



Composition and endemism of the deep-sea hydrothermal vent fauna

Torben WOLFF

Zoological Museum, University of Copenhagen, Universitetsparken 15,

DK- 2100 Copenhagen Ø, Denmark

Fax: +45-35321010, e-mail: twolff@zmuc.ku.dk

Abstract: Based on enumerations from 1997/1998 and personal records, an up-to-date survey of the hydrothermal vent fauna is presented with number of species, genera and families of various taxa. The number of recorded species is 712 and includes species known exclusively from vents (71%), also occurring in cold seeps and/or whale falls (5%), also recorded from non-vent/non-seep environments (9%) or mainly referred to genus only (15%). The number of genera is 373, of families 185. Molluscs, arthropods and polychaetes are the prevailing groups (36, 34 and 18%, respectively). Prosobranch gastropods number almost three fourths of 257 mollusc species, copepods more than one third of 225 crustaceans and phyllodocid polychaetes more than half of 129 polychaetes. Calculation of vent endemism (after deduction of 103 species of doubtful status) shows values far exceeding those found elsewhere in the marine environment. On species level it is 83.4%, with maximum values found in cirripeds (100%), copepods (98%), prosobranch gastropods (89%), and polychaetes (86%). The percentage of endemic genera is 45. All six cirriped and most vestimentiferan genera are endemic, and other high values are within copepods (66%), gastropods (58%), polychaetes (51%) and decapod crustaceans (43%). Fourteen among the families (8%) are found in vents exclusively, eight also in seeps.

Résumé : *Composition et endémisme de la faune des sources hydrothermales profondes.* Fondée sur les listes publiées en 1997 et 1998 et sur des données personnelles, une liste mise à jour de la faune des sources hydrothermales est présentée. Le nombre total d'espèces signalées est 712, nombre qui inclut les espèces exclusivement inféodées aux sources hydrothermales (71%), celles également présentes dans les zones de suintements froids ou sur les carcasses de baleines (5%), celles également trouvées dans d'autres types de milieux (9%), enfin celles identifiées seulement au niveau générique (15%). Le nombre total de genres est de 373, et celui des familles de 185. Mollusques, Arthropodes et Polychètes sont les groupes prédominants (respectivement 36, 34 et 18% du total). Le nombre de Gastéropodes prosobranches représente à peu près les trois quarts des 257 espèces de Mollusques, les Copépodes plus d'un tiers des 225 Crustacés et les Phyllodocidés plus de la moitié des 129 Polychètes. Une fois soustraites les 103 espèces de statut douteux, le taux d'endémisme de la faune des sources hydrothermales atteint des valeurs qui excèdent toutes celles trouvées dans d'autres environnements marins. Le taux d'endémisme au niveau spécifique est de 83 %, avec des valeurs maximales chez les Cirripèdes (100%), les Copépodes (98%), les Gastéropodes (89%) et les Polychètes (86%). Le pourcentage de genres endémiques est de 45%. Les six genres de Cirripèdes et la plupart des genres de Vestimentifères sont endémiques; d'autres valeurs élevées ont été trouvées chez les Copépodes (66%), les Gastéropodes (58%), les Polychètes (51%) et les Décapodes (43%). Quatorze familles (8%) sont endémiques des sources hydrothermales.

Keywords: Hydrothermal vent fauna, Endemism, Cold seeps, Whale carcasses

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Introduction

After the discovery in the late 1970's of the fascinating hydrothermal vent fauna, being totally independent of sun energy, the first fauna enumeration was made by Hessler & Smithey (1983) who very preliminarily listed 22 taxa, with feeding types, mobility and locality in relation to venting activity.

Based on about ten overview articles and many specific papers, I published an article for Scandinavian readers on the vent fauna (Wolff, 1985a). This included the first extensive list of all registered vent animals, with their distribution at Galapagos and 13° and 21° North on the East Pacific Rise (EPR); a paper, including the same list, was published in English (Wolff, 1985b). The number of species listed, identified to species or not, was 93, and the genera numbered 66. The list included details on feeding types and mobility, the occurrence at vents, as well as data on endemism of species and genera. Also in 1985, a list containing 58 described species was published by Newman.

Since 1985, I have continued to keep a detailed list of new records of vent animals. This was done in close contact with Verena Tunnicliffe who was similarly engaged. Her first published list of species (Tunnicliffe, 1991) numbered 236 species and 135 genera. The two later lists, by Desbruyères & Segonzac (1997) and Tunnicliffe et al. (1998), are almost identical and record ca. 440 species (exclusive of fish and cephalopods) and ca. 285 genera.

