DISSERTATION

Titel der Dissertation

Meiobenthic community studies from deep-sea chemosynthetic habitats (hydrothermal vents, cold seeps)

angestrebter akademischer Grad

Doktor/in der Naturwissenschaften (Dr. rer.nat.)

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Dissertationsgebiet (lt. Studienblatt):	A091 444 (Ökologie)
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Wien, am 19. Februar 2009

CONTENT

ZUSAMMENFASSUNG

Hydrothermal- und Sickerquellen der Tiefsee werden von geologischen Prozessen geformt, wobei die Basis allen Lebens in diesen extremen Ökosystemen Chemosynthese ist. In dieser Arbeit werden die Abundanz und Diversität der Meiofauna dieser Habitate untersucht. Die ersten vier Manuskripte geben einen Überblick über die Meiofaunagemeinschaften an den Hydrothermalquellen am Ostpazifischen Rücken, wobei auch eine neue Art beschrieben wird. Obwohl dieses Ökosystem von hoher Primärproduktion geprägt ist, findet man Meiofauna nur in geringer Dichte (~ 100 Individuen 10 cm^{-2}). Die Diversität ist zudem niedrig und nimmt mit abnehmender Toxizität des Hydrothermalflusses zu. Copepodite wurden zum ersten Mal an den Hydrothermalquellen entdeckt. Auch die Hälfte aller identifizierten Arten war bisher unbekannt. Das fünfte Manuskript untersucht Meiofauna von Sickerquellen im Golf von Mexiko. Wie auch an den Hydrothermalquellen, findet man hier Nematoden, Copepoden, Ostracoden and Halacarida in geringer Häufigkeit. Das letzte Manuskript vergleicht Meio- und Makrofauna Gemeinschaften der Hydrothermalquellen. Die meisten Makrofaunaarten sind endemisch während es sich bei den meisen Meiofaunaarten um Generalisten handelt. Die Diversität der Makrofauna ist unimodal entlang des untersuchten Stressgradienten verteilt, im Gegensatz dazu ist die Diversität der Meiofauna invers korreliert mit dem Stressgradienten. Gründe hierfür werden ausführlich diskutiert.

ABSTRACT

Deep-sea hydrothermal vents and cold seeps are extreme ecosystems where geological processes fuel benthic communities with chemosynthetic energy. For this study meiofaunal diversity and abundance were examined from hydrothermal vents at the East Pacific Rise and from cold seeps in the Gulf of Mexico. The first four manuscripts present an overview of meiofaunal vent communities, including a description of a new tegastid copepod. Even though hydrothermal vents are characterized by high *in situ* productivity, meiobenthos is of low abundance (~ 100 individuals 10 cm^{-2}). Diversity is also low and increases with decreasing toxic vent flux. Both copepods and nematodes show diminished diversity at high vent flux and most of them are feeding on detritus. For the first time copepodites were observed at vents. More than half of the identified species are new to science. In addition, meiobenthos from deep-sea cold seeps is described. Major taxon richness (nematodes, copepods, ostracods, halacarids) and low abundance are similar to what has been found at vents. Finally, vent meio- and macrofauna are compared. Macrofauna species are endemic and show unimodal diversity patterns along an environmental stress gradient. In contrast, meiofauna species are generalists and diversity is inversely correlated to this stress gradient. The underlying mechanism such as body size and related species traits, disturbance and productivity are discussed to explain these contrasts between macro- and meiofauna.

INTRODUCTION

Deep-sea hydrothermal vents and cold seeps are among the most unusual and extreme ecosystems in the world’s oceans. Hydrothermal vents are located at back-arc basins and on the mid-ocean ridges, underwater mountain chains with a total length of 75,000 km. They emerge at divergent plate boundaries and are geologically very active, accounting for more than 75% of the total volcanic activity on Earth. Hydrothermal fluid flux, seawater that migrated through the ocean crust and got enriched with toxic hydrogen sulfide and heavy metals, emerges with temperatures of up to 400°C at black smoker sulfide chimneys or as diffuse flow with lower temperatures through cracks in the ocean crust within the Axial Summit Trough (AST) (Van Dover 2000). In contrast, cold seeps occur mostly along passive continental margins. Cold seep fluids originate from petroleum and gas seepage. In the Gulf of Mexico, one of the regions studied for this PhD research, the continental slope is fractured by salt tectonics. Methane rich fluids as well as sulfide, produced by sulfate reduction in the sediments, are the source of energy (Sibuet & Olu1998). Both hydrothermal vent and cold seep ecosystems are primarily fueled by chemosynthesis. This is in stark contrast to the surrounding deep-sea plains, where energy input in form of particulate organic matter is originating primarily from photosynthesis in the surface waters (Etter & Mullineaux 2001).

Bacteria form the basis of the food-web in deep-sea chemosynthetic ecosystems, either as free-living or as symbiotic partners of megafaunal organisms, such as tubeworms and mussels. For the associated fauna, bacteria serve as primary producers, and symbiotic megafauna act as foundation species. The hosts provide space, structure the habitat, change physical and chemical properties, and concentrate food sources (Van Dover 2000, Bruno & Bertness 2001). Since the discovery of hydrothermal vents in 1977, over 500 animal species have been described (Desbruyères et al. 2006). Vent macrofauna can be generally characterized as an endemic, species-poor but biomass-rich community (Tunnicliffe et al. 1998, Van Dover 2002, Tsurumi & Tunnicliffe2003, Govenar et al. 2005). At hydrocarbon seeps, young habitats feature biomass-rich and endemic communities, whereas old habitats show low biomass and background deep-sea faunal communities (Cordes et al. 2009).

Whilst the macrofauna communities are quite well studied at both hydrothermal vents and cold seeps, the ecological role of meiofauna (animals in the size range from 63 µm to 1 mm) is almost unknown, despite its pivotal role in linking bacterial and macrofaunal food webs (Gerlach 1971, Giere 2009). At vents, meiofauna currently contributes to about 20% of total diversity, but this number is expected to rise in the future, as only a few meiofauna studies have been carried out so far and a significant proportion of identified species awaits further formal taxonomic description (Bright 2006). Overall, vent meiofauna occurs in low abundance, and is a species- and taxon-poor community (Vanreusel et al. 1997, Tsurumi et al. 2003, Zekely et al. 2006, Copley et al. 2007, Gollner et al. 2007). At cold seeps, our knowledge of the meiofauna is even less detailed. Hitherto, studies are mostly on taxon level and were carried out in various depths and geographic regions, making it difficult to compare them. Nematodes and copepods appear to be the dominant taxa and abundances vary from very low to extremely high (Levin 2005).

This PhD thesis aims to test and discuss 6 different working hypotheses:

The central objective of this PhD research is to identify and quantify the metazoan and foraminiferan meiobenthic community along a vent flux gradient at the 9°N East Pacific Rise, a chosen prime study region of the international community InterRidge. From the descriptive data, meiobenthic biodiversity is characterized and its underlying mechanisms are discussed. As one example of newly discovered species, a copepod is described taxonomically (Gollner et al. 2006, Zekely et al. 2006, Gollner et al. 2008, Gollner et al. submitted).

(1) The meiobenthic density at 9°50’N EPR hydrothermal vents follows the general trend documented for vent macrobenthos, i.e. high abundance.
(2) The meiobenthic diversity at 9°50’N EPR hydrothermal vents follows the general trend documented for vent macrobenthos, i.e. low species richness.
(3) The meiobenthic diversity accords with diversity patterns predicted by the intermediate disturbance hypothesis (Connel 1978), showing an unimodal diversity pattern along an stress/disturbance gradient.
(4) The meiofauna is vent endemic, similar to what it is known for the macrofauna.

Meiobenthic cold seep community abundances and taxon richness from the Gulf of Mexico are investigated (Bright et al. submitted) in order to compare abundance and major taxon diversity patterns for both chemosynthetic ecosystems.

(5) Meiobenthic abundance from cold seeps is high and similar to hydrothermal vents, as both ecosystems are supported by high *in situ* primary production.

Meiofauna diversity patterns are compared to macrofauna patterns along an environmental stress gradient at the studied vent sites (Gollner & Bright in prep.).

(6) Along an environmental stress gradient the two faunal size classes exhibit similar diversity patterns.

This thesis includes the following manuscripts (in order of presentation):

Gollner S, Riemer B, Martinez Arbizu P, Le Bris N, Bright M (submitted) Community study of meiobenthos from the 9º50´N East Pacific Rise over the full range of hydrothermal vent flux.

Gollner S, Zekely J, Van Dover CL, Govenar B, Le Bris N, Nemeschkal H, Bright M (2006) Benthic copepod communities associated with tubeworm and mussel aggregations on the East Pacific Rise. Cahiers de Biologie Marine 47:397-402

Zekely J, Gollner S, Van Dover CL, Govenar B, Le Bris N, Bright M (2006) The nematode community and trophic structure of three macrofaunal aggregations at 9° & 11°N East Pacific Rise. Cahiers de Biologie Marine 47:477-482

Gollner S, Ivanenko VN, Martinez Arbizu P (2008) A new species of deep-sea Tegastidae (Crustacea: Copepoda: Harpacticoida) from 9°50´N on the East Pacific Rise, with remarks on its ecology. Zootaxa 1866:323-336

Bright M, Plum C, Riavitz LA, Nikolov N, Martinez Arbizu P, Cordes EE, Gollner S (submitted) Epizooic metazoan meiobenthos associated with tubeworm and mussel aggregations from cold seeps of the Northern Gulf of Mexico.

Gollner S, Bright M (in prep) Size matters: contrasting meio – and macrofauna diversity patterns at deep-sea hydrothermal vents.

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Govenar B, LeBris N, Gollner S, Glanville J, Aperghis A, Hourdez S, Fisher CR (2005) Epifaunal community structure associated with *Riftia pachyptila* aggregations in chemically different hydrothermal vent habitats. Marine Ecology Progress Series 305:67-77

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Community study of meiobenthos from the 9º50´N East Pacific Rise over the full range of hydrothermal vent flux

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ABSTRACT

We studied meiobenthos at hydrothermal vents along a gradient of vent flux and their well-characterized megafaunal habitats at the East Pacific Rise 9º50´N region to explore meiobenthic diversity and discuss its possible underlying ecological and evolutionary processes. A total of 52 species were identified at vent habitats which were dominated by hard substrate generalists that also live on bare basalt at ambient deep-sea temperature in the axial summit trough (AST generalists). Some vent species are restricted to a specific vent habitat (vent specialists), but others occur over a wide range of physico-chemical conditions (vent generalists). Additionally, 35 species were only found on cold bare basalt (basalt specialists). At vent sites, species richness and diversity clearly increase with decreasing vent flux from pompei worm (S: 4-7, $H´_{loge}$: 0.11 – 0.45), tubeworm (S: 8 – 23; $H´_{loge}$: 0.44 – 2.00) to mussel assemblages (S: 28 – 31; $H´_{loge}$: 2.34 – 2.60). Our data suggest that with increasing temperature and toxic hydrogen sulfide concentrations, fewer species are being able to cope with these extreme conditions, resulting in less diverse communities. The fact that an unimodal relationship between disturbance and diversity, as predicted by the intermediate disturbance hypothesis was not found, might be due to the lack of non-disturbed habitats within this ecosystem.

Keywords: disturbance, diversity, meiobenthos, hydrothermal vent, hydrothermal flux, community study, East Pacific Rise, deep-sea, meiofauna

INTRODUCTION

Marine communities and ecosystem processes are affected by environmental changes, such as global warming, ocean anoxia, and ocean acidification (Worm et al. 2006). Disturbance is one of the key components ruling diversity and is defined as damage (removal of biomass) or more precisely as an event in time that disrupts communities, changes resources, or influences the physical environment (White & Pickett 1985, Sousa 2001). The intermediate disturbance hypothesis states that highest diversity is found at intermediate disturbance because lower disturbance levels encourage dominant species to consume all resources, whilst at higher levels of disturbance only colonizing species survive (Connel 1978, Menge & Sutherland 1987, Sousa 2001). The same hump-shaped diversity pattern is also expected for communities across an environmental stress-gradient (Menge & Sutherland 1987, Bruno et al. 2003, Scrosati & Heaven 2007). However, in a review on the disturbance effect on diversity, non-significant relationships were the most common (Mackey & Currie 2001).

Deep-sea hydrothermal vents are model systems of physically highly disturbed and stressful marine environments (Van Dover 2000). Dramatic and unpredictable catastrophic volcanic eruptions, tectonic disturbances, rapid changes in vent fluid composition, and the dynamics of waxing and waning vent flux characterize this ecosystem (Childress & Fisher 1992, Fornari et al. 1998). Unstable physico-chemical conditions such as high temperature and pH gradients, the toxicity of vent emissions, and the temporal lack of oxygen impose physiological stress to animals living at such extreme conditions, reducing their rates of biochemical reactions when their values are outside their optimal range of tolerance (Menge & Sutherland 1987, Bruno & Bertness 2001).

Hydrothermal vents are relatively small and patchy habitats within the axial summit troughs (AST) of the mid-ocean ridges - large, continuous and scarcely populated basalt habitats. Vents represent islands where chemosynthetic primary production locally supports high densities of mega- and macrofaunal communities. Primary production is carried out by chemolithoautotrophic bacteria, using the energy provided by the mixing of the reducing hydrothermal fluid flux and oxygenated seawater to fix inorganic carbon (Karl 1995). As part of the free-living microbial community they are the foundation of the food-web at vents. As symbiotic partners, they occur in a variety of associations with animals. These symbioses often act as foundation species in creating and structuring the habitat, modifying their environment by changing the physical and chemical properties, concentrating food sources and thus providing space for associated fauna (Van Dover 2000, Bruno & Bertness 2001).

Worldwide, over 500 animal species have been described from hydrothermal vents and over 90% are considered endemic for this habitat (Tunnicliffe et al. 1998, Desbruyères et al. 2006). The vent macrofauna communities are generally characterized by low diversity and low species richness but high population densities (Hessler et al. 1985, Tsurumi & Tunnicliffe 2003, Van Dover 2003, Govenar et al. 2005).

One of the best-known mid-ocean ridge regions is located at 9º50´N, 104º17´W on the East Pacific Rise (EPR) with a fast spreading rate of 55 mm yr^{-1} (Carbotte & Macdonald 1994). The ridge crest is broad and shallow and lies at a depth of about 2500 m. An axial summit trough (AST) with associated lava channels is ~ 50 m wide and ~ 20 m deep (Fornari et al. 1998). Vent communities at the 9º50'N region are known to be frequent and diverse (Haymon et al. 1991, Shank et al. 1998). The occurrence of characteristic foundation species and associated assemblages shows a striking spatial distribution pattern along a thermal and chemical gradient of hydrothermal fluid flux. Furthermore, several habitat types associated with different styles of venting can be distinguished: high temperature flow (>50°C) with alvinellid polychaetes colonizing sulfide chimneys (e.g. *Alvinella pompejana* and *A. caudata*), vigorous, but moderate temperature flow (<30°C) with vestimentiferans (e.g. *Riftia pachyptila*) growing on basalt, low temperature flow (<5°C) with bivalves (e.g. *Bathymodiolus thermophilus*) on basalt, and very low or no detectable vent flow with suspension feeders (serpulids, barnacles, anemones). The flux can be gradual, but the faunal boundaries are distinct (Hessler et al. 1985, Etter & Mullineaux 2001). In addition, there are habitats with no visible fauna such as the high temperature (up to 400°C) areas of bare sulfide chimneys and bare basalt habitats with no direct influence of hydrothermal fluid flux and ambient deep-sea temperature (Van Dover 2000).

Temperature is not the only parameter influencing the distribution of foundation species. In alvinellid habitats, pH is lower and toxic sulfide concentration is much higher for a given temperature than at any other vent habitat (Le Bris et al. 2003, Le Bris & Gaill 2007). In contrast, the temperature-sulfide relation is more consistent within diffuse flow habitats where bathymodiolins and vestimentiferans are found (Le Bris et al. 2006). At bare basalt where fluid venting is absent, conditions are similar to those in the surrounding seawater, i.e. no sulfide is detectable, pH is neutral, and temperatures are close to ambient (Luther et al. 2001).

The zonation of megafauna along this strong physico-chemical gradient was initially attributed to physiological responses to stress and nutrient requirements (Childress & Fisher 1992, Shank et al. 1998, Luther et al. 2001). Since then, biological factors such as competition and predation, facilitation and inhibition were found to mediate the limits of species distributions, and it has been concluded that correlations with abiotic gradients provide insufficient evidence for inferring causation of zonation along environmental gradients (Micheli et al. 2002, Mullineaux et al. 2003, Matabos et al. 2008).

Our knowledge on the accociated macrofauna of the 9º50´N EPR is limited to tubeworm and mussel habitats. Two chemically different sites with *Riftia pachyptila* as foundation species had similar macrofaunal diversity (S: 19-35, H'_{log2}:1.2-2.1) (Govenar et al. 2005), and were similar in range to the fauna associated with mussels (S: 34-46, H'_{loge}: 1.5 – 1.7) along the EPR (Van Dover 2002, Van Dover 2003). No quantitative information is yet available for pompei worm associated macrobenthos and for the basalt.

The meiofauna (smaller size class of animals and protists passing through a 1 mm sieve and retained on a 63 µm or 32 µm sieve) communities and distribution have been much less studied, although their importance in marine ecosystems has been acknowledged for a long time (Giere 2009). The ecological role of meiofauna is often unknown or not considered, and most studies tend to focus on a single habitat and a single taxon. Currently, meiofauna species contribute to about 20% of the total diversity known from vents. Meiofauna communities generally exhibit low diversity and species richness, and occur in low population densities (Bright 2006). Nematode species diversity was observed at hard substrate mussel habitats along the EPR (Flint et al. 2006, Zekely et al. 2006a, Copley et al. 2007) and in sedimented vents with mussels in the North Fiji Basin (Vanreusel et al. 1997). Qualitative copepod data are available from pompei worm and tubeworm habitats from Juan de Fuca Ridge (Tsurumi et al. 2003), and a quantitative study investigated copepods at the EPR (Gollner et al. 2006). However, so far only two studies have described the entire meiobenthic community on a species level from mussel beds at the 11º N EPR and 23º N Mid-Atlantic Ridge and from tubeworms at the 9°N EPR (Zekely et al. 2006b, Gollner et al. 2007).

Here, we test whether the intermediate disturbance hypothesis, predicting highest diversity at intermediate stress, holds true for the meiobenthic community at the chemosynthetically driven hydrothermal vents. We identified and quantified the entire meiobenthic communities from the main habitat types at the 9º50´N EPR region and documented species diversity, abundance, and distribution according to well-characterized habitat types within this ecosystem. Samples covered the entire range of hydrothermal vent flux from black smoker sulfide chimneys devoid of any visible mega- and macrofauna, to pompei worms at black smokers, tubeworms and mussels at basalt, and bare basalt within the AST. By including samples from basalt with ambient deep-sea temperature and lack of vent fluid emissions in our study, we can estimate the degree of endemicity of vent meiobenthos in this region and discuss underlying ecological and evolutionary processes.

METHODS

Study area

The study was conducted within the axial summit trough (AST) at the 9°50´N 104°17´W region at the East Pacific Rise (EPR) in 2500 meters depth. A total of 22 collections were made at 9 sites, using the submersible DSV *Alvin* in the years 2001 – 2004 (Appendix 1, 2).

Five different habitat types were chosen accordingly to their different hydrothermal flux regimes (extremely high, high, vigorous, low, no flux), termed sulfide (A), pompei worm (B), tubeworm (C), mussel (D), and basalt (E) (Fig. 1). (A) 4 extremely high flux sulfide samples were collected from active high temperature bare sulfide chimneys of the black smokers P-Vent (2003, AD # 3928, 2510 m, 9°50.287´N, 104°17.487´W), Bio9 (2003, AD # 3929, 9°50.319´N, 104°17.482´W), M-Vent (2003, AD # 3930, 9°50.792´N, 104°17.601´W) and BioVent (2003, AD # 3933, 2505 m, 9°50.927´N, 104°17.584´W). (B) 5 high flux pompei worm collections were made at sulfide chimneys of several black smokers colonized by the foundation species *Alvinella pompejana* and *A. caudata* (Michel´s-Vent (P1), Alvinella Pillar (P2), Bio 9 (P3), M-Vent (P4, P5)). (C) 6 tubeworms samples were taken at vigorous flux sites dominated by *Riftia pachyptila* (Tica (T1, T2, T3), Riftia Field (T4, T5, T6)). (D) 3 mussel collections were made at a low flow site colonized by *Bathymodiolus thermophilus* (Mussel Bed (M1, M2, M3)), and (E) 4 basalt collections were taken at bare basalt with no hydrothermal fluid flux, no foundation species and no visible mega- and macrofauna (near Tica (B1, B2, B3) and near Alvinella Pillar (B4) in approximate vicinity of 10 m to tubeworms or pompei worms).

Physico-chemical characteristics

Temperature was measured at all sites prior to sampling. Temperatures were extremely high (244 - 252°C) at sulfides lacking macro- and meiofauna. At the pompei worm habitat temperature was highly variable and changing within seconds from overall 14 - 119°C at the studied sites. The tubeworm sites Tica and Riftia Field were characterized by warm fluids with maximal temperatures of 32°C and 54°C, respectively, and at Mussel Bed we measured a maximal temperature of 10°C (Le Bris et al. 2006). On bare basalt the measured temperature was 2°C, which is in this habitat accompanied by no dectable sulfide and neutral pH (Luther et al. 2001).

We were not able to measure sulfide and pH at the pompei worms prior to sampling. However, several studies from this and other regions of the EPR revealed that the pH is generally acidic with minimal values around pH 4, and sulfide concentrations up to 1520 µM $\sum H_2S$ (Di Meo-Savoie et al. 2004, Le Bris et al. 2005, Le Bris & Gaill 2007). At the tubeworm and the mussel collection sites, we directly measured these parameters prior to sampling: Tica exhibited maximal sulfide concentrations of 283 µM $\sum H_2S$, and minimal pH of 5.7. No iron was detected in the fluid. At Riftia Field, maximal sulfide concentration was only 95 µM $\sum H_2S$. Minimal pH value was 4.4 in the diffuse flow, and substantial concentrations of dissolved ferrous iron were present at this site (up to 42 µM among the tubeworms). *In situ* analysis of vent flux at Mussel Bed showed a minimal pH of 6.7 and maximal sulfide of 151 µM $\sum H_2S$ (Le Bris et al. 2006).

Sample processing

Due to difference in habitat structure it was necessary to use different sampling devices. Tubeworm samples were taken with the hydraulically actuated collection device, named `Bushmaster Jr.´ lined with a net of 63 µm mesh size (Govenar et al. 2005, Gollner et al. 2007). Some additional samples from tubeworm aggregations were taken by the hydraulic arm of *DSV Alvin* at a later time in order to check for presence of meiofauna in the size class between 32 and 63 µm. These control samples were not included in further analyses of the meiobenthic community. Mussel samples were scooped carefully down to the bottom with a linen bag (63 µm) strengthened at its opening by a steel frame and closed by turning the bag. Sulfide, pompei worm, and basalt samples were taken with the hydraulic arm of *Alvin*. A piece of the substrate was very carefully broken off from the habitat and put into the sampling box. Some organisms might have been lost during the approximately 1 meter long transfer to the sampling box on *Alvin*, probably resulting in slight under-sampling of rare species and slight error in species abundances. We are well aware that in most cases, our samples can be only considered semi-quantitative. In all cases the area sampled was photographed before and after sampling in order to estimate the sea floor surface area of samples taken. Samples were separately put into isolated, previously cleaned plastic boxes on the basket of DSV *Alvin*, transported to the surface, and recovered on deck of the ship R/V *Atlantis*. On board, Bushmaster samples from the tubeworm habitat and mussel scoop samples were sieved through a 1 mm and 63 µm net. Sulfide, pompei worm, and basalt samples were sieved additionally through a 32 µm net. In addition the control samples from tubeworm aggregations were sieved through a 32 µm and 63 µm net. All samples were fixed in 4% buffered formalin. Samples taken in 2001 and 2002 were transferred to 70% ethanol after one day, but this step was found unnecessary for the quality of fixation and therefore was not done with the samples taken later.

In the lab, all meiofauna animals were sorted, counted, and identified to higher taxa under a dissecting microscope. Sorting revealed that not a single animal was found in the size class from 32 µm to 63 µm in pompei worm and tubeworm samples. In one out of 4 basalt samples a few juvenile nematodes were found, but no new species were detected. These juveniles were excluded from the study to make this sample comparable to all other samples. Not a single specimen was present in the sulfide samples and this habitat type was therefore excluded from all further analyses. From each sample and each higher taxon (copepods, nematodes, ostracods, acari, foraminiferans) all or at least 300 randomly picked individuals were identified to lowest possible taxon, usually to species level. All species belonging to the permanent meiobenthos (i.e. being in the size class of meiofauna as adults according to Giere 2009) were considered in this study. We also recorded the temporary meiobenthos (i.e. species that belong to the mega- and macrobenthic size class as adults but are meiobenthic during a certain time of their development) and all pelagic species (Calanoida spp., Corycaeidae spp., Oncaeaidae spp.), but both groups were excluded for further analyses of permanent meiobenthos.

A few individuals of Platyhelminthes and numerous Folliculidae (Ciliophora) were detected in some samples but could not be included in further analyses because identification of Platyhelminthes to species level was not possible due to the method of fixation and distinction between live ciliates and empty tubes was not possible. In a previous study we included the single species of Tanaidacea (Gollner et al. 2007), but in the meantime we found that this specific species (*Typhlotanais* sp. 1) can grow to large macrofauna sizes, and we therefore excluded it in this study. Furthermore, the species Harpacticoida sp. 2 in Gollner et al. (2007) could be identified as *Xylora bathyalis*.

Cumulative species-effort curves confirmed that the level of sampling effort (for details on slide preparation, literature used for species identification, and species effort-curves see citations in Gollner et al. 2007), and permuted cumulative species count over samples (number of permutations 999) were sufficient for the studied vent habitats. We are well aware that a total of 4 collected bare basalt samples is insufficient to describe the community of this large habitat and we expect an increase in species numbers with more sampling in the future. Nevertheless, even this limited basalt data set gave us important information for the assessment of endemicity of vent species.

Quantification of abundance

To compare the variable sample areas of single collections with each other, abundance was standardized to 10 cm^2 sample area. We also measured the volume of accumulated sediment within the macrofauna aggregations growing on bare basalt (see Gollner et al. 2007). Standardization of abundance data to 10 ml sediment revealed similar abundance values as for 10 cm^2 standardization at pompei worm and tubeworm habitats and relatively higher abundances at mussel and basalt habitats (data not shown). To compare this study with others we chose to present data based on 10 cm^2 sample area.

Data analyses

Species richness (S), Shannon-Wiener diversity index (H'_{loge}), and Pielou´s evenness index (J´) were calculated from quantitative species-abundance data by DIVERSE subroutine in PRIMER Version 5 package (Clarke & Gorley 2001). For statistical analyses bootstrapping (10000 resamplings each, 2-sided test, routine „FTBOOT“ from the package „computer intensive statistics“ (Nemeschkal 1999)) was used as a well proven method when working with a relatively low number of samples and high variances. We tested for significant differences in abundance (square-root transformed), species richness (square-root transformed), Shannon-Wiener diversity (no transformation), and Pielou’s evenness (no transformation). Significance of correlations was carried out by using Pearson´s r (F-value and t-value calculations by STATISTICA). All significance levels were classical Bonferroni-corrected (p = alpha/n; alpha = 0.05). To evaluate similarity and dissimilarity of samples, Bray-Curtis similarity was created (abundances of species were standardized and square-root transformed to down-weight the importance of very abundant species without losing the influence of rarer species), and similarity percentage (SIMPER) analyses, analysis of similarity (ANOSIM), and multi-dimensional scaling (MDS) plot were performed using PRIMER v5. The BIO-ENV procedure was carried out by PRIMER v5 to link biota to multivariate environmental patterns. Maximum temperature, maximal sulfide, and minimum pH were chosen as abiotic variables having possible effect on meiofauna species and communities. Additionally, we included the volume of sediment from each sample as value to test, because it mainly was composed of organic matter, a known food source for meiofauna (Gollner et al. 2007). Abiotic variables were ln transformed and Euclidean distance was used to create a similarity matrix. For biota, Bray-Curtis similarity from species abundance data was used. Similarities between biotic and abiotic data were afterwards calculated using Spearman´s rank correlation (Clarke & Gorley 2001).

RESULTS

Abundance

We counted a total of 74 315 individuals in 22 samples taken from 5 different habitat types (sulfide, pompei worm, tubeworm, mussel, basalt) within the AST at the 9°50´N EPR region. Not a single specimen was detected in the sulfide samples. Meiobenthic abundance of the other 4 habitats was generally low and varied from 1 to 976 ind. 10 cm^{-2}. Abundances were not statiscically discernable between pompei worms and tubeworms, tubeworms and mussels, tubeworms and basalt habitats. Significantly higher abundances were detected in pompei worms compared to mussels and basalt, and mussels to basalt habitats. Variations in abundance were higher at sites with higher influence of hydrothermal fluid flux, and lower at habitats with low or no vent flux. While abundances of communities at pompei worm and tubeworm habitats ranged from 36 – 474 and 1 – 976 ind. 10 cm^{-2}, mussel and basalt habitats had less abundance variations with 58 – 87 and 1 - 51 ind. 10 cm^{-2} (Table 1, 2).

The meiobenthic community was composed of Copepoda, Nematoda, Ostracoda, Acari, and Granuloreticulosa (Platyhelminthes and Ciliates not included in this study). Overall, copepods was the most abundant higher taxon (1 - 472 ind. 10 cm^{-2}, relative abundance 65% ± 33), with the Dirivultidae (Siphonostomatoida) and harpacticoid copepods being the dominant copepod family and order, respectively, and being present at all sites. Nematodes were absent in the pompei worm habitat. In the other 3 habitats their abundance was highly variable ranging from 1 to 946 ind. 10 cm^{-2}. Foraminiferans were present at all sites, with a maximum of 9 ind. 10 cm^{-2}. Ostracoda were low in abundance (max. 1 ind. 10

cm^{-2}) and restricted to tubeworm, mussel, and basalt communities. Acari were only found in one mussel sample.

The pompei worm communities were dominated by copepods in relative abundance (99 – 100%). A similar, but less pronounced situation was found in the mussel communities (49 – 66%). No clear pattern was discernible in the tubeworm habitat: in 4 out of 6 samples, nematodes dominated (58 - 97%), while in 1 sample copepods dominated (80%), and in one other sample nematodes, copepods, and foraminiferans were about equally present. On the basalt, copepods dominated the communities in abundance in 2 samples (63% and 92%), while foraminiferans were dominant in one sample (72%), and no taxa dominance was found in another sample (Table 1).

