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Are there widespread peracarid species in the deep sea (Crustacea: Malacostraca)?

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Abstract: The global zoogeographic distribution of the most widespread peracarid species occurring in three or more ocean basins below 2000 m is analysed. Basing on the published data we investigated 45 peracarid species, which have a most widespread distribution and most likely are cosmopolitan. Thirty-three species have a wide distribution in the Northern Hemisphere. Most species occur in the North Atlantic, however, 16 of these species occur also in the North Pacific, a more limited number of species occurs in the South Atlantic or South Pacific The Southern Ocean displays some special zoogeographic features and 22 widespread species occur there below 2000 m, including highly eurybathic ones. In total, 11 of the analysed species occur in all oceans. *Eucopia australis* (Lophogastrida), *Munneurycope murrayi* (Isopoda) and *Eurythenes gryllus* (Amphipoda) are the species with the widest distributions. Other peracarids occurring in all oceans are: the isopods *Paramunnopsis oceanica* and *Eurycope sarsi*, the mysid *Caesaromysis hispida* the lophogastrid *Eucopia unguiculata,* the amphipod *Mesopleustes abyssorum* and the tanaids *Exspina typica, Paranarthura insignis* and *Pseudotanais nordenskioldi*. No cumacean species has been reported with an ocean-wide distribution but *Campylaspis glabra* occurs in the Atlantic, Indian and Pacific oceans. Among plenty of rare species in each order there are only few species with wide distribution records. There is evidence from molecular genetic studies that some of the widespread peracarids represent several cryptic species, however, some, *e.g. Eucopia australis*, seem to be truly cosmopolitan species. Geography of sampling is biasing our view of biogeography. The history and quality of taxonomic work as well as the reliability of geographic records (quality control of large databases) limits our investigations of widespread or cosmopolitan species as much as the limited knowledge of variation within most species causes difficulties in defining morpho-species with certainty.

Key words: Antarctic, world oceans, abyssal, cryptic species, biogeography.

Introduction

Since pioneering works by Sanders (1968) and Sanders and Hessler (1969) on the change in abundance and richness from the shelf to the deep sea (defined as beginning at the shelf edge, usually >200 m depth; Clarke and Johnston 2003), the attempts to describe and explain patterns of species diversity have become a major goal in deep-sea biological research. It has been suggested that, on a regional (*e.g.* basin-wide) scale, diversity is influenced by environmental factors like organic-matter fluxes, bottom-water oxygen concentrations, or current velocity and sediment type (Levin *et al.* 2001; McClain and Hardy 2010). However, there is also some evidence for the existence of biodiversity patterns at larger (global) scales; in particular, an apparent decrease in species richness among some taxa from the equator towards higher latitudes (Poore and Wilson 1993; Rex *et al.* 1993; Culver and Buzas 2000). Recently, data on isopod biodiversity of the Southern Ocean (SO) deep sea have challenged the hypothesis of deep-sea latitudinal gradients in the Southern Hemisphere (Brandt *et al.* 2007 a, b). McClain and Hardy (2010) reviewed the dynamics of deep-sea biogeographic ranges and noted that there is evidence for many deep-sea genera and species to be widely distributed regardless of the sediment type.

Grassle and Maciolek (1992) suggested that there may be a vast number of new species in the deep sea. Since then it has become apparent that there is a considerable proportion of undescribed fauna (*e.g.* Poore and Wilson 1993; Lambshead *et al.* 2000; Brandt *et al.* 2007a–c) and that many species do not occur frequently. For example, Brandt *et al.* (2007a–c) found 52% of Antarctic Isopoda to be rare (singletons or doubletons at only one or two of 40 stations). Currently it is unknown, even roughly, how many species inhabit the deep sea, although the most recent and comprehensive analysis of the diversity of the World's oceans (Appeltans *et al.* in press) estimates a total of less than a million species over all depths. Shelf biodiversity is better known because the shelf area has been much better sampled and specimens are recovered in better condition.

Analyses of large-scale distribution patterns in the deep sea are hampered by the large number of potentially rare and undescribed species. Additionally, few species are widespread and many species of the upper bathyal depths also occur on the continental shelf. Within the Census of the Marine Life (CoML), the deep-sea programme CeDAMar (Census of the Diversity of Abyssal Marine Life) attempts to compile a database of all abyssal benthic species records deeper than 2000 m. Data on the most widespread peracarid species were retrieved from the literature and this database, and their distribution is discussed here.

In zoogeography, widespread or particularly disjunctive animal distributions can be caused respectively by dispersal (migration of a taxon across a barrier from A to B) or vicariance (erection of a barrier between A and B, both of which were already inhabited by the taxon, *e.g.* continental drift, plate tectonics) (Stace 1989). Vicariance can also be caused by currents or differences in resource availability (*e.g.*

food falls from overhead blooms (Billet *et al*. 1983)), depth, flow and sediment (*e.g.* Levin *et al*. 2001), or the establishment of physical barriers such as trenches, seamount chains, continents, and basin sills (reviewed by McClain and Hardy, 2010). Larval development might enhance dispersal and range expansion of taxa and compensate for vicariance events in certain taxa. However, direct development often restricts wide distribution and accelerates cryptic speciation (*e.g.* Raupach *et al*. 2007) and endemism. It is generally accepted that species with pelagic larval stages are comparatively good dispersers, while palaeontological evidence exists for narrower distributions in species of marine molluscs with non-pelagic development, which were also more susceptible to extinction than those with pelagic development (Jablonski and Roy 2003; Pearse *et al*. 2009). Yet, it has been shown that dispersal ability and geographic (or bathymetric) range are not necessarily linked, but faunal distributions largely depend on, for example, habitat suitability, fragmentation, and ecological flexibility (*e.g.* Lester *et al*. 2007; Liow 2007). Both development and lifestyle (*e.g.* benthic *vs.* pelagic; vagile *vs.* sessile) influence the zoogeographic distribution of a species. Modern seafaring causes major faunistic changes by transporting larvae and early life stages via ballast water and hull-fouling (Highsmith 1985). Benthic storms or bottom currents have been suggested as mechanisms of deep-sea fauna relocation (*e.g.* Schüller and Ebbe 2007).