In continuation of my vent article in Danish (Wolff, 1985a), I recently published an up-to-date survey of new discoveries in the hydrothermal vents (Wolff, 2002). It also included chapters on the composition of animals, based on a circumstantial list of the number of species, genera and families of the various animal groups, the number of species at major deep-sea vent sites, details about the endemism, and conservation. A version in English of most of these items is the background for the present paper.

Composition

Number of species, genera and families

Table 1 is based on my list of vent taxa up to January 2005. The enumeration has been supplemented with information on special groups provided by several colleagues (see Acknowledgements) and was coordinated with the lists of primarily described species in Gebruk (2002).

Table 1 presents the total number of species, genera and families of animal groups of the deep-sea hydrothermal macrofauna, with percentage of the number of species for each of the taxa listed. Also included are 1) species exclusively in vents, 2) species also represented in cold seeps

and/or associated with whale carcasses, 3) species also known from other (non-vent) environments, and 4) species of doubtful status (mostly referred to genus only and not recorded as being new species). Of a total 712 vent species registered, the four categories number 508, 35, 66, and 103 species – or 71%, 5%, 9% and 15%, respectively.

The main reasons for the apparently significant increase in total number of species since the list in Desbruyères & Segonzac (1997) and Tunnicliffe et al. (1998), from ca. 440 to 712 species, are: 1) about 100 new records since 1997/98, 2) omission in the two lists of several species which, when published, had been stated as true vent forms (mainly some sponges, cnidarians, amphipods, tanaids and isopods), 3) deliberate omission of all fishes and cephalopods, 4) omission of a fair number of species which had been recorded as new but yet undescribed species, 5) almost total omission of a large number of species (now more than 100) which were referred to species only (inclusion of the latter records involves that the total number is on the large size, since some, but probably not many, will eventually be referred to already known vent species).

The total number of genera is 373 of which 151 are found exclusively in vents. A total of 185 families are represented, with 14 in vents only and another eight also in seeps/whale falls (Table 4).

Dominating groups

The molluscs, the arthropods and the polychaetes are the three prevailing groups, amounting to 36.1%, 34.3% and 18.1% of all vent animals (Fig. 1).

There may be two reasons for the particular success of these three groups. First, it is an advantage to find protection inside a shell, an integument or a tube, respectively, against the continuous precipitation of particles in the 'dirty' vent environment. Especially the water inside polychaete tubes may act as a buffer against rapid changes in temperature or chemical properties. Moreover, these three dominating groups are exactly those which also in other marine environments are able to adjust themselves to extreme conditions regarding temperature, salinity, deficiency of oxygen, etc., in opposition to more stenotopic groups like sponges, cnidarians, echinoderms and ascidians.

Molluscs: more than one fourth of all vent animals are snails (Table 1). About 70% of these belong to the Archaeogastropoda, many of which are limpet-shaped. Apart from the two genera, *Alviniconcha* and *Ifremeria* which, with their symbiotic bacteria, are dominating in most of the West Pacific back-arc spreading centres, the others are of moderate or small size (< 1 cm).

More than one third of the gastropod species belong to three families (number of species in parenthesis): Provannidae (24, inclusive three also in seeps), Peltospiridae (22), and Lepetodrilidae (21, one also in

Table 1. Number of macrofauna families, genera and species represented exclusively in hydrothermal vents or also known from cold seeps and/or whale carcasses or elsewhere in the deep sea. Meiofauna nematodes are not considered. Only vent fishes living inside active fields are included (about 90 other fish species hovering in the close surroundings, with occasional visits to the vent fields, are not considered).

Tableau 1. Nombre de familles, genres et espèces de macrofaune signalés exclusivement au niveau des sources hydrothermales ou également au niveau des suintements froids et des carcasses de baleines ou dans d'autres environnements profonds. Les Nématodes de la méiofaune ne sont pas pris en compte. Seuls les poissons vivant au sein des sources actives sont inclus (environ 90 autres espèces fréquentant les environs et visiteurs occasionnels ne sont pas pris en compte).

