evidenziate alcune lacune nelle conoscenze tassonomiche e nella valutazione della fauna ad anfipodi nelle regioni antartica e sub-antartica. I crostacei peracaridi rappresentano il gruppo con il maggior numero di specie nell'Oceano Meridionale, con oltre mille specie strettamente antartiche. Tra di essi gli anfipodi sono ovviamente i più differenziati, con 531 specie antartiche e 821 specie in tutto l'Oceano Meridionale. Alcune cause possibili di questa ampia differenziazione degli anfipodi vengono quindi prese in esame.

Parole chiave: biodiversità, Amphipoda, benthos, Oceano Meridionale, Antartide.

INTRODUCTION

In the Southern Ocean, the Antarctic coastal and shelf ecosystem (ACSE) constitutes the most complex and the most productive ecosystem, the richest in biodiversity, and supposedly the most sensitive to global change effects. To better understand the structure and functioning of the ACSE, in the global warming and ozone depletion perspective, the new SCAR programme "*Coastal - Shelf Ecology of the*

Table I - Peracarid Crustacea species richness compared to other most speciose macrobenthic groups in the Southern Ocean
(B = benthic and benthopelagic; P = pelagic)

	Southern Ocean	*Antarctic only*	Sources
Porifera		300	Barthel, in Sieg & Wägele 1990
Bryozoa		350	Ristedt, in Sieg & Wägele 1990
Mollusca	870	?	Hain, in Sieg & Wägele 1990
Polychaeta	558 (800?) (1)	+650* (2)	(1) Knox & Lowry 1977 (2) Paiva & Wägele, in Sieg & Wägele 1990
Crustacea Peracarida		1004 (B+P)	
Mysidacea		26 (B+P)	Wittmann, in Sieg & Wägele 1990
Amphipoda	821 (B+P) 713 (B)	531 (B+P) 462 (B)	De Broyer & Jazdzewski, 1993, updated
Cumacea	64	51	Ledoyer 1993
Tanaidacea	100	50	Sieg, in Sieg & Wägele 1990
Isopoda		346	Brandt 1991

(* see remarks in the discussion section).

Antarctic Sea-Ice Zone" (EASIZ), proposes for the next decade an integrated study of the ice, water column and benthic subsystems mainly organized around the follow-up of key processes and key-species in a network of reference sites (SCAR 1994). In this framework, to accurately assess the Southern Ocean biodiversity and its role in the ACSE, it seems obvious that more taxonomical expertise and tools are needed, especially in highly diverse and taxonomically difficult groups. On the other hand, in a wider context, several recent papers drew attention to the potential high species richness of the deep sea (Grassle & Maciolek 1992; May 1992; Poore & Wilson 1993) and at the same time some global reviews stressed the gaps in the world marine biodiversity knowledge, especially in the coastal zones and the deep sea (*e.g.* Ray & Grassle 1991, World Conservation Monitoring Centre 1992, Norse 1993).

In the Southern Ocean and in particular in the Antarctic and Subantarctic coastal and shelf ecosystems, the peracarid crustaceans, and first of all the amphipods, obviously constitute an often abundant

(Jazdzewski et al. 1992) and always diverse component of the benthic communities (Table I). The amphipods also commonly occur in the neritic and oceanic communities of the Southern Ocean. Both benthic and pelagic amphipods form a main trophic resource for many Antarctic and Subantarctic fishes (see *e.g.* Gon & Heemstra 1990, Kock 1992) and a number of Southern Ocean seabirds (see *e.g.* Croxall 1987, Puddicombe & Johnstone 1988) and squids (Rodhouse et al. 1992, Ivanovic & Brunetti 1994) regularly prey on pelagic amphipods.

As a first step towards an assessment of the place of the Crustacea Amphipoda in the biodiversity of the Southern Ocean, an inventory, with synonymical bibliography and distributional traits, of all benthic, supralittoral and pelagic Amphipoda (Gammaridea, Caprellidea and Hyperiidea) occurring in the Southern Ocean has been recently drawn up by De Broyer & Jazdzewski (1993). The present paper briefly reviews some results of this inventory and focusses on some aspects of the present state of knowledge of the species and taxonomic diversity, of the geographical and bathymetrical distribution and of the ecofunctional diversity of amphipods, in particular in the Antarctic benthic communities.

Material & Methods

Bibliographical coverage

Since the completion of the checklist of De Broyer & Jazdzewski (1993), based mainly on taxonomical references checked until 31 December 1992, new Southern Ocean taxonomical and distributional information has been provided (until 31 December 1994) by Alonso de Pina (1993), Andres (1993), Coleman (1994), Coleman & Team (1994), Jazdzewski et al. (1996), Klages (1993), Rauschert (1994), Rauschert & Andres (1993, 1994), Vinogradov & Vinogradov (1993), Wakabara *et al.* (1996), and Zeidler (1994). Data from Andres & Rauschert (1990, 1992), overlooked in the checklist, have been taken into account.

