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DIPLOMARBEIT

Epizooic meiobenthic community structure associated with tubeworm and mussel aggregations at deep-sea cold seeps in the northern Gulf of Mexico

Zusammensetzung von epizooischen Meiobenthos-Lebensgemeinschaften assoziiert mit Röhrenwurm- und Muschelaggregationen an den Kalten Quellen der Tiefsee im nördlichen Golf von Mexiko

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INHALTSVERZEICHNIS

ABSTRACT (Deutsch)

Kalte Quellen der Tiefsee sind extreme Habitate, in denen die assoziierte Fauna hohen Konzentrationen an toxischem Sulfid und Methan und geringem Sauerstoff ausgesetzt ist. Während die Makrofauna-Gemeinschaften, assoziiert mit Ölen und Gasen, die best erforschten sind im Golf von Mexiko, ist die kleinere Größenklasse der Meiofauna so gut wie unbekannt. Um die Abundanzen, Diversität und die Zusammensetzung der mit Röhrenwurm- und Muschelaggregationen assoziiert Meiobenthos Gemeinschaft zu untersuchen, wurden sechs Proben in Atwater Valley in einer Tiefe von 2200 m im nördlichen Golf von Mexiko quantitativ gesammelt. Insgesamt wurden 119 Gattungen bestimmt, die von Nematoden und Copepoden dominiert wurden, während Ostracoden, Halacariden, Tanaiden, Kinorhynchen und Isopoden selten waren. Die Abundanzen waren sehr variabel, allerdings sehr gering (7 – 1839 Ind. 10 cm^{-2}) und damit ähnlich denen von den Meiobenthos-Gemeinschaften der Hydrothermalquellen, jedoch geringer als jene der Infauna der Sedimente der Kalten Quellen. Die Anzahl der Gattungen war unterschiedlich und reichte von 44 bis zu 77 in den Röhrenwurmaggregationen und von 22 bis 48 in den Muschelaggregationen. Die Diversität, bei den Röhrenwurmhabitaten ($H'_{\log e}$ 2.46 – 3.66) war leicht höher als bei den Muschelhabitaten ($H'_{\log e}$ 2.11 – 2.97), aber nicht signifikant. Dieser Trend wurde auch bei der assoziierten Makrofauna gefunden und ist kennzeichnend für die dort vorherrschenden Bedingungen. Obwohl die Fauna, assoziiert mit Muscheln höheren Suldifkonzentrationen ausgesetzt ist als jene der Röhrenwürmer, verbessern beide Organismen die umgebenden Bedingungen indem sie das meiste austretende Sulfid selber aufnehmen. Die assoziierte Meiofauna der Kalten Quellen, ist eine diversere und geringere gestresste Gemeinschaft und ähnelt viel mehr der Infauna der umgebenden Tiefsee als der Infauna von Kalten Quellen oder der assoziierten Meiofauna von Hydrothermalquellen, da letztere Gemeinschaften hohen Sulfidkonzentrationen ausgesetzt sind.

EINLEITUNG

Seit der Entdeckung der ersten Kalten Quellen, so genannte *cold seeps*, im Jahre 1984 im Golf von Mexiko (Paull et al. 1984), wurden viele solcher Ökosysteme weltweit gefunden und jedes Jahr folgen neue Berichte über weitere Auffindungen. Kalte Quellen entstehen dort wo Gemische aus Ölen und Gasen, wie Methan und Sulfid aus den Bodensedimenten hervortreten. Kalte Quellen sind weit verbreitet und kommen weltweit, gekoppelt an unterschiedliche geologische Prozesse, sowohl an aktiven als auch passiven Kontinentalrändern in Tiefen zwischen < 15 m und > 7000m vor (Sibuet & Olu 1998, Levin 2005). Von Hydrothermalquellen der Tiefsee, so genannten *hot vents*, unterscheiden sich *cold seeps* deutlich durch wesentlich geringere Temperaturen und langsamere Austrittsgeschwindigkeiten der Flüssigkeiten und Gase (Tunicliffe et al. 2003).

Der Golf von Mexiko liegt auf einem passiven Kontinentalrand und beinhaltet die am besten erforschten Kalten Quellen überhaupt. Ihre Entstehung ist komplex, da dem Golf von Mexiko eine dichte Salzschicht zugrunde liegt. Salzbewegungen sind in dieser Region die Hauptursache für das Austreten von Ölen und Gasen aus dem Sediment. Da Salz dichter ist als das darüber liegende akkumulierte Sediment, drücken daraus entstehende Salzstöcke nach oben und verursachen starke Risse und Spalten im Sediment, wodurch es zum Austritt von Gasen und Ölen aus dem Sediment kommt. Auch Salz tritt an die Sedimentoberfläche aus und bildet dichte Salzseen, so genannte *brine pools* (McDonald et al. 2003, Fisher et al. 2007, Cordes et al. 2007).