Animal Groups	Genera			Species					
	Families	All genera	Vent endemic ¹	All species	% of all vent species	Vent endemic ²	Also at cold seeps/whale falls	Also outside vents	Dubious ³
Porifera, sponges	5	6	0	11	1.6	0	0	3	8
Cnidaria	12	22	2	26	3.7	7	0	10	9
Hydrozoa, hydroids, siphonophores.	7	12	1	11	1.6	2	0	7	2
Anthozoa, sea anemones	3	8	1	11	1.6	5	0	3	3
Others	2	2	0	4	0.6	0	0	0	4
Nemertea, ribbon worms	2	2	1	2	0.3	1	0	0	1
Turbellaria, flatworms	1	1	-	1	0.1	-	-	-	1
Tremadoda, flukes	-	-	-	-	-	-	-	-	-
Acanthocephala	1	1	1	1	0.1	1	0	0	0
Echiura, spoon worms	2	2	0	2	0.3	1	0	1	0
Polychaeta, bristle worms	28	73	37⁴	129	18.1	97	7	9	16
“Vestimentifera”/“Pogonophora”	1	9	9 ⁵	15	2.1	12	3	0	0
Hirudinea, leeches	1	1	1	1	0.1	1	0	0	0
Mollusca	41	107	53	257	36.1	194	25	9	29
Monoplacophora	1	1	1	1	0.1	1	0	0	0
Aplacophora	2	2	1	10	1.4	10	0	0	0
Polyplacophora, chitons	1	2	1	2	0.3	2	0	0	0
Prosobranchia, snails	28	83	48 ⁶	188	26.4	150	14	5	19
Opisthobranchia, nudibranchs	1	1	1	1	0.1	1	0	0	0
Bivalvia, clams, mussels	6	13	1	48	6.7	29	11	2	6
Cephalopoda, octopods	2	5	1	7	1.0	1	0	2	4
Arthropoda	75	138	50⁷	244	34.3	184	2	30	28
Arachnida, water mites	1	5	1	8	1.1	6	0	1	1
Pycnogonida, sea spiders	1	4	1	11	1.6	9	0	2	0
Crustacea	73	129	48	225	31.6	169	2	27	27
Copepoda, water fleas	21	41	27	81	11.4	79	0	2	0
Tantulocarida	1	1	1	1	0.1	1	0	0	0
Ostracoda, mussel shrimps	8	10	0	12	1.7	6	0	0	6
Cirripedia, barnacles, etc.	4	6	6	14	2.0	14	0	0	0
Leptostraca	1	1	1	1	0.1	1	0	0	0
Tanaidacea	1	2	0	8	1.1	0	0	1	7
Isopoda	7	7	1	7	1.0	1	0	0	6
Amphipoda	17	31	0	32	4.5	20	0	12	0
Caridea, shrimps	5	13	7 ⁸	26	3.7	19	1	4	2
Astacidea, lobsters	1	1	0	1	0.1	1	0	0	0
Anomura, galatheids	2	5	1	18	2.5	11	1	2	4
Anomura, lithodes	1	2	0	5	0.7	3	0	2	0
Brachyura, crabs	5	9	5	19	2.7	13	0	4	2
Echinodermata	7	8	1	12	1.7	2	0	4	6
Enteropneusta, acorn worms	1	1	1	1	0.1	1	0	0	0
Pisces, fishes⁸	8	11	3	25	3.5	19	1	0	5
	185	373	151	712	99.9	508	35	66	103

¹ Including genera recorded as new, but not yet described.

² Including species recorded as new, but not yet described.

³ Mainly species referred to genus or family only.

⁴ Four genera also in seeps/whale falls.

⁵ Two genera also in seeps/whale falls.

⁶ Three genera also in seeps/whale falls.

⁷ Two genera also in seeps.

⁸ One genus also in seeps.

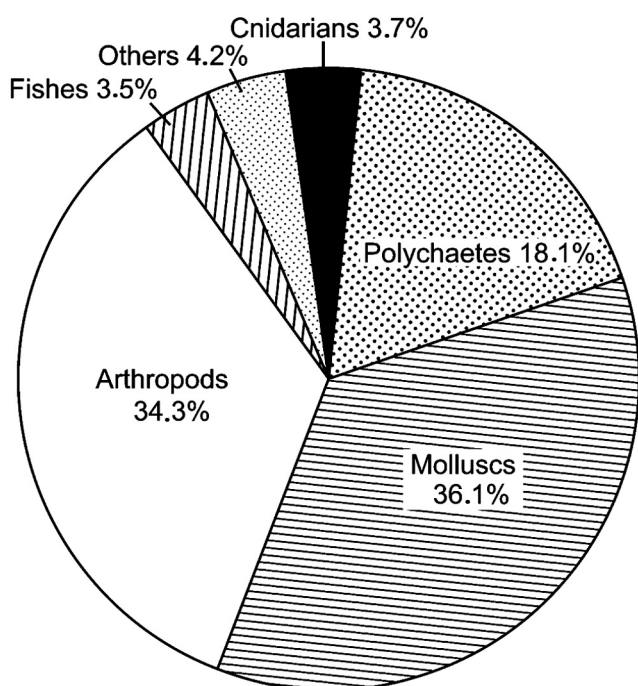


Figure 1. The allocation (%) on major groups of the fauna of the deep-sea hydrothermal vents (including species also occurring in cold seeps and/or whale falls or in non-vent environments).