In the present paper we discuss the validity of the widespread peracarid species in the deep sea (*i.e.* Amphipoda, Cumacea, Isopoda, Tanaidacea, Mysida and Lophogastrida). All peracarids are brooders that release their eggs into a ventral brood pouch (marsupium) in which the offspring develop until they leave the marsupium and begin an independent life. This mode of reproduction can limit dispersal capabilities and thus reduce gene flow. We question whether there are widespread peracarid species based on what we know about species' distribution. According to McClain and Hardy (2010) peracarids are one of the most speciose groups in the deep sea. Any discussion on species with wide zoogeographic distributions is strongly dependent on sampling effort (uneven global coverage), taxonomic knowledge and accuracy, and is thus subject to change. Moreover, molecular approaches have revealed that many species are cryptic and not as widely distributed as once thought (*e.g.* Raupach and Wägele 2006). Here we examine a set of reportedly widely-distributed examples of each major taxon. We discuss what is known about their biology and life-style and review the evidence for the most widespread peracarid deep-sea species.

Material and methods

Data and the species records assembled and analyzed in the present paper were retrieved from the published literature and databases, particularly from WoRMS (Appletans *et al.* 2012), CeDAMar database (http://www.cedamar.org/ Biogeography/), Gary Anderson's webpage (Anderson 2009) and personal databases from CDB, MBP and UMS (Tables 1–2).

Subregions of Tables 1 and 2 are arbitrary divisions of the oceans (Northern and Southern Hemisphere) (Fig. 1). The Arctic Ocean was not considered, as there has been almost no biological sampling at abyssal depths. We include and discuss a species when it occurs in three or more pre-defined areas.

Since the number of species relies on the chosen species definition (besides sampling bias), discussions on biodiversity and biogeography must state on which species concept the conclusions are based. For deep-sea research, the morphological species concept (species are groups of morphologically identical or very similar organisms [Futuyma 1998]) has been the most popular definition in studies of metazoan biodiversity and biogeography. Owing to limited sampling abilities, the biological species concept (species are groups of interbreeding natural populations that are reproductively isolated from other such groups [Mayr 1942]) can seldom be used for the assessment of deep-sea animal distributions. Based on the morphological species concept, we have listed 45 peracarid species, viz. 10 species of Amphipoda (A), 10 species of Cumacea (C), 10 species of Isopoda (I), 3 species of Lophogatrida (L), 5 species of Mysida (M) and 7 species of Tanaidacea (T), in Table 1.

Similarity between defined subregions was assessed based Bray-Curtis similarity index on a presence/absence data matrix. Hierarchical agglomerative clustering was performed using the group average mathod. Nonmetric multidimensional scaling ordination technique (MDS) was also applied. The analysis was performed using PRIMER v6.

The following abbreviations are used in text, Tables and Fig. 1: EIO = East Indian Ocean; WIO = West Indian Ocean; NWP = Northwest Pacific; NEP = Northeast Pacific; SWP = Southwest Pacific; SEP = Southeast Pacific; NEA = Northeast Atlantic; NWA = Northwest Atlantic; SWA = Southwest Atlantic; SEA = Southeast Atlantic; SO = Southern Ocean. The abbreviations of the families and suborders are given in Table 1.

Results

Twenty-six of the 45 widespread peracarid species studied occur in the Northeast Atlantic, 20 in the Southeast Atlantic, 19 in the Northwest Atlantic, 18 each in the Northwest and Northeast Pacific, 17 in the Southern Ocean, 14 in the Southeast Pacific, 13 in the Southwest Atlantic, 11 in the Southwest Pacific, 9 in the west Indian Ocean, and 3 in the East Indian Ocean (Table 1).

Few species occur in all oceans. *Eucopia australis* (L), *Munneurycope murrayi* (I) and *Eurythenes gryllus* (A) have the widest distribution. *Mesopleustes abyssorum* (A), *Caesaromysis hispida* (M), *Eucopia unguiculata* (L), *Eurycope sarsi* (I)

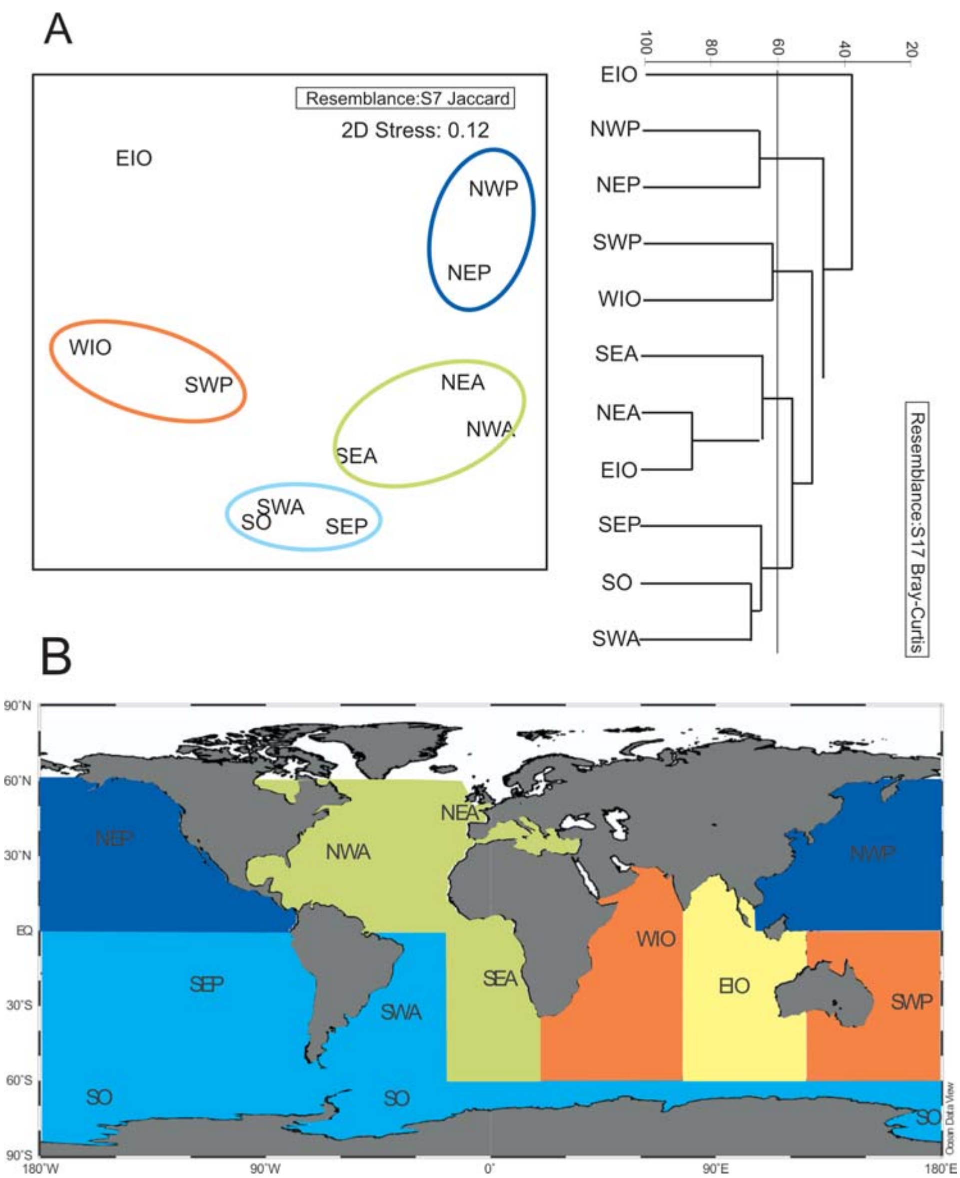

Fig. 1. **A**, similarity of subregions (nMDS/clustering) based on presence/absence of peracarid species. **B**, geographic subregions considered in the analysis. These subregions are not based on zoogeographical results.