Systematic arrangement

Same as used in De Broyer & Jazdzewski (1993) but updated for the caprellid families by Laubitz (1993).

Databases and reference collection

In the perspective to establish a network of "Antarctic Biodiversity Reference Centres", in the framework of both the SCAR "EASIZ"

Programme and the "Systematics Agenda 2000: charting the biosphere" Programme, a global initiative to discover, describe and classify the world's species (SA 2000, 1994), specialized databases have been built or are still in development for recording, by species, taxonomical, ecological, distributional data and bibliographical references. In addition, an extensive reference collection of Southern Ocean amphipods is under development at the "Institut royal des Sciences naturelles", in Brussels, Belgium.

Zoogeographical scheme

The geographical limits used for the Southern Ocean follow Deacon's (1982, 1984) concept *i.e.* all the marine area spreading south of the Subtropical Convergence zone to the Antarctic Continent (Fig. 1). This vast marine zone has been classically divided in two zoogeographical regions (see Hedgpeth 1969, Knox & Lowry 1977, and White 1984): the Antarctic Region, extending from the continent to the Antarctic Convergence and in turn subdivided in the East and West Antarctic sub-regions, and the Subantarctic Region, spreading between the Antarctic and the Subtropical Convergence and subdivided into a Subantarctic Islands sub-region (sometimes treated as two separate Kerguelen and Macquarie sub-regions, see *e.g.* Briggs 1974 and Brandt 1991) and a Magellanic sub-region. For further details see De Broyer & Jazdzewski (1993) and cited references.

Results

1. Species richness and taxonomic diversity

1.1 *The Southern Ocean amphipod fauna*

An overview of the Southern Ocean amphipod fauna is given in Tables II-IV, updated from De Broyer & Jazdzewski (1993). The tables show, for the different zoogeographic regions, sub-regions and bathymetric zones, the number of known taxa of the fauna and its benthic and pelagic components. 896 taxa have been recorded: 724 spp. and subspp. of Gammaridea, 28 spp. of Caprellidea, 69 spp. and subspp. of Hyperiidea as well as 75 unidentified (and in part unidentifiable) taxa (73 Gammaridea, 2 Caprellidea).

The Southern Ocean fauna today represents respectively about 14% of the world marine gammaridean species (world total on 1 July 1986: 4.733 species, from which about 1.200 are freshwater species, according