Figure 1. Contribution (%) des groupes majeurs à la faune des sources hydrothermales (y compris la faune également présente au niveau des suintements froids et/ou des carcasses de baleines ou dans des environnements non hydrothermaux).

seeps), with *Lepetodrilus* and *Provanna* having the greatest diversity with 13 and 7 species living exclusively in vents, and 14 and 10, respectively, in vents and seeps.

Most numerous of the bivalves are the mussels of the genus *Bathymodiolus* which numbers about 21 species (5 also in seeps and several still not described). While the mussels are restricted to vents and seeps, the other large bivalves with symbiotic bacteria, the clams *Calyptogena* and related genera (family Vesicomidae), are apparently immigrants into vents and seeps, being also found in the deep sea elsewhere. *Bathymodiolus* is reported from all major vent sites while the Vesicomidae are absent from the Manus, Fiji and Lau back-arc spreading centres in the SW Pacific and from the Mid-Atlantic Ridge (except a not yet described species of *Calyptogena* at the Logatchev site) and in seeps at Barbados and West Florida (Kojima et al., 2004).

Arthropods: crustaceans make up 93% of the vent arthropods. By far the most diverse group are the copepods which account for more than one third (36%) of all 225 crustacean species (Table 1). They were (varying in numbers from one specimen per species to several thousand) collected with grabs or slurp guns and by washing of tubes of vestimentiferan worms, mussels and larger crustaceans. No less than 52 copepod species (two thirds) belong to the family Dirivultidae (one species also in a cold seep), and almost half of them (23) to the genus *Stygiopontius*. Many copepods live more or less loosely associated with other vent organisms: 11 species with vestimentiferans, 4 with other polychaetes, 14 with bivalves and 5 with shrimps and crabs (Humes & Segonzac, 1998).

The second largest crustacean group are the decapods with 69 species (31%). Most of the 26 species of shrimps belong to Alvinocarididae which – including Mirocarididae (cf. Komai & Segonzac, 2003) – numbers 18 species and occurs only in vents (one species of *Alvinocaris* also in seeps, and another 4 species of *Alvinocaris* are exclusively found in seeps, Komai & Segonzac, 2005).

Most of the galatheids are referable to *Munidopsis*, with 12 species (one also in seep, two also non-vent and three referred to genus only). Of the 19 crab species, 13 (plus two undescribed) belong to the superfamily Bythograeoidea whose 5 genera are restricted to vents.

Polychaetes: more than half (53%) are phyllodocid polychaetes; they include by far the largest family, the scale-worms Polynoidae which, with a total of 44 species, amounts to 34% of all 129 polychaete species. Next in numbers are vestimentiferans and pogonophorans (family Siboglinidae)¹ which includes 14 vestimentiferans and one pogonophoran vent species with 3 also in seeps/whale falls (Schulze, 2003); almost equal in number is the vent endemic family Alvinellidae with 12 species. Several polychaetes are associated with vestimentiferans or bivalves, and some are living in the mantle cavity of the latter.

Rare or absent groups

The most striking paucity is found within the echinoderms which dominate, particularly in biomass, elsewhere in the deep sea. The so far recorded representatives are limited to 5 (partly doubtful) species of holothurians, 4 asteroids and one species each of echinoids, ophiuroids and crinoids. Other rare groups are the sponges and cnidarians except the sea anemones which are, however, always found in the peripheral part of the vent fields. Completely lacking are i.a. xenophyophores, sipunculids, phoronids, bryozoans, brachiopods and ascidians². Some of these groups consist

¹ All vestimentiferan and pogonophoran genera are referred to Polychaeta: order Sabellida, family Siboglinidae (Rouse & Fauchald, 1997).

² Recently, Monniot (2003) recorded the ascidian *Polydistoma azorensis* nov.sp. from or close to vents on the Mid-Atlantic Ridge, but it is not recognized as a vent species (Desbruyères in litt.).

Table 2. Number of macrofauna taxa recorded from all vent sites. Meiofauna nematodes and about 90 species of stray fishes are not considered. EPR: East Pacific Rise.

Tableau 2. Nombre de taxons de macrofaune recensés sur tous les sites hydrothermaux. Les Nématodes de la méiofaune et environ 90 espèces de poissons errants ne sont pas pris en compte. EPR: Ride Est Pacifique.