Diversity

From a total of 22 samples from all studied habitats, 87 species were identified (52 at vent sites, 35 at basalt). Looking at the higher taxa distribution of species from all samples, 56% of species were copepods, followed by nematodes (30%), foraminiferans (7%), ostracods (6%), and acari (1%). The number of total species found in a habitat increased from pompei worm (11 spp.), to tubeworm (31 spp.), to mussel (36 spp.), and to basalt (64 spp.) habitats.

Species richness and Shannon-Wiener diversity were low and increased from pompei worm (S: 4 – 7; H'_{loge}: 0.11 – 0.45), to tubeworm (S: 8 – 23; H'_{loge}: 0.44 – 2.00), and to mussel (S: 28 – 31; H'_{loge}: 2.34 – 2.62) communities and were all statistically significantly different. Pielou's evenness was significantly lower at pompei worms (J': 0.11 – 0.28) compared to tubeworms and mussels (J': 0.15 – 0.91) (Table 1, 2). Diversity measurements from basalt communities (S: 20 – 34; H'_{loge}: 1.18 – 2.74, J': 0.34 – 0.91) were significantly higher than those from pompei worms. Compared to tubeworms, only species richness was higher at basalt, and all diversity measurements from mussels were similar to basalt (Table 1, 2).

Community patterns

Dissimilarity of pompei worm to tubeworm, to mussel and to basalt communities was > 93%, and ANOSIM proved that this was significant ($R = 1$; $p < 0.018$). Tubeworm and mussel communities were 68% dissimilar ($R = 0.53$; $p = 0.24$; n.s.), and tubeworm and basalt communities showed a dissimilarity of 84% ($R = 0.86$; $p = 0.005$). Mussel and basalt communities had a dissimilarity of 75% ($R = 0.56$, $p = 0.06$; n.s.) (Table 2). Multidimensional scaling (MDS) configuration revealed that meiobenthos from distinct habitats formed distinct groups (Fig. 2).

Community and environment

Total meiofauna abundance did not correlate to maximal temperature, maximal sulfide, minimal pH, volume of sediment, and sampled surface area. Maximal temperature correlated significantly inversely with species richness ($r = 0.85$; $p < 0.001$) and with Shannon-Wiener diversity index (r =0.66; p < 0.003). In addition, also minimal pH directly measured at the sample site of tubeworm and mussel habitats and estimated from measurements of previous studies at pompei worm and basalt correlated significantly with species richness (r = 0.88; p < 0.001) and with Shannon-Wiener diversity index (0.66; p < 0.003). An inverse correlation of maximal sulfide with species richness (r = 0.71; p = 0.001) was found, but Shannon-Wiener diversity (r = 0.59; p = 0.011) was not significantly correlated. Both univariate measures of diversity were not correlated with sediment volume and surface area, except for Shannon-Wiener diversity and surface area (r = 0.69; p = 0.002). BIOENV gave the result of the following single abiotic variables which best group the sites, in a manner consistent with the faunal patterns: pH (rank correlation ρ = 0.55), sulfide (ρ = 0.51), temperature (ρ = 0.51), and sediment (ρ = 0.14). Temperature, sulfide, and pH show together a rank correlation of 0.54.

Meiofauna distribution on a broader scale

We summarized the occurrence of species according to habitat and gave them the following type names: AST generalist (species found on basalt and at least in one vent habitat, indicating a broad ecological niche), basalt specialist (species only found on basalt, indicating a more narrow niche), vent specialist (species only found in one vent habitat), vent generalist (species found in at least two vent habitats but not on basalt). Our results include species reports from other studies to gain a more complete picture (Humes 1984, Humes 1987, Humes 1989, Humes 1990, Kornicker 1991, Humes & Lutz 1994, Tsurumi et al. 2003, Ivanenko & Defaye 2006, Zekely et al. 2006b, Gollner et al. 2008) (see Appendix 3). From the 87 identified species we currently can consider 35 species as basalt specialists, 29 species as AST generalists, 12 species as vent generalists, and 11 species as vent specialists. Concerning the vent habitats only, 56% of species are AST generalists, 23% are vent generalists, and 21% are vent specialists.

DISCUSSION

The AST of the midocean ridge at 9°50'N EPR region houses two fundamentally different habitats: (i) the large, continuous basalt which is only scarcely populated by mega- and macrofauna with stable, ambient deep-sea temperatures. (ii) the relatively small, ephemeral, patchy hydrothermal vents at which a distinct zonation of foundation species and their associated faunas along a physical stress gradient of hydrothermal vent flux are found. Despite these profound differences, meiobenthos from both habitats is more similar than we expected. Instead of viewing a community as vent meiobenthos only, we propose to visualize them as AST hard substrate, epibenthic and epizoic deep-sea fauna, characterized by a few higher taxa of animals and protists with low diversity, and low abundances. Overall, distinct communities colonize each habitat in a pattern of diversity inversely correlated with the gradient of hydrothermal vent flux.

Low abundance and low higher taxon diversity

Low meiofauna abundances below 100 ind. 10 cm^{-2} are common for hard substrate vent communities, which stand in contrast to many other marine habitats (see Gollner et al. 2007). At our studied sites, highest abundance was 976 ind. 10 cm^{-2}, but most samples were characterized by <100 ind. 10 cm^{-2}. A similar trend was found in all other comparable meiofauna studies from vents (Dinet et al. 1988, Zekely et al. 2006b, Copley et al. 2007). Bottom-up as well as top-down processes could provide possible explanations. On the one hand, vents are known for their high *in situ* primary production (Van Dover 2000), but neither the quality nor the quantity of particulate organic matter (POM), the major food source for meiofauna, has been studied at diffuse flow vents at the 9°N EPR. At Juan de Fuca Ridge, meiofauna occupies different feeding guilds and POM is shaped by variations of hydrothermal flux (Limén et al. 2007). On the other hand, highly abundant macrofauna possibly preys on smaller fauna.

To our knowledge, only 4 metazoan phyla, Arthropoda, Gastrotricha, Nematoda, Platyhelminthes, and 2 protist phyla, Ciliates and Granuloreticulosa, build the entire meiobenthic community in the 9°50'N EPR region. Gastrotricha were described from artificial devices deployed in this area (Kieneke & Zekely 2007), but we did not encounter them in our study of natural communities. The most species rich taxon in our study is the Copepoda with 49 identified species. Copepoda is also one of the most diversified taxa at hydrothermal vents, contributing about 80 described species, which represents more than 15% of the species documented from vents worldwide (Bright 2006, Ivanenko & Defaye 2006).

Diversity is inversely correlated to vent flux

A clear pattern of diversity emerges from this study of deep-sea hydrothermal vents. Meiobenthos diversity was found to be negatively correlated to the vent flux. While this ecosystem naturally exhibits the full range from extremely high vent flux above the limits of life to absence of vent flux in basalt areas, other types of disturbances such as frequent volcanic eruptions and biological disturbances are present everywhere. The fact that an unimodal relationship between disturbance and diversity as predicted by the intermediate disturbance hypothesis (Connel 1978, Menge & Sutherland 1987) was not found, might be due to the lack of non-disturbed habitats within this ecosystem. In consequence, competitive exclusion leading to a decrease in diversity at non-disturbed habitats might not play a role.

Very high vent flux regimes with temperatures around 250°C as measured on the surface walls of several black smoker chimneys are above the limits for eukaryotic life, currently thought to be about 45-55°C (Lee 2003). These samples lacked any macro- and meiofauna. The foundation species *Alvinella pompejana* and *A. caudata* thrive at the most extreme of vent habitats still populated by animals. Associated animals, such as the dirivultid *Stygiopontius hispidulus* that dominate the meiobenthic community also survive temporal peaks of high flux (Le Bris et al. 2006). For small meiobenthic organisms in general, this threat is thought to be more severe than for large macrobenthic animals due to their limited mobility relative to their small size in reacting to this potential disturbance. However, within the meiobenthos, copepods are considered relatively fast. Observation of live animals after collection showed us that this is also true for vent meiofauna (SG, MB pers. obs.). Their agility might be one of the factors allowing some copepods to invade this habitat, while the more sluggish nematodes, ostracods, and acari are apparently not capable of living in the hot pompei worm habitat.

Physico-chemical characteristics of vent flux impose several physiological stresses and disturbances. With increasing vent flux and increasing amplitude of fluctuations, fewer species are able to cope with the extreme conditions. By comparing meiobenthic communities at different flux regimes and their thriving foundation species, we found that at vent sites, species richness and diversity clearly increased with decreasing vent flux from alvinellid (S: 4-7, H'_{loge}: 0.11 – 0.45), tubeworm (S: 8 – 23; H'_{loge}: 0.44 – 2.00) to mussel assemblages (S: 28 – 31; H'_{loge}: 2.34 – 2.60). Statistical tests show that abiotic parameters of the vent flux are inversely correlated to species richness, and that temperature, sulfide concentration, and pH might have a great influence on the meiobenthic community structure.

Previous studies on nematode and copepod communities do not contradict our results. The nematode community at sedimented vents in the North Fiji Basin, showed lower species diversity in the center of hydrothermal activity than in nearby areas without vent flux (Vanreusel et al. 1997). A copepod community study at *Ridgeia piscesae* tubeworm habitats at the Juan de Fuca Ridge also revealed that vents with reduced fluid flux or sites with undetectable vent fluid harbor more copepod species than higher flux vent sites (Tsurumi et al. 2003). Also a very species poor copepod community was found at sulfide chimneys colonized by *Paralvinella sulfincola*, comparable to what we found at the chimneys colonized by pompei worms. In *P. sulfincola* aggregation the copepod *Stygiopontius quadrospinosus* instead of *S. hispidulus* dominates the communities with 80% relative abundance (Tsurumi et al. 2003).

The relation of disturbance and diversity in marine meiobenthos apparently is equally complex as has been reviewed for a variety of communities, which exhibited unimodel, U-shaped, positive, negative, or no patterns (Mackey & Currie 2001). Similar to our results from hydrothermal vents, also several community studies from intertidal areas showed a negative correlation of diversity with physical disturbance (Ott 1972, Netto et al. 1999, Moreno et al. 2006). In contrast along a gradient caused by glacial discharges of meltwater, ice and till highest taxonomic distinctness was found at the most disturbed areas (Somerfield et al. 2006). Along a salinity gradient in an estuary, the diversity pattern was U-shaped (Warwick & Gee 1984). Studies in oil-polluted areas showed no effect on diversity of nematodes compared to unpolluted sites (Gee et al. 1992, Schratzberger et al. 2003). Heavy metal pollution resulted in diminished taxon diversity (Sundelin & Elmgren 1991, Lee & Correa 2005). Disturbance by macrofauna (predation, physical disturbance, competition for food) shows no overall trend that could predict diversity (Ólafsson 2003).

AST meiofauna and possible underlying ecological and evolutionary processes

More than half of the 52 species found at the 9°50'N EPR vents at pompei worm, tubeworm, and mussel aggregations also inhabit the bare basalt. Taking into account that we only were able to collect 4 samples at the basalt, we expect the number of species currently listed as vent endemics (specialists and generalists) to decline by future collecting. However, we can already see a rough outline of underlying different life histories concerning dirivultid and harpacticoid copepods and nematodes. Some species of the Dirivultidae, a family formerly classified as vent endemic (Heptner & Ivanenko 2002) must now be considered as AST generalistic, as we also encountered them on bare basalt. Interestingly, many of these Dirivultidae showed relatively higher abundance at vent sites and individual species were found in many vent samples while at the basalt most species of Dirivultidae were only detected in a single sample. In contrast, the harpacticoid Copepoda, an order present in many other marine benthic habitats (Giere 2009), were usually more abundant and diverse in the basalt habitat. Nematodes were also more diverse on basalt, e.g. no species was found in the pompei worm habitat, and only very few species were present in the tubeworm habitat (e.g. *Halomonhystera hickeyi*, *Thalassomonhystera fisheri*). These few nematode species can become very abundant at vent habitats, suggesting that some species and/or genera have somehow successfully adapted to the vent environment. Whether the success of vent species is due to physiological adaptations, a very broad physiological tolerance, or due to biological processes remains to be tested.

Disturbances, such as the waxing and waning of vents and even volcanic eruptions, are less dramatic for AST generalists as populations are present nearby on the basalt. Vent generalists have the advantage over vent specialists that shifts in vent flux are tolerated according to the range of physiological capabilities of each species. The number of vents potentially acting as a source for colonization is much higher for generalists, than specific vent types within a given area are for specialists. Consequently, the few vent specialists restricted to one specific habitat are most threatened by disturbances.

Very few basalt samples were taken in the vicinity of vents about 10 meters away from flux, and it is far too early to predict which communities are generally found in this neglected habitat. It has to be noticed that the studied basalt, although not directly influenced by vent flux, might have enhanced food sources compared to more distant bare basalt. We identified species that are also able to live at vent sites, but there were also true basalt specialists, as it could be tested for the harpacticoid copepod *Smacigastes barti* (Gollner et al. 2008). Likely, the basalt specialist meiofauna and/or AST meiofauna extends further into the flanks of the mid-ocean mountain chain until a switch from an epibenthic to infaunal community occurs due to an increase in sediment coverage.

Conclusion

This study underlines the importance of including meiofauna in studies of community ecology. We provide here an inventory of meiobenthic species and diversity patterns found at a deep-sea hydrothermal vent region. While a relationship between meiobenthic diversity and vent flux was found, this physical stress gradient does not necessarily imply that a causal link exists. The advantage of working on a community that is relatively poor in species, is our ability to address, in future work, specific questions on the underlying processes shaping this community.

ACKNOWLEDGEMENTS

This work was supported by the Austrian Science Foundation grant FWF (P16774-B03, P20190-B17 to MB), the National Science Foundation USA (OCE-0002729 to CR Fisher), the International Office Vienna, the Promotion Grants from the University of Vienna, and the TAWNI (training awards for new investigators) by ChEss (to SG). Special thanks to the captain and crew of the RV *Atlantis*, pilots and crew of the DSV *Alvin*, and scientists on board for their expertise and helpfulness during several cruises to the East Pacific Rise. We are grateful to CR Fisher, J Voight and CS Cary for invitations to cruises, and to many taxonomists for describing species (Ostracoda: LS Kornicker, E Harrison-Nelson, R Maddocks) and for their effort in supporting and helping us with species identification (Foraminifera: M Holzmann, G Panieri; Ostracoda: D Danielopol; Nematoda: J Ott, A Vanreusel; Copepoda: R Huys, VN Ivanenko).

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Figure 1. *In situ* photographs of the 5 different habitat types: Sulfide chimney (A), pompei worm habitat with the polychaete *Alvinella pompejana* (B), tubeworm habitat with the vestimentiferan *Riftia pachyptila* (C), the mussel habitat with the mytilid mussel *Bathymodiolus thermophilus* (D), and bare basalt habitat (E).

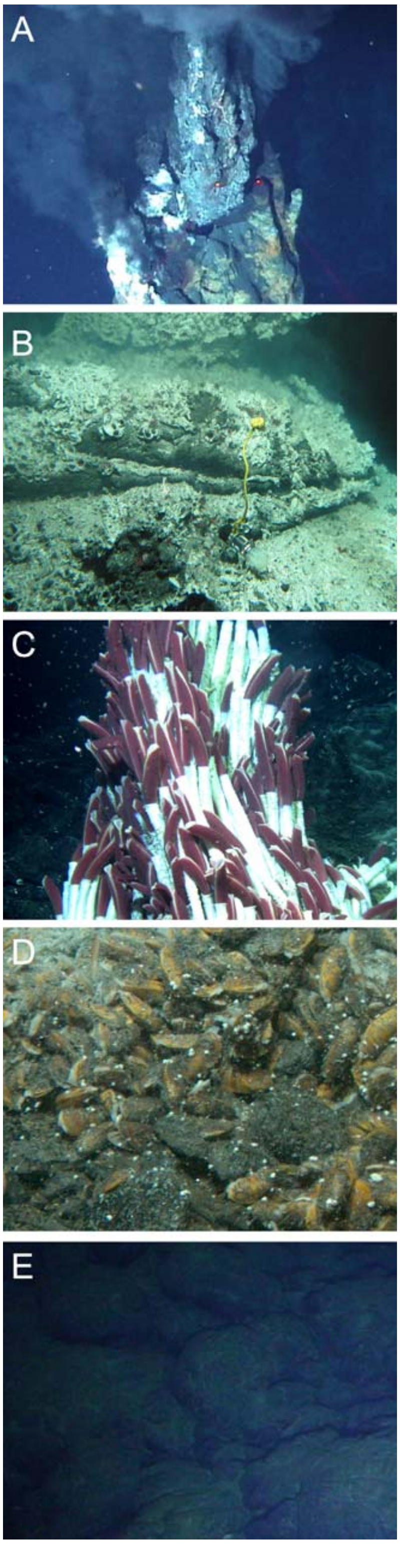


Figure 2. 2-dimensional MDS configuration plot for 18 samples from the pompei worm (P1-P5), tubeworm (T1-T6), mussel (M1-M3), and basalt habitats (B1-B4).

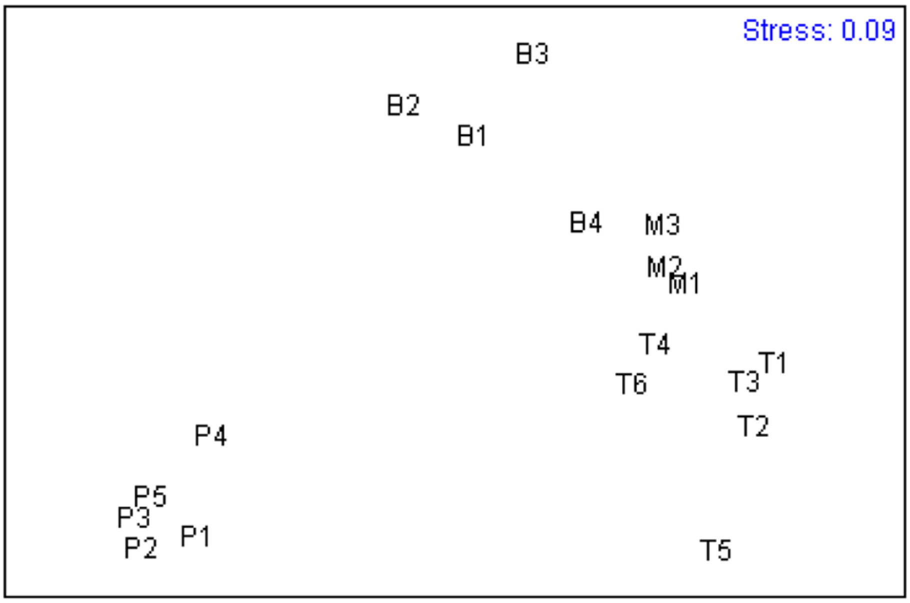


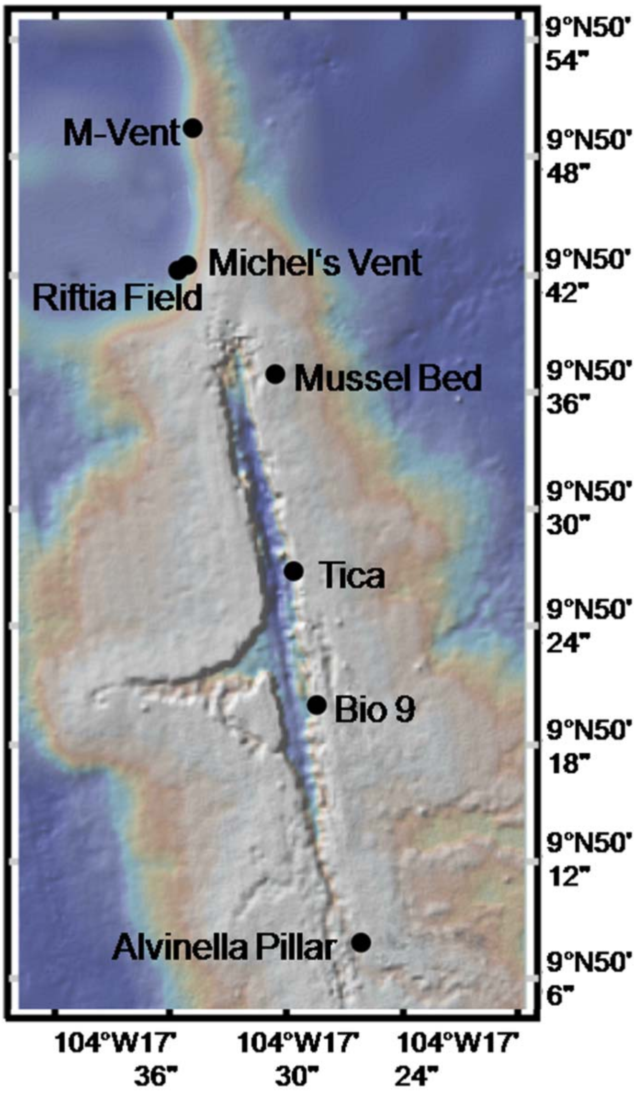
Table 1. Meiofauna abundance, relative abundance of taxa, and the diversity measures species richness (S), Shannon-Wiener diversity (H'_{loge}), and Pielou´s evenness index (J´) are shown for the 18 samples of the habitats: P (pompei worm; P1-P5), T (tubeworm; T1-T6), M (mussel; M1-M3), and B (basalt; B1-B4).

Habitat	**pompei worm communities**					**tubeworm communities**						**mussel communities**			**basalt communities**			
Samples	**P1**	**P2**	**P3**	**P4**	**P5**	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**	**M1**	**M2**	**M3**	**B1**	**B2**	**B3**	**B4**
Abundance (no. individuals)																		
Total	408	7453	1498	252	782	1219	29279	4242	65	60	978	11914	4444	4524	582	141	35	1896
Total ab. 10 cm^{-2}	36	217	266	71	474	20	976	61	1	1	12	87	58	72	13	5	1	51
Relative abundance of taxa (%)																		
Rel. ab. Nematoda [%]	0	0	0	0	0	78	97	76	31	18	58	49	43	29	4	13	34	1
Rel. ab. Copepoda [%]	99	100	99	99	99	18	2	23	38	80	35	49	53	66	23	63	31	92
Rel. ab. Ostracoda [%]	0	0	0	0	0	0	1	1	0	0	2	1	1	1	1	1	9	1
Rel. ab. Acari [%]	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Rel. ab. Foraminifera [%]	1	0	1	1	1	4	1	1	31	2	5	1	2	4	72	23	26	6
Diversity measures																		
S total	5	5	4	6	7	11	17	20	10	8	23	29	31	28	32	25	20	34
H'_{loge} total	0.11	0.45	0.18	0.40	0.21	1.13	0.44	1.35	2.00	1.75	1.72	2.34	2.60	2.42	1.18	2.16	2.74	1.42
J´ total	0.07	0.28	0.13	0.22	0.11	0.47	0.15	0.45	0.87	0.84	0.55	0.69	0.76	0.73	0.34	0.67	0.91	0.40

Table 2. Results of bootstrapping (bt, 10 000 resamplings each) used to test for significant differences in total abundance 10 cm^{-2} (Ab.), species richness (S), Shannon-Wiener diversity (H'_{loge}), and Pielou´s evenness (J´), between the habitats P (pompei worm), T (tubeworm), M (mussel), and B (basalt). Significant results after classical Bonferroni-correction are marked in bold. Dissimilarity results (Diss. %) calculated by SIMPER, and ANOSIM results (R-statistics and possible significance level p) are also shown for habitats.

Habitat	Ab.	S	H'_{loge}	J´	Diss.%	R-stat	p
P - T	0.29	**<0.001**	**<0.001**	**<0.001**	95	1	**0.002**
P - M	**<0.001**	**<0.001**	**<0.001**	**<0.001**	94	1	**0.018**
P - B	**<0.001**	**<0.001**	**<0.001**	**<0.001**	93	1	**0.008**
T - M	0.81	**<0.001**	**<0.001**	0.09	68	0.53	0.24
T - B	0.32	**<0.001**	0.20	0.86	84	0.86	**0.005**
M - B	**0.003**	0.58	0.07	0.24	75	0.56	0.057

Appendix 1. Sample sites within the 9°50´N EPR (East Pacific Rise) region: Alvinella Pillar, Bio 9, Michel´s Vent, M-Vent, Q-Vent (pompei worm habitats), Tica, Riftia Field (tubeworm habitats), and Mussel Bed (mussel habitat). Basalt samples were taken near Tica and Alvinella Pillar.



Appendix 2. Sample information is given on geographical location, year of sampling, sample area, and volume of sediment. We named samples after habitat types and their foundation species (P pompei worm, T tubeworm, M mussel) or their substrate (B basalt); dominant mega-/macrofauna species at sites were *Alvinella pompejana* Debruyéres & Laubier 1980, *Riftia pachyptila* Jones 1981, and the mytilid mussel *Bathymodiolus thermophilus* Kenk & Wilson 1985. High temperature sulfide chimney habitats are not shown because not a single specimen was detected within these samples and this habitat type was therefore excluded from all analyses.

Habitat	**pompei worm communities**					**tubeworm communities**						**mussel communities**			**basalt communities**			
Samples	**P1**	**P2**	**P3**	**P4**	**P5**	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**	**M1**	**M2**	**M3**	**B1**	**B2**	**B3**	**B4**
Site	Michel´s Vent	Alvinella Pillar	Bio9	M-Vent	M-Vent	Tica	Tica	Tica	Riftia Field	Riftia Field	Riftia Field	Mussel Bed	Mussel Bed	Mussel Bed	near Tica	near Tica	near Tica	near A.Pillar
Longitude 9°50.	.709`N	.130´N	.335´N	.826´N	.826´N	.447´N	.447´N	.447´N	.705´N	.705´N	.705´N	.615´N	.613´N	.629´N	.447´N	.447´N	.447´N	.130´N
Latitude 104°17.	.585´W	.438´W	.474´W	.583´W	.583´W	.493´W	.493´W	.493´W	.493´W	.493´W	.493´W	.509´W	.504´W	.512´W	.493´W	.493´W	.493´W	.438´W
Depth (m)	2507	2502	2508	2508	2508	2500	2500	2500	2500	2500	2500	2503	2503	2503	2500	2500	2500	2502
Year of Sampling	2004	2004	2004	2004	2004	2001	2001	2002	2001	2001	2002	2002	2002	2002	2003	2003	2004	2004
Alvin dive #	4063	4065	4069	4070	4072	3731	3732	3846	3730	3734	3843	3845	3847	3852	3952	3952	4063	4064
Sample area (cm^2)	113	343	56	36	17	600	300	700	1300	600	800	1370	770	630	454	263	270	369
Sediment (ml)	17	174	106	138	20	88	165	133	40	37	85	25	15	19	4.9	9.6	2.3	6.5

Appendix 3. Distribution of meiobenthic species in the habitats P (pompei worm), T (tubeworm), M (mussel), and B (basalt). The occurrence of species (indicated by the number 1) in their habitats in this study is compared to those of other studies: M* corresponds to the study of Zekely et al. 2006 who studied meiobenthic communities at the mussel site Buckfield at 11°N EPR. Other findings show additional occurrences of species. Reference is given for each habitat finding. The taxon is given for each species (S = Siphonostomatoida: all found species except *Ecbathyrion prolixicauda* belong to the family Dirivultidae), H = Harpacticoida, N = Nematoda, O = Ostracoda, F = Foraminifera, A = Acari). The type summarizes the overall occurrence of species in their habitat known so far: AST G = axial summit through generalist (species found on basalt and at least in one habitat at vents), B S = basalt specialist (species only found on basalt), V S = vent specialist (species only found in one habitat at vents), V G = vent generalist (species found in at least two habitats at vents and not on basalt).