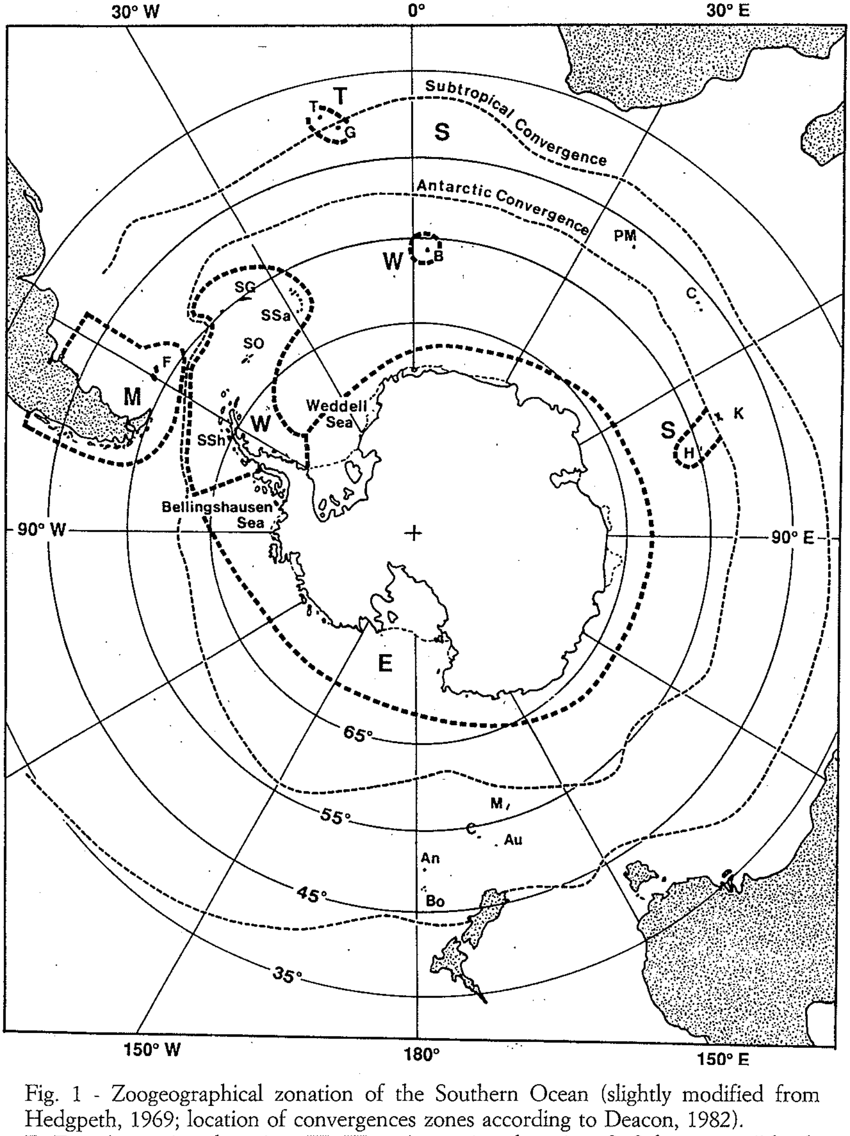

Fig. 1 - Zoogeographical zonation of the Southern Ocean (slightly modified from Hedgpeth, 1969; location of convergences zones according to Deacon, 1982).
E: East Antarctic sub-region; W: West Antarctic sub-region; S: Subantarctic Islands sub-region; T: Tristan da Cunha district; M: Magellanic sub-region.
An: Antipodes Is.; Au: Auckland I.; B: Bouvet I.; Bo: Bounty I.; C: Crozet Is.; Ca: Campbell I.; F: Falkland Is.; G: Gough I.; H: Heard and McDonald Is.; K: Kerguelen Is.; M: Macquarie I.; PM: Prince Edward and Marion Is.; SG: South Georgia; SSa: South Sandwich Is.; SO: South Orkney Is.; SSh: South Shetland Is.; T: Tristan da Cunha Island.
Bold dotted line limits are indicative.

Table II - Total Amphipod Fauna of the Southern Ocean
(from De Broyer & Jazdzewski, 1993, updated)

	GAMM	CAPR	HYPE	*AMPH*
ANTARCTIC REGION *Total spp. (N endemics)* *Total gen. (N endemics)*	470 (369) 175 (47)	18 (4) 8 (1)	43 (8) 22 (1)	*531 (381)* *205 (49)*
East Antarctic subregion N spp. (endemics)	222 (83)	12 (1)	[43 (8)]	*277 (92)*
West Antarctic subregion N spp. (endemics)	376 (197)	17 (1)	[43 (8)]	*436 (206)*
South Georgia district N spp. (endemics)	113 (23)	6 (0)	-	*119 (23)*
Antarctic deep-sea (> 500m) N spp. (endemics)	100 (19)	3 (0)	-	*103 (19)*
SUBANTARCTIC REGION *Total spp. (N endemics)* *Total gen. (N endemics)*	329 (170) 159 (22)	19 (5) 14 (1)	43 (0) 27 (0)	*391 (175)* *200 (23)*
Subantarctic Islands sub-region N spp. (endemics)	186 (73)	9 (3)	[43 (0)]	*238 (76)*
Magellanic subregion N spp. (endemics)	174 (84)	15 (2)	[43 (0)]	*232 (86)*
Tristan da Cunha district N. spp. (endemics)	24 (8)	3 (0)	?	*27 (8)*
Subantarctic deep-sea (> 200m) N spp. (endemics)	49 (18)	12 (1)	-	*61 (19)*
SOUTHERN OCEAN *Total spp. (N endemics)* *Total spp. (N endemics)* Total fam. (N endemics)	*724 (604)* *258 (99)* *54 (3)*	*28 (12)* *17 (5)* *6 (0)*	*69 (9)* *33 (1)* *16 (0)*	*821 (625)* *308 (105)* *76 (3)*
Total unidentified taxa *(not included)*	73	2	0	75
Questioned Southern Ocean records *(not included*	4	1	1	6

to Barnard & Karaman (1991). Today the world marine gammaridean species would amount about 5.300 spp.; see discussion below). For the caprellids, the austral fauna represents less than 11% of the world fauna (which counts more than 247 spp., McCain & Steinberg 1970; Berzin & Vlazova 1982), and for the hyperiids, nearly 30% of the world fauna (world total 233 spp., Vinogradov et al. 1982)

Table III - Benthic Amphipod Fauna of the Southern Ocean
(from De Broyer & Jazdzewski 1993, updated. Unidentified species, questioned records and supralittoral talitrids not included. Benthopelagic species included.)