Region	Area	Species	Genera	Families	Phyla
East Pacific Ocean	Galapagos	90	68	46	7
	SE Pacific, EPR	50 ¹	36	25	7
	10-13°North, EPR	133	97	57	8
	21°North, EPR	103	72	42	6
	Guaymas	67	53	38	3
NE Pacific Ocean	Juan de Fuca, etc.	109	90	61	6
SE Pacific Ocean	Pacific-Atlantic Ridge (PAR)	17+	-	-	-
West Pacific Ocean	Okinawa, etc., Japan	59	48	36	4
	Marianas	34	32	24	5
	Manus	30	28	19	5
	North Fiji	62	49	32	4
	Lau	55	50	30	4
	Kermadec Ridge	13+	-	-	-
Indian Ocean	Rodriquez Triple Junction	36+ ²	-	-	-
Atlantic Ocean	Mid-Atlantic Ridge (MAR)	140	96	67	6
All vent sites (Table 1)		712	373	185	13

¹ A recent survey of 29 sites at 7°25' S, 14° S, 17°25'-35' S, 18°26'-36' S, and 21°25'-33' S (Jollivet et al., 2004) provided names of 10 not previously recorded species and the following tentatively identified taxa: several new species of four polychaete families and new monogenous and digenous Trematoda (group not recorded from vents before), parasitic on three new fish species.

² Combined from records of named taxa, mainly in Hashimoto et al., 2001, Van Dover et al., 2001, Van Dover, 2002, and Southward & Jones, 2003, also including first vent occurrence of Turbellaria. Reference to three unnamed species of gastropods and one copepod and to possible new genera were left out.

Table 3. Number and percentage of endemic species, genera and families in hydrothermal vents and in vents plus seeps and/or whale falls.

Tableau 3. Nombre et pourcentage d'espèces, de genres et de familles endémiques des sources hydrothermales et de l'ensemble sources hydrothermales + suintements froids et carcasses de baleines.

	Total number	Reduction	Only in vents	% endemic	Also in seep and/or whale falls	% endemic	Also outside vents/seeps
Species	712	103 ¹	508	83.4	35	89.2	66
Genera	373	40 ²	151	45.0	9	48.0	173
Families	185	-	14	7.6	8	11.9	-

¹ Unidentified species referred to genus or family only.

² Genera with not yet identified species and not recorded as n.gen.

of colonial animals which, apart from the aberrant siphonophore *Thermopalia*, are absent from the vents.

Two crustacean groups, the tanaids and the isopods which are otherwise abundant in deep-sea sediments, are few in numbers in vent environments (Table 1), and the early, mainly Russian records, have not been verified later³. If the limited number may be explained by the scarcity of suitable sediment habitats, it seems however strange that

none have been recorded from the East Pacific Guaymas vent field which is extraordinarily rich in sediments.

Occurrence at the deep-sea vent sites

Judged from the relatively modest number of recent papers recording and describing new vent species, compared to the flood of such publications in the 1980's and 90's, it seems

³ Several additional tanaids, collected at Juan de Fuca and Lucky Strike (MAR) in 2004, are under study (Kim Larsen, pers. com.).

appropriate to present here a list of the number of taxa recorded from the major vent sites (Table 2).

New hydrothermal vent sites are, however, still being discovered, most significantly in the Indian Ocean (Hashimoto et al., 2001; Van Dover et al., 2001; Van Dover, 2002), on the Pacific-Antarctic Ridge (PAR) in the SE Pacific at 38°S, 111°W (Stecher et al., 2002) and on the southern Kermadec Ridge, New Zealand (Clark & O'Shea, 2001; Webber, 2004).

The lists of animals from particularly the two latter localities are tentative. Thus, from PAR only those taxa which have not previously been recorded from EPR or elsewhere were included in Tables 1 and 2. From the list in Stecher et al. (2002), Türkay (pers. com.) excludes Parachnopa (pelagic holothurians) and comatulid crinoids as true vent forms while another crinoid, *Hyocrianthus* sp., is common in the PAR vent fields (the first record of vent crinoids).

From the Kermadec Ridge, Clark & O'Shea (2001) list about 70 crustacean, mollusc and echinoderm species. However, since the status of most of these as true vent forms is still uncertain, only 13 obvious vent records of seven crustaceans, 5 molluscs and one echinoderm have been included in Tables 1 and 2.

Endemism⁴

Endemism on species level

A total of 83.4% of the vent species are endemic (Table 3): out of the 609 species which have been named so far or are recorded as new but still undescribed species, no less than 508 are restricted to vent habitats. If we include the 35 species which are shared with cold seeps and/or whale falls (i.a. Sibuet & Olu, 1998; Tunnicliffe et al., 1998) the endemism increases to 89.2%.