Exspina typica (T), *Paranarthura insignis* (T) and *Pseudotanais nordenskioldi* (T) are distributed in four oceans. The cumacean *Campylaspis glabra* is reported in three oceans.

Eucopia australis (L) is reported from eleven, and *Munneurycope murrayi* (I) and *Eurythenes gryllus* (A) from ten subregions. The following species have been

Table 1

Peracarid species occurring lower than 2000 m (with the exception of *Munnopsurus giganteus* (I)) and with a wide geographic distribution. Information on bathymetric distribution is provided (see WoRMS for authorities). A, Amphipoda; C, Cumacea; I, Isopoda; L, Lophogatrida, M, Mysida, and T, Tanaidacea: Ap, Apseudomorpha; Ne, Neotanaidomorpha; Ta, Tanaidomorpha. (References for distribution data can be requested from the authors).

Order	Family	Species	Regions	NEA	SEA	NWA	NWP	NEP	SO	SEP	SWA	SWP	WIO	EIO	Min depth	Max depth
A	Eurytheneidae (Eur)	*Eurythenes gryllus*	10	×	×	×	×	×	×	×	×	×	×		550	7800
A	Uristidae (Uri)	*Abyssorchomene abyssorum*	6	×				×		×	×	×	×		900	9120
A	Atylidae (Aty)	*Lepechinella aberrantis*	5		×		×	×				×	×		1421	6330
A	Lysianassidae (Lys)	*Orchomenopsis gerulicorbis*	5	×			×	×		×		×			750	6000
A	Pleustidae (Ple)	*Mesopleustes abyssorum*	4	×				×	×				×		694	3515
A	Alicellidae (Ali)	*Paralicella caperesca*	4	×		×	×	×							1740	6018
A	Uristidae (Uri)	*Abyssorchomene chevreuxi*	3	×					×			×			3076	4970
A	Hirondelleidae (Hir)	*Hirondellea brevicaudata*	3	×			×	×							2000	5940
A	Oedicerotidae (Oed)	*Oediceroides wolffi*	3		×							×	×		1510	4961
A	Phoxocephalidae (Oho)	*Pseudharpinia excavata* + cf.	3	×	×			×							363	4392
C	Bodotriidae (Bod)	*Bathycuma longicaudatum*	4	×			×	×		×					plankton	3279
C	Nannastacidae (Nan)	*Campylaspis bulbosa*	2		×					×					2154	2846
C	Nannastacidae (Nan)	*Campylaspis glabra*	4	×		×	×							×	37	2886
C	Nannastacidae (Nan)	*Campylaspis rubicunda*	4	×		×	×	×							10	2857
C	Nannastacidae (Nan)	*Campylaspis verrucosa*	3	×		×	×								91	4125
C	Bodotriidae (Bod)	*Cyclaspis longicaudata*	4	×		×				×	×				120	5000
C	Lampropidae (Lam)	*Hemilamprops pellucidus*	3		×				×			×			564	2725
C	Leuconidae (Leu)	*Leucon longirostris*	4	×	×	×							×		??	2580
C	Leuconidae (Leu)	*Leucon tenuirostris*	6	×	×	×		×		×	×				2707	4980
C	Bodotriidae (Bod)	*Vaunthompsonia cristata*	4	×	×	×	×								0	2000
I	Munnopsidae (Mun)	*Munneurycope murrayi*	10	×	×		×	×	×	×	×	×	×	×	0 (500?)	7800

Table 1 – *continued.*

Order	Family	Species	Regions	NEA	SEA	NWA	NWP	NEP	SO	SEP	SWA	SWP	WIO	EIO	Min depth	Max depth
I	Munnopsidae (Mun)	*Paramunnopsis oceanica*	7	×	×	×			×	×		×		×	600	3240
I	Munnopsidae (Mun)	*Betamorpha fusiformis*	5	×	×	×			×		×				773	5223
I	Munnopsidae (Mun)	*Eurycope sarsi*	5		×				×	×?	×		×		2086	3962
I	Munnopsidae (Mun)	*Storthyngurella triplispinosa*	5		×			×	×	×	×				2313	6420
I	Munnopsidae (Mun)	*Syneurycope parallela*	5	×	×	×			×		×				1280	5122
I	Munnopsidae (Mun)	*Munnopsoides beddardi*	4	×	×	×		×							363	2580
I	Munnopsidae (Mun)	*Acanthocope galatheae*	3		×				×	×					3670	5585
I	Munnopsidae (Mun)	*Munnopsurus giganteus*	3	×		×	×								36	1426
I	Haploniscidae (Hap)	*Haploniscus bicuspis*	2						×		×				698	5024
L	Eucopiidea (Euc)	*Eucopia australis*	11	×	×	×	×	×	×	×	×	×	×	×	600	6050
L	Eucopiidea (Euc)	*Eucopia unguiculata*	9	×	×	×			×	×	×	×	×	×	700	2500
L	Gnathophausidae (Gna)	*Gnathophausia gracilis*	7	×	×	×				×	×	×		×	1000	5225
M	Mysidae (Mys)	*Caesaromysis hispida*	9		×		×	×	×	×	×	×	×	×	50	3200
M	Mysidae (Mys)	*Boreomysis inermis*	7	×		×	×	×	×	×		×			90	3800
M	Mysidae (Mys)	*Boreomysis plebeja*	7	×	×	×			×	×	×	×			620	5283
M	Mysidae (Mys)	*Katerythrops oceanae*	7	×	×	×					×	×	×	×	200	3000
M	Petalophthalmidae (Pet)	*Petalophthalmus armiger*	7	×	×	×		×			×	×	×		900	4500
T (Ne)	Neotanaidae (Neo)	*Neotanais americanus*	8	×	×	×	×	×	×	×	×				513	8210
T (Ta)	fam, incertae sedis	*Exspina typica*	7	×		×	×		×	×		×	×?		385	4950
T (Ta)	Anarthruridae (Ana)	*Paranarthura insignis*	6	×	×	×		×	×				×		582	5218
T (Ta)	Anarthruridae (Ana)	*Pseudotanais nordenskioldi*	5				×		×		×	×	×		497	7335
T (Ta)	Agathotanaidae (Aga)	*Agathotanais ingolfi*	4	×	×	×	×								1200	5240
T (Ta)	Typhlotanaidae (Typ)	*Peraeospinosus magnificus*	4				×	×	×		×				170	5225
T (Ap)	Apseudidae (Aps)	*Apseudes zenkevitchi*	3			×	×	×							1067	6065