Die Kalten Quellen der Tiefsee bilden mit ihrer assoziierten Fauna einen Ort mit erhöhter Primärproduktion und ein Refugium für eine einzigartige Organismenwelt in einer ansonsten monotonen und nährstoffarmen Tiefsee (Sarrazin & Juniper 1999, Bergquist et al 2003). Alle an Kalten Quellen lebenden Organismen müssen an die gegebenen chemischen Bedingungen, wie erhöhte Sulfid- und Methankonzentrationen, sowie geringe Sauerstoffkonzentrationen angepasst sein (McMullin et al. 2000, Hourdez & Lallier 2007). Trotz dieser relativ rauen Bedingungen, zeichnen sich die Lebensgemeinschaften der Kalten Quellen durch eine hohe Biomasse aus, wobei die Diversität vergleichsweise sehr gering ist (Sibuet & Olu 1998, Levin 2005). Sedimente der Kalten Quellen beherbergen oft ein Konsortium an Bakterien, die große Mengen an Sulfid bilden. Da Sulfid für die meisten Organismen toxisch ist (Bagarinao 1992), ist die Verbreitung der Lebensgemeinschaften und die Artenzusammensetzung stark von dessen Mengen und Vorkommen beeinflusst (Sahling et al. 2002, Levin 2003). Zwei Gruppen von Megafauna, die in Symbiose mit chemoautotrophen und/oder methanotrophen Bakterien leben, dominieren die Kalten Quellen: Vestimentifera, Röhrenwürmer aus der Familie Siboglinidae, Muscheln der Gattung *Bathomodiolus* aus der Familie Mytilidae. Die Röhrenwürmer beherbergen Endosymbionten welche Sulfid als Energiequelle nutzen, während die Endosymbionten einiger *Bathymodiolus* Arten Sulfid oder Methan oder beides als Energiequelle nutzen (Fischer et al. 1997, Childress et al. 1986, Cordes et al. 2009). Muscheln und Röhrenwürmer bilden dichte Aggregationen, die wiederum als eigene Habitate für andere Lebensgemeinschaften unterschiedlicher Größenklassen dienen. Diese dreidimensionalen biogenen Strukturen bieten Lebensraum, Nahrung, und Schutz vor Räubern sowie vor Umweltstress (Bruno & Bertness 2001, Fisher et al. 2007). Röhrenwürmer und Muscheln siedeln dort, wo die Konzentrationen von Methan und Sulfid hoch sind, allerdings halten sie diese niedrig, da sie das meiste der Gase absorbieren bevor sie an die Sedimentoberfläche gelangen oder diese in der Wassersäule absorbieren (McDonald et al. 1989, Scott & Fisher 1995, Nix et al. 1995, Julian et al. 1999, Bergquist et al. 2003). Die Röhrenwürmer nehmen das Sulfid bereits schon innerhalb des Sedimentes auf durch „wurzelähnlicher Verlängerung“ ihrer Körper ins Sediment (Julian et al. 1999) und die Muscheln beziehen es aus dem ihnen umgebenden Wasser (Brand et al. 2007, Cordes et al submitted).

Die assoziierte Makrofauna im Golf von Mexiko ist relative gut bekannt da bereits mehrere Studien darüber durchgeführt wurden, die über eine sehr hohe Abundanz berichten (Cordes et al 2007, Cordes et al submitted). Von welchen Arten solche Aggregationen besiedelt werden, hängt vor allem von den Mengen an Sulfid und Methan ab, die sich im Wasser um die Muscheln und Röhrenwürmer befinden (Bergquist et al. 2003, 2005, Cordes et al. 2005, Cordes et al. 2006). Nichts ist hingegen bekannt über das assoziierte Meiobenthos, obwohl es in benthischen Gemeinschaften von wichtiger Bedeutung ist. Es umfasst Tiere und Protisten in der Größenklasse zwischen 32 µm und 1 mm (Gerlach 1971, Giere 2009). Wie in den meisten anderen marinen Lebensräumen auch, sind die Nematoden die dominanteste Gruppe des Meiobenthos von Kalten Quellen, gefolgt von den Copepoden (Giere 2009). Auch andere Taxa der Meiofauna, wie Ostracoden, Halacariden, Gnathostomuliden, aber auch Turbellarien, zählen zur *cold seeps* Gemeinschaft (Powell et al. 1981, 1983). Auf Grund der relativ jungen Forschungsgeschichte der Meiofauna von chemosynthetischen Systemen existieren bisher nur wenige Arbeiten über diesen wichtigen Bestandteil der benthischen Fauna an Kalten Quellen.

Alle bisherigen Studien beziehen sich auf jene Meiobenthosgemeinschaften, die das Sediment bewohnen, die so genannte Infauna. Meistens werden dabei lediglich Abundanzen oder Biomassen der höheren Taxa beschrieben und nur ansatzweise die Diversität auf Artniveau bestimmt. Studien, die Diversitätsmuster beschreiben, beziehen sich hauptsächlich auf die Artenzusammensetzung der Nematoden. Resultate der Sedimentinfauna zeigen meist eine erhöhte Abundanz mit geringer Diversität und hoher Dominanz (z.B. VanGaever 2006,2009a, 2009b). Bright et al. (submitted) gaben als erste einen Einblick in die mit Muscheln und Röhrenwürmern assoziierten Meiobenthosgemeinschaften im Golf von Mexiko. Die Abundanzen des Meiobenthos waren sehr gering (gewöhnlich < 100 Ind. 10 cm^{-2}) und bestanden lediglich aus 4 höheren Taxa: Nematoda, Copepoda, Halacaridae und Ostracoda. Allerdings ist die Artenzusammensetzung und somit die Diversität dieses epizooischen Meiobenthos noch unbekannt.

Die vorliegende Studie identifiziert und quantifiziert als erste die gesamte Meiobenthosgemeinschaft assoziiert mit Muschel- und Röhrenwurmhabitaten im nördlichen Golf von Mexiko. Folgende Fragen sollen damit beantwortet werden: 1. Ist die Abundanz der Meiobenthosgemeinschaft hoch oder niedrig und was sind die Ursachen? 2. Ist die Diversität hoch oder niedrig und wovon ist eine hohe oder niedrige Diversität abhängig? 3. Gibt es Unterschiede in der Gemeinschaftsstruktur zwischen dem assoziierten Meiobenthos und der Sedimentinfauna an den Kalten Quellen?