Species	**taxon**	**TYPE**	**P**	**T**	**M**	**B**	**M***	**other findings**	**reference**
Aphotopontius limatulus	S	AST G			1	1	1	site Clam acres (with clams?)	Humes 1987
Aphotopontius mammillatus	S	AST G		1	1	1	1	vestimentiferans	Ivanenko & Defaye 2006
Aphotopontius probolus	S	AST G		1		1		mussel, vestimentiferans, crab trap	Humes 1990
Ceuthocetes introversus	S	AST G		1	1	1		vestimentiferans and *Calyptogena*	Ivanenko & Defaye 2006
Ceuthoecetes acanthothrix	S	AST G		1	1	1	1	vestimentiferans and *Calyptogena*	Ivanenko & Defaye 2006
Ecbathyrion prolixicauda	S	AST G	1		1	1	1	no	
Scotoecetes introrsus	S	AST G		1	1	1	1	vestimentiferans	Ivanenko & Defaye 2006
Stygiopontius flexus	S	AST G	1	1		1		siboglinids	Ivanenko & Defaye 2006
Stygiopontius hispidulus	S	AST G	1	1		1		bivalves, polychaetes	Ivanenko & Defaye 2006
Stygiopontius paxillifer	S	AST G	1		1	1		site Clam acres (with clams?)	Humes 1989
Stygiopontius quadrispinosus	S	AST G				1		sulfides, vestimentiferans, no flux	Tsurumi et al. 2003
Ameira sp. 1	H	AST G	1		1	1		no	
Amphiascus sp.1	H	AST G			1	1		no	
Halectinosoma sp. 1	H	AST G	1	1	1	1	1	no	
Halophytophilus sp.1	H	AST G	1			1		no	
Xylora bathyalis	H	AST G		1	1	1		no	
Anticoma sp.1	N	AST G			1	1	1	no	
Chromadorita sp.1	N	AST G		1	1	1	1	no	
Halomonhystera hickeyi	N	AST G		1	1	1		no	

Species	**taxon**	**TYPE**	**P**	**T**	**M**	**B**	**M***	**other findings**	**reference**
Leptolaimus sp.1	N	AST G			1	1	1	no	
Microlaimus sp.1	N	AST G			1	1		no	
Paralinhomeus sp.1	N	AST G			1	1	1	no	
Thalassomonhystera fisheri	N	AST G		1	1	1	1	no	
Prionotoleberis styx	O	AST G				1		site Clam acres (with clams?)	Kornicker 1991
Thomontocypris gollnerae	O	AST G		1	1	1		no	
Thomontocypris brightae	O	AST G		1	1	1		no	
Xylocythere vanharteni	O	AST G		1	1	1		no	
Abyssotherma pacifica	F	AST G	1	1	1	1		no	
Deuterammina sp. 1	F	AST G		1	1	1		no	
Exrima sp. 1	S	B S				1		no	
Ameiropsis sp.1	H	B S				1		no	
Argestes sp.1	H	B S				1		no	
Atergopedia sp.1	H	B S				1		no	
Ectinosoma sp. 1	H	B S				1		no	
Ectinosoma sp. 2	H	B S				1		no	
Idomene sp. 1	H	B S				1		no	
Idomene sp. 2	H	B S				1		no	
Idomene sp. 3	H	B S				1		no	
Leptotachidia sp. 1	H	B S				1		no	
Mesochra sp. 1	H	B S				1		no	
Sarsameira sp. 1	H	B S				1		no	
Smacigastes barti	H	B S				1		on artificial substrates on basalt	Gollner et al. 2008
Stenocopia sp. 1	H	B S				1		no	
Stenocopia sp. 2	H	B S				1		no	
Stenocopia sp. 3	H	B S				1		no	
Astomonema sp. 1	N	B S				1		no	
Chromadora sp. 1	N	B S				1		no	
Chromadorida sp. 1	N	B S				1		no	
Chromadorida sp. 2	N	B S				1		no	
Euchromadora sp. 1	N	B S				1		no	
Eurystomina sp. 1	N	B S				1		no	
Metoncholaimus sp. 1	N	B S				1		no	
Microlaimus sp. 2	N	B S				1		no	

Species	taxon	TYPE	P	T	M	B	M*	other findings	reference
Monhysterida sp. 1	N	B S				1		no	
Monhysterida sp. 2	N	B S				1		no	
Paracyatholaimus sp. 1	N	B S				1		no	
Paracyatholaimus sp. 2	N	B S				1		no	
Prooncholaimus sp. 1	N	B S				1		no	
Rhabdocoma sp. 1	N	B S				1		no	
Syringolaimus sp. 1	N	B S				1		no	
Tripyloides sp. 1	N	B S				1		no	
Foraminifera sp. 2	F	B S				1		no	
Foraminifera sp. 3	F	B S				1		no	
Foraminifera sp. 4	F	B S				1		no	
Aphotopontius acanthinus	S	V G		1				on crabs, limpets, bac. mats	Humes & Lutz 1994
Aphotopontius arcuatus	S	V G	1		1		1	bivalves	Ivanenko & Defaye 2006
Aphotopontius flexispina	S	V G		1				bivalves	Ivanenko & Defaye 2006
Ceuthoecetes aliger	S	V G		1	1		1	vestimentiferans and *Calyptogena*	Ivanenko & Defaye 2006
Nilva torifera	S	V G			1		1	vestimentiferans and *Calyptogena*	Ivanenko & Defaye 2006
Rhogobius contractus	S	V G		1	1		1	no	
Stygiopontius sentifer	S	V G	1				1	polychaetes, in tubes of *Alvinella*	Ivanenko & Defaye 2006
Stygiopontius stabilitus	S	V G	1	1				*Paralvinella*	Humes 1990
Bathylaophonte pacifica	H	V G		1			1	invertebrates	Ivanenko & Defaye 2006
Daptonema sp. 1	N	V G		1	1			no	
Halomonhystera sp. 1	N	V G		1	1		1	no	
Polycopetta pax	O	V G		1	1			no	
Aphotopontius hydronauticus	S	V S		1				no	
Benthoxynus tumidiseta	S	V S		1				vestmentiferans	Humes 1984
Stygiopontius mucroniferus	S	V S		1				no	
Ameira sp. 2	H	V S			1			no	
Bradya sp. 1	H	V S			1			no	
Diosaccinae sp.1	H	V S			1			no	
Harpacticoida sp. 1	H	V S		1				no	
Tetragoniceps sp. 1	H	V S			1			no	
Paracanthonchus sp.1	N	V S			1		1	no	
Forminifera sp. 1	F	V S		1				no	
Lohmannella sp. 1	A	V S			1			no	

Benthic copepod communities associated with tubeworm and mussel aggregations on the East Pacific Rise

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ABSTRACT

Variability in the structure of the meiobenthic copepod communities was studied among three vent sites on the East Pacific Rise. One of the sites was dominated by the mussel *Bathymodiolus thermophilus,* and the other two of the sites were dominated by the tubeworm *Riftia pachyptila*. In addition to the differences in the dominant megafauna, the maximum temperatures were much lower at the mussel-dominated sites, and the temperature to sulfide ratio was different between the tubeworm-dominated sites. A total of 22 vent endemic siphonostomatoid copepod species and 5 harpacticoid copepod species were identified among the three sites. Copepod abundance was low at all sites (< 1-31 ind. 10 cm^{-2}). Species richness ranged from 6-14, Shannon-Wiener diversity indices from 1.3-2.3, and Pielou's evenness indices between 0.6-0.9 were found. Differences were detected in abundance and Shannon-Wiener diversity between the mussel site and one tubeworm site. Multivariate analyses pointed to a relative homogenous mussel bed community and a heterogenous tubeworm community. The majority of species were primary consumers feeding on detritus. Both copepod sexes and, for the first time, all copepodite stages were detected in the samples.

Keywords: meiobenthic copepods, hydrothermal vent, *Bathymodiolus thermophilus, Riftia pachyptila,* East Pacific Rise, community structure

INTRODUCTION

Copepoda is one of the largest and most diversified taxa at hydrothermal vents. They are estimated to contribute more than 15% of the total species described from vents worldwide (Tunnicliffe et al. 1998). The most important order is the Siphonostomatoida, with more than 50 described species including the families Dirivultidae and Ecbathyriontidae, which are largely endemic to vents (Humes 1988, Heptner & Ivanenko 2002). Even with the large number of described species, our knowledge of the variability in copepod community structure, as well as the geographic distribution and habitat selection of individual species is limited. In this study, we focused on the identification and quantification of the meiobenthic copepod communities from three sites on the northern East Pacific Rise. We also explored the influence of the dominant megafaunal species *Riftia pachyptila* Jones, 1981 and *Bathymodiolus thermophilus* Kenk & Wilson, 1985 and hydrothermal fluid flux on the structure of the copepod communities.

MATERIAL AND METHODS

In December 2001 and December 2002, quantitative collections of either mussel-dominated or tubeworm-dominated communities were made at three hydrothermal vent sites on East Pacific Rise at ~ 2500 meters depth: Tica (9°50.447´N, 104°17.493´W), Riftia Field (9°50.705´N, 104°17.393´W), and Buckfield (11°24.90´N, 103°47.20´W). At Tica, large aggregations of the tubeworm *Riftia pachyptila* were visibly dominant, but the mussel *Bathymodiolus thermophilus* was also present. At the time of sampling in 2002, this site was characterized by warm fluids with maximum temperatures of 18°C, maximum sulfide concentrations of 176 µM $\sum H_2S$, and slightly acidic pH. The more sparse and patchy aggregations of tubeworms at Riftia Field lacked mussels and in 2002 exhibited similar maximum temperatures of 23°C but maximum sulfide concentrations were 35 µM $\sum H_2S$ and minimal pH was below 5 (see Le Bris et al. 2006). At Buckfield, mussels formed a dense bed, and temperatures ranged between ~2 and 10°C (Van Dover pers. obs.) (Table 1). No data on sulfide concentrations and pH were available for this site. Both, *R. pachyptila* and *B. thermophilus* formed aggregations on hard substrate, and small amounts of sediment, consisting primarily of particulate organic matter and a few mineral grains, accumulated between the tubes and between the shells and byssal threads of the mussels.

Three quantitative samples were taken at each of the three sites, Tica (TC1, TC2 in 2001 and TC3 in 2002), Riftia Field (RF1, RF2 in 2001 and RF3 in 2002) and Buckfield (BF1, BF2 and BF3 in 2001) using two collection devices. The tubeworm aggregations were sampled with the “Bushmaster Jr.” (300-1300 cm^2 sample area) (Govenar et al. 2005), and mussel aggregations were sampled with the “mussel pot” (531 cm^2 sample area) (Van Dover 2002). Meiofauna was retained on 63 µm mesh-sized net, passing through a 1 mm net, fixed in 4% buffered formalin for 24 h, and stored in 70% ethanol. In order to compare these large sample areas to other meiofauna studies, we standardized all samples to 10 cm^2. All copepods were counted, and at least 300 individuals per sample were identified to species level, until an asymptote was obtained for the cumulative species effort curve constructed for each sample (Fig. 1). Planktonic species were excluded in this study because this community, albeit closely related to the benthic environment, is not part of the meiobenthos (Giere 1993). Biomass of the vent endemic siphonostomatoid copepods was calculated according to their body form (see Heptner & Ivanenko 2002). Body volume of harpacticoid copepods was estimated (Volume = Length x $Width^2$ x Conversion factor corresponding to body form) and was then multiplied by the specific gravity of 1.13 (for meiobenthos in general) to obtain wet mass in mg (see Feller & Warwick, 1979). The trophic status of each species was determined according to the mouth structure of copepods, according to the classification determined by Heptner & Ivanenko (2002). Univariate (S, H'_{loge}, J´) and multivariate measurements (cluster-analysis, SIMPER, ANOSIM; data were standardized and square-root transformed) were calculated using PRIMER v5 Package (Plymouth Marine Laboratory; Clarke & Gorley 2001). Student´s t-tests were used to test significant differences in abundance and species richness. Due to the relatively small number of samples, bootstrapping (1000 resamplings each, two-sided test; routine “FTBOOT” from the package “computerintensive statistics” by Nemeschkal 1999) was used to test for significant differences in abundance, species richness, and Shannon-Wiener diversity indices among the three sites. Results from statistical analysis were classical Bonferrroni-corrected ($p = \alpha/n$; $\alpha = 0.05$).

RESULTS AND DISCUSSION

Hydrothermal vents on the East Pacific Rise are highly variable habitats inhabited by distinct mega- and macrofaunal communities dominated by the tubeworm *Riftia pachyptila* or the mussel *Bathymodiolus thermophilus* found in vigorous to moderate diffuse flow areas (Shank et al. 1998). Since at the time of sampling, the tubeworm dominated sites Tica and Riftia Field were known to exhibit higher overall maximum temperatures than the mussel site Buckfield, but differed in their maximum sulfide concentrations and minimum pH (Le Bris et al. 2006; Table 1), we expected a divergence in copepod community structure among the three different sites. Our findings showed that despite differences in environmental characteristics and dominant megafauna, univariate and multivariate analyses revealed that the meiobenthic copepod community composition (e.g. abundance, S, $H'_{\log e}$) and trophic structure were similar among the tubeworm dominated sites. The mussel dominated site Buckfield and the tubeworm dominated site Riftia Field showed differences in abundance and Shannon-Wiener diversity index, but were similar in species richness and trophic structure. Differences in the distribution and relative abundance of species among samples reflect a relative homogenous mussel bed community and a highly heterogeneous tubeworm community.

We identified a total of 27 species from all three sites. Similar to other studies from the Mid-Atlantic Ridge (Zekely et al. 2006) and the Juan de Fuca Ridge (Tsurumi et al. 2003), vent endemic siphonostomatoid copepods dominated the communities on the East Pacific Rise. The highest relative abundance of siphonostomatoids with little variation among samples occurred at the mussel bed Buckfield (96-97%). At the tubeworm-dominated site Tica, siphonostomatoid relative abundance was also high, but the intra-site variation was larger (87-97%), while the lowest relative abundance was found at Riftia Field (75-86%) (Table 1). Harpacticoid copepods, known form a variety of shallow-water and deep-sea habitats, apparently play a minor role at vents with the exception of one senescent vent site at the Juan de Fuca Ridge (Tsurumi et al. 2003).

Only 6 of 27 species were collected in mussel bed samples and in tubeworm aggregations (Table 3). *Scotocetes introrsus* Humes, 1987 was the most abundant shared species among sites. Other siphonostomatoids were patchily distributed among samples at all sites, while harpacticoids were rare in all samples. *Aphotopontius mammilatus* Humes, 1987 and *A. rapunculus* Humes & Segonzac, 1998 appeared to be a consistent part of the copepod community at Buckfield, contributing more than 10% of the total abundance at the mussel bed, while these species were either present in lower abundances or absent in the samples from the tubeworm-dominated sites. On the other hand, the three parasitic *Ceuthocetes* species were relatively more abundant at the tubeworm-dominated sites.

All univariate measures of community structure (S, H'_{loge}, J', abundance, biomass) were quite similar among sites (Table 1). Species richness (S) varied from 6 to 14 species in a single sample, but differences among sites were not significant (Table 2). Shannon-Wiener diversity indices were low at all sites (H'_{loge} = 1.3 to 2.3; Tables 1 & 2). Pielou's evenness indices were similar and high (J´ = 0.6 to 0.9), with similar proportions of all species. Also biomasses estimated for the 3 samples from each site were similar and dominated by the large-sized siphonostomatoids (Table 1). Copepod abundances well below 80 ind. 10 cm^{-2} seem to be the rule at hydrothermal vents (Dinet et al. 1988, Tsurumi et al. 2003, Zekely et al. 2006). The three hard substrate communities in this study follow this trend. Abundances at Tica (12.8 ± 10.9 ind. 10 cm^{-2}) were similar to those of Riftia Field (1.4 ± 1.7 ind.10 cm^{-2}) and Buckfield (26.2 ± 2.8 ind. 10 cm^{-2}). Only at Riftia Field and Buckfield abundances were different (Tables 1 & 2).

Multivariate analyses differentiated a distinct homogenous mussel-dominated community at Buckfield and a highly heterogeneous tubeworm-dominated community at Tica and Riftia Field. At the mussel bed, samples were highly similar (SIMPER: 86%) indicating a rather homogenous assemblage, while among the tubeworm aggregations, intra-site similarities were low (SIMPER: Tica 40%, Riftia Field 45%). The dendrogram based on Bray-Curtis similarity reflects these patterns (Fig. 2). ANOSIM showed a global R of 0.63 at a significance level of 1.4% pointing to 3 slightly different communities.

Out of 16 species found at Tica and 17 species found at Riftia Field, the majority of 13 species (76% of total species at Tica and 81% of total species in Riftia Field) co-occurred at both tubeworm sites. In contrast, only 43% of total species in the mussel bed (6 out of 14 species) also occurred at the tubeworm-dominated sites and 43% of total species were restricted to the mussel bed indicating different assemblages. However, whether these differences between copepod communities at tubeworm aggregations from the East Pacific Rise 9°N vent sites and a mussel bed from 11°N are due to local factors, such as distinct flow regimes or the dominant megafauna, or due to regional-scale differences, possibly created by the Clipperton transform fault dividing the East Pacific Rise, remains to be studied.

Little is known on the geographic distribution of copepod species at vents. In previous studies, most samples were collected and described from a single vent. The majority of species we found among the tubeworm and mussel aggregations in this study were already known from the northern East Pacific Rise. However, *Aphotopontius probolus* Humes, 1990 was described from the Galapagos Rift, and *Bathylaophonte pacifica* Lee & Huys, 1999 was reported from the southern East Pacific Rise (Ivanenko & Defaye 2006) before they were discovered at our study sites.

Copepods are usually a very abundant part of the benthos in a variety of habitats, and play an important role in the food web by linking the microbial community and the macrofauna (Giere 1993). Although copepods are known to have representatives at all trophic levels, from primary consumers to secondary and tertiary predators and parasites, at the hydrothermal vents sites in this study, deposit feeders dominated the copepod community, with a total of 24 of 27 total species. Parasites were represented by the three species of *Ceuthocetes*, and predators were absent. Trophic status can be inferred from mouth structures (Heptner & Ivanenko 2002). While direct feeding observations have yet to be conducted, the mouthparts of many vent siphonostomatoids appear to be suitable for feeding on finely grained particles. Furthermore, bacteria embedded in mucus were found in the foreguts of such copepod species (Dinet et al. 1988). The dominance of primary consumers in the meiobenthic copepod community could be important for the transfer of organic matter at hydrothermal vents.

The role of parasitic copepods at hydrothermal vents is less understood. For example, *Ceuthocetes* species are thought either to feed on mucus and/or cut round holes into the host tissue and obtain their food through these holes (Heptner & Ivanenko 2002, Ivanenko & Defaye 2006). So far, they have been found associated with tubeworms or the clam *Calyptogena magnifica* Boss & Turner, 1980 (Ivanenko & Defaye 2006). In our samples they were also associated with the mussel *Bathymodiolus thermophilus*.

Little is known about the population structure, reproduction, and dispersal of vent copepods. Female dominated copepod communities are often found in diverse shallow-water habitats (Giere 1993) and were also reported from a vent site at Juan the Fuca Ridge (Tsurumi et al. 2003). Also, the majority of species in our samples showed a female bias or completely lacked males (*Aphotopontius hydronauticus* Humes, 1989, *A. probolus*, *A. acanthinus* Humes & Lutz, 1994). On the other hand, some parasitic species, such as *Ceuthocetes acanthothrix* Humes, 1987, *C. aliger* Humes & Dojiri, 1980, and *C. introversus* Humes, 1987 and the primary consumer *Scotocetes introrsus* Humes, 1987 were male dominated. While underlying mechanisms of population and community dynamics of female or male dominated species cannot be fully understood when samples are collected at a single time point, the occurrence of certain larval stages in benthic samples at least points to specific life history traits and dispersal capabilities. Copepodite stages from I to V were found at the two tubeworm-dominated sites, and a particularly high number of copepodites was present at Tica. At the mussel-dominated site Buckfield, copepodites from stage III to V were found, but in lower overall abundance than the tubeworm-dominated sites (Table 1). The differences in occurrence of copepodite stages between tubeworm and mussel communities cannot be explained by possible seasonality in reproduction cycles since all samples were taken in the same month of the year. Early copepodite stages have not been found previously in vent samples, suggesting pelagic dispersal (Tsurumi et al. 2003, Ivanenko 1998). However, from our findings we infer that at least in some species living among tubeworm aggregations, development through copepodite stages I to V occurs in the benthic environment. It has to be kept in mind, however, that many copepods, adults or larvae, are known to frequently migrate from the benthic to the pelagic environment in order to disperse, reproduce, search for food, or escape predators (Giere 1993).

ACKNOWLEDGMENTS

This work was supported by the Austrian Science Foundation grant FWF (P16774-B03 to M. Bright), National Science Foundation USA (Biological Oceanography to C. L. van Dover; OCE-0002729 to C. R. Fisher), Ifremer and the European Community (Ventox project EVK3-1999-00056P to N. Le Bris), International Office Vienna and Promotion Grant University of Vienna (to J. Zekely and S. Gollner). We thank the captains and crews of the R/V *Atlantis* and the pilots and crews of the DSV *Alvin* for their expertise in sample collections, and C.R. Fisher for invitation to the cruises and his scientific input. We are grateful to R. Huys, V. N. Ivanenko, and P. Martínez-Arbizu for their input in copepod identification and ecology.

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Figure 1. Cumulative species-effort curves for copepods based on cumulative number of species for samples with > 300 individuals (Tica: TC1, TC2, TC3; Riftia Field: RF3; Buckfield: BF1, BF2, BF3).

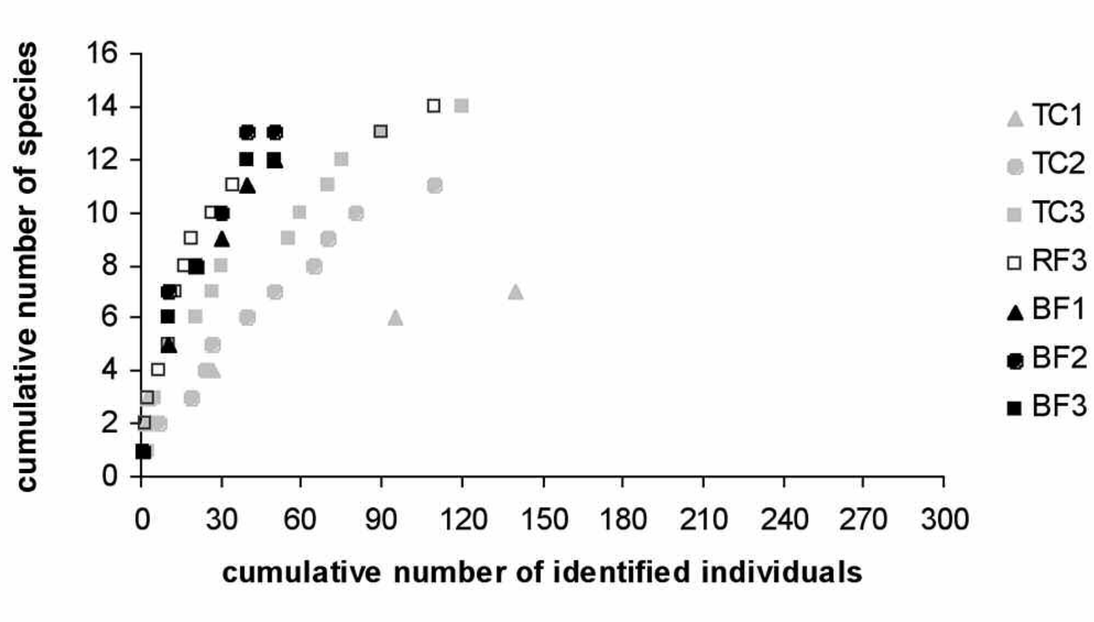

Figure 2. Hierarchical cluster diagram for group average linking, based on Bray-Curtis community similarity values from the nine samples (Tica samples: TC1, TC2, TC3; Riftia Field samples: RF1, RF2, RF3; Buckfield samples: BF1, BF2, BF3).

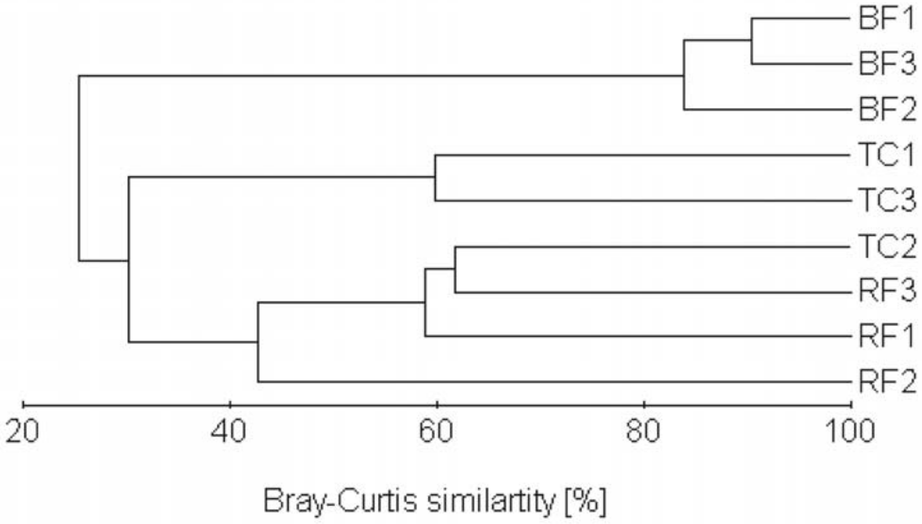

Table 1. Characteristics of collection sites and benthic copepod communities according to sites.

	Tica	Riftia Field	Buckfield
Maximum temperature [°C]	18[c]	23[c]	~ 2 - 10
Maximum $\sum H_2S$ [µM]	176[c]	35[c]	N/A
Maximum iron [µM]	0[c]	42[c]	N/A
Minimum pH	5.7[c]	4.4[c]	N/A
Dominant megafauna	*R. pachyptila*	*R. pachyptila*	*B. thermophilus*
Sediment [ml $10cm^{-2}$]	1.5 - 5.5	0.3 - 1.1	0.1 - 0.2
Total abundance [ind. per sample]	217 - 983	25 - 342	1224 - 1624
Abundance[a] [ind. 10 cm^{-2}]	4 - 27	<1 - 4	23 - 31
Abundance[b] [ind. 10 cm^{-2}]	3 - 24	<1 - 3	23 - 29
Adults : Copepodites	5.9 ± 3.6 : 1	18.7 ± 22.4 : 1	38.0 ± 25.2 : 1
Biomass [mg wet weight 10 cm^{-2}]	0.32 - 2.88	0.02 - 0.42	1.47 - 3.01
Species richness	7 - 14	6 - 14	12-13
Shannon-Wiener diversity	1.3 - 2.3	1.5 - 2	2.1 - 2.3
Pielou’s evenness	0.6 - 0.9	0.8	0.9
Dirivultid copepods [%]	87 - 97	75 - 86	96 - 97
Harpacticoid copepods [%]	3 - 13	14 - 25	3 - 4
Deposit feeders [%]	5 - 92	73 - 100	84 - 91
Parasites [%]	8 - 95	0 - 27	9 - 16
Predators [%]	0	0	0

[a] Abundance [ind. 10 cm^{-2}] including copepodites.

[b] Abundance [ind. 10 cm^{-2}] excluding copepodites, as it was used to calculate diversity indices.

[c] Measured in 2002 (Le Bris et al. 2006)

Table 2. Bootstrapping and students t-test (two-sided, $t_{4df} = 2.776$, p-value in parentheses) was used to test for differences in abundance (Ab, ind. 10 cm^{-2}) and species richness (S) between the three sites (Tica versus Riftia Field, Tica versus Buckfield, Riftia Field versus Buckfield). Bootstrapping was used to test for differences in Shannon-Wiener diversity (H'_{loge}). Results are given prior Bonferroni corrections.

	TC vs RF	TC vs BF	RF vs BF
Ab	0.01 (0.09)	0.02 (0.13)	0.003 (0.01)[a]
S	0.49 (0.60)	0.21 (0.44)	0.05 (0.23)
H'_{loge}	0.90	0.03	0.003[a]

[a] significant after Bonferroni corrections ($p < 0.05$)

Table 3. Relative abundance (%) of copepod species from nine samples (Tica: TC1, TC2, TC3; Riftia Field: RF1, RF2, RF3; Buckfield: BF1, BF2, BF3). Relative abundances > 10 % are marked in bold. [a] Harpacticoid copepods

	TC1	TC2	TC3	RF1	RF2	RF3	BF1	BF2	BF3
Species from three sites									
Aphotopontius mammilatus Humes, 1987		0.4	**10.4**			1.6	**16.3**	**15.8**	**27.2**
Bathylaophonte pacificaa Lee & Huys, 1999		0.4			5.4		0.9		0.9
Ceuthocetes acanthothrix Humes & Dojiri, 1980	**27.3**	3.0	**15.8**			4.7	3.7	1.6	3.3
Ceuthocetes aliger Humes, 1987	**36.0**	1.9	**16.7**			6.2	**12.6**	6.9	9.1
Halectinosoma sp.1[a] Boeck, 1872		4.9	2.3	4.2			1.8	4.3	3.3
Scotocetes introrsus Humes, 1987		**58.9**	1.8	**45.8**	**16.2**	**39.5**	**11.4**	**13.5**	**12.7**
Species from two sites									
Aphotopontius hydronauticus Humes, 1989	1.2		**10.4**	4.2		4.7			
Aphotopontius probolus Humes, 1990	2.5		8.1	8.3		1.6			
Benthoxynus tumidiseta Humes, 1989		**14.1**	1.4		**40.5**				
Ceuthocetes introversus Humes, 1987	**31.7**	3.0	**14.9**		**27.0**	4.7			
Stygiopontius flexus Humes, 1987		4.2	1.4	**16.7**	2.7	9.3			
Stygiopontius hispidulus Humes, 1987		1.1				7.0			
Xylora bathyalis[a] Hicks, 1988		8.0	0.9	**20.8**	2.7	**17.1**			
Aphotopontius rapunculus Humes & Segonzac, 1998	0.6		3.2				**10.8**	**11.8**	**17.5**
Species from a single site									
Aphotopontius acanthinus Humes & Lutz 1994	0.6		**12.2**						
Aphotopontius flexispina Humes, 1987			0.5						
Harpacticoida sp.1[a]						0.8			
Harpacticoida sp.2[a]					5.4	1.6			
Stygiopontius mucroniferus Humes, 1987						0.8			
Stygiopontius stabilitus Humes, 1987						0.8			
Aphotopontius arcuatus Humes, 1987								2.0	
Aphotopontius limatulus Humes, 1987							4.6	5.6	3.9
Ecbathyrion prolixicauda Humes, 1987							8.6	**17.8**	5.1
Exrima dolichopus Humes, 1987							2.2	5.3	1.8
Nilva torifera Humes, 1987							9.8	9.5	6.3
Rhogobius contractus Humes, 1987							**17.4**	5.3	8.8
Stygiopontius sentifer Humes, 1987								0.7	

Nematode communities associated with tubeworm and mussel aggregations on the East Pacific Rise

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ABSTRACT

The meiobenthic nematode community of three different vent sites at the East Pacific Rise was studied in order to determine whether the abundance, species richness, diversity and trophic structure were similar. The sites Tica and Riftia Field were dominated by the tubeworm *Riftia pachyptila,* and the Buckfield site was dominated by the mussel *Bathymodiolus thermophilus*. The nematode communities of all three sites were low in abundance (< 1 up to 46 ind. 10 cm^{-2}), except one sample from Tica with almost 1000 ind. 10 cm^{-2}. The communities at all sites consisted entirely of primary consumers, mostly deposit feeders. Species richness and Shannon-Wiener diversity indices were low and similar at both tubeworm sites and slightly but significantly higher at the mussel site. Multivariate analysis revealed that the species dissimilarity among the three sites was greater than 50 %, indicating distinct communities at each site.

Keywords: hydrothermal vent, meiobenthos, nematodes, *Riftia pachyptila*, *Bathymodiolus thermophilus*, East Pacific Rise

INTRODUCTION

Ecological community studies address the distribution and abundance of organisms. The spatial and temporal heterogeneity of a habitat can play an important role in the structure of a community (Begon et al. 1999). Most ecological studies at hydrothermal vents have focused on mega- and macrofauna. The few studies of the meiofauna, (animals and protists passing through a 1 mm and retained on a 63 µm mesh-sized sieve) (see Giere 1993), have indicated that the meiobenthos is a significant part of the hydrothermal vent community (Dinet et al. 1988, Shirayama 1992, Vanreusel et al. 1997, Zekely et al. 2006). Nematoda is one of the dominant meiobenthic taxa and is known from a variety of terrestrial, freshwater, and marine shallow-water and deep-sea habitats (Giere 1993). Vanreusel et al. (1998) were the first to describe the structure of a vent nematode community from mussel aggregations at soft-sedimented hydrothermal vents at the North Fiji Back-Arc Basin. The abundance and composition of nematodes were significantly different between active sites, inhabited by *Bathymodiolus brevior* Cosel & Métivier, 1994 and inactive vent sites, devoid of megafauna (Vanreusel et al. 1997).

The aim of this study was to investigate and compare the nematode communities of three hydrothermal vent sites on the northern East Pacific Rise, which differ in environmental characteristics, including the occurrence of the structuring large animals *Riftia pachyptila* Jones, 1981 and/or *Bathymodiolus thermophilus* Kenk & Wilson, 1985. These megafaunae create a unique three-dimensional habitat with considerable interstitial space in which small macro- and meiobenthic animals, including nematodes, live. They are a suitable structural habitat for biodiversity and community structure comparisons at hydrothermal vents.