identified from more than five subregions: *Caesaromysis hispida* (M) *and Eucopia unguiculata* (L) in nine; *Neotanais americanus* (T) in eight; *Exspina typica* (T), *Boreomysis inermis* (M), *Boreomysis plebeja* (M), *Gnathophausia gracilis* (L), *Katerythrops oceanae* (M), *Petalophthalmus armiger* and *Paramunnopsis oceanica* (I) in seven, *Paranarthura insignis* (T) and *Leucon tenuirostris* (M) in six. *Pseudotanais nordenskioldi* (T), *Betamorpha fusiformis*, *Eurycope sarsi*, *Storthyngurella triplispinosa*, *Syneurycope parallela*, *Abyssorchomene abyssorum* (A), *Lepechinella aberrantis*, *Orchomenopsis gerulicorbis* are reported from five subregions.

Thirty-three species have a wide distribution in the Northern Hemisphere (Table 2). Most species occur in the North Atlantic; however, 16 of these species also occur in the North Pacific (Table 2), a more limited number of species occurs in the South Atlantic or South Pacific. Twelve species have not been recorded from the NEA. Within this group of species, seven are true deep-sea species occurring below 1000 m depth, five also occur above 1000 m. Twenty-two species occur in the SO and most of these are also in the North or South Atlantic or Pacific Oceans.

The MDS analysis of peracarid deep-sea species recorded in the eleven regions of the world ocean revealed four clusters (Fig. 1 A, B). One of them (cluster 4) assembled eastern and western sides of the North Pacific (NWP + NEP); two others (cluster 1 and 2) comprised three regions each: cluster 2 shown similarity of Eastern and Western North Atlantic and Southern East Atlantic (NWA + NEA + SEA), while cluster 1 showed similarity of regions on both sides of South America and the Antarctic (SWA + SEP + ANT). Intriguingly, West Indian Ocean appeared to be more similar to Southern East Pacific rather than East Indian Ocean; this last region displayed no similarity with any other region of the world.

Discussion

Peracarida analyses

Amphipoda. — To date, only 328 benthic, demersal and benthopelagic species among about 7000 marine amphipod species (Vader 2005) have been found below 2000 m. These species belong to 144 genera and 39 families. These numbers are reduced to 173 species, 87 genera and 37 families below 3000 m and 100 species, 66 genera and 31 families below 4000 m. Among the 328 spp. found below 2000 m only 29 spp. appear to be distributed in two or more oceans. Only 11 of these most-widespread species are truly benthic, the remaining 18 species are demersal or benthopelagic, 10 representative species are listed inTable 1.

The widespread peracarid species analysed all belong to families comprising a significant number of deep-sea species. Few amphipod families, however, are composed of predominantly bathyal and abyssal species: Alicellidae, Hyperiopsidae, Lepechinellidae, Pardaliscidae, Stilipediidae, Synopiidae, and Vitjazianidae. Only the Alicellidae and Hyperiopsidae have very widespread representatives. The superfamily Lysianassoidea (with 11 families or informal family groups) constitutes an important part of the abyssal amphipod fauna comprising 23% of the species found below 2000 m, 35% of the species found below 3000 m and 31% of the species found below 4000 m. At the genus level, abyssal endemism is quite low (5%) (Barnard and Karaman 1991).

Many lysianassoid amphipods are distributed in multiple abyssal basins or even worldwide (Thurston 1990). Several lysianassoid species are scavengers, known to swim above the seafloor in search of food falls, suggesting that they can disperse over long distances (Ingram and Hessler 1983). Abyssal lysianassoids have been found several hundred meters above the seafloor (Thurston 1990), *e.g.* *Eurythenes gryllus*, occurring up to 1800 m above the seafloor (Baldwin and Smith 1987). Measures of swimming rates of scavenging amphipods (*E. gryllus*) have shown that they are sufficiently fast to swim up weak currents, but they can also be carried long distances by stronger currents (Laver *et al*. 1985). Moreover, most lysianassoids search pelagically for mates, which may also increase the probability of passive dispersal by currents (Conlan 1991).

Cumacea. — In total 1634 cumacean species and 140 genera of recent Cumacea are known. Forty-two genera have a wide distribution (represented in three or four oceans) but only 26 of them have representatives below >2000 m.

At the species level we know 356 deep-sea species, with 48 eurybathic species and 190 species living exclusively in 2000 m or deeper. However, most of these 356 deep-sea species are restricted to one ocean, and only 25 species are reported from two or more oceans. *Campylaspis bulbosa* and *Leucon tenuirostris* are truly deep-sea species while most other cumaceans have a wide depth-distribution.

The cumaceans are benthic animals that are more or less burrowed in the substratum for most of their lives. Mature males are known to move into the water column for a substantial period of time during the mating season, and females release their offspring during a brief rise into the water column (Valentin and Anger 1977, Dauvin and Zouhiri 1996). As most of the cumaceans are known to live in soft sediment, which indicates almost no current, there is not much chance for passive dispersal. However, there remains the question: how can individuals of disjunct populations belong to one gene pool? Unfortunately there are few molecular data of widely distributed cumacean species. For the widespread species *Leucon intermedius*, occurring in several locations in the Southern Ocean, low divergences of 16S rRNA sequences were observed between specimens from the Weddell and the Ross Sea (Rehm *personal communication*).