Um jene Fragen beantworten zu können, wurden jeweils drei Proben von Muschel- und Röhrenwurmaggregationen und ihrer assoziierten Fauna in Atwater Valley (AV) im nördlichen Golf von Mexiko in einer Tiefe von ungefähr 2200 m, gesammelt. Mit Hilfe des bemannten U-Boots DSV *Alvin* und dem ferngesteuerten Roboter ROV *Jason* und unter Einsatz zweier speziell entwickelter Geräte, dem „Bushmaster Jr.“ (Bergquist et al. 2003) zur Beprobung von Röhrenwurmaggregationen und dem „Mussel Pot“ (Vandover et al. 2002) zur Beprobung von Muschelaggregationen, wurden quantitativ Proben gesammelt. An Bord der Schiffe R/V *Atlantis* und R/V *Ronald H. Brown* wurde die assoziierte Fauna mit gefiltertem Seewasser von der Megafauna gespült und anschließend gesiebt, um die kleinere Größenklasse von der Macrofauna zu trennen. Anschließend wurde das Meiobenthos in 4% Formalin fixiert und nach Wien für weitere Analysen gebracht. Die Proben wurden unter einem Stereomikroskop untersucht und die sich darin befundenen Organismen wurden gezählt und nach höheren Taxa geordnet. Anschließend wurden die Tiere auf Objektträger fixiert und unter einem Lichtmikroskop auf Gattungsniveau bestimmt. Aus den so gewonnen Daten wurde die Abundanz des Meiobenthos kalkuliert, die Diversität bestimmt und weitere univariate und multivariate Analysen durchgeführt.

Mit dieser Studie wurde es zum ersten Mal möglich die Meiobenthosgemeinschaften, assoziiert mit Muscheln- und Röhrenwürmerhabitaten dieses außergewöhnlichen Ökosystems zu charakterisieren.

Epizooic meiobenthic community structure associated with tubeworm and mussel aggregations at deep-sea cold seeps in the northern Gulf of Mexico

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*Extraction and counting of meiofauna, identification of higher taxa, identification of nematodes, statistical analyses, developed concept of manuscript with M. Bright & S. Gollner, writing of manuscript

ABSTRACT

Deep-sea cold seep are considered to be extreme environments where the associated fauna is exposed to high levels of toxic hydrogen sulfide, high concentrations of methane and low oxygen concentrations. While macrofaunal communities associated with extensive hydrocarbon oil and gas seeps in the Gulf of Mexico are one of the most well studied, the smaller size class of meiofauna is virtually unknown. To study the abundance, diversity, and community structure of mussel and tubeworm associated epizooic meiobenthos, a total of six quantitative samples were collected at Atwater Valley in 2200 m depth in the northern Gulf of Mexico. A total of 119 genera were identified, dominated by nematodes and copepods, and ostracods, halacarids, tanaids, kinorhynchs and isopods were rare. Abundances were highly variable but overall very low (7 - 1839 ind. 10 cm^{-2}) and similar to epizooic communities at vents but much lower than those of infaunal seep communities. Genera richness was variable and ranged from 44 to 77 in tubeworm bushes and from 22 to 48 in mussel beds. The diversity was slightly higher but not significantly different in tubeworm bushes ($H'_{\log e}$ 2.46 – 3.66) than in mussel beds ($H'_{\log e}$ 2.11 – 2.97), a trend also found in the associated macrofauna communities corresponding well to environmental conditions. While seep epifauna hosted by mussels experience higher levels of toxic sulfide than those at tubeworms, overall both habitats ameliorate the environmental conditions by taking up most of the sulfide-emanations. The associated seep meiobenthos is a higher diverse and low stressed and disturbed benthic community and much more similar to the surrounding deep-sea infauna than to the low diverse seep infauna and vent epifauna, both exposed to high levels of toxic sulfide and low oxygen.

INTRODUCTION

Extreme environments such as deep-sea cold seeps and hydrothermal vents are characterized by relatively low diversity and high biomass. At cold seeps, sediments are fueled with high concentrations of methane and high levels of hydrogen sulfide but have low oxygen concentrations (Sibuet & Olu 1998, Levin 2005). Because hydrogen sulfide is toxic to most organisms (Bagarinao 1992) the diversity and the distribution of faunal communities are strongly affected by sulfidic conditions (Sahling et al. 2002, Levin 2003). Most faunal investigations at seeps have focused on large megafaunal communities such as the chemoautotroph vestimentiferan tubeworms and mytilid mussels (Sibuet & Olu 1998, Levin 2005) and their distribution and abundance has been connected to the rate of methane and sulfide (McDonald et al., 1989, Sibuet & Olu 1998).