MATERIAL AND METHODS

Nine megafaunal aggregations were sampled, three each at the sites Riftia Field (9°50.705´N, 104°17.493´W, 2500 m depth) and Tica (9°50.447´N, 104°17,493´W, 2500 m depth) (both dominated by the tubeworm *Riftia pachyptila*, but *Bathymodiolus thermophilus* mussels also occurred at Tica) and three at the site Buckfield (11°24.90´N, 103°47.20´W, 2480 m depth), where the mussel *B. thermophilus* was the dominant megafaunal species (Table 1). All megafaunal aggregations assembled on bare basalt and small amount of sediment, mostly particulate organic matter with few mineral grains, accumulated between tubes and/or shells. In 2002, chemical concentrations of $\sum H_2S$ and ferrous iron, pH and temperature were measured at the collection sites *in situ* with the *"Alchimist"* (Le Bris et al. 2006). At Riftia Field the maximum temperature was 23°C, sulfide concentrations were up to 35 µM $\sum H_2S$, minimum pH was 5, and dissolved ferrous iron concentrations were as high as 42 µM. At Tica, maximal temperatures were similar to Riftia Field (maximum 18°C), but the chemistry of the fluid was significantly different (maximal sulfide concentrations up to 176 µM $\sum H_2S$, neutral pH, ferrous iron was not detected) (Le Bris et al. 2006; Table 1). At the time of collection of mussels at Buckfield, maximum temperatures were approximately between 2 and 10°C (Van Dover, pers. obs.). No chemical measurements were conducted during sampling at Buckfield.

Quantitative tubeworm samples at Riftia Field and Tica were taken using DSV *Alvin* and a hydraulically actuated collection net named the "Bushmaster Jr." in December 2001 and December 2002 (sampling area up to 60 cm in diameter; for details see Govenar et al., 2005). The mussel samples at Buckfield were collected with the "mussel pot" sampling device (531 cm^2 collection area) with DSV *Alvin* in December 2001 (for details see Van Dover 2002). On board the ship, megafaunal aggregations were immediately disassembled and rinsed 3 times with 10 µm filtered seawater to wash off associated fauna and sediment. To extract the meiofaunal community, the samples were washed through a series of sieves (63 µm, 250 µm, 1 mm sieve size), fixed in 4% buffered formalin for 24 h, and stored in 70% ethanol. The nematode community was sorted and individuals were counted under a dissection microscope. If present, 300 nematodes per sample were haphazardly chosen and mounted in glycerin for identification to the lowest possible taxon level.

Due to the different sizes of the sampled areas (300 cm^2 to 1300 cm^2 for tubeworm aggregations and 531 cm^2 for mussel aggregations) and in order to compare these large sample areas with each other and to other meiofauna studies, we standardized the abundance to 10 cm^2 surface area. Individual biomass (µg wet weight) of nematode species was estimated according to Andrassy (1956) [wt (µg) = length (µm) x width^2 (µm) / 1600000; wt = µg wet weight, L = length (from anterior to posterior end) and W = maximum diameter of body]. All identified specimens were measured and the total biomass of the nematode community was estimated by the summation of the mean biomass of each measured species by the total abundance of each species in each sample.

The trophic status of the nematodes was determined by morphology and classified into primary consumers, parasitic and predatory secondary and tertiary consumers, following Wieser (1953).

To illustrate the degree of heterogeneity and dominance patterns, k-dominance curves were constructed for each sample by plotting the relative abundance of each species against the decreasing rank of dominant species. To describe the nematode community structure, species richness (S), Pielou's evenness index (J´), and Shannon-Wiener diversity index ($H'_{\log e}$) were calculated. The Students t-test was used to test significant differences in abundance (square-root transformed) and species richness (square-root transformed). Due to relative small number of samples, bootstrapping (1000 resamplings each, two-sided test; Nemeschkal 1999) was used to test for significant differences in abundance, species richness, and Shannon-Wiener diversity indices among the three sites (Nemeschkal 1999). Results from statistical analysis were Bonferroni-corrected ($p = \alpha/n$; $\alpha = 0.05$). Hierarchical clustering was used to compare communities of the three sites. The similarity matrix for cluster analysis was generated using Bray-Curtis similarity values calculated from square-root transformed, standardized abundance data. All univariate indices and multivariate measures were performed using the PRIMER v5 package (Plymouth Marine Laboratory; Clarke & Gorley 2001).

RESULTS AND DISCUSSION

At the East Pacific Rise striking spatial patterns of typical megafauna assemblages along a gradient of hydrothermal fluid flux are common (e.g. Shank et al. 1998). Hydrothermal vent sites of vigorous to moderate diffuse flow such as Tica, Riftia Field, and Buckfield are often densely populated by large aggregations of tubeworms and/or mussels. Assembled on bare basalt, the tubes or shells and byssal threads of these animals provide a highly structured three-dimensional habitat in which little sediment accumulates. Nematodes, one of the most divers and abundant meiofaunal taxa in virtually all marine benthic habitats, were found to be a consistent but small part of the associated epifaunal community. In this study, the diversity of nematodes was extremely low with very few species present in low abundance and biomass. The presence of these impoverished nematode communities at the northern East Pacific Rise stands in contrast to those of sedimented vent sites from other biogeographical regions, such as from the North Fiji Back-Arc Basin (Vanreusel et al. 1997). Multivariate analyses of community structure revealed that each site, differing in environmental characteristics, harbored its own distinct community. Furthermore, the similarity of both tubeworm sites was higher with univariate measures than the similarity of each tubeworm site to the mussel site.

Inferred from mouth structure analyses, the nematode communities associated with tubeworms and mussels were entirely comprised of deposit feeders; whereas in other habitats, nematode communities are dominated by primary consumers but consumers of higher trophic levels are usually present (see Giere 1993). No predators were collected in this study.

In eight out of nine samples, abundances ranged from only < 1 to 46 ind. 10 cm^{-2}, with biomasses ranging from 0.001 to 0.006 mg 10 cm^{-2} (Table 1). Although statistically not significantly different, one exceptional sample from Tica (946 ind. 10 cm^{-2}; 0.164 mg 10 cm^{-2}; Table 1) fell within the well-known range of nematode abundance from other shallow-water or deep-sea habitats and might point to a patchy distribution (see Giere 1993) at hydrothermal vents. The only species co-occurring at all sites was *Thalassomonhystera* sp. 1. It dominated relatively consistently between 84 and 94% to the total community at Tica and between 45 to 49% at Buckfield, while its contribution between 0 and 60% at Riftia Field was highly variable (Table 2).

As expected, univariate and multivariate measures of community structure point to distinctly different communities along an environmental gradient. Although inferred from a total of nine samples only and a few physicochemical data available for these sites, it appears that the nematode communities were affected by abiotic key factors such as temperature and sulfide concentrations, known to be critical for hydrothermal vent animals. Nevertheless, the dominant megafauna structuring the habitat might have a basic influence on its associated community, since the degree of similarity was higher between both tubeworm sites than between those and the mussel site. The tubeworm communities, at the time of sampling, were exposed to similar maximal temperatures near 20°C, in contrast to the mussel bed at Buckfield with maximum temperatures ranging from 10°C to slightly above ambient (~ 2°C) temperatures (Table 1). Also, the age of the communities, quite different between the three sample sites, might have an influence on the structure of the nematode communities. The mussel bed Buckfield is older (> 10 yrs; Dreyer et al. 2005) and exhibited a more divers macrobenthic community than Riftia Field (< 10 yrs; Van Dover 2000), while Tica is the youngest habitat (< 7 years; Van Dover 2000) with the lowest diversity. Univariate measures of community structure revealed clear differences between the tubeworm and mussel bed communities. A total of only three species from Riftia Field and four species from Tica were identified. The few species found, were unevenly distributed among samples and sites. Species richness and Shannon-Wiener diversity were low and not significantly different between Riftia Field and Tica (Table 3). In contrast, nine species were found at Buckfield, and species richness and Shannon-Wiener diversity were significantly higher than both of the tubeworm sites (Table 3). The same trends held true for Pielou's evenness. The more pronounced similarity among the both tubeworm dominated nematode communities as well as the distinct community associated with the mussel bed was also evident in the k-dominance curves (Fig. 1).

Multivariate analyses (SIMPER) revealed that the species dissimilarity between sites was > 50% between Tica and Buckfield, > 60% among Tica and Riftia Field and > 80% between Riftia Field and Buckfield (see also Fig. 2). These patterns were also supported by an analysis of similarity (ANOSIM; global R = 0.942, p = 0.4). The similarity between Tica tubeworm and the Buckfield mussel communities was due to the homogeneity among the samples with Bray-Curtis similarity values > 85% at Tica and > 80% at Buckfield (Fig. 2). The latter mussel bed community was characterized by six out of nine species that lacked at the other sites. In contrast, the Riftia Field community was rather heterogeneous. The similarity among the Riftia Field samples was < 70%, due to the variable relative abundance of *Thalassomonhystera* sp. 1 (60%, 10% and 0%) and that one sample was composed entirely of a representative of undescribed genus of Monhysteridae sp. 2 (Table 2). The picture emerging from the available data on hydrothermal vent nematode distribution and community structure available so far points to a small community composed of a few, mostly yet undescribed species belonging to generalistic genera well known from many shallow-water and deep-sea environments. Deep-sea hydrothermal vent communities appear to have no strong affinities to other communities from sulfidic environments such as the ‘thiobios’ of sulfidic sediments, shallow-water vents, or cold seeps, despite the presence of reducing chemicals and hypoxia (Vanreusel et al. 1997).

In general, nematode diversity (species richness, Shannon-Wiener diversity) as well as nematode abundance is low at deep-sea hydrothermal vents. At a finer scale however, the East Pacific Rise communities from 9° and 11°N in this study were even less abundant than those from 21°N (Dinet et al. 1988), the Guaymas Basin (Dinet et al. 1988), and the Iheya Ridge (Shirayama 1992), and less abundant and less diverse than those the North Fiji Back-Arc Basin (Vanreusel et al. 1997). The difference between the sites in this study and other hydrothermal vent sites maybe due to the substrate, but many other factors (e.g. the physico-chemical factors, the geographic locations) may contribute as well. Sediments through which hydrothermal fluid percolates or mussel aggregations accumulated above the sediments appear far more suitable for nematodes than mussel or tubeworm aggregations developing on bare basalt. While *in situ* experiments yet have to determine the exact location of nematode distribution within such aggregations either epibenthically on the tubes or shells and/or endobenthically within the little sediment accumulating between large animals, nematode communities are generally more diverse and more abundant in sediments than on hard substrate (Giere 1993).

ACKNOWLEDGEMENTS

This work would not have been possible without the captain and the crew of the R/V *Atlantis* as well as the pilots and technicians of DSV *Alvin* for their efforts in sample collections. Additionally we are grateful to C. R. Fisher for invitations to several cruises and his scientific input. We are most grateful to Ann Vanreusel (University of Ghent), given support on nematode ecology. This research was financially supported by grants of the Austrian Science Fund FWF (P16774-B03 to M. Bright), the National Science Foundation USA (OCE-0002729 to C. R. Fisher), Ifremer and the European Community (Ventox project EVK3-1999-00056P to N. Le Bris), the National Science Foundation (Biological Oceanography to C L. van Dover), and by the International Office Vienna and Promotion Grants of the University of Vienna (to J. Zekely and S. Gollner).

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Figure 1. Mean cumulative dominance of nematode species from the three sites (TC = Tica; RF = Riftia Field; BF = Buckfield); relative abundances of species were plotted against species rank (i.e. number of species) for each sample.

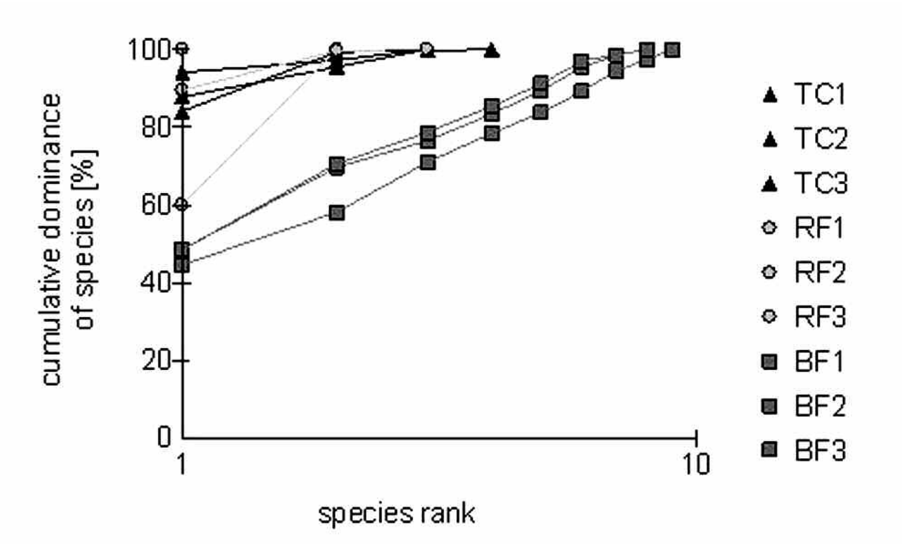

Figure 2. Hierarchical cluster diagram for group average linking based on Bray-Curtis similarities of nematode species from the nine samples (Tica samples: TC1, TC2, TC3; Riftia Field samples: RF1, RF2, RF3; Buckfield samples: BF1, BF2, BF3).

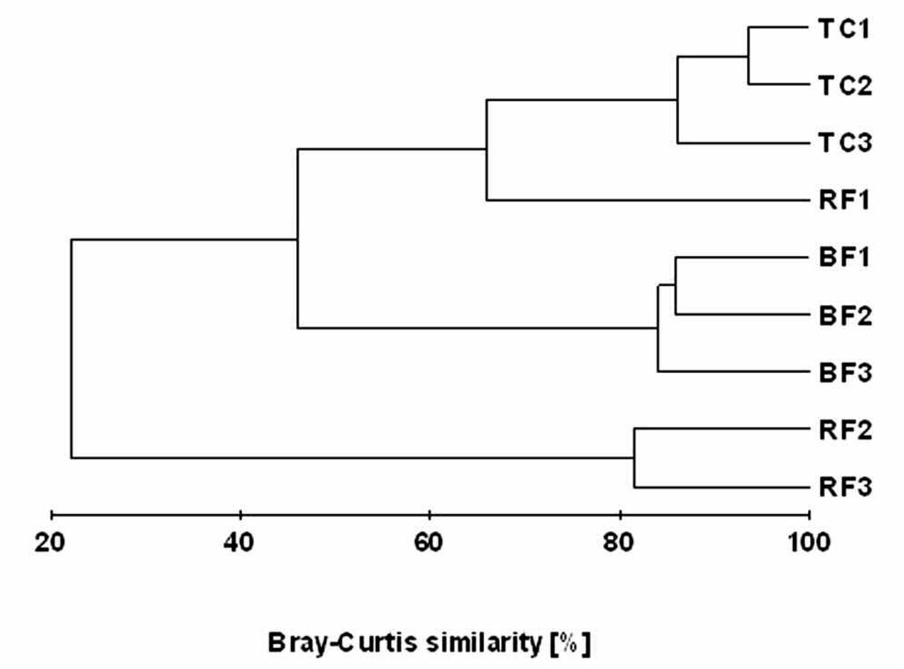

Table 1. Characteristics of collection sites (*measured in 2002; Le Bris et al. 2006) and nematode communities according to sites.

Site	Riftia Field	Tica	Buckfield
Maximum temperature [°C]	23*	18*	10
Maximum ·H_2S [µM]	35*	176*	N/A
Maximum ferrous iron [µM]	42*	0*	N/A
Minimum pH	4.4*	5.7*	N/A
Dominant megafauna	*R. pachyptila*	*R. pachyptila*	*B. thermophilus*
Total abundance	11 - 573	951 - 28369	51 - 66
Abundance 10 cm^{-2}	<1 - 7	16 - 946	1 - 2
Species richness	1 - 3	3 - 4	8 - 9
Shannon-Wiener diversity	0.4 - 0.7	0.3 – 0.5	1.5 – 1.7
Pielou’s evenness	0.3 - 0.9	0.2 - 0.4	0.7 - 0.8
Biomass [mg wet weight 10 cm^{-2}]	< 0.001 – 0.001	0.002 – 0.16	< 0.0001

Table 2. Relative abundance (%) of nematode species occurring at Tica (TC), Riftia Field (RF) and Buckfield (BF).

Site	**TC1**	**TC2**	**TC3**	**RF1**	**RF2**	**RF3**	**BF1**	**BF2**	**BF3**
Species from three sites									
Thalassomonhystera fisheri	8	94	84	60		10	48	45	49
Species from two sites									
Chromadorita sp. 1			< 1				7	5	1
Monhysteridae sp. 1	7	3	15				21	13	8
Monhysteridae sp. 2	5	3	< 1	40	100	90			
Species from one site									
Anticoma sp. 1							2	3	
Daptonema sp. 1						< 1			
Leptolaimus sp. 1							6	3	7
Megadesmolaimus sp. 1							6	5	6
Paracanthonchus sp. 1							3	5	6
Paralinhomoeus sp. 1								7	1
Theristus sp. 1							7	14	22

Table 3. Bootstrapping and Students t-test (two-sided, t_{4df} = 2.776, in parentheses) was used to test for differences in abundance (Ab, ind. 10 cm^{-2}) and species richness (S) between the three sites (TC = Tica; RF = Riftia Field; BF = Buckfield). Bootstrapping was used to test for differences in Shannon-Wiener diversity (H'_{loge}). Results are given prior Bonferroni corrections. * Significantly different (after Bonferroni corrections; $p < 0.05$).

	TC vs RF	TC vs BF	RF vs BF
Ab	0.026 (1.487)	0.026 (1.491)	0.744 (0.015)
S	0.058 (1.91)	0.003* (-10.035)	0.027* (6.849)
H'_{loge}	0.826	0.003 *	0.003 *

A new species of deep-sea Tegastidae (Crustacea: Copepoda: Harpacticoida) from 9°50´N on the East Pacific Rise, with remarks on its ecology

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ABSTRACT

Both male and female of the new deep-sea species *Smacigastes barti* sp. nov. (Tegastidae, Sars) are described in detail. Copepoda is one of the most diversified taxa at deep-sea hydrothermal vents, but only one species of the family Tegastidae has been described from this habitat and other deep-sea environments. *Smacigastes barti* is the second species of the genus *Smacigastes* Ivanenko & Defaye, 2004, and was found in artificial substrates deployed in the vicinity of and 0.5 m from tubeworm aggregations at the 9°50´N region on the East Pacific Rise at 2500 meters depth. The derived character states of the new species are the lack of coxal endite in the maxilla, and 2-segmented exopods of swimming legs 2 and 3, being the latter result of fusion of the 2 proximal segments. An identification key to all known genera of Tegastidae is provided. Interestingly the distribution of *S. barti* showed that it does not tolerate elevated temperatures and/or the presence of hydrogen sulfide or oxygen fluctuations, although both species of this genus were found in deep-sea chemosynthetic environments.

Keywords: copepoda, harpacticoida, Tegastidae, hydrothermal vent, deep-sea

INTRODUCTION

Deep-sea hydrothermal vents are globally widespread extreme environments located at the mid-ocean ridge systems. Driven by *in situ* primary production via chemosynthesis, a special vent fauna thrives under highly fluctuating conditions along a gradient of temperature and toxic chemicals such as hydrogen sulfide (Van Dover 2000). Copepoda is one of the most diversified taxa at hydrothermal vents contributing with about 80 described species, which represents more than 15% of the species documented from vents worldwide (Humes & Segonzac 1988, Tunnicliffe et al. 1998, Bright 2006). About 50 described vent copepod species belong to the order Siphonostomatoida, remarkably to the presumably vent-endemic family Dirivultidae Humes & Dojiri. Only 12 species of harpacticoid copepods have been described from vents so far, but this group has been less studied and it is thought that the diversity of this group might be higher (Heptner & Ivanenko 2002, Ivanenko & Defaye 2006).

Copepods of the family Tegastidae (Crustacea, Copepoda, Harpacticoida) are characterized by a laterally compressed amphipod-like body, by a modified male genital complex, and by a claw-like mandible in the nauplii (Lang 1948, Ivanenko et al. 2008). Currently 59 species belonging to 6 genera have been described. Except for the deep-sea species *Smacigastes micheli* (Ivanenko & Defaye 2004), all tegastid species have been found in shallow water habitats in association with algae, bryozoans and/or cnidarians (Chislenko 1967, Medioni & Soyer 1968, Chislenko 1977, Humes 1981a, 1981b, 1984, Ferrari et al. 2007). In a previous paper, *S. micheli* was reported from artificial substrates as a part of a colonization experiment deployed at the active chimney „Eiffel Tower" on the Mid Atlantic Ridge (Ivanenko & Defaye 2004). Here, we describe a new species of the genus *Smacigastes* from deep-sea hydrothermal vents on the East Pacific Rise and provide remarks on its ecology.

MATERIALS AND METHODS

Copepods were collected during cruises AT7-26 and AT11-03 on board of the RV *Atlantis* to the Northern East Pacific Rise in November 2002 and 2003. Specimens were found associated with artificial substrates that were used to imitate the natural *Riftia pachyptila* Jones tubeworm aggregations. Each artificial aggregation consisted of 80 PVC (polyvinyl chloride) tubes of four different size classes. Four of these artificial aggregations were deployed within assemblages of *R. pachyptila*, ~50 cm from *R. pachyptila*, and ~20 m from the natural aggregations at the site Tica (9°50.447´N, 104°17.493´W) at 2500 meters depth. After collection, copepods were fixed in 4% formalin for 24 hours, and transferred to 70% ethanol for shipment and storage (for details see Govenar & Fisher 2007).

For light microscopy, specimens were dissected in glycerin under a Leica MZ8 microscope. Copepods and/or parts of copepods were mounted on slides using glycerin

(Higgins & Thiel 1988). Specimens were examined, and drawings were made with bright-field or differential interference contrast, using a Leica DMR compound microscope.

For scanning electron microscopy (SEM), copepods were dehydrated through a series of graded ethanol, acetone and HMDS (hexamethyldisilazane) concentrations, mounted on aluminium stubs, and sputtered with gold (Nation 1983). Specimens were observed using a Philips XL 20 scanning electron microscope.

The description is mainly based on the female holotype and the male paratype 1, which were drawn using light microscopy. Additional SEM pictures from paratypes were used to show more details. For long-term preservation the holotype and paratypes are all mounted on slides in glycerin. The type material is deposited in the Forschungsinstitut and Naturmuseum Senckenberg, Frankfurt am Main, Germany (Holotype, Paratypes 1-8), and in the Oberösterreichische Landesmuseen, Biologiezentrum Linz, Austria (Paratypes 9-13).

DESCRIPTIVE PART

Order HARPACTICOIDA Sars
Family Tegastidae Sars
Genus *Smacigastes* Ivanenko & Defaye

Type species
Smacigastes barti sp. nov.

Type material
Holotype dissected f#, 19 slides (nr. SMF 31411)
Paratype 1: dissected m#, 13 slides (nr. SMF 31412)
Paratype 2: f# (nr. SMF 31413)
Paratype 3: m# (nr. SMF 31414)
Paratype 4: f# (nr. SMF 31415)
Paratype 5: m# (nr. SMF 31416)
Paratype 6: f# (nr. SMF 31417)
Paratype 7: m# (nr. SMF 31418)
Paratype 8: dissected copepodite stage V, 3 slides (nr. SMF 31419)
Paratype 9: f# (nr. OLML 2007/199)
Paratype 10: m# (nr. OLML 2007/200)
Paratype 11:f# (nr. OLML 2007/201)
Paratype 12: m# (nr. OLML 2007/202)
Paratype 13: copepodite stage V (nr. OLML 2007/203)

Type locality

East Pacific Rise (EPR); 9°50.447´N, 104°17.493´W; 2500 m depth. The site Tica is located on the EPR between the Clipperton and Sequeiros transform faults. The site was colonized by the giant tubeworm *Riftia pachyptila* in 1997 (Fornari et al. 2004). Type material was collected from artificial substrates (PVC hoses) deployed in 2002, and recovered one year later (see Govenar & Fisher 2007).

Etymology

The species is named in honor of Breea Govenar who designed the artificial devices from which specimens were collected (BART: Breea´s Artificial Riftia Tubes).

Female

Body (Fig.1a, 1b, 2a) laterally compressed, weakly chitinized, with short sensilla and few pores. Total length of female holotype (rostrum to posterior margin of telson) 420 µm, greatest width 180 µm. Rostrum rounded and prominent (Fig. 1a). Prosome 4-segmented (cephalothorax and 3 somites bearing legs 2 to 4) (Fig. 2a). Urosome (Fig. 2b) 5-segmented: first urosomite with leg 5, genital-double somite with ventral depression and one gonoporus covered by flap of the minute leg 6 (Fig. 1c, 5b, 5c), and 2 postgenital somites plus telson with furca. Furca 3 times as long as wide, with 7 setae of different length (Fig. 2c).

Antennule (Fig. 2d) 7-segmented; formula of setation: 1, 10, 9, 3+aesthetasc, 6, 4, 6+aesthetasc.

Antenna (Fig. 2e) with small coxa and elongate basis with 1 seta and a field of cuticular spinules. Exopod 2-segmented, proximal segment with 1 inner setae, distal segment with 3 apical setae; endopod 2-segmented, proximal segment with 1 median seta, distal segment with 4 inner setae, 6 terminal setae and a hyaline frill subdistally at outer margin.

Labrum (Fig. 2a) projecting over shield of cephalothorax in lateral view.

Mandible (Fig. 3a) with gnathobase (not shown); palp 2-segmented, with 2 distal setae on basis and 1-segmented endopod bearing 1 outer and 3 terminal setae.

Maxillule (Fig. 3b, c) with praecoxal arthrite bearing 8 spines; coxal endite with 1 seta; exopod with 2 setae; basis elongate with 1 median and 4 terminal setae.

Maxilla (Fig. 3d). Syncoxa with two endites, proximal endite with 1, distal endite with 3 spines. Allobasis with 3 lateral setae, two subdistal and one apical spine.

Maxilliped (Fig. 3e, f) 3-segmented, subchelate; syncoxa elongated with 1 distal seta; basis with 2 rows of spinules; endopod 1-segmented, produced into a strong claw, with 2 proximal setae and an inner row of short spinules.

Swimming legs 1-4 biramous; armature formula as in Table 1.

Leg 1 (Fig. 4a) with 1-segmented rami.

Leg 2 and leg 3 (Fig. 4b, 4c) with 3-segmented endopods and 2-segmented exopods; proximal segments of exopods elongated, derived by fusion of former proximal and middle segment.

Leg 4 (Fig. 4d) with 3-segmented rami. Distal exopod segment with a slightly modified inner seta into a spine (Fig. 5a).

Leg 5 (Fig. 5b) with baseoendopod and exopod; baseoendopod with 1 basal outer seta, 3 inner setae, 1 terminal spine, and 1 small terminal outer seta; exopod with 3 outer elements (proximal seta-like; middle and distal ones spine-like), and 2 terminal spines.

Leg 6 a small flap with 1 minute seta (Fig. 5c).

Single egg sac with three eggs, located ventrally between fifth legs (Fig. 1b, 1c, 2a).

Male differs from female in the following:

Length of paratype 1 (Fig. 1d, 6a), 325 µm; greatest width, 150 µm. Genital-double somite (Fig. 1e, 5e) produced ventrally into a large, elongated prominence bearing distally asymmetrical genital flap representing leg 6.

Antennule (Fig. 6b) 10-segmented; setation formula as follows: 1, 10, 6+a, 1, 7+aesthetasc, 1, 2, 1, 4, 7+aesthetasc.

Leg 5 (Fig. 5d) 2-segmented; basis with 1 outer seta, exopod with 1 outer proximal seta, 1 outer subdistal spine, and 2 terminal spines.

Leg 6 (Fig. 1e, 5e) a membranous genital flap on the left side.

One spermatophore stored inside the genital double-somite (Fig. 5e).

Copepodite stage V

Leg 2 (Fig. 6c) and Leg 3 (Fig. 6d) consist of 3-segmented exopods (in contrast to adult) and 2-segmented endopods (shortly before division into the adult 3-segmented endopod).

TAXONOMICAL REMARKS

Smacigastes barti sp. nov. belongs to the family Tegastidae. This family is characterized by a laterally compressed, amphipod-like, strongly chitinized and sculptured body (Lang 1948, Huys et al. 1996). Six genera belong to the family Tegastidae, namely *Tegastes* Norman, *Smacigastes* Ivanenko & Defaye, *Parategastes* Sars, *Syngastes* Monard, *Feregastes* Fiers, and *Arawella* Cottarelli & Baldari. *Smacigastes* apomorph characters are its elongate furca and its weakly chitinized body. The other genera can be distinguished by the segmentation of legs 2-4. The key to genera of Tegastidae presented by Huys et al. (1996: 290) and Boxshall and Halsey (2004: 392) turned out to contain typographic inconsistencies. Here, we propose a new identification key that also includes the recently described genus *Smacigastes* (Table 2).

The new species belongs to the genus *Smacigastes* and shares with *S. micheli* the following distinguishing characters: a 10-segmented male antennule, presence of female leg 6, and a furca being 3 times as long as wide. Further, both species share a weakly chitinized body, distinguishing them from other tegastids having, according to the family diagnosis, strongly chitinized bodies (Lang 1948, Huys et al. 1996). *Smacigastes micheli* shows 3-segmented exopods of leg 2 and 3. The presumed derived features of *S. barti* are the fusion of proximal exopodal segments 1 and 2 in legs 2 and 3, and the loss of coxal endite of the maxilla.

Interestingly females of *Smacigastes barti* and *Arawella alexandri* Cottarelli & Baldari possess a slender P5, which contrast to all other species of Tegastidae. The females of the other tegastid species have either a swollen baseoendopod and normal exopod (some species of *Tegastes*, *Smacigastes micheli*, *Ferregastes wellensi* Fiers, *Parategastes caprinus* Wellerhaus, *P. haphe* Leigh-Sharpe, *P. sphaericus* Claus), a swollen endopod and exopod (some *Tegastes*, *Parategastes coetzeei* Kunz, *P. conexus* Humes, *P. herteli* Jakob), a swollen baseoendopod and a reduced exopod (*Tegastes georgei* Marcus & Masry, *T. chalmersi* Thompson & Scott, *Syngastes* spp.), or a single swollen rami (*Syngastes* spp. Monard). Most modified female baseoendopods are found in the genera *Syngastes* and *Parategastes* with leaf-shaped leg 5. Interestingly, instead of having a broad leg 5, *A. alexandri* developed a special genital somite, produced ventrally into an eaves-shaped structure, and *S. barti* shows a ventral depression of the genital-double somite. We think that the shape of female P5 is important as this is the structure holding and protecting the eggs of tegastids, ensuring the survival of species. However, the development of female P5 has never been discussed or included as a character in tegastid taxonomy. A slender P5 is a plesiomorphic character and consequently, *Smacigastes* might be a relatively ancient tegastid genus, as already proposed by Ivanenko & Defaye (2004b).