As far as the individual groups are concerned (Table 1), species of 4 genera of Cirripedia, *Scillaelepas*, *Arcoscalpellum*, *Altiterruca* and *Hexalasma*, have previously been recorded as belonging to the vent fauna. Their non-vent status has, however, been confirmed by Bill Newman (pers. com.), leaving 14 species (5 yet undescribed) which are all restricted to vents. If the 3 species of vestimentiferans which also occur in seeps/whale falls are excluded, the remaining 11 vestimentiferans and one pogonophoran are also 100% endemic.

A similar extraordinarily high vent endemism of 97.5% is found in the 81 represented copepods, of which only 2 species are also recorded from the deep sea elsewhere. Almost equally high values are found within the snails: 89% when both unidentified species and the 14 species occurring also at seep/whale fall sites are excluded, and 97% endemism with inclusion of the latter. The corresponding values for the polychaetes are 86 and 92%.

Table 1 indicates a limited endemism for the moderately adapted cnidarians. Also the number of proper vent fishes (mainly the eelpout family Zoarcidae) is rather modest, being only 22% of the total number of recorded fish species; the majority of the fishes (about approximately 90 species) have mainly or entirely been observed roaming in the periphery of the vent sites (Bischoito et al., 2002). Apparently a similar vent occurrence applies to amphipods where no less than about one third have previously been recorded from the deep sea in general and are probable intruders from outside. If these 12 amphipod species, are excluded the overall vent species endemism even increases to 85%, not including seep/whale fall species, and to 91% when these are counted in.

Endemism on genus level

As far as genera are concerned, the overall endemism is 45%, and 48% when including seep occurrence (Table 3). The endemism of 6 cirriped and 7 vestimentiferan genera (excluding two also in seeps) is 100% (Table 1). The third highest endemism is found within the copepods (66% of a total of 41 genera). Other groups with many endemic genera are the snails (58% of 83 genera, excluding three also in seeps/whale falls), the polychaetes (51% of 73 genera, excluding four also in seeps) and the decapod crustaceans (43% of 30 genera, excl. one also in seeps). In contrast to the many endemic snail genera, only one of the 13 bivalve genera (the highly diverse *Bathymodiolus*) is endemic to vents and seeps.

Fairly many of the endemic genera number 3-4 species, rather few 5-7, and the following amount to at least 10 species: the polychaete genus *Paralvinella* (10), the gastropod genera *Lepetodrilus* (14, including one species also in seeps), *Phymorhynchus* (10) and *Provanna* (10, including 3 also in seeps), the mussel *Bathymodiolus* (at least 21, including 5 species also in seeps), and finally the copepod genera *Aphotopontius* with 12 and *Stygiopontius* with no less than 23 species.

⁴ During correspondence with Andrey Gebruk (Moscow) on vent endemism of certain taxa, he advised me not to use this term, maintaining that "endemic" means restricted to a geographic region, not to a biotope – "like rain forests or caves or temporary ponds or sand bottoms". Instead he and his collaborators felt that 'vent endemic' should be replaced by 'vent obligate', a term which means precisely restricted to a certain type of habitat (Mironov et al., 2002). I addressed various colleagues for comments. Alan Southward (Plymouth) agreed that 'vent endemic' is quite incorrect usage, mentioning that the term 'obligate' is much employed by microbiologists. Bill Newman (La Jolla), on the contrary, considered that "the word 'endemic' applies to organisms restricted to a particular region or environment, regardless of how limited, and therefore it is properly applied to families, genera and species restricted to vent and seep communities". Others (including myself) also felt that 'endemism', when speaking of vent habitat, has become generally accepted through usage.

The only non-endemic genus with about equally many species is the galatheid crab genus *Munidopsis* with 12 species (two also non-vent) and numerous species elsewhere in the deep sea.

Endemic subfamilies

The polychaetes contain three endemic subfamilies and the snails and cirripeds one each. In addition, one more polychaete subfamily and the mussels (subfamily Bathymodiolinae) include also species occurring both in vents and seeps.

Endemic families

Fourteen among the 185 families (8%) are found in vents only, with 8 additional ones also in cold seeps and/or associated with whale falls. The number of genera and species of endemic families is listed in Table 4. Some gastropod families and most vent crabs belong to vent endemic superfamilies.