Environmental conditions such as fluctuating physico-chemical conditions, food availability, competition and predation have strong influence on diversity. In very stressful habitats, diversity is low and directly regulated by the physical environment. Highest diversity is found at intermediate stress levels where competition of mobile and sessile species plays an important role, whilst in benign environments, under the influence of predation effects, low diversity is expected (Menge & Sutherland 1987, Bruno & Bertness 2001, Scrosati & Heaven 2007). Habitat heterogeneity also plays an important role in decreasing or increasing diversity (Therriault & Kolasa 2000). The "habitat heterogeneity hypothesis" states that structurally complex habitats support an increase in species diversity due to the provision of more niches and diverse ways of exploiting environmental resources (MacArthur & Wilson 1967). Habitat-forming foundation species increase the complexity of a habitat and can alter the environment in ways that reduces stress or disturbance, thereby creating suitable living conditions for other species, which would not otherwise have been able to exploit the habitat (Jones et al. 1994, 1997). Such mussel beds and tubeworm bushes provide living space, favourable settlement conditions, food resources and refuge from predators (see Bruno & Bertness 2001, Fisher et al. 2007).

Various communities such as macro- and meiofauna inhabit as infauna reduced seep sediments and/or live as epifauna in association with foundation species such as mussels and tubeworms. Vestimentiferan tubeworms and mytilid mussels settle where sulfide and methane are abundant but keep these chemical compounds within and around their aggregations low (Cordes et al. 2009). Vestimentiferans are able to take up sulfide already beneath the sediment surface due to the posterior growth of their tubes into the substrate (Julian et al. 1999, Freytag et al.2001) and mytilid mussels obtain sulfide from the surrounding water through their gills (Brand et al. 2007, Cordes et al submitted).

In the Gulf of Mexico (GoM) many cold seep communities were described and new seep sites continue to be discovered. Hydrocarbon seeps in the Gulf of Mexico are complex as they are generated due to salt tectonics which causes deep cracks and faults that carry gases, petroleum and brines upward from the sub-bottom to the sediment surface (Kennicutt et al. 1988, McDonald et al. 2003, Fisher et al. 2007). Recently, studies on hydrocarbon seeps on the lower continental slope (> 1000 m depth) were conducted, including the lately explored seeps in Atwater Valley (AV) (McDonald et al. 2003, Cordes et al. 2007, Roberts et al. 2007). The macrobenthic communities associated with tubeworm and mussel communities are well studied in the Gulf of Mexico and are known to be highly abundant within these aggregations (Bergquist et al. 2003, Cordes et al., 2005, 2007). The number of species of associated macrobenthos is usually below 100 (e.g. Bergquist et al. 2003a, 2005 Cordes et al. 2005, 2007, Cordes et al. sumitted). In contrast, nothing is known about the associated smaller size class.

To date, all meiofaunal seep studies concentrated on communities inhabiting seep sediments. These investigations documented meiobenthic infaunal communities that dwell in sediments covered by bacterial mats at shallow seeps (Montagna & Spies 1985, Powell et al. 1983, Palmer et al. 1998) and at greater depths (Robinson et al. 2004, Van Gaever 2006, Sergeeva & Gulin 2007, Van Gaever 2009a). Meiofauna living in sediments underneath siboglinid tubeworms (Soltwedel et al. 2005, Van Gaever 2006, Van Gaever 2009a) and vesicomyid clams (Shirayama & Ohta 1990, Olu et al. 1997, Sommer et al. 2007) were also studied. General patterns arising from these investigations show mostly enhanced meiofaunal abundances (e.g. Olu et al. 1997, Soltwedel et al. 2005, Van Gaever et al 2006, Van Gaever et al. 2009a). Several studies concentrated on the diversity of nematodes, which exhibited low species richness and high dominance of single species relative to non-seep conditions (for details see Vanreusel et al. submitted).

Bright et al. (submitted) reported the first abundance data of epizooic, metazoan meiobenthos in the Gulf of Mexico and documented a remarkably low meiobenthic abundance represented by few higher taxa. In this study we investigate in detail the diversity and abundance of the entire metazoan epizooic meiobenthos associated with three mussel and three tubeworm aggregations at deep-sea cold seeps in the northern Gulf of Mexico.

We hypothesize that tubeworm and mussel aggregations create a relatively low stressed and low disturbed habitat in an otherwise toxic environment and therefore will support highly diverse meiobenthic communities. In addition, we compare the community patterns of the epizooic meiobenthos to the studies of sediment infauna at cold seeps.

MATERIAL AND METHODS

Study site

Collections at two different hydrocarbon seeps were obtained during cruises in 2006 and 2007 at Atwater Valley (AT 340) on the lower continental slope of the northern Gulf of Mexico. Atwater Valley is located south of the Mississippi Canyon (Cordes et al. 2007) and consists of a bathymetric high with three mounded areas on the eastern edge of the Mississippi Canyon along its transition from a canyon to a submarine fan. Three samples were collected at mussel aggregations dominated by *Bathymodiolus brooksi* Gustafson, Turner, Lutz & Vrijenhoek 1998 and three samples were collected from tubeworm aggregations consisting of *Escarpia laminata* Jones 1985 and *Lamellibrachia ssp.*.

Sample collections

Mussel and tubeworm aggregations were collected using the submersible DSV *Alvin* supported by RV *Atlantis* in 2006 and using the ROV *Jason* supported by the NOAA Ship *Ronald Brown* in 2007. Three quantitative samples of mussel aggregations were taken: M-AV1, M-AV2 and M-AV3 (Table1) using the hydraulically actuated “mussel pot” sampling gear. The sampling pot (531 cm^2 surface area, 26 cm diameter) was lined with a tightly net (Van Dover 2002, Cordes et al. 2010) and pushed into a mussel bed until it reached the sediment bottom and was closed. Also, three quantitative samples of tubeworm aggregations, T-AV1, T-AV2 and T-AV3 (Table1) were taken with the hydraulically actuated “Bushmaster Jr.”, lined with a 63 µm net, 2800 m^2 surface area (Berquist et al. 2003, Gollner et al. 2007). The Bushmaster device was manoeuvred over a tubeworm aggregation and was then tightly closed. To avoid loss of animals during the transport to the surface, the collected samples were separately placed into plastic boxes on the baskets of the submersible/ROV.