Isopoda. — About 1300 species from 92 genera and 21 families occur below 2000 m depth. Most deep-sea isopod families and genera seem to have a world-wide distribution, while on the species level the distribution appears to be much more restricted. Munnopsidae, a family of the Asellota, contains at least nine subfamilies and over 320 species and is geographically widely distributed in the deep sea (Table 1). Most isopod species included in this analysis are munnopsids (9), only one belongs to the Haploniscidae. While *Munneurycope murrayi* and *Paramunnopsis oceanica* are pelagic, *Munnopsurus giganteus* is benthopelagic, and *Betamorpha fusiformis, Eurycope sarsi, Acanthocope galatheae, Storthyngurella triplispinosa, Syneurycope parallela* and *Haploniscus bicuspis* are benthic. *Munneurycope murrayi* is the species with the widest bathymetric distribution (0–7800 m), *Munnopsurus giganteus* with the narrowest bathymetric distribution (36–1426 m). *Eurycope sarsi, Acanthocope galatheae*, and *Storthyngurella triplispinosa* occur only deeper than 2000 m. *Munnopsurus giganteus* has only been reported shallower than 2000 m until now, however it is one of the most widely distributed species geographically. Most of the widespread Isopoda listed are known from the Southern Ocean (8 species), followed by the SEA (7 species) and NWA (6 species). Nine of the isopod species occur in the Atlantic, six species in the Pacific Ocean and three species are recorded from the Indian Ocean. The ANDEEP (Antarctic benthic DEEP-sea biodiversity: colonisation history and recent community patterns) project has recovered 674 species of Isopoda (between 774 and 6348 m depth (Brandt *et al*. 2007a–c). 97% of these species were Asellota and 87% are “apparently” endemic). Species richness was highest around 3000 m depth: for example, 92 species of Isopoda were sampled at a single location in 3100 m depth (Brandt *et al.* 2007). Members of family Munnopsidae can swim with their posterior pereopods that have paddle-like carpi and propodi (Hessler and Strömberg 1989; Wilson 1989; Wägele 1989). This ability may be the reason why most of the isopod species that are widely distributed (Table 1) belong to the Munnopsidae. The most widespread genus *Eurycope s.l.* is not monophyletic and already seven different genera have been separated from it (Wilson and Hessler 1981; Wilson 1983; Wilson 1989; Malyutina and Brandt 2006; Malyutina 2008), however, it has been shown still to be paraphyletic (Osborn 2009). Besides Munnopsidae, some species of Haploniscidae were widely distributed, although, they cannot swim. The Haploniscidae living on the seafloor are able to walk efficiently and show a different distribution pattern. Species of *Haploniscus* were shown to consist of cryptic species in the Antarctic (Brökeland and Raupach 2008).

In widespread species with disjunctive distributions, the occurrence of sibling species is not uncommon. An example is the munnopsid genus *Gurjanopsis* recently erected comprising *G. australis* from the Weddell Sea (Antarctic) and the morphologically similar Arctic deep-sea species *G. incisa* (Malyutina and Brandt 2007a). *Microcope*, a genus of tiny benthic munnopsids, consists of one species from the Kurile-Kamchatka Trench and two species from the Weddell Sea and the Cape Basin (Malyutina 2008). In addition to these remote but similar species, other deep-sea munnopsids from the SO have similar, probably convergent, species in the North Atlantic, the Arctic and the North Pacific. *Munnopsis typica* (Arctic) and *M. australis* (Antarctic), *Eurycope vicarius* (Eastern Antarctic) and *E. brevirostris* (Arctic and North Atlantic) and a new species *Eurycope* sp. aff. *dahli*

(Antarctic) and *E. dahli* (Arctic) are examples of such pairs of similar species. Two undescribed Antarctic species of *Munnopsurus* from the ANDEEP collection are similar to the Arctic species *M. giganteus* and *M. longipes*. A new benthopelagic species from the Weddell Sea, *Paramunnopsis* sp., is similar to the Arctic species *P. justi* (Malyutina and Brandt 2007b). These disjunct distributions are based on the present-day documented ranges of the species and might be due to sampling bias. Many of these species are rare and molecular data are not available. We believe that at least some of the species identifications summarized in our Tables 1 and 2 are doubtful and require careful morphological and genetic studies.

Dispersal ability undeniably has an impact on species' range sizes, thus pelagic species are presumed to be more widespread than those associated with the sea bed. However, *Munneurycope murrayi* (Walker, 1903), a holopelagic widespread species, is species complex. Examination of 18S and COI from numerous specimens collected off central California, the Gulf of California, and the Gulf of Mexico showed the presence of at least five genetically distinct species. Furthermore, the data suggest there are multiple cryptic species and even that more than a single species exists at a single location and depth.

Mysida and Lophogastrida. — Most of the widespread deep-sea mysids have a meso- or bathypelagic distribution and yet are not restricted to the deep sea. Only the lophogastrid *Gnathophausia gracilis* occurs exclusively deeper than 1000 m.

Tanaidacea. — Recent Tanaidacea are represented by 1080 nominal species in 233 genera, 23 families and three suborders. Exactly half of all nominal species have been recorded below 200 m, and 30% (324 species) occur below 2000 m depth. Among the three suborders, only the Neotanaidomorpha is an exclusively deep-sea taxon. The other two – Apseudomorpha (Ap) and Tanaidomorpha (Ta) – have representatives with wide depth ranges in all types of habitats (Błażewicz--Paszkowycz *et al*. 2012). Both groups contain truly deep-sea genera, members of which never or rarely occur above abyssal depths (*e.g. Leviapseudes* (Ap)*, Carpoapseudes* (Ap)*, Langapseudes* (Ap)*, Eliomosa* (Ap), and *Monstrotanais* (Ta), *Robustochelia* (Ta) and *Stenotanais* (Ta). Some deep-sea genera, such as *Peraeospinosus*, *Tanaella* and *Collettea*, each with a world-wide distribution, also inhabit the Antarctic shelf, supporting the polar emergence hypothesis (Knox and Lowry 1977; Błażewicz-Paszkowycz 2005).

Agathotanais ingolfi, *Peraeospinosus magnificus, Leviapseudes zenkevitchi* and *Pseudotanais nordenskioldi* are examples of tanaidaceans that were initially described from a specific locality and later, dubiously, recorded from a second, remote area.

Exspina typica is parasitic on holothurians (Alvaro *et al*. 2011). It is considered that holothurian planktonic larvae could affect distribution of *E. typica* and that the tanaid and its host could have synchronized life cycles, but the mechanism of such a synchrony remains unknown.

Recent studies highlights that some earlier, apparently disparate, records of deep-sea species in fact mask distinct sibling species, unrecognized by previous inadequate taxonomy (Błażewicz-Paszkowycz, Bamber and Jóźwiak, submitted). Shallow-water species previously assumed to be widespread or even cosmopolitan (*Leptochelia* "*dubia*", *Sinelobus stanfordi*, *Hexapleomera robusta*) have been found to be aggregates of a number of quite distinct species, often with very localized distributions (*e.g.* Edgar 2008; Bamber 2010).

Tanaidacea are semi-sessile peracarids; they commonly burrow or build tubes (Tanaidomorpha) thus showing limited dispersal ability, probably consisting of only a few meters during their short lifetime. Furthermore, the possibility of dispersal by floating algae or anthropogenic means (see Bamber 2012) can be ruled out for deep-sea species. Benthic storms and upwelling are often suggested as factors enabling the dispersal of peracarids of low mobility (Reidenauer and Thistle 1985). Tanaids can be disturbed or transported by such catastrophic episodes (Larsen 2005), but this does not explain the disjunctive distributions of some of the rare species.