Endemism on higher level

Of vent taxa higher than superfamily, the endemic suborder Brachylepadomorpha comprises the earliest sessile barnacles, appearing in Upper Jurassic, and containing a single recent species, *Neobrachylepas relicha* (Newman & Yamaguchi, 1995) (from the Lau Back-Arc Basin in the West Pacific), the most primitive of living sessile barnacles. The monophyletic gastropod group Neomphalina is endemic and comprises one superfamily (Neomphaloidea) and provisionally three families (Table 4); the taxonomic status of this group is still unsettled (A. Warén pers. com.).

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Table 4. Vent endemic families and families found also in seeps/whale falls, with their number of genera and species.

Tableau 4. Familles endémiques des sources hydrothermales et familles endémiques de l'ensemble sources hydrothermales + suintements froids et carcasses de baleines.

Vent endemic	Genera	Species
Polychaeta		
Archinomidae	1	1
Alvinellidae	2	12
Gastropoda		
Dendrotonidae	1	1
Neomphalidae ¹	4	7
Peltospiridae ¹	10	22
Melanodrymiidae ¹	3	9
Sutilizonidae	3	5
Crustacea		
- Copepoda		
Lubbockiidae	1	1
Ecbathyriontidae	1	1
Misophtriopsidae	1	1
- Cirripedia		
Brachylepadidae	1	1
Neoverrucidae	2	2
- Brachyura (crabs)		
Bythograeidae ²	5	15
Hemichordata (acorn worms)		
Saxipendidae	1	1
Found exclusively in vents and seeps/whale falls		
Polychaeta		
Nautiliniellidae	3	5 ³
Gastropoda		
Neolepetopsidae	3	9 ⁴
Pyropeltidae	1	4 ⁵
Lepetodrilidae ⁶	4	21 ³
Provannidae	4	24 ⁷
Crustacea		
- Copepoda		
Dirivultidae	13	52 ⁸
- Cirripedia		
Eolepadidae	4 ⁹	9
- Caridea (shrimps)		
Alvinocarididae ¹⁰	7	18 ³

¹ In separate superfamily: Neomphaloidea.

² In separate superfamily: Bythograeoidea.

³ One also in seep.

⁴ One also in seep, two restricted to seeps.

⁵ Three also in seeps/whale falls.

⁶ In separate superfamily: Lepetodrilidae.

⁷ Three also in seeps; at least ten more (genus *Provanna*) in seeps only.

⁸ One found exclusively in seep.

⁹ One genus and species in seep only.

¹⁰ Komai & Segonzac (2003) synonymized the endemic family Mirocarididae with Alvinocarididae and recognized only one species of *Mirocaris*.