The segmentation of leg 1 to leg 4, the character used to distinguish between shallow water tegastids, of *Smacigastes barti* is similar to the genus *Parategastes.* Beside the apomorph characters of *Smacigastes*, the new species also differs from *Parategastes* in the number of segments of the female and male antennule (7-segmented and 10-segmented antennule in the female and male of *S. barti*, but 6-segmented and 7-segmented antennule in the female and male of *Parategastes*), number of segments of the antennal exopod (2-segmented in *S. barti,* but 1-segmented in *Parategastes*), shape of female leg 5 (slender in *S. barti*, but endopod transformed into a broadened flap in *Parategastes*), length of furca (long in *S. barti*, but shorter than wide in *Parategastes*) (Lang 1948, Jakob 1953, Wellerhaus

1970, Kunz 1980, Humes 1984, Huys et al. 1996). The 2-segmented exopods of leg 2 and leg 3 and the elongated proximal segments result from the fusion of the proximal and middle segments. The setation-formula II-2 of the first elongated exopodal segment of leg 2 and 3 indicates a fusion process. Huys & Boxshall 1991 proposed a setal formula of I-1 and I-1 for the proximal and middle exopodal segments of leg 2 and 3 for the harpacticoid ancestor. The fusion process could be proved by studying copepodites of stage V of *Smacigastes barti* having 3-segmented exopods of P2 and P3 (see Fig. 6c, 6d).

Shallow-water tegastid genera can be separated by the segmentation of legs 2-4. *Tegastes* has 3-segmented endo- and exopods of leg 2, 3 and 4. The proximal and middle exopodal segment of leg 2 and 3 are fused in *Arawella, Smacigastes, Parategastes,* and *Syngastes*. Further, *Syngastes* shows a proximal fusion of segments 1 and 2 on the exopod of leg 4. Probable plesiomorphic characters of *Smacigastes micheli* are the 3-segmented endopods and exopods of leg 2, 3 and 4 (Ivanenko & Defaye 2004). Fused proximal and middle exopodal segments of legs 2 and leg 3 were found by us in *Smacigastes barti* and 2 other undescribed deep-sea tegastid species also belonging to the genus *Smacigastes*. One species was found in samples taken from Gulf of Mexico cold seeps and can be distinguished from *S. micheli* only by shorter spines on the female leg 5 baseoendopod and by its body length (one third shorter). A suture between the first two exopodal segments of leg 2 and leg 3 were observed only from the posterior dorsal view (not from the anterior view) in this cold-seep species. Such suture was not observed in *S. barti*, but a fissure between those segments was observed instead. The other undescribed deep-sea species, found in wood-falls from Gorda Ridge, shows a complete fusion of the proximal exopod segments. These findings might show a general trend in Tegastidae, having fusion-processes of exo- and endopodal segments. Whether the fusion processes point to a parallel evolution of shallow-water and deep-sea tegastids, or to characters already developed before the colonization of the deep-sea remains to be discussed.

ECOLOGICAL COMMENTS

Thus far copepods of the family Tegastidae from deep-sea hydrothermal vents have mostly been observed in association with artificial and hard substrates. *Smacigastes barti*, together with a variety of other copepods, nematodes, ostracods and foraminiferans, were found between PVC hoses used to imitate the tubeworm *Riftia pachyptila* (Govenar et al. 2007, pers. obs. SG). Short-term (~ 10 days) and long-term (~ 1 year) deployments were both colonized by *S. barti*, indicating that the species is able to quickly colonize newly formed habitats. Only a few specimens of *S. barti* were found up to now on natural basalt (pers. obs. SG). *Smacigastes micheli* as well as many other copepods were captured in a specially designed array consisting of 4 trays with an artificial substrate of small glass beads, protected from large carnivorous animals by a mesh. It was positioned between *Bathymodiolus azoricus* mytilids at temperatures ranging from 5-13°C at the site Lucky Strike on the Mid Atlantic Ridge for ~1 year (Ivanenko & Defaye 2004a, 2004b). The yet undescribed tegastid species of the genus *Smacigastes* from the Gorda Ridge was found to be associated with artificially positioned wood. Only copepods of another new and yet undescribed tegastid species of the same genus were among natural tubeworm aggregations in the Gulf of Mexico cold seeps. The reasons for the attractiveness of artificial substrates are difficult to decipher. Artificial substrates are a system in an early succession stage as they represent a newly opened habitat without former colonizers (Connel & Slayter 1977). It might be that both species, *S. barti* and *S. micheli,* are fugative species, typical for early succession stages, being able to colonize newly opened habitats that are free of competition.

Smacigastes barti was found associated with artificial substrates deployed at the tubeworm-dominated site Tica on the EPR 9°50´N at 2500 meters depth, but was never found within the natural tubeworm aggregations at the same site (see Gollner et al. 2007). The natural habitat was colonized by *Riftia pachyptila* and was characterized by moderate hydrothermal vent flux with maximum temperatures of 18°C, maximum sulphide concentrations of 176 µM $\sum H_2S$, and minimum measured pH close to neutrality (Le Bris et al. 2006). Four artificial aggregations each were deployed in an high flow zone within *Riftia pachyptila* specimens, in a low flow zone with less influence of toxic hydrothermal fluid flux ~50 cm away from *R. pachyptila*, and ~20 m away from the natural aggregations with no influence of hydrothermal fluid flux and constant deep-sea water temperature of approximately 2°C (Govenar & Fisher 2007). The natural *Riftia pachyptila* community at the site Tica was colonized mostly by dirivultid copepods and only some harpacticoid copepods, but not a single tegastid was found (for details see Gollner et al. 2006). Interestingly, the artificial aggregations were successfully colonized by the new tegastid species and from a total of 30 identified *S. barti* specimens, 14 females, 11 males and 4 copepodites were observed. There was no difference in the relative abundance percentage of tegastids in short-term and long-term deployments. 2.2 – 2.8% of all identified copepods were *S. barti* in the far away zone, and 0 – 2.6% were found 50 cm away, respectively. Not a single specimen was found within the artificial tubes in the high flow zone, except for one artificial aggregation that was originally positioned within *R. pachyptila* but fell out after some time into the low flow zone and is therefore counted to the low flow zone. This indicates that *S. barti* lacks the capability to tolerate varying temperatures, and sulfide concentrations of vent flux.

The amphipod-like body of shallow-water tegastids has been interpreted as an adaptation to their co-existence with algae, bryozoans or cnidarians (Huys & Boxshall 1991, Ivanenko & Defaye 2004). Tegastids have never been detected in deep-sea samples from deep-sea abyssal plains (pers. obs. PMA). Their body-shape might not be suitable to live in mesopsammal habitats, whose members are usually characterized by worm-shaped bodies allowing them to crawl easily between sand grains (Giere 1993). All of the presently discovered members belonging to the deep-sea tegastids were found close to or in association with hard-substrate chemosynthetic environments. Both *Smacigastes barti* and *S. micheli* were sampled at deep-sea hydrothermal vents. Two other yet undescribed deep-sea tegastid species were found at Gulf of Mexico seeps and at wood falls from Gorda Ridge, respectively. These findings point to a preference of deep-sea tegastids for hard-substrate nutrient-rich environments.

ACKNOWLEGEMENTS

This work was supported by the Training AWards for New Investigators (TAWNI) given by ChEss to SG, and the Austrian Science Foundation grant FWF (P16774-B03 given to Monika Bright). The research of VNI was supported by the Census of Diversity of Abyssal Marine Life (CeDAMar) and the Russian Foundation for Basic Research (Grant 06-04-48918-a). We are grateful to the captains and crews of the R/V *Atlantis*, to the pilots and crews of the DSV *Alvin* for their expertise in sample collections, and to Breea Govenar and Charles R. Fisher for providing the material. We would like to thank Julia Zekely for help in sorting out copepods, and Monika Bright, Bas van de Schootbrugge and two anonymous reviewers for carefully reading the manuscript and their scientific input. Gisela Moura is gratefully acknowledged for refreshing discussions on tegastid systematics.

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Figure 1. *Smacigastes barti* sp. nov. SEM photos: f# paratype: A, habitus, ventral (rostrum indicated by arrow); B, habitus, lateral; C, genital-double somite with leg 6 (see arrow); m# paratype: D, habitus, lateral; E, spermatophore reservoir with opened gonopore and leg 6 (see arrow). Scale bars A, B, D 100 µm; C, E 20 µm.

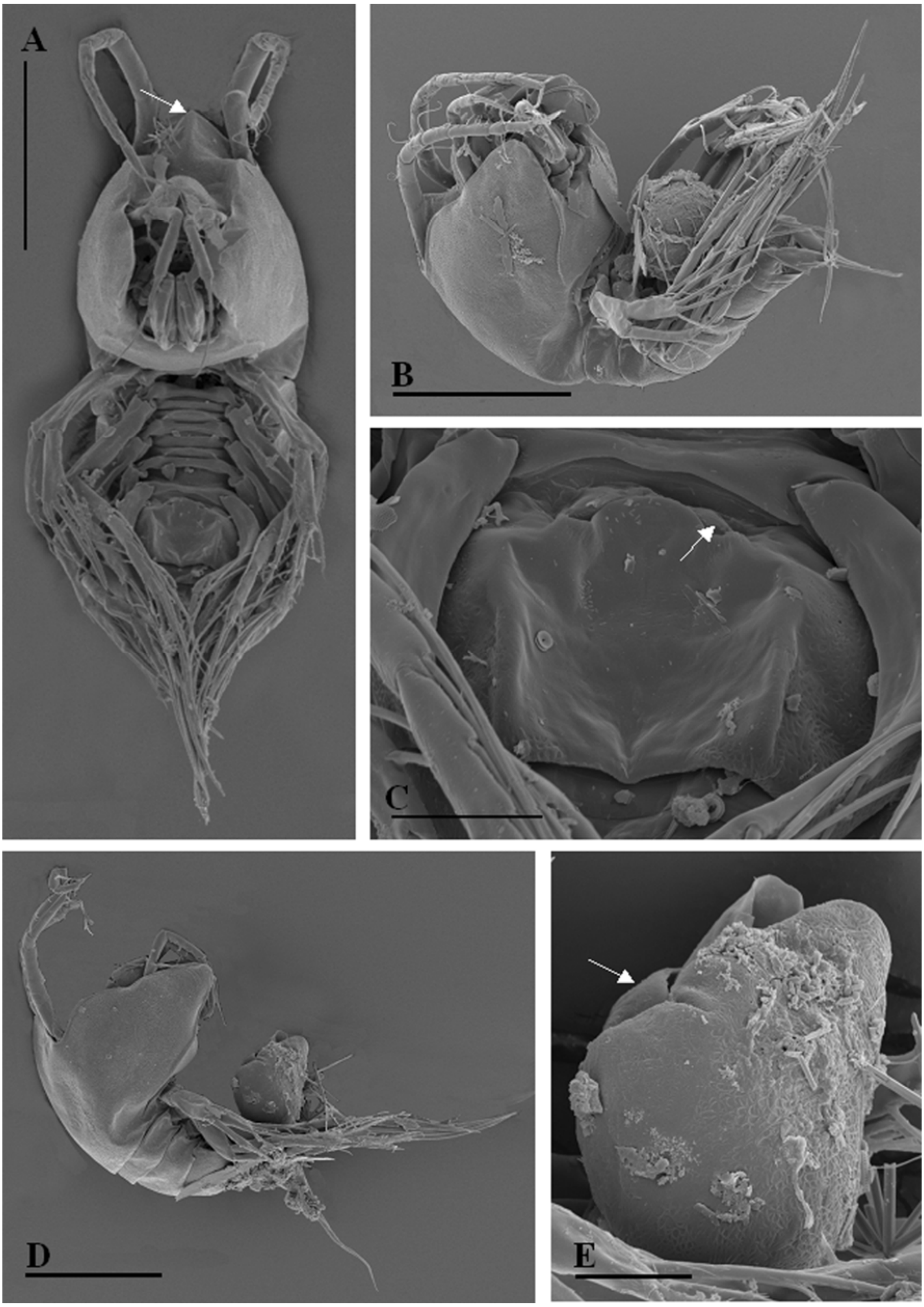

Figure 2. *Smacigastes barti* sp. nov. f# holotype LM drawings: A, habitus, lateral (labrum indicated by arrow); B, urosome, ventral; C, furca, ventral; D, antennule (a seta on 2nd segment broke and is indicated by a circle); E, antenna (frill indicated by arrow). Scale bars A 100 µm; B-E 50 µm.

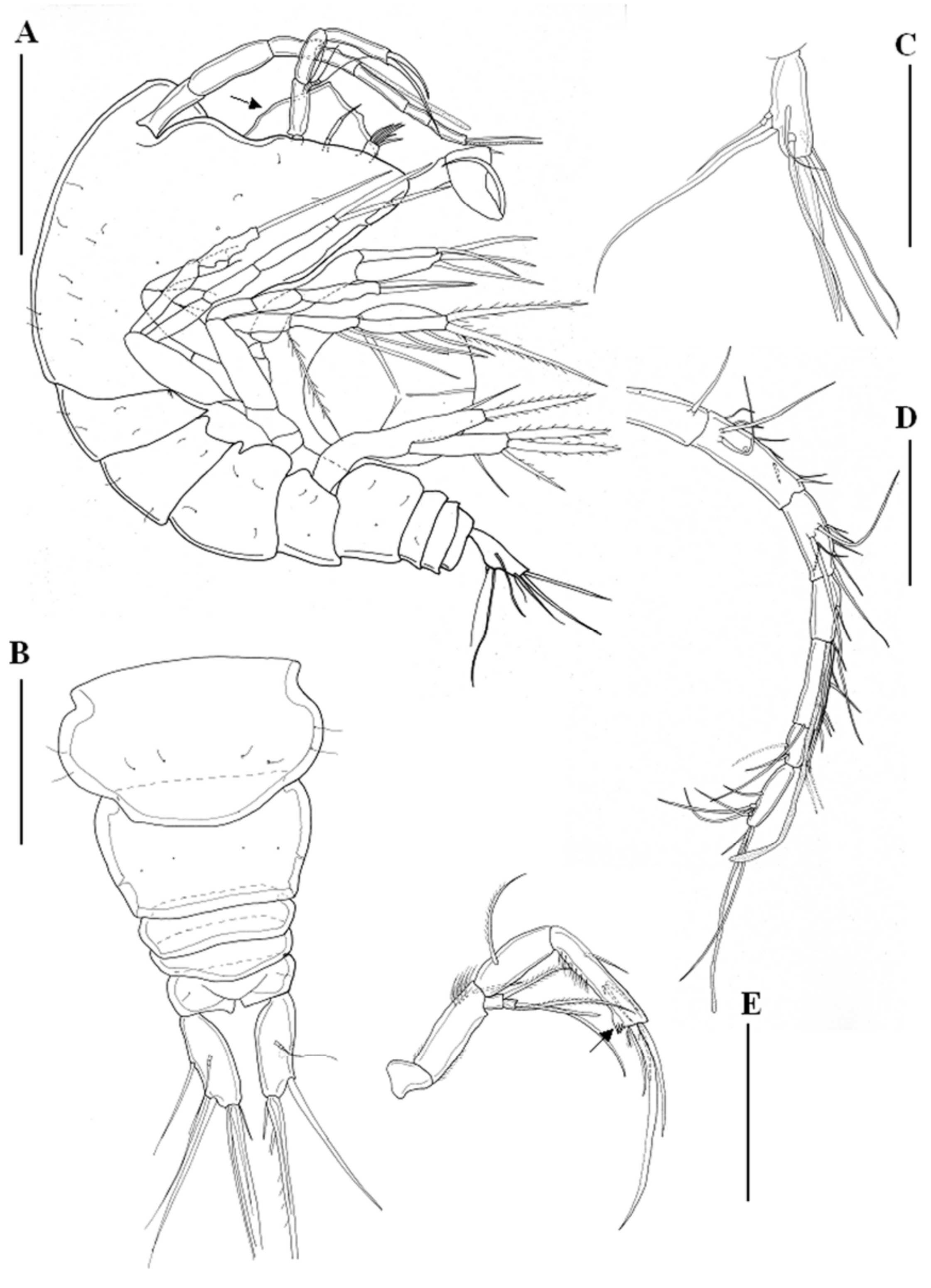

Figure 3. *Smacigastes barti* sp. nov. f# holotype LM drawings: A, mandible; B, maxillule; C, maxillule (different view, from m# paratype 1); D, maxilla; E, maxilliped, posterior; F, maxilliped, anterior. Scale bars A-D 10 µm; E, F 50 µm.

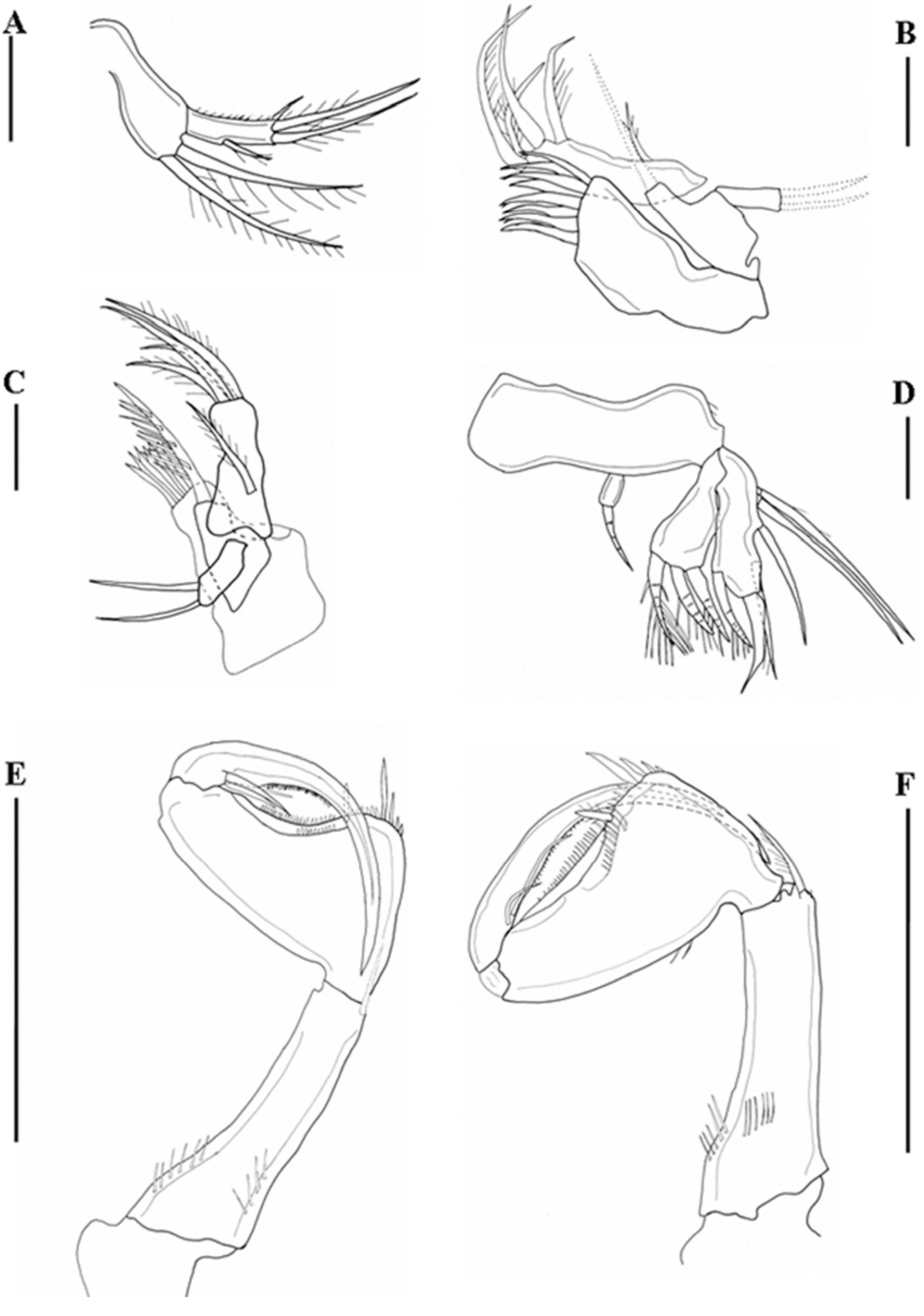

Figure 4. *Smacigastes barti* sp. nov. f# holotype LM drawings: A, leg 1; B, leg 2; C, leg 3; D, leg 4. Scale bars A-D 50 µm.

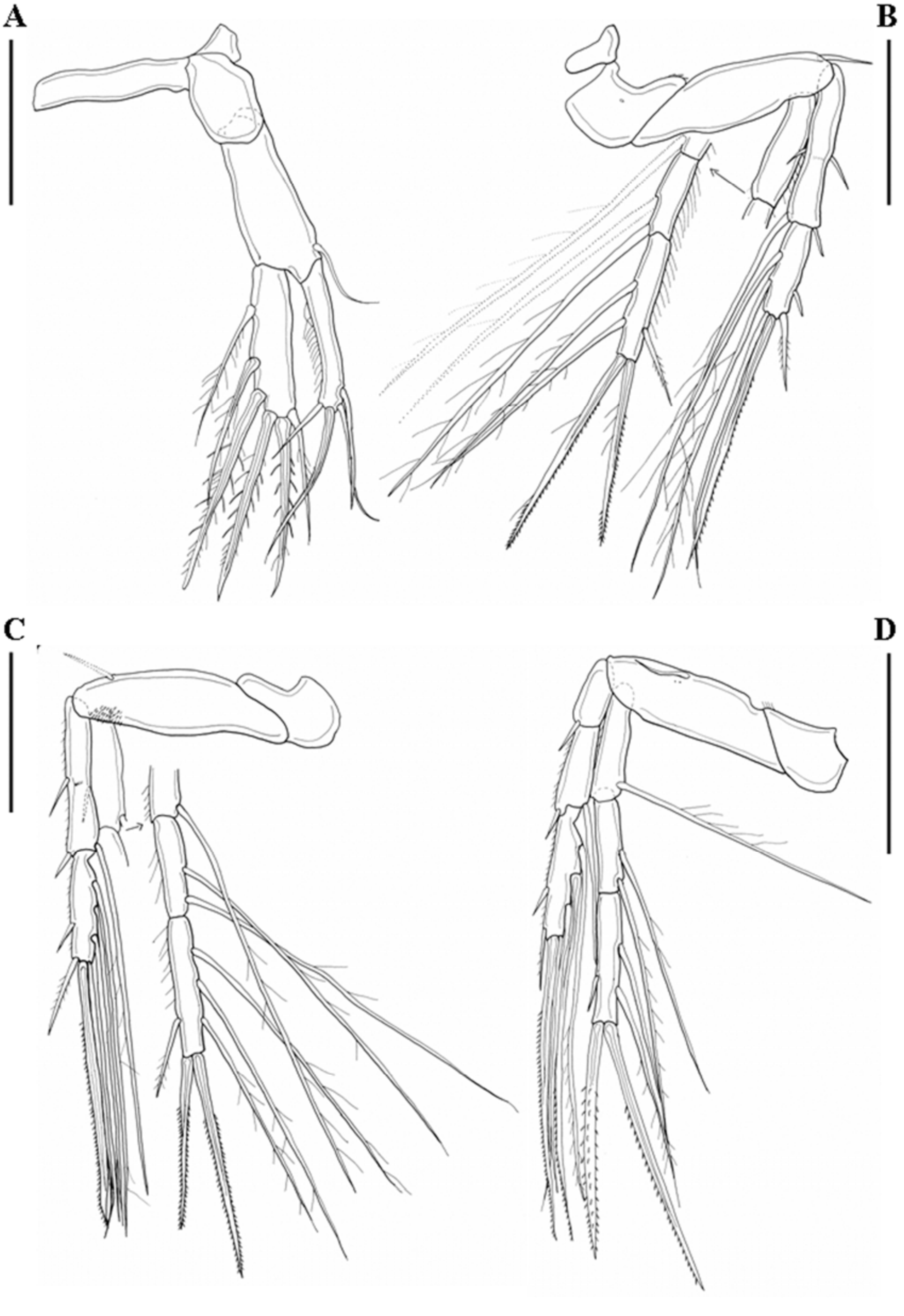

Figure 5. *Smacigastes barti* sp. nov. f# holotype: A, distal endopod segment of leg 4; B, leg 5; C, leg 6 (f# paratype 2); m# paratype 1 LM drawings: D, leg 5; E, leg 6 (see arrow; m# paratype 3). Scale bars A, C-E 50 μm; B 100 μm.

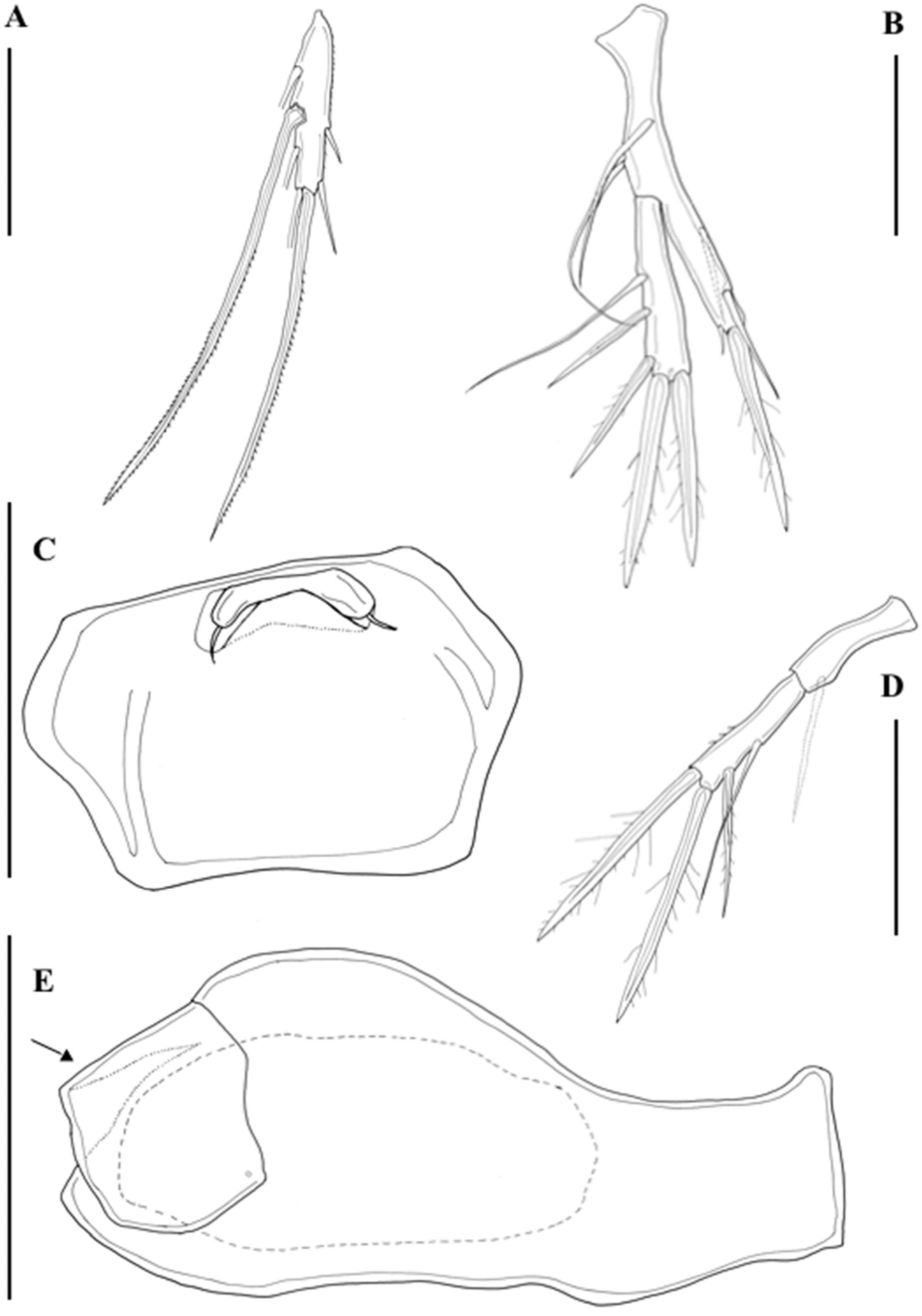

Figure 6. *Smacigastes barti* sp. nov m# paratype 1 LM drawing: A, habitus, lateral; B, antenulle; paratype 8 copepodite stage V LM drawings: C, leg 2; D, leg 3. Sclae bares A-D 50 µm.

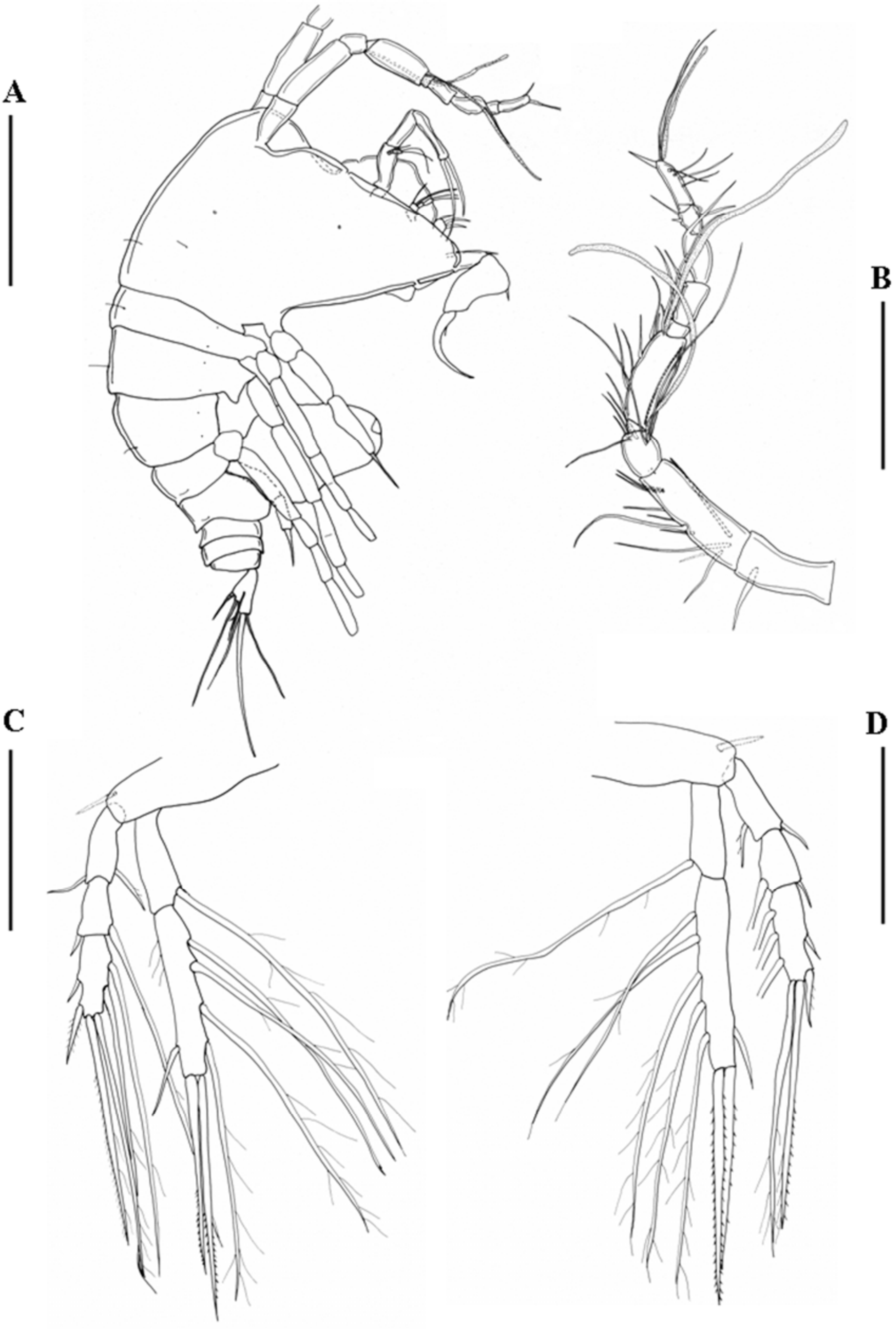

Table 1. Spine and setal formula of legs 1-4 of *Smacigastes barti* sp. nov.