On board of the research vessels, mega- and macrofauna were immediately washed with 32 µm filtered seawater to extract the associated fauna and the sediment. The samples were sieved through a set of 1 mm to separate the meiofauna from macrofauna. The volume of sediment, which was trapped between mussels and tubeworms, of the fraction smaller than 1 mm was measured and then sieved through a net with 32 µm mess size. The retained meiofauna was then fixed in 4% buffered formalin. The larger size fractions were saved for additional studies by collaborators (see Cordes et al. 2010). Mussels and tubeworms were identified, counted and measured on board of the ship.

Quantification of abundance

In the laboratory the samples were centrifuged to separate the meiofauna from the sediment by using a density centrifugation technique with a medium consisting of a Silicapolymer (Fa. Levasil®) mixed with Kaolin (McIntyre and Warwick, 1984; Veit-Koehler, 2008). Due to the high sediment volume of the samples T-AV1 (7,5 l total volume), M-AV2 (3,6 l total volume) and M-AV3 (390 ml total volume), these samples were subsampled by haphazardly splitting the samples. The samples T-AV2, T-AV3 and M-AV1 were totally processed.

Meiofaunal organisms were counted under a dissecting microscope and identified to the lowest possible taxonomic classification. If present, 300 individuals per taxon were randomly picked out from each sample while the remaining organisms were counted only. The Nematoda were mounted on glycerine slides and identified to genus level according to Platt & Warwick (1983), Platt & Warwick (1988), and Warwick et al. (1998). The Copepoda, were mounted on glycerine slides and identified according to Huys et al. 1996 and Boxshall & Halsey 2004. All other taxa (Ostracoda, Tanaidacea, Halacaridae) were sent to specialists for further identification. The abundance of temporary meiofauna and the presence of benthic foraminiferans were recorded but were not included in this study of the permanent metazoan meiobenthos. Crustacean nauplii were also collected but only included in analyses of the abundance of higher taxa due to the difficulty of identification of these animals. As a result of detailed identifications of meiofauna to the genus level, there are minor differences in abundance data of halacarids and ostracods than those reported in Bright et al. submitted due recognition of dead animals, empty carapaces, or isolated valves. In order to make comparisons between the samples and to other meiofauna investigations, all abundance data were standardized to 10 cm^2 sample area.

Ecological indices and statistical analyses

Genera richness (G), the diversity indices Pielou's evenness (J'), Shannon-Wiener diversity ($H'_{\log e}$) and estimated genera richness (EG(n)) were calculated from genera abundance data using Primer v6 package (Clarke, KR, Gorley, RN, 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth). The same software was used to generate cumulative *k*-dominance curves to establish dominance patterns and genus heterogeneity within the two different habitats.

Student's t- tests were performed to assess significance in abundance, genera richness, Pielou's evenness, sediment volume, tubeworm- and mussel surface area and relative abundance between the two habitats. To follow a normal distribution, data were square-root transformed for abundance and genera richness, ln transformed for sediment volume and surface area, and arcsine transformed for relative abundance. Due to the small number of samples and high variances, bootstrapping was also used to test for significant differences between the habitats for each parameter (10000 resamplings each, t-test, 2-sided test, routine ”FTBOOT” from the package ”computer intensive statistics” (Nemeschkal, 1999).

Hierarchical clustering and non-metric multidimensional scaling (MDS) ordination using PRIMER v6 was performed to establish similarity and dissimilarity between and within tubeworm- and mussel aggregations using a Bray-Curtis similarity matrix generated from standardized and square-root transformed genera abundance data to facilitate the contribution of the less common genera and to down- weigh the highly abundant genera (Bray & Curtis, 1975, Clarke & Warwick, 2001). One-way analysis of similarities (ANOSIM) was performed to test for significant differences in the community structure between the two habitats. To determine which genera have the greatest contribution to similarities within a habitat and dissimilarities between habitats, SIMPER (similarity percentage) analyses were carried out.

Several correlations were done to determine whether a significant relationship existed between surface area and total meiobenthos, nematode and copepod abundance and genera richness using Pearson’s r (F-value and t-value calculations by STATISTICA). The same analyses were performed with the volume of sediment. All results were classical Bonferroni-corrected (p = alpha/n; alpha = 0.05).

RESULTS

Abundances

A total of six samples of associated permanent metazoan meiobenthic communities from tubeworm- and mussel aggregations, three samples from each habitat, were studied at Atwater Valley cold seeps in the northern Gulf of Mexico. The total abundances of meiobenthos were highly variable and not significantly different between the two different habitats. They ranged between 1903 to 126 325 individuals per sample (Table 2) and were positively correlated with the total volume of the sediment ($r^2 = 0.80$, $p = 0.02$) (Fig.1). No correlation of abundance and surface area of tubes and mussel shells was found ($r^2 = 0.01$, $p = 0.86$). Also, when standardized to 10 cm^2 sample area, we found no significant difference in abundance between tubeworm and mussel aggregations ($p = 0.13$), in mussel beds between 73 and 1839 ind. 10 cm^{-2} and in tubeworm aggregations 7 to 451 ind. 10 cm^{-2} were found (Table 2).