Zoogeography: geographic range, endemism and dispersal

Only 11 of the peracarid species analysed have been recorded in all oceans following the CeDAMar database (Tables 1 and 2). These 11 species are geographically the most widespread and potentially cosmopolitan deep-sea species, but represent a tiny fraction of the more than 3000 peracarid species recorded from below 2000 m.

The similarity analysis of the widely-distributed peracarid composition (Fig. 1A) revealed generally poor correlation between the species-clustering and the subregion clustering. The similarity between the regions (Fig. 1A,B) in general reflects the movement of the deep-sea currents (thermohaline circulation) for example showing NWA and NEA similar to SEA, but SWA, that remains under the influence of Antarctic Bottom Water (ABW) shows more similarity to SA than to any other part of the Atlantic.

The poor similarity of EIO to the other regions is an artefact caused by the low representation of taxa from this region (Table 1), and in our studies only represented by eight records of mainly pelagic or benthopelagic peracarids (Table 2).

The Pacific is the oldest of the oceans. We might therefore expect that the highest number of species have arisen in this region and that many widespread or even cosmopolitan species would occur there. Instead, we found that most of the examined species were recorded from the North and South Atlantic. This contradiction may be explained by the more extensive sampling which has been undertaken of the geologically younger Atlantic compared to the Pacific.

The Southern Ocean displays some special features in zoogeography. While the Antarctic continental shelf is well-isolated from the shelves of South America, Africa and Australia, the Antarctic deep sea is not isolated from the adjacent deep-sea basins. Due to the almost isothermal water column, many species occur over wide depth ranges (see next paragraph) and can easily migrate up and down the continental shelf displaying submergence or emergence into the deep SO. The 22 widespread species (Table 1) occurring in the SO have also been reported in the North or South Atlantic or Pacific Oceans, however it is unknown whether their origin lies in the Antarctic shelf or deep sea, as assumed for isopod taxa (Wilson 1989; Brandt 1992). Their ancestors might have migrated into the Antarctic deep sea (submergence) during glacial cycles or might have colonised the SO shelf (emergence) for example since the opening of the Weddell Sea in Jurassic times (Thomson 2004; McClain and Hardy 2010). The Southern Ocean is an example of a region that has undergone a large-scale zoogeographic change where taxa might have survived the thermal drop in ocean bottom temperatures during the Cretaceous (Clarke and Johnston 2003; Brandt 2005), in the deep slope or even deep-sea areas around the continent (Thatje *et al.* 2005). In this period, zoogeographic ranges changed and some faunal elements even became extinct (*e.g.* benthic decapods). These environmental and community changes opened up new ecological niches and the potential for enormous adaptive radiations within some peracarid taxa, like the amphipods and isopods. Enhanced speciation and eurybathy during glacial and interglacial periods of ice-sheet extensions and retreats is a further cause of zoogeographic change (Brey *et al.* 1996; Held 2003; Leese *et al.* 2008).

Speciation processes result from evolution in isolation over long periods of time and are connected with a high level of endemism (60–90%) as described for Antarctic peracarid crustaceans (*e.g.* White 1984; Clarke and Crame 2003; Brandt 2005). The degree of apparent isopod endemism in the Antarctic deep sea is high (87%; Brandt *et al.* 2007 a, b), as is tanaidacean endemism (66%). This high endemism could be due to the numerous rare species or to a sampling artefact (which may explain the rare species records). A bias in geographic coverage exists for deep-sea sampling (Stuart et al. 2008).

Many marine taxa have been suggested to have a worldwide distribution (*e.g.* Knowlton 1993; Moura *et al.* 2007; Meyer *et al.* 2008), while others seem to have only restricted ranges. Potential factors shaping species' range sizes have often been discussed in the literature (*e.g.* Gaston 2000; Pfenninger 2004; Lester *et al.* 2007; Liow 2007) and include dispersal ability, habitat suitability, ecological tolerance and changes in habitat through time (McClain and Hardy, 2010). Why marine organisms are distributed as they are, however, remains poorly understood. Furthermore the evaluation of species' range sizes may be skewed by several factors such as inaccurate taxonomic identifications, lack of distinction of cryptic species and uneven geographic and bathymetric sampling (*e.g.* Pfenninger and Schwenk 2007). Deep-sea samples do not cover as much geographic area as those from the continental shelves (sampling bias). In many abyssal samples the proportion of species new to science is high (*e.g.* Smith *et al.* 2008), and many of the deep-sea species appear to be geographically and bathymetrically restricted (*e.g.* Brandt *et al.* 2007 a, c; Smith *et al.*

Table 2

Geographic occurrence of the most widespread peracarids in areas based on Table 1, grouped into the clusters from Fig. 1A. Information on lifestyle is provided.

Taxon	Species	Presence	NEA	SEA	NWA	NWP	NEP	SO	SEP	SW	SWP	WIO	EIO	Min depth	Max depth	Lifestyle
Cluster 1																
I	*Haploniscus bicuspis*	4						×		×				698	5024	benthic
T	*Peraeospinosus magnificus*	4				×	×	×		×				170	5225	benthic
T	*Pseudotanais nordenskioldi*	5				×		×		×	×	×		497	7335	benthic
Cluster 2																
A	*Hirondellea brevicaudata*	3	×			×	×							2000	5940	demersal
A	*Paralicella caperesca*	4	×		×	×	×							1740	6018	demersal
C	*Campylaspis glabra*	4	×		×	×							×	37	2886	benthic
C	*Campylaspis rubicunda*	4	×		×	×	×							10	2857	benthic
C	*Campylaspis verrucosa*	3	×		×	×								91	4125	benthic
C	*Vaunthompsonia cristata*	4	×	×	×	×								0	2000	benthic
II	*Munnopsurus giganteus*	3	×		×	×								36	1426	benthopelagic
T	*Agathotanais ingolfi*	4	×	×	×	×										benthic
T	*Apseudes zenkevitchi*	3			×	×	×							1067	6065	benthic
Cluster 3																
A	*Mesopleustes abyssorum*	4	×				×	×				×		694	3515	benthic
A	*Pseudharpinia excavata* + cf.	3	×	×			×							363	4392	benthic
C	*Leucon longirostris*	4	×	×	×							×		??	2580	benthic
I	*Munnopsoides beddardi*	3	×	×	×		×							363	2580	benthopelagic
T	*Paranarthura insignis*	6	×	×	×		×	×				×		582	5218	benthic
Cluster 4																
A	*Abyssorchomene abyssorum*	6	×				×		×	×	×	×		900	9120	benthopelagic
A	*Orchomenopsis gerulicorbis*	5	×			×	×		×		×			750	6000	demersal
C	*Bathycuma longicaudatum*	4	×			×	×		×					plankton	3279	benthic
M	*Boreomysis inermis*	7	×		×	×	×	×	×		×			90	3800	bathypelagic
T	*Exspina typica*	7	×		×	×		×	×		×	×		385	4950	benthic