Legs	**Coxa**	**Basis**	**Exopod**	**Endopod**
Leg 1	0-0	1-0	2, I, 1	1, II, II1
Leg 2	0-0	1-0	II-2; II, I, 3	0-1; 0-2; I, II, 2
Leg 3	0-0	1-0	II-2; II, I, 4	0-1: 0-2; 1, II, 3
Leg 4	0-0	1-0	I-0; I-1; II, I1, 1I1	0-1; 0-2; I, II, 2

Table 2. Key to genera of Tegastidae. In parenthesis number of described species of the genus.

1 Caudal rami 3-times longer than wide............................ *Smacigastes* (2)
- Caudal rami short 2

2 P2-P3 endopods 2-segmented…………………………… *Arawella* (1)
-P2-P3 endopods 3-segmented…………………………….. 3

3 P2-P3 exopods 2-segmented... 4
- P2-P3 exopods 3-segmented…………………………….. 5

4 P4 endopods 2-segmented……………………………… *Syngastes* (23)
- P4 endopods 3-segmented……………………………….. *Parategastes* (6)

5 P4 endopods 2-segmented……………………………… *Feregastes* (1)
- P4 endopods 3-segmented……………………………….. *Tegastes* (37)

Epizooic metazoan meiobenthos associated with tubeworm and mussel aggregations from cold seeps of the Northern Gulf of Mexico

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ABSTRACT

The abundance and higher taxonomic composition of the epizooic metazoan meiobenthic communities associated with mussel and tubeworm aggregations of hydrocarbon seeps at Green Canyon, Atwater Valley, and Alaminos Canyon in depths between 1400 and 2800 meters were studied and compared to the infaunal community of non-seep sediments nearby. Epizooic meiofaunal abundances of associated meiobenthos living in tubeworm bushes and mussel beds at seeps were extremely low (usually <100 ind. 10 cm^{-2}), similar to epizooic meiofauna at deep-sea hydrothermal vents, and the communities were composed primarily of nematodes, copepods, ostracods, and halacarids. In contrast, epizooic meiobenthic abundance is lower than it has been reported in previous studies for infauna from seep sediments. Interestingly, non-seep sediments contained higher abundances and higher taxonomic diversity, than epizooic seep communities.

Keywords: Gulf of Mexico, meiobenthos, meiofauna, copepods, nematodes, cold seeps, abundance, vestimentifera, *Bathymodiolus*

IINTRODUCTION

The size class of meiofauna is defined as the portion of the community passing through a 1 mm sieve and being retained on a 32 µm sieve. This community comprises protists and metazoan animals that remain small even when adult (permanent meiofauna), and animals which temporarily belong to this size class during their larval/juvenile development (temporary meiofauna). As a part of the sediment infauna, meiobenthos has been studied extensively worldwide from many different habitats, but less attention has been paid to the hard substrate epibenthic or epizooic, and epiphytal meiobenthos (Giere 2009).

At cold seeps, a variety of geologically diverse, reducing habitats can be distinguished by the presence of microbial mats or macro/megafaunal communities (see Sibuet & Olu 1998, Levin 2005). While some animals such as e.g. thyrasid bivalves or frenulate and *Sclerolinum* siboglinids inhabit the sediment and only the anterior part of their tube extends above the sediment surface, vestimentiferan tubeworms, bathymodioline and vesicomyid bivalves, or sponges can build large physical structures above the sediment surface and create habitat as foundation species for an associated macro- and meiofaunal community. In general foundation species influence the abundance, composition and structure of the associated community (Hacker & Gaines 1997) and can provide food resources, living space, favorable settlement conditions, refuge from predators and/or refuge from environmental stress (see Bruno & Bertness 2001).

Meiobenthic community studies at cold seeps are scarce and mainly restricted to assessments of abundance, biomass, and composition of higher taxa. They cover a wide geographical and depth range from shallow-water sands between 10 to 20 m down to deep-sea muds at 5000 m. They comprise various types of hydrocarbon gas and oil seep (Montana & Spiess 1985, Palmer et al. 1988, Shirayama & Ohta 1990, Olu et al. 1997, Sommer et al. 2002, Robinson et al. 2004, Soltwedel et al. 2005, Van Gaever et al. 2006, Sergeeva & Gulin 2007), gas hydrates (Sommer et al. 2002), and brine seeps (Powell et al. 1983, 1986), but are exclusively describing the infaunal meiobenthos from sediments covered by bacterial mats or by vesicomyid clams or were taken from sediments inhabited by frenulates and *Sclerolinum* (called pogonophorans) or in the periphery of mussel beds. Further, some sediments with discharge of methane but devoid of any visible microbial mat or animals were also studied.

The Gulf of Mexico was the site of the first discoveries of cold seeps in the 1980s (Paull et al. 1984, Kennicutt et al. 1985), and several ecological community studies have been carried out since then. Most studies have been completed at seeps located shallower than 1000 meters, but more recently some included also deeper sites (see Cordes et al. 2007, Roberts et al. 2007). Tubeworm bushes, mainly composed of mixed populations of *Lamellibrachia lymesi* and *Seepiophila jonesi* were studied from the upper Louisiana slope

(Berquist et al. 2003, Cordes et al. 2005). The tube surface area taken as a measure of habitat size increased the overall surface between 2.6 to 26 fold over the uncolonized seafloor (Berquist et al. 2003). In deeper waters of the lower slope, vestimentiferan aggregations are primarily composed of *Escarpia laminata* (Brooks et al. 1990, Cordes et al. 2007). There are a number of foundation species of mussels on the lower slope, and beds may consist of single species such as *Bathymodiolus brooksi* (at Atwater Valley) and *B. childressi* (Mississippi Canyon), or mixed populations of *B. brooksi* and *B. childressi* (Alaminos Canyon) or *B. brooksi* and *B. heckerae* (Florida Escarpment) (Cordes et al. 2007).

The macrofauna associated with the upper slope communities are fairly well known (Berquist et al. 2003, 2005, Cordes et al. 2005, 2006), and the deeper communities are becoming more well characterized (Turnipseed et al. 2003, Cordes et al. 2007, Cordes et al., this issue). Seep meiofauna studies at the Gulf of Mexico were conducted for the shallow brine seep sand communities at East Flower Garden (Powell et al. 1983, 1986, Jensen 1986) and the hydrocarbon seep bacterial mat communities at Alaminos Canyon (2200m), Green Canyon (about 700 m), and Atwater Valley (about 2000 m) (Robinson et al. 2004). The epifaunal foraminiferan communities associated with tubeworm bushes on the upper slope was also studied in detail (Sen Gupta et al. 2007), but no study on the associated metazoan meiobenthos has been carried out so far.

This study examines the abundance and higher taxonomic composition of epizooic, permanent, metazoan meiobenthos associated with aggregations of tubeworms and mussels from three different locations at Green Canyon (GC), Atwater Valley (AV), and Alaminos Canyon (AC) in the Gulf of Mexico. In addition, non-seep sediment cores were taken in the vicinity of such aggregations at GC. The following questions were addressed: 1) Do abundance and higher taxonomic composition differ between geographical regions? 2) Do abundance and higher taxonomic composition differ between mussel and tubeworm aggregations? 3) Is the seep epizooic metazoan meiobenthic community similar to seep infauna or non-seep sediments? 4) Are there similarities in abundance and higher taxonomic composition of seep and hydrothermal vent communities associated with mussels and tubeworms?

METHODS

Study area

The study was conducted at the three hydrocarbon seep locations Green Canyon 852 (GC, depth 1400 m), Alaminos Canyon 818 (AC, depth 2800 m), and Atwater Valley 340 (AV, depth 2200 m) of the lower continental slope of the Gulf of Mexico (for further details see this volume). During two cruises in 2006 and 2007, a total of 13 samples were taken with the submersible DSV Alvin (2006) and ROV Jason (2007). Five samples of each foundation group were collected at two different seep habitats: mussels M-GC1, M-GC2, M-GC3, M-AV1, M-AC1; tubeworms T-GC1, T-GC2, T-GC3, T-AV1, T-AV2 and three samples of non-seep sediments were taken as controls (S-GC1, S-GC2, S-GC3) in close vicinity (< 3 m distance) to seep megafauna communities (Table 1).

Sample collections

Epifauna collections were carried out with the quantitative sampling devices 'Mussel Pot' (531 cm^2) for mussel aggregations (for further detail of the collection device see Cordes et al., this issue) and 'Bushmaster Jr.' (2800 cm^2) for tubeworm aggregations (for further detail see Urcuyo et al. 2003, Berquist et al. 2003). Infauna of non-seep sediment was collected with 6.3 cm diameter push cores. Samples were separately put into isolated, previously cleaned plastic boxes on the basket of DSV *Alvin* or ROV *Jason*, transported to the surface, and recovered on deck of the ship RV Atlantis or NOAA Ship Ron Brown. On board, the macro and megafauna of 'Bushmaster' and 'Mussel Pot' samples was carefully rinsed with cold 32 µm filtered seawater before we removed them from the samples in order to avoid loss of smaller fauna. Mussels and tubeworms of each collection were identified and counted (Table 1). The samples were sieved through a 1 mm mesh size to separate macro- from meiofauna. Before sieving the samples though a 32 µm sieve, we measured the volume of sediment of the entire sample < 1 mm. The meiofauna fraction was fixed in 4% buffered formalin. The larger size fractions were retained for complementary studies by collaborators (see Cordes et al., this issue).

The push core sample S-GC1 was split into 3 parts along the entire length, the other two samples S-GC2 and S-GC3 were split into half and these parts were used for the present analyses. In order to estimate the sediment depth distribution of meiobenthos in these samples, we checked the fraction deeper than 5 cm carefully on board of the ship. Since one sample lacked any specimens, and two samples only contained a single nematode, we only took the upper 5 cm of these samples, and fixed them in 4% buffered formalin without sieving.

Quantification of abundance

To extract meiofauna from the sediment, we used a density centrifugation technique with a medium consisting of a Silicapolymer (Fa. Levasil®) mixed with Kaolin (McIntyre & Warwick 1984, Veit-Koehler 2008). Except for sample T-AV1, all other samples were totally processed and the entire meiofauna community was counted and identified to higher taxon level. Sample T-AV1 was extremely large (7.5 l sediment including meiofauna after sieving through a 1 mm net), therefore a subsample of 217 ml was processed and total abundance was estimated.

All taxa belonging to the permanent metazoan meiobenthos were considered in this study. We noticed the presence of crustacean nauplii but did not include them in further analyses due to the fact that they could not be assigned to a specific higher crustacean taxon. We also recorded the protist meiobenthos, but did not include them in this study of permanent, metazoan meiobenthos.

Data analyses

Total abundance of meiobenthos was standardized to 10 cm^2 sample area and additionally to 10 cm^2 surface area of mussel shells and tubeworm tubes. The surface of mussels and tubeworms were estimated for the main foundation species *Bathymodolus brooksi, B. childressi, B. heckerae*, *Esparpia laminata*, and *Lamellibrachia* spp. by measurements of lengths and widths for each individual in the collection (see Cordes et al., this issue for methods). To test for significant differences in abundances among habitat types in the Green Canyon samples, data were square-root transformed and bootstrapping was used as this is a well proven method when working with a relatively low number of samples and high variances (10000 resamplings each, t-test, 2-sided test, routine ”FTBOOT” from the package ”computer intensive statistics” (Nemeschkal 1999). Results were classical Bonferroni-corrected ($p = \alpha/n$; $\alpha = 0.05$). To evaluate similarity and dissimilarity among all samples, a Bray-Curtis similarity matrix was generated (abundance data from 10 cm^2 sample area were square-root transformed, but were not standardized in order to better recognize differences caused by total abundances), and similarity percentage (SIMPER) analysis, analysis of similarity (ANOSIM), and multi-dimensional scaling (MDS) ordination were performed using PRIMER v5 (Clark & Warwick 2001).

RESULTS

Abundance

The total abundance of the permanent, metazoan meiobenthos associated with mussel and tubeworm aggregations of most samples from three different locations at the Northern Gulf of Mexico was extremely low and ranged from 1 to 81 ind. 10 cm^2 sample area. However, one tubeworm aggregation sample (T-AV1) from Atwater Valley (AV) revealed a total abundance between one and two orders of magnitude higher (447 ind. 10 cm^{-2}) than the nine other seep samples. Non- seep sediment control samples showed abundance values from 870 to 1523 ind. 10 cm^{-2} sample area (Table 2).

Green Canyon (GC) was the only site where the number of samples was sufficient to statistically compare the abundances among mussel and tubeworm associated communities, and among the seep communities and adjacent non-seep sediments. We found no significant difference between mussel and tubeworm meiobenthos abundance ($p = 0.19$), but significantly lower abundances at both seep communities than in non-seep sediments (both: $p = 0.003$).

The mussel beds at AV, AC and one sample from Green Canyon (M-GC3) were exclusively built by *Bathymodiolus brooksi*. In addition, *B. childressi* co-occurred in two GC samples, contributing with 50% and 63.2%, respectively to the total mussel abundance. Also the tubeworm aggregations of all collections were mixed populations of *Escarpia laminata* and one or two species of *Lamellibrachia* (Table 1). As foundation species forming biogenic habitat, tubeworms and mussels considerably increase the surface area and thus the potential living space for meiobenthos. By estimating the actual surface of the foundation species, we found an increase of surface in both types of aggregations between 1.78 to 6.03 fold. The ratio of sample area to the surface area of tubes/shells was similar between the two biogenic habitat types, but was more variable in tubeworm bushes (1.78 to 6.03), than mussel beds (3.07 – 5.46) (Table 1).

By assuming that the surface of foundation species was the actual living space of associated meiobenthos, we standardized the total abundance of this community to the surface area and calculated even lower densities only between 1 and 3 ind. 10 cm^2. Again, one tubeworm sample (T-AV1) contained much greater densities of meiobenthos (20 ind.10 cm^{-2}) (Table 2). T-tests on abundance per surface area of GC samples revealed similar results as calculations per sample area with similarly low abundances found in the seep habitat types (mussel and tubeworm: $p = 0.15$; seep and non-seep: both $p = 0.003$).

Taxonomic diversity

The seep metazoan meiobenthic communities were composed of the higher taxa Nematoda, Copepoda, Ostracoda, and Halacarida. In addition, naupli larvae were found in seven out of ten samples with variable abundances but were excluded from analyses due to the impossibility of assignment to a specific crustacean taxon. The protist phylum Foraminifera was also represented in all seep samples.

In all five tubeworm samples from three different locations, the most prominent taxa were the nematodes with relative abundances between 57 to 90 % followed by the copepods (10 – 43 %). Ostracods and halacarids were relatively rare, often found with relative abundances below 1% and below 0.5% respectively (Figure 1).

The relative distribution of higher taxa was more variable in mussel bed samples. In three samples (M-GC3, M-AV1, M-AC1), nematodes dominated (66 – 82%) followed by copepods (17 – 30%), while in two samples (M-GC1, M-GC2) copepods were most abundant (82 and 99%). Ostracods were found in four, halacarids in three out of five samples. In two of these more diverse communities, both ostracods and halacarids reached relative abundances between 1 and 5%.

The non-seep control sediments collected in close vicinity to mussel and tubeworms aggregations at GC additionally harbored the taxon Kinorhyncha. The community was primarily composed of nematodes (80 - 81%), followed by copepods (16 -19%), ostracods, halacarids, and kinorhynchs (all < 1%). It was remarkable that nauplii and foraminiferans were absent from these samples.

Community patterns

SIMPER and ANOSIM analyses did not demonstrate significant differences between mussel bed and tubeworm aggregation meiobenthic communities at the taxonomic level examined. There were also no significant differences among sites, despite the differences in depth (GC 1400 m, AV 2200 m, AC 2800 m) (Table 3). However, there were strong differences detected between non-seep sediment communities and tubeworm and mussel associated communities (> 74% Bray-Curtis dissimilarity), and these differences were significant in the ANOSIM (R = 0.64; p = 0.04 for tubeworm/sediment; R = 0.81; p = 0.02 for mussel/sediment). Multidimensional scaling (MDS) ordination revealed that metazoan meiobenthos from seep habitats and from adjacent non-seep sediments formed distinct groups, with the exception of sample T-AV1 which exhibited relatively high similarity to non-seep communities (Figure 2).

DISCUSSION

The epizooic metazoan meiobenthic communities associated with tubeworm and mussel structure at cold seeps in the Gulf of Mexico can be characterized as a community composed of a limited number of higher taxa including the Nematoda, Copepoda, Ostracoda, and Halacarida, occurring in remarkably low abundances. As such, these seep communities are similar to epizooic meiobenthic vent communities associated with the mussel genus *Bathymodiolus* or vestimentiferan tubeworms. However, these communities associated with biogenic habitats differ from the infaunal communities studied from sands of shallow-water seeps and clays of deep-water seeps, which show much higher abundances compared to the epizooic meiobenthos from our studied sites.

Tubeworm aggregations and mussel beds are not only colonized by meiobenthos but also by a diverse and abundant macrobenthic community at the GOM cold seeps. In these same samples, mussel-associated macrofauna were present in densities between 235.5 and 1196.3 ind. m^{-2} (0.2 and 1.2 ind. 10 cm^{-2}) and tubeworm-associated macrofauna were between 35.9 and 127.9 ind. m^{-2} (0.04 and 1.3 ind. 10 cm^{-2}) (Cordes et al. this issue). In other samples from the upper slope, macrobenthic abundances calculated per sample area ranged from 209 to 9590 ind. m^2 (0.2 to 9 ind. 10 cm^{-2}) (Berquist et al. 2003), and abundances standardized to the tube surface vary from 4 – 233 ind. m^{-2} on the upper slope (Cordes et al. 2005), and 134.3 – 606.6 ind. m^{-2} on the lower slope (Cordes et al. 2007).

Abundances per mussel shell surface from the Florida Escarpment, a different site in Atwater Valley, and Alaminos Canyon were between 160.1 and 4457.8 ind. m^{-2} (Cordes et al. 2007). It appears that the macro- and megafauna are relatively well represented in such aggregations fueled by *in situ* primary production, while small meiobenthic animals are relatively scarce. In general the interaction between macrofauna and meiofauna are thought to be negative for the smaller size class, as adult large animals are potentially predators and/or dislocate meiofauna by movements. In addition, the juvenile macrofauna, temporarily in the meiofauna size class while growing up, can act as predators or competitors (Bell and Coull 1980). If the seep meiofauna community is regulated by such top-down or by bottom-up processes remains to be studied.

Overall, the abundances and higher taxonomic composition of meiobenthos associated with tubeworm and mussel habitats from cold seeps in this study are quite similar to those at hydrothermal vents (Table 4). The epizooic communities of both environments are low in abundance (usually below 100 ind. 10 cm^{-2}) and are mostly dominated by nematodes. In addition, communities with equal nematode to copepod distribution, copepod dominated (this study, Tsurumi et al. 2003, Zekely et al. 2006, Gollner et al. 2007), or foraminiferan dominated communities have also been found (Gollner et al. 2007).

While the present study describes the epizooic meiobenthos from cold seeps, all other meiobenthic seep studies concern the infauna inhabiting seep sediments (Table 4). They range from very shallow sites down to 5000 meters depth, come from different geographic regions and a variety of seep types, mostly hydrocarbon gas or gas/oil seeps, but also gas hydrates and brine seeps. Most samples were taken from sites covered by bacterial mats or colonized by frenulate and sclerolinid tubeworms, or were taken from underneath clam beds, but sometimes also from sites devoid of any microbial or megafaunal community. In addition to different approaches in extraction techniques and size classes included in the meiofauna fraction, there are also large variations in which part of the meiobenthic community was analyzed. Some include the entire permanent (metazoan and protist) and temporary meiobenthos, and some only parts. Overall, no trends in abundance according to depth, geographic regions, seep types, or habitat types are apparent.

Associated epizooic metazoan meiobenthos from seeps (1 – 81 ind. 10 cm^{-2}) and vents (1 – 976 ind. 10 cm^{-2}), as well as vent infauna from sediments (1 – 1075 ind. 10 cm^{-2}), seems to be overall lower in abundance than infaunal meiobenthos from seeps (1 – 11292 ind. 10 cm^{-2}). Low abundances of seep infauna were only detected in anoxic sediments of the Black Sea and in some samples from a brine seep at East Flower Garden Banks (Powell et al. 1983, Sergeva and Gullin 2007). All other infaunal abundances are at least above 100 ind. 10 cm^{-2} and most exceed 1000 ind. 10 cm^{-2} (Table 4). The vast majority of epizooic and infaunal vent and seep meiobenthic samples are dominated by nematodes, usually followed by copepods. Other dominant taxa include gnathostomulids and platyhelminthes in highly sulfidic brine seep samples (Powell et al. 1983), and rotifers in gas hydrate samples (Sommer et al. 2002).

Although in several meiobenthic studies of seeps the nearby non-seep deep-sea samples were found to be lower in abundance than the seep sediment samples (Olu et al. 1997, Robinson et al. 2004, Soltwedel et al. 2005, Van Gaever et al. 2006), our study could not confirm this trend. In general, the abundance of meiobenthos in the deep sea has been found to decrease with depth due to a decrease in POM flux in addition to sedimentary factors such as calcium carbonate content and sorting. Ranges between 100 and 1000 ind. 10 cm^{-2} at shallower depths and between 10 and 100 ind. 10 cm^{-2} at deep sites are considered quite typical (see Giere 2009). Based on a very large data set from the GOM deep-sea meiobenthos carried out between 200 and 3000 meters depth, a range between 600 to 9500 ind. 10 cm^{-2} was found (Baguley et al. 2006). Calculated from the correlation between abundance and depth, approximately 2500 ind. 10 cm^{-2} are expected in about 1500 meters depth (Baguley et al. 2006). This estimation is not only much higher than the actual abundances we found at the tubeworm and mussel aggregations, but also higher than in our comparable non-seep sediment samples (870 – 1523 ind. 10 cm^{-2}) taken in close vicinity to seeps and thus most likely exposed to higher POM due to the primary *in situ* production in this chemosynthetic based environment.

ACKNOWLEDGEMENTS

This study has been financially supported by Austrian Science Foundation grants FWF P16774-B03 and P20190-B17 to M.B. and the Mineral Management Service Contract #1435-01-05-39187 to TDI-Brooks International. We would like to thank Charles R. Fisher for his invitation to collaborate with us and his continuous support and enthusiasm for including meiofauna in the larger framework of community ecology at seeps. We also would like to thank the captains and crews of the R/V *Atlantis*, NOAA Ship Ron Brown and the expedition leaders and crews of DSV *Alvin* and ROV *Jason* for their expertise and valuable assistance.

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Figure 1. Relative abundance (%) of taxa for meiobenthos (5 mussel community samples, 5 tubeworm community samples, 3 non-seep sediment samples). Nematoda, Copepoda and others (including Ostracoda, Halacarida, and Kinorhyncha) were present.

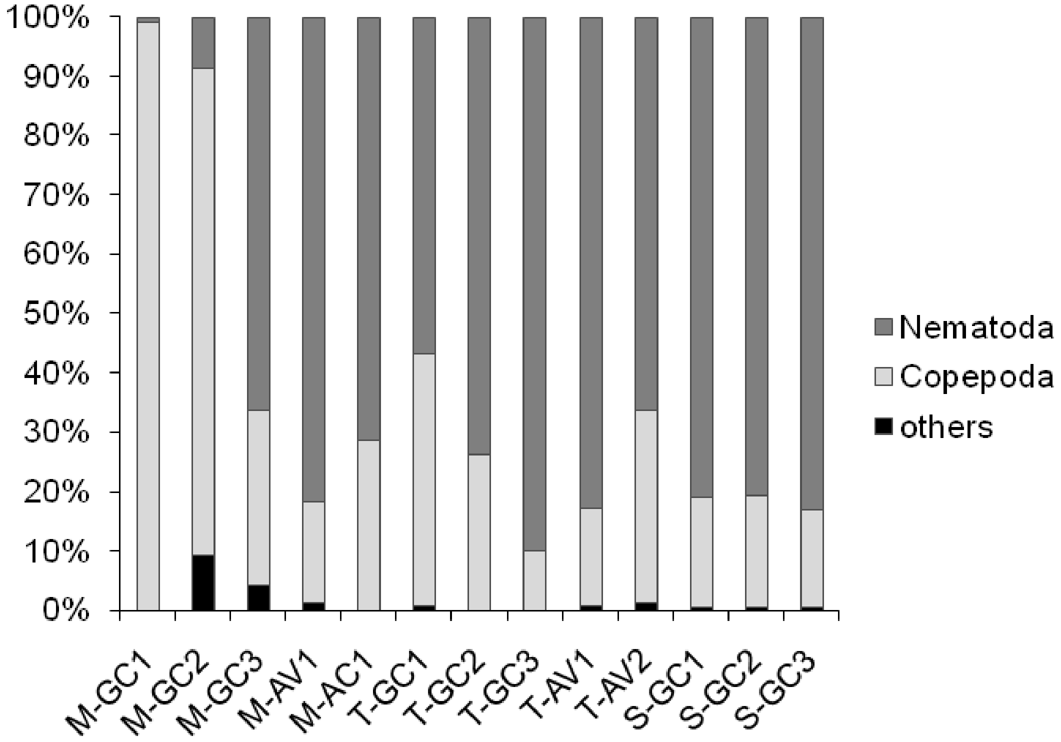

Figure 2. 2-dimensional MDS configuration plot for 13 samples from 5 mussel community samples (M-GC1, M-GC2, M-GC3, M-AV1, M-AC1), 5 tubeworm community samples (T-GC1, T-GC2, T-GC3, T-AV1, T-AV2), and 3 non-seep sediment samples (S-GC1, S-GC2, S-GC3) from 3 different depths.

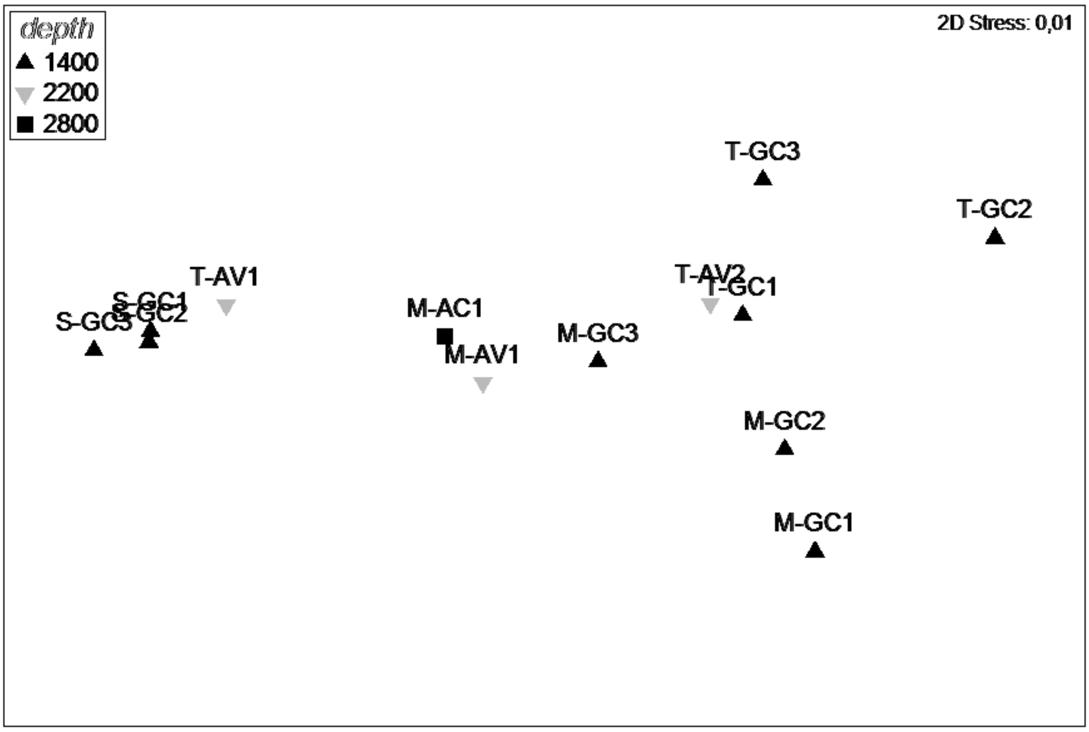

Table 1. Sample information is given on geographical location, site, dive number (AD *Alvin* dive, JD *Jason* dive), latitude, longitude, depth, sample area ('footprint' of sediment surface above which the mussel pot or the bushmaster sampling device was placed; is equal to diameter of mussel pot and maximal diameter of bushmaster), surface area (total area of tubeworm tubes or mussel shells surfaces calculated per sample), surface area per sample area (total sample area per total surface area), volume of sediment (collected between mussels or tubeworms), and megafauna listed per species (% contributing to total megafauna).