Nematodes and copepods dominated at both habitats in all samples, followed by nauplii and ostracods. Halacarids and tanaids occurred at both sites but not in all samples. Isopods and kinorhynchs were only found at the tubeworm aggregation T-AV3 (Table 2). Foraminferans were present at every habitat type but were excluded from this study of permanent metazoan meiobenthos. Nematodes and copepods were significantly correlated with the total volume of sediment (both: $r^2 > 0.70$, $p = 0.02$) but not with the surface area of the foundation species (both: $r^2 = 0.01$, $p > 0.8$).

Between 47 and 1650 nematode ind. 10 cm^{-2} were found in mussel beds, while only 4 to 370 ind. 10 cm^{-2} were found in the tubeworm bushes. Similarly, the copepods were more abundant in mussel- (10 to 162 ind. 10 cm^{-2}) than in tubeworm aggregations (3 to 73 ind. 10 cm^{-2}) (Table 2). However, these differences were not significant (nematodes: $p = 0.12$; n.s., copepods: $p = 0.18$; n.s.). The same trend was found for nauplii with 15 to 28 ind. 10 cm^{-2} at mussel aggregations, and ≤ 3 ind. 10 cm^{-2} at tubeworm aggregations. Members of other taxa showed a low contribution to the meiobenthos (< 1 ind. 10 cm^{-2}), except the ostracods at sample T-AV1 with 2 ind. 10 cm^{-2} and at sample M- AV2 with 3 ind. 10 cm^{-2}.

Also, the relative abundance of the two most dominant taxa, nematodes and copepods, was not statistically discernable between the two habitats (nematodes: $p = 0.25$; n.s., copepods: $p = 0.006$; n.s.). At both habitats nematodes dominated with 60 to 80 %, followed by the copepods with 16 to 38 % in tubeworm bushes and 65 to 90 % in mussel beds followed by the copepods with 9 to 13 %. The relative abundance of nauplii varied considerably in mussel beds (1 to 21 %), while it was similar, but relatively low (1 to 3 %) in tubeworm bushes (Fig.2). Other taxa showed at values of less than 1 % for relative abundance.

Diversity indices

We identified a total of 119 genera (belonging to 54 families); 58 genera occurred at the mussel habitat and 108 at the tubeworm habitat (Table 3). Genera richness (G) and the values of Pielou' evenness (J), Shannon- Wiener (H'log e), and EG (300) indices are listed in Table 4.

Genera richness was neither positively correlated with surface area of the tubeworm tubes and mussel shells ($r^2 = 0.47$, $p = 0.10$) (Fig.3), nor with the sediment volume ($r^2 < 0.01$, $p = 0.90$). It ranged between 44 and 77 genera in tubeworm bushes and was higher than in mussel beds (G 22 to 48) but this was not significant. Pielou's evenness ranged from 0.59 to 0.84 in tubeworm aggregations. In mussel beds, Pielou's evenness values were between the lowest and highest values of tubeworm bushes (0.67 to 0.76). Shannon-Wiener indices were relatively high at both sites (H'log e 2.11 to 3.66).

Nematode genera richness was high at the tubeworm field varying from 27 to 43 and high at the mussel aggregation M-AV1 (30 genera), whereas at the two other samples, M-AV2 and M-AV3 a low value was observed (both 16). The same pattern was observed for the copepods, where the number of genera was higher at the tubeworm habitat (13 to 30 genera) than at the mussel bed (5 to 15).

The tubeworm habitat was characterized by a genus rich nematode association. Representing 2.5 to 33.6 % of total meiobenthic genera, *Desmodora* was the most abundant meiobenthic genus. *Leptolaimus* had a relative abundance of 1 to 7.2 % and *Daptonema* of < 1 to 8 %. *Comesa* was only high in abundance in one sample (18 % of total meiobenthic genera in T-AV1) as well as *Oncholaimus* (8.7%) and *Prochromadorella* (6.5%) in T-AV2. Further, the nematode community in tubeworm aggregations consisted of *Odontanticoma* (9 and 3.1 %) and *Calyptronema* (8.5 and 5.6 %) in the samples T-AV2 and T-AV3, respectively. No other genera contributed more than 5 % to the total abundance in any sample in this habitat (Table 3). The mussel beds were inhabited by a slightly different nematode community, which was characterized by less but more dominant species: *Paracanthonchus* (2.7 – 27.5 %), *Thalassomonhystera* (11.8 – 21.1 %), *Linhomoeus* (2.2 – 22.4 %). However, the two habitats shared two abundant genera *Leptolaimus* and *Desmodora* (Table 3).

Overall 48 copepod genera were identified, with the harpacticoids being the dominant copepod taxon with a contribution of 40 genera. The genus *Amphiascella* dominated at T-

AV2 (14.6 %) and T-AV3 (8.4 %), while at T-AV-1 the relative abundance is low (< 1 %). At the mussel bed the most abundant harpacticoid genus was *Ameira* (5.3 – 7.9 % of the meiobenthic abundance). The other 8 copepod genera belonged to the cyclopoids (5 genera), calanoids (2 genera), and poecilostomatids with the parasitic genus *Enalcyonium* that had a relative abundance of 8.6 to 19.3 % in tubeworm samples and 2.5 to 6.3 % mussel samples. The relative abundance of the copepodites of the total meiobenthos was 6.2 – 18.6 % at the tubeworm and 2.5 – 6.2 % at mussel habitat.