Table 2 – *continued.*

Taxon	Species	Presence	NEA	SEA	NWA	NWP	NEP	SO	SEP	SW	SWP	WIO	EIO	Min depth	Max depth	Lifestyle
Cluster 5																
A	*Eurythenes gryllus*	10	×	×	×	×	×	×	×	×	×	×		550	7800	benthopelagic
C	*Cyclaspis longicaudata*	4	×		×				×	×				120	5000	benthic
C	*Leucon tenuirostris*	6	×	×	×		×		×	×				2707	4980	benthic
I	*Betamorpha fusiformis*	5	×	×	×			×		×				773	5223	benthic
I	*Munneurycope murrayi*	10	×	×		×	×	×	×	×	×	×	×	0 (500?)	7800	pelagic
I	*Paramunnopsis oceanica*	7	×	×	×			×	×		×		×	600	3240	pelagic
I	*Syneurycope parallela*	5	×	×	×			×		×				1280	5122	benthic
M	*Boreomysis plebeja*	7	×	×	×			×	×	×	×			620	5283	bathypelagic
M	*Caesaromysis hispida*	9		×		×	×	×	×	×	×	×	×	50	3200	mesopelagic
L	*Eucopia australis*	11	×	×	×	×	×	×	×	×	×	×	×	600	6050	?
L	*Eucopia unguiculata*	9	×	×	×			×	×	×	×	×	×	700	2500	bathypelagic
L	*Gnathophausia gracilis*	7	×	×	×				×	×	×		×	1000	5225	?
M	*Katerythrops oceanae*	7	×	×	×					×	×	×	×	200	3000	meso-bathypelagic
M	*Petalophthalmus armiger*	7	×	×	×		×			×	×	×		900	4500	bathypelagic
T	*Neotanais americanus*	8	×	×	×	×	×	×	×	×				513	8210	benthic
Cluster 6																
C	*Campylaspis bulbosa*	2		×					×					2154	2846	benthic
I	*Acanthocope galatheae*	3		×				×	×					3670	5585	benthic
I	*Storthyngurella triplispinosa*	5		×			×	×	×	×				2313	6420	benthic
I	*Eurycope sarsi*	5		×				×	×	×		×		2086	3962	benthic
Cluster 7																
A	*Oediceroides wolffi*	3		×							×	×		1510	4961	benthic
A	*Lepechinella aberrantis*	5		×		×	×				×	×		1421	6330	benthic
Cluster 8																
A	*Abyssorchomene chevreuxi*	3	×					×			×			3076	4970	demersal
C	*Hemilamprops pellucidus*	3		×				×			×			564	2725	benthic

2008). This apparent endemism may be an artefact of undersampling in the abyss, and severely hampers the assessment of range sizes.

As all peracarids brood their young and thus lack pelagic larvae, it is not surprising that only 11 species were identifiable as widespread or even cosmopolitan species. However, peracarid orders differ greatly in mobility: some are suprabenthic and can actively swim (*e.g.* mysids, munnopsid isopods, many amphipods), while others are bottom dwellers (*e.g.* cumaceans, tanaidaceans). One would expect differences in dispersal abilities of species to be reflected in their range sizes. Mysids and lophogastrids are pelagic and thus should have a higher potential to disperse by ocean currents compared with benthic peracarids, suggesting pelagic species may have wider zoogeographic distributions. As hypothesised, the mysid *Eucopia australis* showed the widest distribution across all regions (Table 1; Fig. 1).

Cryptic species

Molecular studies have recently documented that quite a number of widely distributed species are indeed assemblages of cryptic species, genetically distinct but not distinguishable morphologically (*e.g.* Wilson *et al*. 2007; Raupach *et al*. 2007, 2009; Vogler *et al*. 2008). On the contrary, genetic analyses have also revealed the existence of truly cosmopolitan species in some planktotrophic taxa (Meyer *et al*. 2008) and also peracarid brooders (C. Held pers. communication). As cryptic speciation has been found to be common across all taxonomic groups and regions (Pfenninger and Schwenk 2007), each of the reported species in this paper need to be examined individually.

France and Kocher (1996) observed a high genetic divergence between the non-abyssal (<3200 m) and abyssal (>3500 m) fauna. The most widespread deep-sea amphipod *Eurythenes gryllus* was shown to be a complex of several genetically divergent taxa which were vertically stratified (Bucklin *et al*. 1987; Stoddart and Lowry 2004; Thurston *et al*. 2002). A similar result was documented for the hadal lyssianassoid *Hirondellea gigas* (France 1993).

In contrast, in other lysianassoid amphipods low intraspecific divergences were observed. A population genetic study on *Abyssorchomene* sp. showed evidence of high gene flow between abyssal populations inhabiting different Californian continental basins, suggesting panmixia. The sills and ridges separating these basins did not act as barriers to gene flow (France 1994). More recently, very low COI divergences have been observed in an undescribed species of *Abyssorchomene*, between specimens from the Antarctic Peninsula, the eastern Weddell Sea and the Ross Sea, between 310 and 4700 m depth. Furthermore, *Abyssorchomene plebs* and *Pseudorchomene coatsi* also showed a high level of eurybathy and extended geographic distribution in the Southern Ocean (Havermans *et al*. 2011).

Four species: *Lepechinella aberrantis*, *Mesopleustes abyssorum*, *Oediceroides wolffi* and *Pseudharpinia excavata* have a benthic lifestyle and probably swim only small distances. Due to their limited dispersal ability, their wide distribution (Table 1) should be questioned and a more accurate analysis might reveal hidden or cryptic species. This was the case for *Oediceroides wolffi* and *Pseudharpinia excavata* where significant morphological variability has been detected (Barnard 1962, 1964).