	GAMM	CAPR	*AMPH*
ANTARCTIC REGION			
Total spp. (N endemics)	451 (361)	11 (44)	*462 (365)*
Total gen. (N endemics)	264 (46)	7 (1)	*171 (47)*
East Antarctic N spp. (endemics)	206 (79)	5 (1)	*211 (80)*
West Antarctic N spp. (endemics)	360 (193)	10 (1)	*370 (194)*
Bathyal Antarctic (> 500m) N spp. (endemics)	79 (7)	3 (0)	*82 (7)*
Abyssal Antarctic (> 2000m) N spp. (endemics)	20 (14)	0 (0)	*20 (14)*
SUBANTARCTIC REGION			
Total spp. (N endemics)	326 (172)	17 (5)	*343 (177)*
Total gen. (N endemics)	157 (22)	13(1)	*170 (23)*
Subantarctic Islands N spp. (endemics)	184 (73)	7 (3)	*191 (76)*
Magellanic N spp. (endemics)	170 (85)	13 (2)	*183 (87)*
Tristan du Cunha N spp. (endemics)	21 (8)	3 (0)	*24 (8)*
Bathyal Subantarctic (> 200m) N spp. (endemics)	40 (14)	12 (1)	*52 (15)*
Abyssal Subantarctic (> 2000m) N spp. (endemics)	11 (5)	1 (0)	*12 (5)*
SOUTHERN OCEAN			
Total spp (N endemics)	*692 (596)*	*21 (12)*	*713 (608)*
Total gen. (N endemics)	*251 (95)*	*16 (5)*	*267 (100)*
Total fam. (N endemics)	*54 (3)*	*5 (0)*	*59 (3)*

In terms of species richness, it clearly appears that the Amphipoda count among the most diverse benthic groups in the Antarctic region of the Southern Ocean (Fig. 2) where the peracarid Crustacea are the most speciose animal group (Table I).

A review of the taxonomic diversity and the geographic distribution of the 20 most speciose gammaridean amphipod families has been made by Knox & Lowry (1977).

Table IV - Pelagic Amphipod Fauna of the Southern Ocean
(from De Broyer & Jazdzewski 1993, updated. Unidentified species and questioned records not included. Benthopelagic species included.)

	GAMM	HYPE	*AMPH*
ANTARCTIC REGION			
Total spp. (N endemics)	29 (9)	43 (8)	*72 (17)*
Total gen (N endemics)	18 (2)	22 (1)	*40 (3)*
SUBANTARCTIC REGION			
Total spp. (N endemics)	7 (0)	43 (0)	*50 (0)*
Total gen (N endemics)	5 (0)	27 (0)	*32 (0)*
SOUTHERN OCEAN			
Total spp. (N endemics)	*38 (9)*	69 (9)	107 (18)
Total gen (N endemics)	*19 (2)*	*33 (1)*	*52 (3)*

An updating is underway and some preliminary considerations appears in Jazdzewski et al. (1996).

1.2. *Present state of faunal survey*

1.2.1. Geographical and bathymetrical coverage

The littoral and shallow sublittoral zone of many places of the West Antarctic can nowadays be considered relatively well known, but the deeper shelf zones in particular are still understudied both in West and East Antarctic. The amphipod fauna – and the benthos in general – of the deep surroundings of South Georgia and the South Orkneys, the South Sandwich Islands, Bouvet Island and the surrounding seamounts, Heard and Mac Donald Islands, the Western Weddell Sea, the Bellingshausen and Amundsen Seas, the shelves extending between the Amundsen and the Ross Seas are still poorly known. Klages et al. (1995) recently reported briefly on the poor species richness and low abundance of the amphipod and isopod fauna of the Bellingshausen Sea shelf.

In the Subantarctic region, the New Zealand Subantarctic Antipodes and Bounty Islands are other nearly complete whitespots. On the other hand, the Magellanic region, which is characterized by an extensive network of straits and channels linking two oceans and by the large East Patagonian shelf, obviously remains understudied in comparison with the Antarctic Peninsula and the Scotia Arc region. Taking into account its relatively high faunal affinities with the Subantarctic Islands, the abundance of algae dwelling species which can be transported by algal