Halacarids as well as tanaidacaeas were represented by a single genus each at both habitats; *Copidognathus* and *Pseudotanais*, contributed less than 1 % to the total meiobenthic abundance, but were not found in each sample. *Xylocythere* was the most dominant ostracod genus occurring at all six samples but with low abundances (< 1 %). The other ostracod genera (7) were rare. Further, one individual of kinorhynchs identified as *Echinoderes* and one individual of isopod, which was unidentifiable due to bad fixation, were found at T-AV3 (Table 3).

Community pattern

An MDS plot based on the meiobenthic genera abundances revealed a cluster of two mussel bed samples (M-AV2 and M-AV3), while the other mussel bed sample and the three tubeworm samples together were clearly separated from each other (Fig. 4). Figure 5 shows a dendrogramm on genera level where the two mussel bed samples (M-AV2 and M-AV3) are grouped together, whilst the third mussel bed sample clusters with the three tubeworm samples.

Results of the SIMPER analyses separated the two habitats from each other with an average dissimilarity of 64.87 %. The nematode genera *Paracanthonchus* and *Desmodora* contributed with 5.43 %, and 4.21 % respectively, the most to the dissimilarity of the two habitats, followed by the copepod genus *Amphiascella* with 3.93%. At the tubeworm field the average similarity was 40.43 %. The nematode genus *Desmodora* contributed on average 10.63 % to the similarity of the three samples. The mussel habitat showed a higher average similarity of 57.11 %. The nematode genus *Thalassomonhystera* contributed with 15.31 % to the similarity of the three mussel aggregations. The communities were compared by a one-way, crossed ANOSIM but the analysis did not point out any significant difference (global R = 0.63, p = 0.1) between the two habitats.

The genera-level *k* –dominance curve based on the richness of genera for all six samples revealed dominance by a single genus for the samples T-AV1, M-AV2 and M-AV3, whereas the lowest curve of sample T-AV3 described the lowest dominance and highest diversity (Fig. 6).

DISCUSSION

The permanent metazoan epizooic meiobenthos associated with tubeworm- and mussel aggregations at deep-sea cold seeps in the northern Gulf of Mexico can be characterized as a relatively genus rich hard substrate community represented by 7 higher taxa, occurring in low abundance. Interestingly, these patterns of epizooic meiobenthic cold seep communities are much more similar to those found in deep-sea sediments but differ from those reported for cold seep sediments, where the meiobenthic infauna shows much higher abundances but lower diversity. The high diversity found at these hard substrate cold seep communities could be explained by the habitat modification by mussels and tubeworms that create a relatively low stressed and disturbed habitat compared to the extreme stressed cold seep sediments where animals are exposed to high levels of toxic sulfide and low oxygen.

The emerging pattern of low abundance of epizooic meiobenthic communities differs from the infauna inhabiting seep sediments. This pattern was already demonstrated by a recent study at deep-sea cold seeps in the Gulf of Mexico, where hard substrate seep communities such as those dominated by mussels or tubeworms have abundances usually below 100 ind. 10 cm^{-2} but can reach values of several hundreds (Bright et al. submitted). The present study confirms this general trend. A wide range between 7 and 1839 ind. 10 cm^{-2} points to a highly patchy distribution. In contrast, cold seep sediments are inhabited by infaunal meiobenthos often exceeding 1000 ind. 10 cm^{-2} (Montagna & Spies 1985, Montagna et al. 1987, Palmer et al. 1988, Olu et al. 1997, Soltwedel et al. 2004, Sommer et al. 2007, Van Gaever et al. 2006, Van Gaever 2009a). Lower abundances than for the epizooic meiobenthos are reported only in some samples of anoxic sediments of the Black Sea (< 6 ind. 10 cm^{-2}; Sergeeva & Gulin 2007) and from a brine seep at East Flower Garden Bank in the Gulf of Mexico (< 2 ind. cm^{-2}; Powell 1983). Top down processes were suggested to negatively influence epizooic meiobenthos at cold seeps as macrobenthos is abundant in mussel and tubeworm aggregations in the Gulf of Mexico (Cordes et al. 1997, Cordes et al. submitted, Bright et al. submitted). Van Gaever et al. (2009a) detected a negative affect of macrofauna on meiobenthos, where predation seems to be the determining factor in limiting meiofaunal abundances.

In contrast, the structure of the soft bottom substrate could facilitate settlement of infauna due to a much greater surface area than hard substrate. This assumption is consistent with Danovaro and Fraschetti (2002), who suggested that consistency and structure of the habitat substratum are the leading factor of regulating meiofaunal abundances. The abundances of the sediment infauna from marine habitats shows an average 1000 to 2000 ind. 10 cm^{-2}, whereas at greater depths these abundances become reduced and range between 10 to 100 ind. 10 cm^{-2} (Giere 2009). In the deep sea of the northern Gulf of Mexico abundances about 1380 ind. 10 cm^{-2} at depths about 2150 m were found (Baguley at al. 2006).

In general cold seeps are considered extreme environments due to the stressful conditions of elevated sulfide and low oxygen concentrations that allows only a few specialized species to colonize such habitats, albeit often in high numbers. However, exactly at such locations vestimentiferan tubeworms and mytilid mussels, which live in symbiosis with chemosynthetic bacteria, thrive in dense aggregations. By taking up sulfide, these foundation species ameliorate the environmental conditions and thus facilitate colonization of a more diverse associated faunal community. While small, tubeworms take up sulfide with their plume extended into the water column. When larger they grow into the sediment and take up sulfide already below the surface through their posterior extended tubes, the so-called roots (Julian et al. 1999), whereas the anterior end grows further away from the surface and the aggregation gains in height, thereby providing an additional non-toxic habitat (Bergquist et al. 2003a). While the aggregation becomes older, a decline in sulfide concentrations occurs (Cordes et al 2005b), thereby making an even more benign habitat available. For mussels, a certain amount of sulfide must be present around the aggregations, as they gain the reduced compounds through their mantle cavity (Cordes et al. submitted).