Sample	**M-GC1**	**M-GC2**	**M-GC3**	**M-AV1**	**M-AC1**	**T-GC1**	**T-GC2**	**T-GC3**	**T-AV1**	**T-AV2**	**S-GC1**	**S-GC2**	**S-GC3**
location	Green Canyon	Green Canyon	Green Canyon	Atwater Valley	Alaminos Canyon	Green Canyon	Green Canyon	Green Canyon	Atwater Valley	Atwater Valley	Green Canyon	Green Canyon	Green Canyon
site	GC 852	GC 852	GC 852	AT 340	AC 818	GC 852	GC 852	GC 852	AT340	AT 340	GC 852	GC 852	GC852
dive number	AD 4186	AD 4187	JD 278	JD 276	AD 4192	AD 4186	AD 4187	JD 273	JD 277	JD 270	AD4177	AD4177	AD4177
latitude	27°06.357	27°06.656	27°06.380	27°25.197	26°10.819	27°06.371	27°06.676	27°06.370	27°38.839	27°38.694	27°10.633	27°10.633	27°10.633
longitude	91°09.974	91°09.937	91°09.953	88°21.853	94°37.380	91°09.968	91°09.932	91°09.967	88°22.429	88°21.843	91°16.608	91°16.608	91°16.608
depth (m)	1410	1406	1408	2200	2744	1409	1406	1410	2175	2192	1450	1450	1450
sample area (cm^{-2})	531	531	531	531	531	2800	2800	2800	2800	2800	10.33	15.5	15.5
surface area (cm^{-2})	1670	1630	2140	2190	2900	15060	4980	8050	12740	16870	10.33	15.5	15.5
surface area per sample area	3.15	3.07	4.03	4.12	5.46	5.38	1.78	2.88	4.55	6.03	1.00	1.00	1.00
sediment (ml)	no info	no info	41.21	21	42	no info	no info	5.89	7500	16	41	107	88.5
megafauna	mussels	mussels	mussels	mussels	mussels	tubeworms	tubeworms	tubeworms	tubeworms	tubeworms	no	no	no
Bathymodiolus brooksi (%)	50	36.8	100	100	100								
B.childressi (%)	50	63.2											
Lamellibrachia ssp. (%)						71.4	85.3	45.6	74.5	67.3			
Escarpia laminata (%)						28.6	14.7	54.6	5.5	32.7			

Table 2. Meiobenthic abundance is shown as total abundance, individuals 10 cm^{-2} sample area, and ind. 10 cm^{-2} surface area for all 13 samples (5 mussel community samples, 5 tubeworm community samples, 3 non-seep sediment samples); additionally total abundances of foraminifera and nauplii are listed (not included in analyses).

sample	**M-GC1**	**M-GC2**	**M-GC3**	**M-AV1**	**M-AC1**	**T-GC1**	**T-GC2**	**T-GC3**	**T-AV1**	**T-AV2**	**S-GC1**	**S-GC2**	**S-GC3**
total abundance													
Nematoda	2	19	723	2513	3087	1005	181	1389	103618	1547	735	1089	1964
Copepoda	240	179	323	519	1229	759	64	153	20461	755	168	253	388
Ostracoda	0	11	14	22	3	3	0	1	1002	22	5	6	5
Halacarida	0	9	31	19	0	7	0	0	0	7	0	0	1
Kinorhyncha	0	0	0	0	0	0	0	0	0	0	0	1	2
total	**242**	**218**	**1091**	**3073**	**4319**	**1774**	**245**	**1543**	**125081**	**2331**	**908**	**1349**	**2360**
ind. 10 cm^{-2} sample area													
Nematoda	0.04	0.36	13.62	47.33	58.14	3.59	0.65	4.96	370	5.53	711.52	702.58	1267.10
Copepoda	4.52	3.37	6.08	9.77	23.15	2.71	0.23	0.55	73	2.70	162.63	163.23	250.32
Ostracoda	0.00	0.21	0.26	0.41	0.06	0.01	0.00	0.00	4	0.08	4.84	3.87	3.23
Halacarida	0.00	0.17	0.58	0.36	0.00	0.03	0.00	0.00	0	0.03	0.00	0.00	0.65
Kinorhyncha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00	0.00	0.65	1.29
total	**4.56**	**4.11**	**20.55**	**57.87**	**81.34**	**6.34**	**0.88**	**5.51**	**447**	**8.33**	**878.99**	**870.32**	**1522.58**
ind. 10 cm^{-2} surface area													
total	**0.29**	**0.27**	**1.02**	**2.81**	**2.98**	**0.24**	**0.10**	**0.38**	**20**	**0.28**	**878.99**	**870.32**	**1522.58**
total foraminifera ind.	NA	NA	NA	33	10	NA	NA	NA	3629	68	0	0	0
total nauplii ind.	0	92	0	788	1118	55	10	0	864	82	0	0	0

Table 3. Dissimilarity results (Diss. %) calculated by SIMPER, and ANOSIM results (R-statistics and possible significance level p) are shown for mussel compared to tubeworm communities, and mussel and tubeworm communities to non-seep sediment communities. Additionally, seep sites at different depths (1400 m, 2200 m, 2800 m) are compared with each other.

	Diss%	R-Stat	p
mussel - tubeworms	54	0,15	0,13
mussel - sediment	**74**	**0,81**	**0,02**
tubeworm - sediment	**74**	**0,64**	**0,04**
seep: 1400 m - 2200 m	55	0,25	0,13
seep: 1400 m - 2800 m	62	0,56	0,14
seep: 2200 m - 2800 m	35	0,56	1

Table 4. List of meiobenthic infaunal and epifaunal studies from vents and seeps, listed according to type of seep or vent, depth, sampling device, extraction/sieving technique, components of meiobenthos included in study (m metazoan permanent, p protist permanent, t temporary meiobenthos), habitat, abundance 10 cm^{-2}, and reference.

location	**type**	**depth (m)**	**sampling**	**extraction/sieving**	**fauna**	**habitat**	**abundance (10 cm^{-2})**	**reference**
seep infauna								
East Flower Garden	brine seep	72	grab	sieving >63 µm	m + t	bac mats	1 - 240	Powell et al. 1983
Isla Vista, Santa Barbara Channel	oil/gas	15	corer	decantation	m(+p?)+t	bac mats	1360	Montagna & Spies 1985
	oil/gas	19	corer	decantation	m(+p?)+t	bac mats	2500	Palmer et al. 1988
Hatsushima, Sagami Bay	gas	1100 - 1200	corer	sieving >63 µm	m+p+t	underneath calms	371 -414	Shirayama & Ohta 1990
Barbados prism	gas	5000	corer	no data	m(+p?)+t	sediment center	116	Olu et al. 1997
	gas	5000	corer	no data	m(+p?)+t	underneath clams	6541 - 8438	
	gas	5000	corer	no data	m(+p?)+t	near clams	845 - 1893	
Hydrate Ridge, off Oregon	gas hydrate	800	corer	centrifugation >32 µm	m+t	bac mats	623 - 965	Sommer et al. 2002
	gas hydrate	800	corer	centrifugation >32 µm	m+t	underneath clams	1021 - 1566	
Dnieper Canyon, Black Sea	gas	182 - 252	corer	sieving 64 µm - 1 mm	m+p+t	bac mats	2.39 - 52.50	Sergeeva & Gulin 2007
Hakon Mosby, Barents Sea	gas	1280	corer	sieving 32 -500 µm	m+p+t	sediment center	4471	Soltwedel et al. 2005
	gas	1280	corer	sieving 32 -500 µm	m+p+t	in Pogonophora	2878 - 3899	
	gas	1280	corer	sieving 32 -500 µm	m+p+t	bac mats	3475	
Hakon Mosby, Barents Sea	gas	1286 - 1288	corer	centrifugation >32 µm	m+t	sediment center	513.2 ± 38.4	Van Gaever et al. 2006
	gas	1286 - 1288	corer	centrifugation >32 µm	m+t	in Pogonophora	1741.3 ± 577.8	
	gas	1286 - 1288	corer	centrifugation >32 µm	m+t	bac mats	11292.1 ± 2256.2	
seep epifauna								
Gulf of Mexico	gas	1400 - 2800	bushmaster	centrifugation 32 µm - 1 mm	m	ass. Vestimentifera	0.88 - 447	this study
	gas	1400 - 2800	mussel pot	centrifugation 32 µm - 1 mm	m	ass. mussels	4.11 - 81.34	this study
vent epifauna								
Juan de Fuca Ridge	vent	2300	grab	sieving >63 µm	m+p	ass. *Paralvinella*	14 - 87	Tsurumi et al. 2003
Mid Atlantic Ridge	vent	3492	mussel pot	centrifugation >63 µm	m+p	mussel	36 - 46	Zekely et al. 2006
N East Pacific Rise,	vent	2480	mussel pot	centrifugation >63 µm	m+p	mussel	25 - 32	
N and S East Pacific Rise	vent	2491 - 2690	mussel pot	centrifugation >62 µm	m+p	mussel	22 - 116	Copley et al. 2007
N East Pacific Rise	vent	2500	bushmaster	centrifugation >63 µm	m+p	ass. Vestimentifera	1 - 976	Gollner et al. 2007
vent infauna								
Guaymas, East Pacific Rise	vent	2000	corer (?)	centrifugation >63 µm	m+t	bac mats	1 to 81	Dinet et al. 1988
Bay of Plenty, New Zealand	vent	4 to 12	corer	sieving >50 µm	m+p	bac mats	1 to 241	Kamenev et al. 1993
Matupi Harbour, Papua New Guinea	vent	0 to 27	corer	sieving >500 µm	m+p	bac mats	2 to 131	Tarasov et al. 1999
Aegean Sea, Mediterranean Sea	vent	10	corer	elutriation >63 µm	m+p	bac mats	0 to 1075	Thiermann et al. 1997

Size matters: contrasting meio – and macrofauna diversity patterns at deep-sea hydrothermal vents

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ABSTRACT

The effects of disturbance and changes in productivity are considered key factors shaping diversity. However, communities characterized by specific body sizes and intrinsic life traits are usually not taken into account. Meiofauna traits include direct development, adult dispersal, short generation times, and mobility. In contrast, macrofauna traits are planktonic larval development and dispersal, long generation times, and mobile and sessile lifestyles. Further, macro- and meiofauna in general differ in reactions to stress and food requirements. Meiofauna is more threatened by stress and has relatively lower food demands, while macrofauna is more stress tolerant and requires relatively more food. We use deep-sea hydrothermal vents and adjacent bare basalt in the axial summit trough of the East Pacific Rise 9°50' N region as natural experiments to explore *in situ* diversity of meio- and macrofauna at various productivity and disturbance gradients. Our results show, that the two communities reacted different to disturbance and productivity conditions. Macrofauna diversity pictured a unimodal diversity pattern along an environmental stress gradient, while meiofauna diversity was negatively correlated to stress. By scaling the degree of productivity and disturbance experienced by animals of two different size classes we provide an explanation for the contrasting diversity patterns. Food requirements were found to play a major role, especially in the food-limited, low productivity basalt habitat. Lower food demands and shorter generation times of meiofauna lead to a highly diverse, permanent community. Higher food demands and longer generation times of macrofauna resulted in a low diverse, transient, non-reproductive community. At vents we found that reproduction strategies and related dispersal capabilities in conjunction with food requirements at different life history stages were important factors, leading to a generalistic meiofauna but a vent endemic macrofauna. Low physiological fitness of meiofauna could be responsible for the negative-to-stress correlated diversity pattern along a hydrothermal flux gradient. Macrofauna with higher fitness and more versatile lifestyles was less influenced by hydrothermal stress leading to a more complex, unimodal diversity pattern. Our study shows that models predicting diversity should not neglect body size related communities traits.

Keywords: life traits, diversity, disturbance, productivity, function of size, meiofauna, macrofauna, hydrothermal vent

INTRODUCTION

Unraveling the underlying mechanisms that control biodiversity are of great interest in today's world. The insurance hypothesis states that biodiversity stabilizes communities and ecosystems (Petchey et al. 2002). Body size is known to influence biodiversity in a significant way (Hildrew et al. 2007). In general, there are many advantages of large size, such as increased fecundity, success in size-dependent competition for resources, escape from size-limited predators, greater diet breadth, greater physiological homeostasis, and tolerance of environmental fluctuations. Costs of large size include the risk of dying before breeding, higher energy requirements, enhanced parasitism, and raised environmental stress of less agile semi-sessile species (Brown & Sibley 2006).

Animals occur in a wide range of body size, from less than 100 μm up to several meters. In the marine environment, the small meiofauna (animals passing through a 1 mm and being retained on a 32 μm net) and the large macrofauna have distinct life traits (Giere 2009). Looking at life histories of different sized organisms can improve our understanding of populations' dynamics. Adaptations associated with small size are direct benthic development, dispersal as adults, short generation times (< 1 year), semelparity, attainment of an asymptotic final body size, trophic specialization (selective particle feeding), and mobility. In contrast, macrofauna traits are often characterized by planktonic larval development and dispersal, long generation times (>1 year), iteroparity, permanent growth, less selective feeding, and mobile and sessile life styles (Warwick 1984). Warwick et al. (2006) used various sized meshes in an intertidal sand to test if diversity changes gradually with chosen size range, similar to what was found in freshwater stream communities (Schmid & Schmid-Araya 2007), or if there are size-dependent communities. Two separate communities, traditionally characterized as 'meiofauna' and 'macrofauna', showed contrary diversity, suggesting that body size and its related traits, which are fundamentally different in marine and freshwater animals, are important in marine environments (Warwick et al. 2006).

Fenchel & Finley (2003) proposed to include size and its related life traits when studying species distribution and the degree of endemism. Microbes and protists are cosmopolitan due to huge population sizes of small organisms (Fenchel & Finley 2003). High abundances make local extinction almost impossible and dispersal capabilities are very good. Also for small animals, it is suggested that they are cosmopolitan, but possibly with a stronger habitat selection than protists (Fontaneto et al. 2006).

Despite the differences in life traits and distribution capabilities of different sized organisms the possible effects on biodiversity patterns are widely not considered and not observed yet. One of the most studied topics to explain diversity patterns, are the influence of disturbance and productivity changes on diversity.

Disturbance, is defined as damage (removal of biomass) or as an event in time that disrupts communities and changes resources or the physical environment (White & Pickett 1985, Sousa 2001). The intermediate disturbance hypothesis predicts unimodal diversity patterns along an increasing disturbance gradient (Connel 1978). The same pattern is also expected along stress gradients (Menge & Sutherland 1987, Bruno et al. 2003, Scrosati & Heaven 2007). However, in natural systems, disturbance effect on diversity can be positive, negative, linear, unimodal, and U-shaped (Mackey & Currie 2001).

Productivity, is the rate of energy flow to a system (e.g. mg C m^{-2} yr^{-1}), but studies and theoretical models often use measures like biomass, energy availability, growth rate, or a measure of productivity at one trophic level (e.g. primary productivity) (Mittelbach et al. 2001, Scholes et al. 2005). The original productivity hypothesis, predicting increasing diversity with increasing productivity, has been rejected since the 70ies (Pielou 1975). Instead, an unimodal diversity pattern along a gradient is now considered as the most common diversity pattern (Grime 1973, Mittelbach et al. 2001).

Combining both disturbance and productivity, Huston (1979, 1994) developed the dynamic equilibrium hypothesis, which states that diversity is influenced by frequency of reduction (disturbance) and rate of displacement (competitive displacement, growth rate, productivity). Diversity depends on the level of both factors. Although there is general support for the model, a protist microcosm experiment with various levels of energy and disturbance failed to provide unequivocal evidence (Scholes et al. 2005). Haddad et al. (2008) pointed out that species' autecological traits predict the effects of disturbance and productivity on diversity. They showed with an experiment that growth rate and the ability to recover from disturbance were related to how severely a species is affected by disturbance, and that competitive ability of a species tends to be less important.

In this study, we use deep-sea hydrothermal vents as natural experiments to explore *in situ* diversity of the different sized meio- and macrofauna communities along various productivity and stress gradients. Vents are species poor, hence, they allow us to analyze the whole community relatively easy. The vent ecosystem offers the full range of environmental stress gradients, with extreme high stress/disturbance at high temperature black smokers to low stress at bare basalt with no toxic vent flux. Productivity is very high at vents, fueled by *in situ* chemoautotroph production by bacteria, but is very low at the bare basalt habitat with no *in situ* primary production but in close vicinity to vents (Etter & Mullineaux 2001).

Whereas the distribution of foundation species such as pompei worms, tubeworms, and mussels is relatively well known at hydrothermal vents, knowledge on the associated macrofauna is more limited. At Juan de Fuca Ridge a succession model using macrofaunal groups showed that habitats with more severe venting conditions had fewer species (groups) than those that were characterized by moderate vent flux (Sarrazin et al.1997, Sarrazin et al. 1999, Sarrazin & Juniper 1999). Quantitative studies on species richness within the moderate zone with *Ridgeia piscesae* as foundation species, revealed similar diversity at different succession stages, temperatures, locations, or year of collection (Govenar et al. 2002, Tsurumi & Tunnicliffe 2003). At the East Pacific Rise (EPR), macrofauna from two chemically different sites with *Riftia pachyptila* as foundation species showed similar diversity (S: 19 - 35, H'_{log2}: 1.2 - 2.1) (Govenar et al. 2005). Macrofauna associated with mussels along the EPR are similar in diversity (S: 34 - 46 , H'_{loge}: 1.5 – 1.7), but show lower values at the Mid Atlantic Ridge (Van Dover 2002, Van Dover 2003). Although these studies provided interesting results for the vent habitats, differences in standardizations and locations do not allow predicting macrofauna diversity along an environmental gradient.

In a previous study, we explored meiofauna diversity along an increasing hydrothermal flux gradient at the EPR (Gollner et al. submitted). The observed inverse correlation between stress and meiofauna diversity patterns was explained by fewer species tolerating extreme conditions, resulting in less diverse communities in more extreme habitats. In that study it was suggested that the expected unimodal diversity pattern was not found due to the lack of non-disturbed habitats (Gollner et al. submitted). Although the basalt in the vicinity of vents, showing high meiofauna diversity, is not exposed to toxic hydrothermal fluid emissions, the relatively frequent volcanic eruptions and biotic disturbances are causing an intermediate disturbed habitat, which is in general expected to show high diversity (Connel 1978).

Here, we compare meio- and macrofauna diversity from the same samples from various hydrothermal vent habitats along stress and productivity gradients. Huston (1979) assumed that changes in environmental variables are affecting populations basically in the same way. If this is true, meio- and macrofauna diversity should respond similar to changing environments. Instead, we observe a unimodal diversity pattern in the macrofauna but a negative-to-stress correlated pattern in the meiofauna size class. Thus, factors influencing diversity must be different for the meio- and macrofauna communities, and therfore we investigated the degree of differences in life traits of these two communities in relation to disturbance and productivity. We conclude that body size and its related traits are the main underlying causes of diversity.

METHODS

Study sites and habitat characterization

We have chosen the well known midocean ridge at the 9°50' North East Pacific Rise (EPR) as our prime study region. The ridge crest is in 2500 m depth, and the axial summit trough (AST) is ~50 m wide and ~20 m deep (Fornari et al. 1998). The majority of the AST is bare basalt, scarcely populated by macrofauna, with stable ambient deep-sea temperatures of 2°C, and no vent flux. Within this AST, we find patchily distributed typical megafauna foundation species along a decreasing thermal and chemical gradient: pompei worms (*Alvinella pompejana and A. caudata*) thrive at high flow (>50°C), tubeworms (e.g. *Riftia pachyptila*) at moderate temperature flow (<30°C), mussels (e.g. *Bathymodiolus thermophilus*) at low temperature flow (<5°C), and suspension-feeders grow close to the periphery (Etter & Mullineaux 2001). Physico-chemical conditions are generally more toxic and more fluctuating at higher temperatures (Di Meo-Savoie et al. 2004, Le Bris et al. 2006). Beside the permanent stress and disturbance caused by vent flux, animals in the AST are killed by frequent volcanic eruptions, occurring in 1991 and 2006 at the studied region (Shank et al. 1998, Tolstoy et al. 2006). Quantitative samples were collected with the submersible *Alvin* from pompei worm (sites: Alvinella Pillar, Bio 9, M-Vent, Michels Vent), tubeworm (sites: Tica, Riftia Field), mussel (at Mussel Bed site collections for meiofauna; at Biovent, Eastwall, Trainstation site collections for macrofauna), and bare basalt habitats (sampled near Tica and Alvinella Pillar) within ~2 km in the AST from 1999 until 2004 (number and size of samples see Table 1; details on sampling method, coordinates, and depth of sites see Van Dover 2003, Govenar et al. 2005, Gollner et al. submitted).

Temperature was measured *in situ* prior to sampling at all habitat types (maximal values in habitats: pompei worm 119°C, tubeworm 54°C, mussel 10°C, basalt 2°C). Additionally, maximal sulfide, and minimal pH was recorded *in situ* at tubeworm sites (95 – 283 µM $\sum H_2S$, 4.4 – 5.7 pH), and mussel aggregations at the Mussel Bed site (151 µM $\sum H_2S$, 6.7 pH) (Le Bris et al. 2006). At bare basalt no temperature anomalies were detectable, indicating absence of sulfide and normal pH of seawater (Luther et al. 2001). At pompei worms we could not measure the toxicity of vent flux but maximal values of up to 1520 µM $\sum H_2S$, and pH ~4 are known for this habitat in this region (Di Meo-Savoie et al. 2004, Le Bris & Gaill 2007).

Primary production has to our knowledge never been measured in detail in this region. In general, biomass of foundation species is highest for tubeworms (8-15 kg m^{-2}), and medium for mussels (2-10 kg m^{-2}) and pompei worms (5 kg m^{-2}) (see Giere et al. 2003). No foundation species are present at bare basalt, and also almost no macrofauna is visible, pointing to extremely low biomass. Overall, vent habitats are characterized by high production, whereas the bare basalt habitat experiences very low production (Van Dover 2000).

Data analyzes

After sampling, fauna was separated into the meio- and macrofauna. Macrofauna was fixed in 4% buffered formaldehyde and stored in 70% ethanol. For the meiofauna the latter step was found unnecessary. Animals were identified to lowest possible taxon, usually to species level. Meiofauna and macrofauna from the same samples were analyzed from pompei worm, tubeworm, and basalt habitats. Macrofauna data from mussels are from the sites Biovent, Eastwall, and Trainstation (Van Dover 2003); meiofauna data from mussels are from the site Mussel Bed (Gollner al. submitted). All sites are within the same region.

Details on meiofauna species composition from all 4 habitats can be found in Gollner et al. (2007, submitted). Macrofauna data from tubeworm (Govenar et al. 2005) and mussel (Van Dover 2003) habitats were recalculated for comparisons with meiofauna to species abundances per 10 cm^2 sea floor area. Macrofauna abundance and species composition from pompei worm and basalt habitats were analyzed and are shown in Appendix 1. The foundation species *Alvinella caudata*, *A. pompejana*, *Bathymodiolus thermophilus* (and its subtenant *Branchipolynoe symmytilida*), *Tevnia jerichonana*, *Oasisia alvinae*, and *Riftia pachyptila* were excluded from analyses as they mostly rely on their symbiotic partners, are not in direct competition for resources, and should have different mechanisms to deal with stress as the associated fauna.

Univariate diversity measures were calculated from quantitative species-abundance data by DIVERSE subroutine in PRIMER Version 5 package (Clarke & Gorley 2001). Univariate results (abundance, species richness, Shannon-Wiener diversity) of different habitat types from different size classes were transformed and tested for significant differences using bootstrapping (10000 resamplings each, 2-sided t-test, routine „FTBOOT“ from the package „computer intensive statistics“ (Nemeschkal 1999). Testing for possible biotic and abiotic correlations were carried out using Pearson´s r (F-value and t-value calculations by STATISTICA). All significance levels were classical Bonferroni-corrected ($p = \alpha/n$; $\alpha = 0.05$).

RESULTS

From ~225 000 counted individuals a total of 159 species was identified for this study (Table 1, Table 2). Total species richness of both size classes was similar at tubeworm, mussel, and basalt habitats (75 to 87 spp.), but very low at the pompei worm habitat (19 spp.). 55% of species belonged to the meiofauna size class and 45% to the macrofauna. Comparing total species richness of meio- and macrofauna revealed quite similar values at pompei worms (meio: 11 spp., macro: 8 spp.), tubeworms (meio: 31 spp., macro: 44 spp.), and mussels (meio: 36 spp., macro: 51 spp.), but very different ones at bare basalt (meio: 64 spp., macro: 22 spp.). Dominant meiofauna taxa were copepods and nematodes, dominant macrofauna taxa were mollusks and annelids (Table 1, 2). Macrofauna found on basalt were mostly juveniles, while adult macrofauna dominated at vents. All life history stages including adult meiofauna were found in all habitats.

Meiofauna species richness and Shannon-Wiener diversity index of studied communities were generally low and significantly increased from pompei worm (mean S: 5; mean H'_{loge}: 0.3), to tubeworm (S: 14; H'_{loge}: 1.4), and to mussel habitats (S: 29; H'_{loge}: 2.5). Total found species number was clearly highest at basalt (total S: 64), but species richness and diversity were similar between the mussel and the basalt habitat (S: 28; H'_{loge}: 1.9) (Figure 1, Table 1, Appendix 2).

Macrofauna species richness and Shannon-Wiener diversity index were generally low. Similar low values were found at pompei worm and basalt habitats (mean S: 5, 9; mean H'_{loge}: 1.1, 1.3). Significantly higher species richness was observed at mussels and tubeworms (S: 17; S: 25). Shannon-Wiener diversity index was only significantly higher at tubeworms (H'_{loge}: 1.7) (Figure 1, Table 1, Appendix 2).

We compared meiofauna with macrofauna species richness, and found them to be similarly low at pompei worms, significantly higher for macrofauna at tubeworms, and significantly higher for meiofauna at mussels and basalt habitats. Shannon-Wiener diversity index was significantly higher for macrofauna at pompei worms, similar at tubeworms and basalt, and significantly higher for meiofauna at mussel habitats (Figure 1, Appendix 2).

Meiofauna species richness and Shannon-Wiener diversity index were inversely correlated to vent flux (S: all $p \leq 0.001$; temperature $r = 0.69$, pH $r = 0.88$, sulfide concentration $r = 0.71$; H'_{loge}: temperature and pH both $p = 0.003$, $r = 0.66$, sulfide concentration: $p = 0.01$, $r = 0.59$). Macrofauna species richness and diversity were not correlated to these parameters.

Overall, meiofauna abundance was low (~100 ind. 10 cm^{-2}). Macrofauna abundance was extremely high (287±262 ind. 10 cm^{-2}) at tubeworms, high at mussels, and similarly low at pompei worm and basalt habitats (~4 ind. 10 cm^{-2}) (Table 1, Appendix 2).

The majority of meiofauna species at deep-sea hydrothermal vents was not endemic to vent habitats but occurred also on the bare basalt with no vent flux. 40% of all meiofauna species are basalt specialists (see Gollner et al. submitted). Macrofauna revealed 60% of species were restricted to vents (24% vent generalists, 36% vent specialists), and only 7% of species were basalt specialists. 33% of macrofauna species were found at vents and on basalt. Most species on the basalt were juveniles (Marcus & Tunnicliffe 2002, Micheli et al. 2002, Mullineaux et al. 2003, Govenar et al. 2004, Desbruyères et al. 2006, Govenar & Fisher 2007, Galkin & Goroslavaskaya 2008, Matabos 2008; see Appendix 3).

DISCUSSION

Predicting diversity without considering community traits might not be appropriate for marine ecosystems because similar conditions in terms of disturbance and productivity do not create similar diversity patterns in meiofauna and macrofauna communities. In contrast to an expected similar pattern in meio- and macrofaunal communities, we see an unimodal diversity pattern along an environmental stress gradient for macrofauna, but a negative correlation of meiofauna diversity with increasing stress. Intrinsic community traits of meio- and macrofauna are the best predictors of diversity patterns. Generation time and size-related food demand regulates diversity in low productivity systems. Over evolutionary time scales, distinct reproduction strategies and food demands have influence on the ecological state of vent communities, resulting in a generalistic meiofauna but vent-restricted macrofauna community. Body-size related physiological fitness can determine diversity in stressful habitats.

Diversity and size related traits in low productive habitats

Generation time and size-related food demand are the most important factors influencing diversity in low productivity systems. At the low productivity basalt habitat, this results in a highly diverse, permanent small-sized meiofauna but a low diverse, transient non-reproductive macrofauna. Short intrinsic generation time, and low food requirements (Peters 1983) until individuals attain their asymptotic final body size and reach maturity, allow establishing a diverse and fertile meiofauna community on basalt, including basalt specialists and AST generalists. Our results are in accordance with studies reporting a diverse copepod community from bare basalt at the Juan de Fuca Ridge, and a rich nematode community in sediments near hydrothermal vents (Vanreusel et al. 1997, Tsurumi et al. 2003). In contrast, large macrofauna species with their long generation times and higher food demands cannot sustain themselves on basalt with little food until they reach maturity. The lack of adult individuals in most macrofauna species found, points to the fact that reproduction might not be possible for the majority of species in this habitat. In consequence, macrofauna diversity on basalt cannot be high. Low abundant and low diverse macrofauna was also reported from artificial substrates positioned in the vicinity of vents (Govenar & Fisher 2007). Marcus & Tunnicliffe (2002) observed decreasing body size in two vent gastropods with increasing distance from vents at Juan de Fuca Ridge. They speculated that juvenile macrofauna takes advantage of the relatively safe basalt habitat, which is less threatened by competition and predation of adult macrofauna. We predict that macrofauna growing up on the basalt has to migrate into the food-rich vent habitat to sustain their energy needs and to reproduce.

Ecological state and size related traits at hydrothermal vents

Intrinsic reproduction strategies of different sized organism and distinct food demands per generation time lead to opposite ecological states of meio- and macrofauna at deep-sea hydrothermal vents. The generalistic meiofauna with low food demands and good dispersal capabilities can live and migrate within the whole AST as larvae, or juveniles or adults. Many meiofauna animals exhibit direct development and can disperse, either active or passive through currents, during all phases of life (Giere 2009). The majority of vent meiofauna species can live due to their relative low food demands also as adults on the nearby basalt. We expect that they migrate within the AST to other vent fields and can endure at least a certain time (if not forever) on the low productive basalt. We predict that the loss of highly productive vent habitats due to the waning of vent fields or volcanic eruptions is not a major problem for meiofauna populations, since nearby populations not effected by eruptions or loss of vent fields are theoretically everywhere in the AST. Our observation of a generalistic AST hard substrate meiofauna community confirms the general cosmopolitan distribution of organisms below 1 mm in size (Fenchel & Finley 2003, Fontaneto et al. 2006). Cosmopolitism of small organism is explained by large absolute population sizes, their high probability of dispersal and low probability of extinction. However, whether or not vent meiofauna is indeed cosmopolitan in distribution remains to be tested.

Due to their high food requirements, the vent macrofauna is forced to stay very close to the high productive vents. In addition, most vent macrofauna species (except e.g. fish) cannot disperse far as adults. Adults can hardly drift with currents due to their large size and heavy weight. Instead, many have planktonic dispersal via larvae (Warwick 1984). Vent larvae are produced in large numbers and are distributed via ocean currents along the AST (Mullineaux et al. 2005). If they settle too far away from vents, they might starve to death before they reach maturity. For this reason, we agree that most macrofauna species are restricted to vents (Tunnicliffe et al. 1998).

Size, different life styles and the related capacity to deal with hydrothermal stress

Small body size and intrinsic lower physiological resistance against physico-chemical disturbance give rise to negative-to-stress correlated meiofauna diversity patterns at the disturbed vent habitats. Higher physiological fitness and broader life style traits of mobile, semi-sessile, and sessile macrofauna should principally favor higher species richness of large animals in stressful and food rich environments. However, in the extreme pompei worm habitat, where only escapers survive and sessile animals rarely do, the disturbance thus results in similarly low diversity of both size classes.