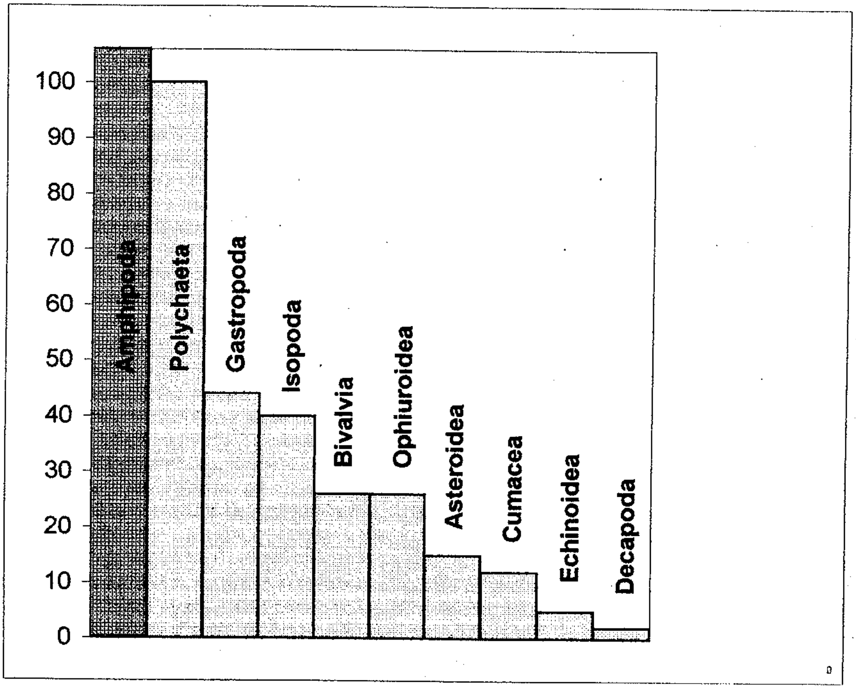

Fig. 2 - The most speciose benthic groups in Admiralty Bay, King George Island, West Antarctic (from Jazdzewski et al., 1996).

rafts, and its location in the West Wind Drift zone, Knox & Lowry (1977) suggested it could have been a center of origin for a part of the Subantarctic fauna. Joint German – Chilean – Italian detailed investigations of the macrobenthos of the Magellan Strait and Beagle Canal areas have recently been undertaken (RV "Victor Hensen" Campaign 1994) and a great amount of diverse amphipod material has been collected (De Broyer & Rauschert 1996).

In addition, the slope fauna and the abyssal basins fauna all around the Antarctic are largely unknown. Vinogradov & Vinogradov (1993) recently investigated the South Orkney Trench to a depth of 6.420 m and, not unexpectedly, provided new records of bathypelagic and benthopelagic amphipods previously unreported from the Southern Ocean.

1.2.2. Ecological coverage

If the pelagic (and less diverse) fauna is probably well sampled today (except in the bathypelagic and hadopelagic ranges), the multistored

and patchily distributed Antarctic epibenthos is far from completely and adequately sampled (White 1984) despite substantial progress in the last decade. Even when intensively sampled, by classical gears like trawls, grabs or box corers, it is well known that a benthic area can reveal additional species – sometimes abundant and ecologically significant –, when less commonly used gears like *e.g.* suprabenthic (or hyperbenthic) fine meshed sledges and baited traps are systematically used. For instance, the use of traps baited for the first time with slightly decaying algae at 400 to 500 m depth, in Admiralty Bay, King George Island, brought an unexpected high number of specimens of a new species of *Oradarea* which indicates the presence of a probably significant herbivore population well below the phytal zone (De Broyer & Jazdzewski, unpubl.).

Arnaud (1992) recently underlined some common limitations encountered when sampling the Antarctic macrobenthos: irregularity of sampling in space and time ("opportunistic sampling", generalized lack of winter sampling); lack of adequate samplers for rough hard and mixed bottoms prevailing in these regions; deficient and incomplete sorting due to lack of specialists on board or to lack of time, or both; absence of record of useful information such as relative abundance of the species in the sample, coloration in life, associations of organisms (before separation by sorting); lack of efficient sampling strategies (*e.g.* for specific habitat and microhabitat determination),.... All these limitations obviously hold true for benthic amphipod sampling.

1.3. *Taxonomical knowledge*

Among the Southern Ocean Gammaridea, 279 spp. (or 38%) are known only from the original material. On the other hand, 191 new species (26%) were described in the last two decades and 127 spp. (17%) only in the last decade.

A good number of Antarctic and Subantarctic species remains incompletely or inadequately described: type material needs to be carefully checked and redescribed and previous identifications clarified. Some genera (*Paramoera*, *Uristes*,...) are still very confused. Barnard and Karaman (1991) recently emphasized the general fact that "many early descriptions have become almost worthless" and that "ultimate clarification of many species must come now and in the future from meticulous restudy of old materials in the process of working out new generic monographs on a global basis". Another limitation is the present lack of clear and complete scheme of family-level entities in the two

Southern Ocean most speciose groups of families: Eusiridae *s.l.* and Lysianassidae *s.l.* or, better, Lysianassoidea (see recent progress in Bousfield & Shih, 1994).

Finally, large collections of material remain unstudied or are often too slowly processed due to lack of taxonomical expertise and tools.

2. Species diversity

In addition to the number of species and higher taxa evaluation, another classical way to quantify biodiversity (on this particular topic see Hawksworth 1994) is the calculation, at the community or regional level, of species diversity or eveness (equitability) indices combining species richness and relative abundance of species. The quantitative species composition and diversity of comparable communities in the East and West Antarctic or the Subantarctic have not often been evaluated and compared (see White 1984) but, as remarked by Arntz et al. (1994), appropriate quantitative data, ideally based on same collecting gears, sieving procedures and area extensions, are still rather few.