Some widely-distributed Antarctic isopod shallow water "species" are in fact several cryptic species or even paraphyletic genera as documented for *Eurycope* (Wilson and Hessler, 1981; Osborn 2009) *e.g.*: *Ceratoserolis trilobitoides* (Serolidae), *Glyptonotus antarcticus* (Valvifera) (Held 2003), *Betamorpha fusiformis* (Munnopsidae) (Raupach *et al*. 2007), *Acanthaspidia drygalskii* (Acanthaspidiidae) (Raupach and Wägele 2006) and species of the genus *Haploniscus* (Brökeland and Raupach, 2008). Therefore it is likely that some of the identifications of *B. fusiformis*, which is reported throughout the Atlantic, should be revised. *Serolis paradoxa* populations from Patagonia and from the Falkland Islands do not show effective gene flow, suggesting again that these are also two cryptic species (Leese *et al*. 2008).

Bathymetric ranges of widespread abyssal peracarids

Depth and factors related to it have often been found to structure communities more than geographic distance (*e.g.* France and Kocher 1996; Held and Wägele 2005, Zardus *et al*. 2006). Zonation patterns in the deep-sea are likely to be due to hydrostatic pressure, which is often described as the dominant physical force preventing ascent or descent beyond a species' observed depth range (Belyaev 1989). However, additional physical and ecological forces such as temperature, sediment granulometry, competition and predation may also influence the depth range a species can inhabit (France and Kocher 1996; Blankenship *et al*. 2006). Temperature seems indeed to be a controlling factor in the deep sea in general (France 1994), as well as oxygen concentration (White 1987) and sediment (Brandt and Piepenburg, 1994). Midwater anoxic events can vertically isolate bathyal and abyssal faunas and trigger allopatric speciation (White 1987). In the amphipod *Eurythenes gryllus*, pronounced genetic divergences between abyssal and non-abyssal populations indicate barriers to gene flow between these bathymetric zones (France and Kocher 1996).

Most of the widespread peracarid species examined here occur across wide depth ranges and thus are eurybathic (Table 1). For example, all but one of the 29 examined amphipod species have depth ranges spanning more than 2000 m and ten species more than 4000 m. One species (the amphipod *Abyssorchomene abyssorum*) occurs between 900–9120 m. In the SO, eurybathy has been attributed to glacial and interglacial cycles of the Holocene (Brey *et al*. 1996; Thatje *et al.* 2005). It has been suggested that most of the shelf and continental slope around Antarctica were unfavourable environments for benthic invertebrates to survive glacial periods (Thatje *et al*. 2005: 534) which migrated to the deep sea and recolonized the Antarctic continental shelf from the deep during the following interglacial.

Numerous tanaidaceans are known to show a wide bathymetric range (*e.g.* 7–2223 m for *Pseudosphyrapus anomalus* (G.O. Sars, 1869) and 40–6710 m for *Collettea cylindrata* (G.O. Sars, 1882). Larsen (2005) discussed this phenomenon and stated that tanaidaceans show substantial pressure tolerance owing to the fact that selection might have favoured enzymatic adaptations in abyssal organisms (Siebenaller 1978; Siebenaller and Somero 1978). The opposite was concluded by Błażewicz-Paszkowycz and Bamber (in press) based on tanaidaceans collected in the Bass Strait (SE Australia) from a wide range of depths down to 3000 m. Their results suggested a restriction in the species distributions horizontally in band-shaped basins and vertically to zones of a few hundred meters.

At present there are 320 known cumacean species, of which approximately 20% is reported to live below 2000 m depth. A large number of these species (107) are recorded from less than 200 to greater than 2000 m depth, indicating a high degree of eurybathy. Of the 35 most-widespread species known, 23 have depth ranges less than 200 to 2000 m and deeper. Most of them are described from polar regions and deep-sea regions adjacent to polar regions, indicating a preference for cold temperature rather than for bathymetric pressure.

The predominantly pelagic widespread mysids and lophogastrids shown in Table 1 also have depth ranges of more than 2000 m indicating that eurybathy is common in this group as well.

Taxonomic reliability

Species names and their respective geographical distribution can be retrieved from different databases (*e.g.* OBIS, WoRMS, GBIF). These databases document that some peracarid species have a wide zoogeographic distribution, however, all of these databases depend on correct identifications of the species. Often there is no quality control (checking of correctness of identifications) and therefore species names in databases, as well as in ecological surveys, may be subject to misidentifications. Species identifications often depend on identification keys or – even more commonly – on a comparison with the original descriptions, which are often incomplete because of little knowledge of variation within a group of closely-related species, cryptic species or paraphyletic taxa. In addition to that, many families and genera lack extensive systematic revisions that are urgently needed.

For example, tanaidaceans received little taxonomic attention for decades apart from a few monographs (see Błażewicz-Paszkowycz *et al.* 2012). The lack of taxonomic recognition has been the direct reason for species misidentification and, in consequence, an incorrect assessment of their distribution. The taxonomy of tanaidaceans has received more attention in the last two decades and since 1990 a further 347 new species have been described, equivalent to 32% of all know tanaidaceans. Those studies have contributed to the revision of some higher taxa and additional information on their distribution. In consequence, species formerly considered to be cosmopolitan, widely distributed or bipolar, were found under closer examination to be cryptic taxa with limited distributions.

The same is true for other peracarids, *e.g.* new data from the Antarctic deep sea added 15.3% to the world's known marine isopod diversity, which roughly stands at ~4,400 species (Kensley 1998; Brandt *et al.* 2007b).

It appears that most of the widespread species according to current records discussed here might represent aggregates of similar, closely-related or cryptic species whose distinction will rely on competent and detailed taxonomy; were that to be undertaken, the total of eleven widespread species discussed above may well reduce to two (the pelagic *Eucopia australis* and the parasitic *Exspina typica*) or even fewer. We believe that there are in fact very few widespread deep-sea peracarid species, and possibly none, in the definition of widespread used here.

Future studies

In the previous sections we referred to potential taxonomic problems with databases lacking quality control and to taxonomic problems of some taxa. Many genera and families of peracarid orders need to be revised, and, therefore, Peracarida is a taxon difficult to study. It must also be emphasized that the practice of identifying species to existing taxa despite being found far from previous locations, which was common in the 19th and 20th centuries, is inappropriate in the non-dispersive Peracarida. Indeed, the default option should be to assume that species described from disparate localities are most likely to be distinct. High biodiversity, the large number of potentially rare species or singletons in deep-sea samples, the fact that many species (usually >90%) are new to science, as exemplified for the SO Isopoda (Brandt *et al.* 2007a–c), and vanishing taxonomic expertise are all challenges to deep-sea investigations in addition to those listed by McClain and Hardy (2010). Training young scientists in taxonomy and maintaining career opportunities for taxonomists is therefore as important as intensified genetic, phylogenetic or phylogeographic studies.

The present paper is important in the context of basic ecological studies and conservation of biodiversity, which might be threatened by *e.g.* deep-sea mining and waste dumping because it covers large-scale biogeographic distributions of deep-sea species which are difficult to sample and usually rare.

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