Escape from heat and high levels of toxic chemicals is necessary in extreme, disturbed habitats. The pompei worm habitat is one of the most extreme habitats on Earth, and the “hottest” animal on Earth, the foundation species *Alvinella* spp., is found there in high abundances (Cary et al. 1998). This foundation species is creating a less toxic habitat for itself, by building tubes and actively ventilating them with cold oxygenated seawater by quickly moving around (Le Bris & Gaill 2007). The associated fauna is species poor and species richness is similar in meio- and macrofauna communities. Both size classes deal in a similar way with the extreme stress of highly fluctuating hydrothermal flux that cause temperatures to change within seconds (Di Meo-Savoie et al. 2004). These animals are fast-moving and thus can probably avoid small-scale disturbance. Copepods are the most successful taxon in terms of abundance and species richness and they are very fast escapers (McGurk 1986, pers. obs. MB and SG). In the meiofauna size class only copepods were detected, but not a single slow-moving nematode was present. The fast swimming and relatively large-sized (~1.2 mm in length) copepod *Stygiopontius hispidulus* (Humes 1987) dominated the meiofauna community with up to 90% (Gollner et al. submitted). The two most successful macrofauna species are the fast swimming amphipod *Ventiella sulfuris* and the incredibly fast snake-like moving polychaete *Hesiolyra bergi* (pers. obs. MB), that is only known from this specific habitat type. Our escaper hypothesis of associated fauna in the pompei worm habitat is supported by a temperature experiment with *H. bergi*, which showed that this species is not tolerating temperatures exceeding 40°C and thus has to avoid extreme temperatures (Shillito et al. 2001). Sessile species cannot escape and have to tolerate the vent flux, which is an extreme challenge in a habitat where temperature peaks of 120°C are common. Consequently, sessile and semi-sessile species are rarely found in the pompei worm habitat. Only 2 limpets (*Lepetodrilus galriftensis* and *L. elevates*), were present in low abundance in our samples. Overall, a similar macrofauna species composition was also observed in another study at pompei worm habitats (Galkin & Goroslavskaya 2008).

Diversity of both macro- and meiofaunal classes is higher at the tubeworm habitat due to decreased hydrothermal stress relative to the pompei worm habitat. Higher physiological fitness and broader range of life styles as mobile, semi-sessile and sessile macrofauna result in higher macrofauna than meiofauna diversity at the tubeworm habitat. The surface-area-to-volume ratio is greater for smaller animals, thus chemical compounds and changing temperatures might be more dramatic for the small size class (Townsend & Thompson 2007). Macrofauna exhibits greater physiological homeostasis and hence tolerance of environmental fluctuations (Brown & Sibley 2006). Their larger size and thicker carapaces (e.g. crustaceans) or stronger shells (e.g. gastropods) make them better protected against physical and chemical stress. In contrast to the solely mobile meiofauna, the macrofauna has mobile, semi-sessile, and sessile representatives. In terms of abundance and species richness macrofauna communities at tubeworms are numerically dominated by semi-sessile limpets (Govenar et al. 2005). These mollusks can withstand physico-chemical stress by sticking themselves very tight to the ground with their strong foot (Garrity 1984). Limpets are known to be very resistant against environmental changes, and they are for example also successful in highly disturbed rocky shores (Tomanek & Helmuth 2002).

The mussel habitat is characterized by less extreme vent flux than the tubeworm habitat, and we expected more species in relation to the tubeworm habitat. This pattern is observed for meiofauna, being very sensitive to environmental changes, but not for macrofauna. In contrast, the macrofauna diversity is lower than the meiofauna diversity, and lower than the macrofauna diversity at tubeworms. It is difficult to decipher, why this macrofauna pattern is observed as we find similar macrofauna species composition in both habitats.

At the mussel habitat, lower productivity might cause higher competition for food resulting in lower diversity of mussel associated macrofauna, as predicted by the intermediate productivity hypothesis (Grime 1973). However, this is extremely speculative since food availability has to our knowledge never been measured in the tubeworm and the mussel habitat.

Additional surface area provided by foundation species not only increases habitat complexity, but can also facilitate species coexistence and thus enhance diversity (Bruno & Bertness 2001). Mussels and tubeworms can build complex three-dimensional structures, creating many micro-niches. In studies on the effect of tube surface area on species richness, it was found that enhanced area favored species richness (Tsurumi & Tunnicliffe 2003, Govenar et al. 2005). Interestingly, larger tube surface area had no effect on meiofauna diversity (Gollner et al. 2007). There are no data available on mussel surface area. However, since the collected mussels for this study were smaller and less abundant than the collected tubeworms, we speculate that larger provided surface area and niches might cause enhanced macrofauna diversity at the studied tubeworm habitat. Mussel beds can also become several meters thick, similar to tubeworms. Therefore, we cannot predict that under all circumstances lower diversity in these aggregations is the rule. However, the mussel and tubeworm habitats are fundamentally different to the pompei worm and basalt habitat, as already discussed.

Comparison to previous meiofauna and macrofauna patterns along environmental gradients in marine habitats

Based on previous studies it has been concluded that different life traits might influence diversity. A comparison of the reaction of nematodes and macrofauna to changed disturbance and productivity in an mesocosm experiment revealed that the response of nematodes was not always similar to macrofauna (Austen & Widdicombe 2006). In a glacial fjord, taxonomic distinctness of macrofauna was U-shaped along the disturbance gradient, whilst nematodes showed a positive relationship. However, species richness was similar at all observed sites (Somerfield et al. 2006). Austen & Widdicombe (2006) and Somerfield et al. (2006) explained the different patterns to have been caused by the design of the experiment or by different sampling methods. They also stated that the different ecology of the groups could be a reason for the observed differences.

Another study observed meio- and macrofauna in carbonate systems and compared diversity of the sublitoral, flats, pools, and lagoons (Netto et al. 1999). Interestingly, in the examined place both, meio- and macrofauna consisted of nematodes and polychaetes. There were differences in diversity (meiofauna was more diverse), but interestingly diversity patterns along the observed habitats were changing in a similar way. This supports our view that not only size but also life traits (which were in this case similar) have major influence on diversity.

Conclusions

Our study shows that models predicting diversity should integrate body size related community traits, since intrinsic life traits of marine meio- and macrofauna result in different response of communities to changing productivity and disturbance. Here we attempted to scale the degree of productivity and disturbance experienced by animals of two different size classes and provided an explanation for the contrasting diversity patterns. Developing a model that incorporates intrinsic community traits that includes all living beings in an environment will be a future challenge to overcome.

ACKNOWLEDGEMENTS

This work was financed by the Austrian Science Foundation grant FWF (P20190-B17 to MB) and the National Science Foundation USA (OCE-0002729 to CR Fisher). The Captain and crew of the RV *Atlantis*, pilots and crew of the DSV *Alvin*, and scientists on board were helping us on several cruises to the East Pacific Rise. This work would not have been possible without the continuous help of numerous taxonomists (M Holzmann, G Panieri, D Danielopol, J Ott, A Vanreusel, P Martinez Arbizu, R Huys, VN Ivanenko, S Hourdez).

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Figure 1. Habitat types (basalt, mussel, tubeworm, pompei worm) and their hydrothermal vent flux characteristics, showing high flux at the pompei worm habitat and low flux at the mussel habitat. Box & Whisker plots demonstrate species richness and Shannon-Wiener diversity index (H'_{loge}) with standard error and standard deviation for meiofauna (white boxes) and macrofauna (grey boxes). Significant differences between meiofauna and macrofauna in a habitat are indicated by *, differences between the four meiofauna habitats (white boxes) are indicated by small case letters, differences between the four macrofauna habitats (grey boxes) are indicated by capital letters.

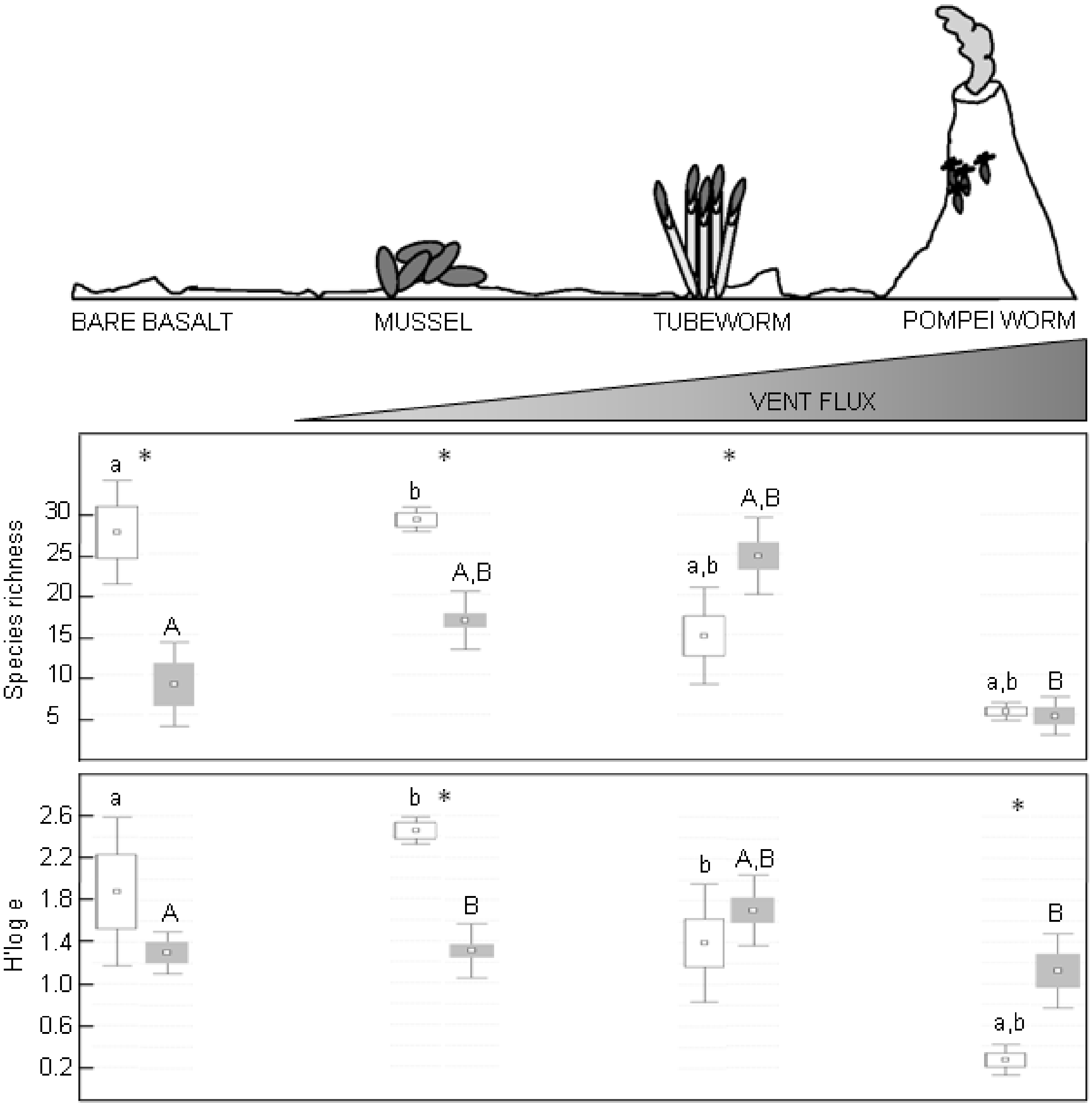

Table 1. Number of samples, total sampled area, total faunal abundance, abundance per 10 cm^2 (± standard deviation), total species richness (S), mean species richness (± standard deviation), and mean Shannon-Wiener diversity index H'_{loge} (± standard deviation) are shown for each habitat (P = pompei worm, T = tubeworm, M = mussel, B = basalt) for meiofauna and macrofauna.

	Meiofauna				Macrofauna			
	P	T	M	B	P	T	M	B
Number of samples	5	6	3	4	5	8	17	4
Total sampled area (cm^2)	565	4300	2770	1356	565	4900	9027	1356
Total abundance	10 394	35 842	20 882	2 654	188	119 933	35 017	477
Ab. (ind. 10 cm^{-2})	213±175	178±391	72±15	18±23	4±1	287±262	39±23	3±4
S total	11	31	36	64	8	44	51	22
S	5±1	14±6	29±2	28±6	5±2	25±5	17±4	9±5
H'_{loge}	0,3±0,1	1,4±0,6	2,5±0,1	1,9±0,7	1,1±0,4	1,7±0,3	1,3±0,3	1,3±0,2

Table 2. Number of species per taxon found in the axial summit trough (AST), in vent habitats (Vent), and in single habitats (P = pompei worm, T = tubeworm, M = mussel, B = basalt). Total number of species is shown for meiofauna, macrofauna, and all fauna. Relative percent (%) of species numbers is given for meio- and macrofauna.

	AST	**Vent**	**P**	**T**	**M**	**B**
Meiofauna						
Nematoda	26	10	0	5	10	23
Copepoda	49	33	10	19	19	32
Acari	1	1	0	0	1	0
Ostracoda	5	5	0	4	4	4
Foraminifera	6	3	1	3	2	5
Macrofauna						
Annelida	28	24	4	18	17	13
Arthropoda	10	9	1	4	8	4
Chordata	1	0	0	0	0	1
Cnidaria	1	1	0	0	1	0
Echinodermata	1	1	0	1	1	0
Mollusca	30	30	3	21	23	4
Nemertea	1	1	0	0	1	0
Total meiofauna	87	52	11	31	36	64
Total macrofauna	72	66	8	44	51	22
Total fauna	159	118	19	75	87	86
% meiofauna	55	44	58	41	41	74
% macrofauna	45	56	42	59	59	26

Appendix 1. Macrofauna species abundance per 10 cm^2 is shown for each sample from the pompei worm habitat (P1 – P5) and the basalt habitat (B1 – B4). For each species the taxon is given (AN = Annelida, AR = Arthropoda, CH = Chordata, MO = Mollusca). Bold numbers indicate abundance > 1 individual per 10 cm^2. (unid. juv. = unidentified juvenile).

species	taxon	P1	P2	P3	P4	P5	B1	B2	B3	B4
Alvinella caudata	AN	**1.06**	**0.35**	**3.37**	**2.54**	**1.21**				
Alvinella pompejana	AN	**3.10**	**1.31**	**2.48**	**6.76**	**3.03**				
Amphisamytha galapagensis	AN	0.09	0.06				0.53	0.68		0.05
Archinome rosacea	AN						0.20	0.27		
Branchinotogluma sp. 1	AN									0.22
Flabelliderma sp. 1	AN						0.02		0.04	0.03
Galapagomystides aristata	AN									0.05
Glycera tesselata	AN							0.15		
Hesiolyra bergi	AN	0.97	0.61	0.89	**3.38**	0.61				
Hesiospina vestimentifera	AN									0.05
Polychaete unid. juv.	AN									0.03
Polynoid polychaete unid. juv.	AN							0.04		
Lepidonotopodium williamse	AN									0.03
Nectochaeta larvae	AN			0.18						
Nereis sandersi	AN						0.13	0.11		
Nicomache arwidsoni	AN							0.11		
Ophryotrocha akessoni	AN	0.18	0.12	0.18		0.61	0.02			0.73
Paralvinella grasslei	AN	0.35	0.41	0.35	2.54					0.05
Syllidae sp. 1	AN						0.02			
Amphipod sp. 4	AR						0.02	0.04		
Bythograea thermydron	AR		0.06	0.00						
Dahlella caldariensis	AR									0.22
Typhlotanais sp.1	AR						0.02			0.22
Ventiella sulfuris	AR	**1.06**	**2.13**	0.18		**2.42**	0.07			**6.88**
Tunicat	CH								0.04	
Gorgoleptis spiralis	MO									0.03
Gastropod unid. juv.	MO						0.15	0.19		
Limpet unid. juv.	MO						0.11	0.23		0.11
Lepetodrilus ovalis	MO									0.11
Lepetodrilus cristatus	MO									0.03
Lepetodrilus elevatus	MO		0.03	0.35					0.19	0.81
Lepetodrilus galriftensis	MO		0.03	0.18						
Rhynchopelta concentrica	MO								0.04	0.16

Appendix 2. Results of bootstrapping (bt, 10 000 resamplings each) used to test for significant differences in total abundance 10 cm^{-2} (Ab.), species richness (S), and Shannon-Wiener diversity index (H'_{loge}) between the habitats P (pompei worm), T (tubeworm), M (mussel), and B (basalt) for meiofauna (Table A) and macrofauna (Table B). Table C shows bootstrapping results for meiofauna versus macrofauna in the four habitat types (P, T, M, B) tested for abundance (ind. 10 cm^{-2}), species richness (S), and Shannon-Wiener diversity (H'_{loge}). Higher (>) and lower (<) values of meiofauna (me) and macrofauna (ma) indices are indicated for each habitat. Significant results after classical Bonferroni-correction are marked in bold.

A

	Meiofauna		
Habitat	**Ab.**	**S**	**H'_{loge}**
P - T	0.29	**<0.001**	**<0.001**
T - M	0.81	**<0.001**	**<0.001**
M - B	**0.003**	0.58	0.07
P - M	**<0.001**	**<0.001**	**<0.001**
P - B	**<0.001**	**<0.001**	**<0.001**
T - B	0.32	**<0.001**	0.20

B

	Macrofauna		
Habitat	**Ab.**	**S**	**H'_{loge}**
P - T	**<0.001**	**<0.001**	**<0.001**
T - M	**<0.001**	**<0.001**	**0,001**
M - B	**<0.001**	**0.003**	0,93
P - M	**<0.001**	**<0.001**	**<0.001**
P - B	0.51	0.09	0.29
T - B	**<0.001**	**<0.001**	**0.002**

C

	Meiofauna-Macrofauna					
Habitat	**Ab.**		**S**		**H'_{loge}**	
P	**<0.001**	me >	0.476		**<0.001**	ma >
T	0.178		**<0.001**	ma >	0.180	
M	**<0.001**	me >	**<0.001**	me >	**<0.001**	me >
B	0.082		**<0.001**	me >	0.062	

Appendix 3. Distribution of macrofauna species in the habitats P (pompei worm), T (tubeworm), M (mussel), and B (basalt). The occurrence of species (indicated by the number 1) in their habitats in this study is compared to those of other studies. Other findings present additional occurrences of species. Reference is given for each habitat finding. The taxon is indicated for each species (AN = Annelida, AR = Arthropoda, CH = Chordata, CN = Cnidaria, EC = Echinodermata, MO = Mollusca). The type summarizes the overall occurrence of species in their habitat known so far: AST G = axial summit through generalist (species found on basalt and at least in one habitat at vents), B S = basalt specialist (species only found on basalt), V S = vent specialist (species only found in one habitat at vents), V G = vent generalist (species found in at least two habitats at vents and not on basalt).

Species	**taxon**	**TYPE**	**P**	**T**	**M**	**B**	**other findings**	**reference**
Amphisamytha galapagensis	AN	AST G	1	1	1	1	*Alvinella*, *Ridgea*, mussel, serpulid, periphery	Marcus & Tunnicliffe 2002, Micheli et al. 2002 Galkin & Goroslavskaya 2008
Ophryotrocha akessoni	AN	AST G	1	1	1	1	serpulid, periphery	Mullineaux et al. 2003, Govenar & Fisher 2007
Paralvinella grasslei	AN	AST G	1	1	1	1	*Alvinella*	Galkin & Goroslavskaya 2008
Ventiella sulfuris	AR	AST G	1	1	1	1	*Alvinella*, mussel, periperhy	Govenar & Fisher 2007, Galkin & Goroslavskaya 2008
Lepetodrilus elevatus	MO	AST G	1	1	1	1	*Alvinella*, mussel, serpulid, periphery	Micheli et al. 2002, Galkin & Goroslavskaya 2008
Bythograea thermydron	AR	AST G	1	1	1		periphery	Govenar & Fisher 2007
Archinome roscea	AN	AST G		1	1	1	*Alvinella*, mussel	Galkin & Goroslavskaya 2008
Galapagomystides aristata	AN	AST G		1	1	1	*Riftia*	Govenar et al. 2004
Hesiospina vestimentifera	AN	AST G		1	1	1	*Ridgea*, mussel, periphery	Marcus & Tunnicliffe 2002, Galkin & Goroslavskaya 2008
Lepidonotopodium williamse	AN	AST G		1	1	1	mussel	Galkin & Goroslavskaya 2008
Nereis sandersi	AN	AST G		1	1	1	*Riftia*	Govenar et al. 2004
Dahlella caldariensis	AR	AST G		1	1	1	*Alvinella*, mussel	Galkin & Goroslavskaya 2008
Gorgoleptis spiralis	MO	AST G		1	1	1	*Riftia*	Govenar et al. 2004
Rhynchopelta concentrica	MO	AST G		1	1	1	*Riftia*	Govenar et al. 2004
Ophiura	EC	AST G		1	1		periphery, mussel	pers. obs.

Species	**taxon**	**TYPE**	**P**	**T**	**M**	**B**	**other findings**	**reference**
Bathymagarites symplector	MO	AST G		1	1		*Alvinella*, mussel, periphery	Govenar & Fisher 2007, Galkin & Goroslavskaya 2008
Lepetodrilus pustulosus	MO	AST G		1	1		*Alvinella*, serpulid, periphery	Micheli et al. 2002, Matabos et al. 2008
Levensteiniella kincaidi	MO	AST G		1	1		*Ridgea*, periphery	Marcus & Tunnicliffe 2002
Typhlotanais sp.1	AR	AST G		1		1	no	
Lepetodrilus cristatus	MO	AST G		1		1	*Alvinella*, *Riftia*, mussel	Galkin & Goroslavskaya 2008, Matabos et al. 2008
Paralvinella pandorae	AN	AST G		1			*Ridgea*, periphery	Marcus & Tunnicliffe 2002
Nicomache arwidsoni	AN	AST G			1	1	periphery	Marcus & Tunnicliffe 2002
Clypeosectus delectus	MO	AST G			1		periperhy	Govenar & Fisher 2007
Glycera tesselata	AN	AST G				1	reported from vents	Hourdez pers. comm.
Branchinotogluma sp. 1	AN	B S				1	no	
Flabelliderma sp. 1	AN	B S				1	no genus reported at vents	Hourdez pers. Comm.
Syllidae sp.1	AN	B S				1	no	
Amphipod sp. 4	AR	B S				1	no	
Tunicat	CH	B S				1	no	
Nodopelta rignae	MO	V G	1	1			*Alvinella*	Desbruyères et al. 2006
Branchinotogluma sandersi	AN	V G		1	1		*Alvinella, Ridgea*	Govenar et al. 2002, Galkin & Goroslavskaya 2008
Branchinotogluma hessleri	AN	V G		1	1		*Riftia, Ridgea, Calyptogena*	Govenar et al. 2002, Desbruyères et al. 2006
Branchiplicatus cupreus	AN	V G		1	1		*Riftia, Calyptogena*	Desbruyères et al. 2006
Eulalia papillosa	AN	V G		1	1		*Riftia, Calyptogena*	Desbruyères et al. 2006
Iphionella risensis	AN	V G		1	1		mussel	Galkin & Goroslavskaya 2008
Lepidonotopodium riftense	AN	V G		1	1		*Riftia*	Govenar et al. 2004
Opisthotrochopodus alvinus	AN	V G		1	1		*Riftia*	Govenar et al. 2004
Alvinocaris lusca	AR	V G		1	1		*Alvinella*, mussel	Galkin & Goroslavskaya 2008, Matabos et al. 2008
Cyathermia naticoides	MO	V G		1	1		vestimentiferan, mussel	Micheli et al. 2002, Galkin & Goroslavskaya 2008
Eulepedopsis vitrae	MO	V G		1	1		mussel	Galkin & Goroslavskaya 2008
Lepetodrilus ovalis	MO	V G		1	1		*Alvinella*, mussel	Galkin & Goroslavskaya 2008
Melanodrymia aurantiaca	MO	V G		1	1		no	
Pachydermia laevis	MO	V G		1	1		*Alvinella*, mussel	Galkin & Goroslavskaya 2008, Matabos et al. 2008
Peltospira delicata	MO	V G		1	1		no	

Species	taxon	TYPE	P	T	M	B	other findings	reference
Peltospira operculata	MO	V G		1	1		*Alvinella*	Matabos et al. 2008
Hesiolyra bergi	AN	V S	1				*Alvinella*	Galkin & Goroslavskaya 2008
Lepetodrilus galriftensis	MO	V S	1				no	
Branchinotogluma grasslei	AN	V S		1			*Riftia*	Govenar et al. 2004
Lepidonotopodium atalantae	AN	V S		1			no	
Prionospio sandersi	AN	V S		1			*Riftia*	Desbruyères et al. 2006
Gorgoleptis emarginus	MO	V S		1			no	
Gymnobelia sp.1	MO	V S		1			no	
Helicoradomenia sp.1	MO	V S		1			no	
Neomphalus fretterae	MO	V S		1			no	
Glycerid	AN	V S			1		no	
Polychaete ganglionate	AN	V S			1		no	
Polychaete sp.1	AN	V S			1		no	
Amphipod sp. 1	AR	V S			1		no	
Amphipod sp. 2	AR	V S			1		no	
Amphipod sp. 3	AR	V S			1		no	
Pycnogonid	AR	V S			1		no	
Tanaid	AR	V S			1		no	
Anemony	CN	V S			1		no	
Aplacophora sp.1	MO	V S			1		no	
Aplacophora sp.2	MO	V S			1		no	
Levensteineri plicata	MO	V S			1		no	
Provanna cross hatch	MO	V S			1		no	
Provanna ios	MO	V S			1		no	
Provanna lineated	MO	V S			1		no	
Provanna riblet	MO	V S			1		no	
Nemertea	NE	V S			1		no	

CONCLUSION

Despite the high *in situ* primary production at hydrothermal vents and cold seeps, abundance of meiobenthos is low. This is in contrast to the working hypotheses that both ecosystems should support high meiofauna abundance, similar to what is known for the macrofauna (rejecting hypotheses 1 and 5). Competition for food and/or predation by rich macrofauna could be reasons. Interestingly, nematodes and copepods at mussel and tubeworm aggregations at hydrothermal vents were mostly primary consumers. Vent and seep meiofauna is taxon poor and includes copepods, nematodes, ostracods, acari, and foraminiferans. Additionally, at vents, platyhelminthes and folliculid ciliates were observed. Overall, similar to many other meiobenthic studies, nematodes and/or copepods dominate the communities in abundance and species richness.

Species richness of hydrothermal vent meiobenthos is similarly low as macrofauna (agrees with hypothesis 2). Meiobenthic diversity is inversely correlated to the environmental stress (vent flux) gradient (rejecting hypothesis 3). This questions the generally proposed unimodal diversity pattern along a disturbance gradient for vent meiofauna. It is suggested that with increasing temperature and toxic hydrogen sulfide concentration, fewer meiofaunal species are able to cope with these extreme conditions. This finding is supported by prior studies that investigated copepods and nematodes at different vent and non vent locations (Vanreusel et al. 1997, Tsurumi et al. 2003).

Most hydrothermal vent meiobenthic species are not endemics but generalists and can live in various vent habitats, in addition to the AST (axial summit trough) (rejecting hypthesis 4). This is in contrast to the bare basalt community where many species cannot migrate into vent habitats. One of these bare basalt specialists is *Smacigastes barti* Gollner et al. 2008, that does neither tolerate elevated temperatures nor the presence of hydrogen sulfide, and/or oxygen fluctuations.

Surprisingly, the community diversity pattern along an environmental stress gradient was hump-shaped for macrofauna but negatively-shaped for meiofauna, showing that models predicting diversity but neglecting species traits should not be used for marine ecosystems (rejecting hypothesis 6). We hypothesize that species body size and its related traits are the main underlying causes of diversity. Low productive systems can only sustain a high diverse small-sized fauna with short generation time and low food demands. Low physiological fitness of small sized meiofauna leads to a negative-to-stress correlated diversity pattern along the hydrothermal flux gradient. Macrofauna, with higher fitness and more lifestyle types, is less influenced by hydrothermal stress leading to a more complex, unimodal diversity pattern. Distinct reproduction strategies and food demands control vent communities' ecological state, resulting in a generalistic meiofauna but vent restricted macrofauna community.

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ACKNOWLEDGEMENTS

“If you feel good, your work is also good”. This motto from my supervisor Prof. Dr. Monika Bright is central to this PhD thesis. I thank Monika for the many great opportunities I had over the past few years, especially my two dives with the deep-sea submersible *Alvin*, exploring the incredible hydrothermal vents in 2500 meters depth. The research cruises in which I could participate and my international conference visits were real eye-opening experiences. My PhD research has been a rocky road, not in the least due to volcanic eruptions that required some rethinking. That was not always easy – but Monika you always supported and helped me, being both colleague and friend.

I am also grateful to the Marine Biology Department crew in Vienna: it is great fun being there!
Jörg Ott - thank you for your advices whenever ecological questions arose.
Ingrid, Sigrid, Irmi, Chrisi, Andrea, Bettina R, Bettina P, Harald and many more - thanks for inspiring discussions, helping when help was needed, and joyful days, evenings and nights!

Pedro Martinez Arbizu and his team at the DZMB in Wilhelmshaven (Germany) always gave me a very warm welcome and continuous help in identifying copepods. I always enjoyed my visits – I’ll be back, more than once!

Mama and Papa, you always encouraged me to go my own way. Andi – lovely brother with your crazy molecules. Van de Schootbrugge’s, my second family. Ju and Anna, my very close friends. Thank you all for your continuous support!

Bas - it is wonderful to explore life with you every day. You gave me tremendous support during my PhD, motivating me, being my mainstay, being critical and never careless about what I do. Thank you also for your understanding when I am traveling around the world for weeks due to my job. You are a very special person.

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2005	Final examination of studies of Biology (with excellence)
2003-2005	Master thesis at the Department of Marine Biology: Community study of tubeworm associated meiobenthos from two chemically different hydrothermal vents sites at the East Pacific Rise (supervisor Dr. Monika Bright)
1999-2005	Studies of Biology (Ecology) with main focus on Marine Biology at the University of Vienna, Austria
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Electron microscopy techniques (TEM and SEM, element analysis)
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2003 Participant in the marine ecological field course, marine biological station STARESO (Station de Recherches Sous-Marines et Océanographiques), Calvi, Corse
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Conferences

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2008 General Assembly European Geosciences Union, Vienna, Austria (invited talk)
2007 „13th international Meiofauna Conference“, Brasilia, Recife (talk, posters)
2006 General Assembly European Geosciences Union, Vienna, Austria (talk)
2005 „Third international Symposium on Hydrothermal Vent & Seep Biology“, San Diego, USA (posters)
2004 „Twelfth international Meiofauna Conference“, Italy, Ravenna (poster)

Publications

Govenar B, Le Bris N, Gollner S, Glanville J, Aperghis A, Hourdez S, Fisher CR (2005) Epifaunal community structure associated with *Riftia pachyptila* aggregations in chemically different hydrothermal vent habitats. Marine Ecology Progress Series 305: 67-77

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Submitted

Gollner S, Riemer B, Martinez Arbizu P, Le Bris N, Bright M (submitted) Community study of meiobenthos from the 9º50´N East Pacific Rise over the full range of hydrothermal vent flux

Bright M, Plum C, Riavitz LA, Nikolov N, Martinez Arbizu P, Cordes E, Gollner S (submitted) Epizooic metazoan meiobenthos associated with tubeworm and mussel aggregations from cold seeps of the Northern Gulf of Mexico.

In preparation

Gollner S, Bright M (in prep) Size matters – contrasting meio- and macrofauna diversity patterns at deep-sea hydrothermal vents