On the other hand, the rarefaction curve method (Hurlbert, 1971) allows to estimate the potential number of species in a standardized sample and has been largely used in recent estimations of deep sea species richness (see discussion). For the deep shelf and slope of the south-eastern Weddell Sea, for example, the amphipod species diversity expressed by the Hurlbert index [E(S n)] appears to be the highest among the investigated groups (Bivalvia, Gastropoda, Isopoda, Decapoda, Holothuroidea, Ophiuroidea, Polynoidea) indicating a probability to meet 36 different species among a sample of 100 specimens (Brey et al. 1994). It must be noted that these results are based on quantitative data obtained by the "multiboxcorer" (Gerdes et al. 1992, *e.g.*) which seems to underestimate vagile epifaunal Crustacea as indirectly indicated by Jarre-Teichmann et al. (in press).

3. Ecofunctional diversity

An important aspect of the assessment of the biodiversity of Southern Ocean amphipods – which is still poorly studied – is the detailed knowledge of the diversity of ecomorphotypes and of the ecological roles of species or functional groups of species, which is – generally speaking – of greater significance for the ecologist than the species richness or the taxonomic diversity. As clearly stated by Ray (1988), the ecological diversity approach would require for instance identification

of species which are important contributors to ecosystem processes, help structuring their communities, enhance productivity and help recycling essential nutrients. In this context, it may be worth mentioning that the trophic type of the great majority of the Southern Ocean species is still unknown and, on the other hand, that the habitats and microhabitats of many Southern Ocean species remain to be identified precisely. A preliminary approach of the functional role of the amphipod taxocenosis in a Eastern Weddell Sea benthic community, taking simultaneously into account their trophic and spatial resources, their mode of life and their trophic strategies, indicated a high ubiquity and rather highly diverse ecological roles (De Broyer & Klages 1990b, and unpublished data).

4. Zoogeography

4.1. *Geographical and bathymetrical distribution.*

The distribution in the East or West Antarctic sub-regions, in the Subantarctic Islands sub-region (including the Tristan da Cunha district) and in the Magellanic sub-region has been documented and synthesized by De Broyer & Jazdzewski (1993) as well as the bathymetrical distribution of the benthic and pelagic species (Tables II-IV).

The circumantarctic distribution (*i.e.* in both East and West Antarctic sub-regions) is shown by 121 species or 26.1% of all benthic species occuring in the Antarctic region (or 16.9% of all Southern Ocean benthic species). Among these species, 47 species or 10.1% of all Antarctic benthic species (or 6.5% of all Southern Ocean species) are circumantarctic endemics. It must be noted here that, faunal surveys progressing, more and more East or West Antarctic species appear of circumantarctic occurrence. On the other hand, the circumcontinental distribution (or the occurrence in several locations around the East Antarctic) is a well-known trait of the Antarctic benthos (Dayton 1990) shared by the benthic amphipods.

4.2. *Endemicity*

Taking into account the recent additions, endemicity rates have been recalculated from De Broyer & Jazdzewski (1993) for the different components of the fauna and are presented in Table V.

Endemism is relatively low among the 107 Southern Ocean pelagic

Table V - Endemicity rates of the Southern Ocean Amphipod Fauna

	GAMM	*CAPR*	*HYPE*	*AMPH* benthic	*AMPH* pelagic	*AMPH*
ANTARCTIC REGION						
% endemic spp.	78.5	22.2	18.6	*79.0*	*24.6*	71.7
% endemic gen.	26.8	12.5	4.5	*27.4*	*7.5*	*23.9*
East Antarctic sub-region % endemic spp.	37.3	8.3	-	*37.9*	-	*33.4*
West Antarctic subb-region endemic spp.	52.3	5.8	-	*52.4*	-	*47.2*
South Georgia district % endemic spp.	20.3	0	-	*19.3*	-	*19.3*
Antarctic deep-sea (>500 m) % endemic spp.	19.0	0	-	*19.5*	-	*18.4*
SUBANTARCTIC REGION						
% endemic spp.	51.6	26.3	0	*51.6*	*0*	*44.7*
% endemic gen.	13.8	7.1	0	*13.6*	*0*	*11.5*
Subantarctic Islands sub-region % endemic ssp.	39.2	33.3	-	*39.7*	-	*31.9*
Magellanic sub-region % endemic spp.	48.2	13.3	-	*50.0*	-	*37.0*
Tristan da Cunha district % endemic spp.	33.3	0	-	*38.0*	-	*29.6*
Subantarctic deep-sea (> 200 m) % endemic spp.	36.7	8.3	-	31.1	-	*31.1*
SOUTHERN OCEAN						
% endemic spp.	*83.4*	*42.8*	*13.0*	c85.2	*17.3*	*76.1*
% endemic gen.	*38.3*	*29.4*	*3.0*	*37.4*	c5.7	*34.0*
% endemic fam.	*5.5*	*0*	*0*	c5.0	*0*	*3.9*

species with a rate of 17.3%, against 24.6% for the 72 species occuring in the Antarctic Region itself.