References

- Biscoito M., Segonzac M., Almeida A.J., Desbruyères D., Geistdoerfer P., Turnipseed M. & Van Dover C. L. 2002. Fishes from the hydrothermal vents and cold seeps - an update. *Cahiers de Biologie Marine*, **43**: 359-362.
- Clark M.R. & O'Shea S. 2001. Hydrothermal vent and seamount fauna from the southern Kermadec Ridge, New Zealand. *InterRidge News*, **10**: 14-17.
- Desbruyères D. & Segonzac M. 1997. *Handbook of Deep-Sea Hydrothermal Vent Fauna*. Editions IFREMER, Brest, 279 pp.
- Gebruk A. V. (Ed.) 2002. *Biology of Hydrothermal Systems*. Scientific Press Ltd., Moscow, 543 pp. (In Russian)
- Hashimoto J., Ohta S., Gamo T., Chiba H., Yamaguchi T., Tsuchida S., Okudaira T., Watabe H., Yamanaka T. & Kitazawa M. 2001. First hydrothermal vent communities from the Indian Ocean discovered. *Zoological Science*, **18**: 717-721.
- Hessler R. R. & Smithey W. M. 1983. The distribution and community structure of megafauna at the Galapagos Rift hydrothermal vents. In: *Hydrothermal Processes at Sea-floor Spreading Centres* (P.A. Rona, K. Boström, L. Laubier & K.L. Smith eds), pp.735-770. Plenum Press, New York.
- Humes A.G. & Segonzac M. 1998. Copepoda from deep hydrothermal sites and cold seeps: description of a new species of *Aphotopontius* from the East Pacific Rise and general distribution. *Cahiers de Biologie Marine*, **39**: 51-62.
- Jollivet D. & 23 collaborators 2004. The BIOSPEEDO cruise: a new survey of hydrothermal vents along the South East Pacific Rise from 7°24'S to 21°33'S. *InterRidge News*, **13**: 20-26.
- Kojima S., Fujikura K. & Okutani T. 2004. Multiple trans-Pacific migrations of deep-sea vent/seep-endemic bivalves in the family Vesicomidae. *Molecular Phylogenetics and Evolution*, **32**: 396-406.
- Komai T. & Segonzac M. 2003. Review of the hydrothermal vent shrimp genus *Mirocaris*, redescription of *M. fortunata* and reassessment of the taxonomic status of the family Alvinocarididae (Crustacea: Decapoda: Caridea). *Cahiers de Biologie Marine*, **44**: 199-215.
- Komai T. & Segonzac M. 2005. A revision of the genus *Alvinocarididae* Williams and Chace (Crustacea: Decapoda: Caridea: Alvinocarididae), with description of a new genus and a new species of *Alvinocarididae*. *Journal of Natural History*, **39** : 1111-1175.
- Mironov A.N., Gebruk A.V. & Moskalev L.I. 2002. Biogeography of hydrothermal vent communities and obligate hydrothermal taxa. In: *Biology of Hydrothermal Systems* (A.V. Gebruk ed), pp. 410-455. Scientific Press Ltd., Moscow. (In Russian)
- Monniot F. 2003. Ascidiées coloniales de la ride médio-atlantique recoltées à proximité de sites hydrothermaux. *Cahiers de Biologie Marine*, **44**: 353-360.
- Newman W.A. 1985. The abyssal hydrothermal vent invertebrate fauna: a glimpse of antiquity? *Biological Society of Washington Bulletin*, **6**: 231-242.
- Newman W. A. & Yamaguchi T. 1995. A new sessile barnacle (Cirripedia, Brachylepadomorpha) from the Lau Back-arc Basin, Tonga; first record of a living representative since the Miocene. *Bulletin du Muséum national d'Histoire naturelle*, 4^e série, **17A**: 211-243.
- Rouse G.W. & Fauchald K. 1997. Cladistics and polychaetes. *Zoologica Scripta*, **26**: 139-204.
- Schulze A. 2003. Phylogeny of Vestimentifera (Siboglinidae: Annelida) inferred from morphology. *Zoologica Scripta*, **32**: 321-342.
- Sibuet M. & Olu K. 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. In: *Tropical Studies in Oceanography* (C.R. Smith, L.S. Mullineaux & L.A. Levin eds). *Deep-Sea Research II*, **45**: 517-565.
- Southward A.J. & Jones D.J. 2003. A revision of stalked barnacles (Cirripedia Thoracica: Scapellomorpha: Eolepadidae: Neolepadinae) associated with hydrothermalism, including a description of a new genus and species from a volcanic seamount off Papua New Guinea. *Senckenbergiana maritima*, **32**: 77-93
- Stecher J., Türkay M. & Borowski C. 2002. Faunal assemblages on the Pacific-Antarctic Ridge near the Foundation Seamount Chain (37° 30' S, 110° 30' W). *Cahiers de Biologie Marine*, **43**: 271-274.
- Tunnicliffe V. 1991. The biology of hydrothermal vents: ecology and evolution. *Oceanography and Marine Biology, Annual Review*, **29**: 319-407.
- Tunnicliffe V., McArthur A.G. & McHugh D. 1998. A Biogeographical Perspective of the Deep-Sea Hydrothermal Vent Fauna. *Advances in Marine Biology*, **34**: 353-442.
- Van Dover C.L. 2000. *The Ecology of Deep-sea Hydrothermal Vents*. Princeton University Press, 424 pp.
- Van Dover C.L. 2002. Trophic relationships among invertebrates at the Kari hydrothermal vent field (Central Indian Ocean). *Marine Biology*, **141**: 761-772.
- Van Dover C.L. & 26 collaborators 2001. Biogeography and ecological setting of Indian Ocean hydrothermal vents. *Science*, **294**: 818-823.
- Webber W.R. 2004. A new species of *Alvinocarididae* (Crustacea: Decapoda: Alvinocarididae) and new records of alvinocaridids from hydrothermal vents north of New Zealand. *Zootaxa*, **444**: 1-26.
- Wolff T. 1985a. Oaser i dybhavet. De hydrotermiske væld og deres fantastiske dyreliv. [Oases in the deep sea. The hydrothermal vents and their fantastic animal life]. *Naturens Verden*, **68**: 393-416. (In Danish)
- Wolff T. 1985b. The composition and distribution of the hydrothermal vent fauna. *Deep-Sea Newsletter*, **11**: 9-13.
- Wolff T. 2002. Nye opdagelser i de hydrotermiske væld, dybhavets varme kilder. [New discoveries in the hydrothermal vents, the heat-sources of the deep sea]. *Naturens Verden*, **85**: 1-40.