On the other hand, the benthic amphipod fauna of the Southern Ocean comprises 713 species (85.2% endemics) of which 462 are distributed in the Antarctic region (79.0% endemics) and 343 in the Subantarctic region (51.6% endemics). Endemicity at the genus level attains 37.4% for the whole Southern Ocean fauna, 27.4% for the Antarctic and 13.5% for the Subantarctic region, respectively.

For the benthic gammaridean amphipods specifically, comparison with the results of Knox & Lowry (1977, but data of end 1975), shows similar but slightly reduced rates of endemicity: 85.2% instead of 90% of species and 37.4% instead of 40% of genera are today considered Southern Ocean endemics. The Subantarctic islands sub-region (184 spp. today, 99 benthic spp. in 1975) has a endemicity rate of 39.2%, versus 50%. The Magellanic sub-region (with larger limits in this treatment) counts 170 spp. with 48.2% endemics, versus 121 spp. and 53% endemics in 1975. The West Antarctic or Scotia sub-region has today 360 gammaridean spp. (52.3% endemics), versus 206 spp. and 46% in 1975, differences explained by the increased sampling effort in the Scotia Sea and the Peninsula areas and the recent description of many new species.

Finally, the East Antarctic counts 206 benthic species, with 37.3% endemics, versus 162 spp. and 43% endemics in 1975. This reduced rate seems mainly due to the discovery of former East Antarctic species at shelf depths in the West Antarctic.

Discussion

This brief review revealed that the peracarid Crustacea are the most speciose of all (macrobenthic) animal groups in the Antarctic and, supposedly, in the whole Southern Ocean.

Are the amphipods in turn the most speciose Antarctic macrobenthic (ordinal) group as well?

The question has not much interest *per se*: more usefully, it draws attention to the common confusion made when evaluating species richness between the Antarctic region *sensu stricto* (south of the Polar Front) and the too often loosely defined Southern Ocean or "Antarctic Seas". This is illustrated for instance in Table I by the number of over 650 spp of Polychaeta "in der Antarktis..." cited by Paiva & Wägele (in Sieg & Wägele 1990): according to Knox & Lowry's (1977) evaluation, this number seems to refer more to the whole Southern Ocean than to the strictly Antarctic region.

How many more amphipod species in Antarctica and the whole Southern Ocean?

Recent speculations about the potential number of deep-sea benthic species have advanced numbers of half a million (May 1992), 5 million (Poore & Wilson 1993) to several tens of million (Grassle & Maciolek 1992) of macrobenthic species for the bathyal and abyssal fauna of the

World Ocean. Whatever the real potential number – which seems anyway at least one order of magnitude larger than the presently known benthic fauna – these stimulating papers primarily indicated the general lack of knowledge of the marine fauna in general and of the slope and deep-sea in particular. This is especially true around the Antarctic where the fauna below 500 or 600 m (the shelf break depth) is largely unknown (Arnaud 1992, De Broyer & Jazdzewski 1993). It would probably be of outstanding interest to undertake a complete transect from a relatively well prospected East Antarctic shelf area (like the Eastern Weddell Sea) along the slope to the contiguous abyssal basin, to study *e.g.* the faunal composition and the phylogenetic links between the Antarctic shelf and the abyssal faunas, the diversity gradient, the differences in structure and composition of the successive benthic assemblages, the habitat heterogeneity, and the limits of the species eurybathy.

The last decade intensive surveys of the Eastern Weddell Sea shelf, mostly to a depth of 500-600 m, with some limited sampling to 2000 m (Andres 1986, Coleman 1994, Coleman & Andres 1988, Coleman & Team 1994, De Broyer & Klages 1990a, unpubl., Klages 1991, 1993, Voss 1988) revealed so far less than 10% of species new to science but large samples remain to be worked out and, obviously, additional new taxa are expected. The recent Arctic fauna survey by Tzvetkova (1996) indicated an increase by 8% of the recorded low and high Arctic species in comparison with Gurjanova's (1951) data, already resulting from rather intensive sampling.

On the other hand, judging for instance from recent and on-going profound revisions of the Iphimedids and related families by Coleman and Stenothoids by Rauschert & Andres, its seems clear that precise taxonomical studies and in particular detailed redescriptions and careful checking of previous records could bring a non-negligible amount of new Antarctic and Subantarctic species. The revision process of the whole Antarctic benthic amphipod fauna is now underway (Andres, Bellan-Santini, Coleman, De Broyer, Jazdzewski, Rauschert, Vader, Wakabara, in prep.) with the objective of publishing the amphipod volumes of the series "Synopses of the Antarctic Benthos" (Wägele & Sieg, editors), using as a model the remarkable volumes "The Amphipoda of the Mediterranean" (Ruffo et al., 1982, 1989, 1993). This careful and comprehensive revision of the Mediterranean amphipod fauna, allowed to increase from 270 (Chevreux & Fage 1925) to 453 the number of known species from this area (Bellan-Santini & Ruffo 1996),

probably now the best known, with the North Atlantic fauna for which an inventory was recently made by Palerud & Vader (1991).

About 6,000 species of Amphipods (more than 90% Gammaridea) have been described until July 1986. On the average 110 new species per year (or between 1.9% and 3.3% of the known world species) were described unabated from 1965 to 1986 (Barnard & Karaman 1991). Some authors speculated the total world amphipod fauna could reach 25,000 or 30,000 spp. (Bousfield 1979; Schminke unpubl.). Does this mean the Southern Ocean fauna (including the deep sea) could amount to five times the present numbers of species *i.e.* about 2,000 species for the Antarctic only and about 4,000 for the whole Southern Ocean?

Taking into account the expected progresses in taxonomic revisions, and provided extensive and adequate sampling is pursued, we are of the opinion that 50 to 100% additional species could be discovered in the Southern Ocean, including the slope and abyssal floor.

Is this high amphipod diversity unparalleled in other oceans?

A preliminary comparison with the Arctic fauna (Jazdzewski et al. 1996), classically considered much poorer than the Antarctic fauna, showed that the species richness of the North Polar region could be at the same level as the Antarctic one. But this is probably a very preliminary conclusion: when comparing the sampling effort, it seems evident that the North Polar region has been more thoroughly studied so far (Tzvetkova, 1996) than the Antarctic region. On the other hand, any comparison between the two polar regions meets the problem of definition and limits of the Subarctic region not homologous to the Subantarctic and also, may be, the question of the inclusion of true brackish water elements of the North Siberian seas in the balance. The same conclusions about sampling effort holds true for the Mediterranean fauna which, with 453 benthic Gammaridean and Caprellidean amphipod species (Bellan-Santini & Ruffo, 1996) appears at first sight very comparable to the Antarctic fauna (531 benthic and pelagic spp. versus 462 benthic spp.). Such kind of comparison remains to be made on firm zoogeographical and bathymetrical basis and between regions with similar degree of faunal knowledge.

What are the potential causes of the high Antarctic amphipod diversity?

Faunal diversification is the result of two different kinds of processes: long-term, evolutionary processes involving speciation and geographic dispersal (or more generally all regional and historical processes which determine the number of species able to be present in a community) and

short-term ecological processes which assure the maintenance of the diversity, which involve all physical factors and local biotic interactions controlling the numbers of actually coexisting species (Gage & Tyler 1991).

For explaining the generally high diversity of the Antarctic benthos, the long evolutionary history in isolation in a relatively constant and predictable environment has been invoked on one hand and biological disturbance, spatial heterogeneity and the nature of trophic regime were put forward at the ecological level on the other (Lipps & Hickman 1982; Arntz et al. 1994).

The causes of the successful radiation in the Southern Ocean and in particular of Antarctic benthic amphipods are not fully understood and have probably to be sought among these several evolutionary and biological/ecological factors. One ecological factor, already mentioned by Knox & Lowry (1977), seems to be of great importance in creating bottom fauna diversity. This is the extraordinary important share of poorly sorted, coarse terrigenic materials in bottom sediments around the whole Antarctic continent, reaching very far from the continent on the deep Antarctic shelf. All stones dropped from icebergs that permanently calve off the Antarctic ice-cap glaciers create numerous nuclei of substrates allowing development of a rich fauna of sessile filter-feeders like Porifera, Bryozoa or Ascidiacea. These animal groups flourishing in the Antarctic sublittoral serve in turn as an ideal habitat for an extremely diversified vagile fauna, including of course many amphipod crustaceans.

In addition to this habitat heterogeneity factor, some other causes specific to amphipods can be invoked:

— Amphipods are primarily a cold water adapted group (Barnard & Barnard 1983) which radiated more successfully in cold seas.

— Reproductive isolation can probably occur rather quickly in some groups of amphipods (Kinne 1954, cited by Watling & Thurston 1989):

– they are brooders (like all peracarids), which implies limited dispersal of juveniles.

– many soft bottom burrowers, sponges dwellers or associates of other sessile benthonic filter feeders are sedentary or weakly motile or have very limited swimming periods (reproductive males) (see Conlan 1991, Bousfield & Shih 1994).

— Decapods are quasi absent in the Antarctic leaving open their habitual niches for peracarids.

— An increasing part of benthic amphipods can be suspected to be

narrow specialists associated with diverse sessile benthos (e.g. Iphimediidae and related families, see Coleman, 1989a, b, 1990). This implies effects of niche fragmentation by specialization and maybe coevolution.

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