Thus, the habitat created by such foundation species is much more moderate than the underlying sulfidic sediments, where the communities are exposed to high sulfidic conditions and low oxygen availability (Ahoron & Fu 2000, Arvidson et al. 2004, Joye et al. 2004, Dattagupta et al. 2008). Entire tubeworm bushes in relatively advanced successional stages (Bergquist et al 2003a, 2003b, Cordes et al. 2005b) similar to the once we studied are known to consume most of the sulfide before it is released from the sediment and also mussels taking up sulfide and/or methane above the sediment surface may keep the environment below the toxicity threshold for epizooic meiobenthos. Sulfide concentrations in the water around tubeworm aggregations similar in composition of size structure to those we studied are very low (<1 µM) above the sediment and rarely exceed 4 µM while almost no sulfide is detectable around the plumes of the tubeworms (Scott & Fisher 1995, Freytag et al. 2001, Bergquist et al. 2003b, Cordes et al. 2005a, Cordes et al. 2009). Sulfide levels in the water surrounding mussel aggregations, if detectable at all, vary between 1 and 6 µM and can sometimes reach values up to 100 µM or even more (Smith et al. 2000, Bergquist et al. 2004, Bergquist et al. 2005). In addition, sulfide shifts reversely with oxygen concentrations (Levin et al. 2001).

Thus, epizooic meiobenthos has a great oxygen supply in the surrounding epibenthic water, which is required as most meiofaunal organisms have high oxygen demands (Giere 2009).

Consistent with the intermediate stress hypothesis (Menge & Sutherland 1987), the epizooic meiobenthos associated with mussel and tubeworm aggregations in the Gulf of Mexico is a relatively high diverse community, represented by 119 genera and Shannon diversity as well as Pielou's evenness were high at both sites ($H'_{\log e} \geq 2$, $J' \geq 0.6$). Although slightly higher genera richness and Shannon diversity are found in tubeworm compared to mussel associated meiobenthos, these differences are not statistically significant, which might be due to the low number of samples we studied. A similar trend was found for the associated macrobenthos, for which much more data are available (Bergquist et al. 2003a, Bergquist et al. 2005, Cordes et al. 2005b, Cordes et al. 2006 Cordes et al. 2007, Cordes et al. submitted). Mussel beds, considered the initial stage of succession (Bergquist et al. 2003a) with moderate amounts of sulfide seeping from the sediment surface are colonized by epizooic macrobenthos exhibiting high endemicity and relatively low diversity ($H'_{\log e} < 2$; Cordes et al submitted). Upon colonization and growth of tubeworms and replacement of mussels (Bergquist et al. 2003a), sulfide concentrations start to decline due to sulfide mining through the roots of tubeworms in the sediment. The associated macrobenthic community gradually shifts to a more diverse community ($H' = 0.8$ to 3.1) composed of non-endemic species with lower tolerance of sulfide (Cordes et al. submitted).

In contrast to the relatively diverse epizooic meiobenthos at seeps, the seep sediments apparently are inhabited by infaunal meiobenthos characterized by a low diversity, although data are only available for the nematodes (Jensen 1986, Shirayama & Ohta 1990, Jensen et al. 1992, Van Gaever et al. 2006, 2009a, 2009b). A recent review of Vanreusel et al. (submitted) reveals a relatively low genera richness (18 ± 16), low diversity ($H'_{\log e} = 1.4 \pm 1.1$) and evenness ($J' = 0.5 \pm 0.3$) at cold seep sediments worldwide. Whereas low or even no dominance was found for associated epizooic meiobenthos, the infaunal communities where often dominated by single nematode genera. High dominance was recorded at seeps in the Norwegian margin (*Halomonhystera*; Van Gaever et al. 2006, Van Gaever et al. 2009a), in the Gulf of Guinea (*Sabatieria* and *Desmodora*; Van Gaever et al. 2009b), in the North Sea (*Astomonema*; Dando et al. 1991) and at a shallow seep site in the Gulf of Mexico (*Desmolaimoides*, Jensen, 1986). These genera dominating the seep infaunal meiobenthos are presumably able to exploit this high productive habitat due to better tolerance to environmental stress than most other deep-sea organisms (Van Gaever et al. 2006, 2009a, b).

The diversity and community structure of epizooic meiobenthos associated with hard-substrate communities is similar to those at the surrounding deep-sea. The sediments of the deep sea are generally characterized by a relatively high local diversity of the benthic fauna (Hessler & Sanders 1967, Grassle and Maciolek 1992, Gage 1996, Levin 2001). Although most of the deep-sea studies documented community patterns of macrobenthos, the species richness of meiobenthos is estimated at least to be as high as those of the larger size fraction (Gage 1996). Cold seeps are fueled with high in situ primary production due to chemosynthesis (Sibuet & Olu 1998, Levin 2005) whereas the deep sea depends on photosynthesis sinking from the euphotic zone to the deep sea bottom. Although these two habitats differ in food supply they can be both characterized by low temperature anomalies and small-scale disturbance events (Sanders 1968, Grassle & Morse-Porteous 1987, Tunnicliffe et al. 2003). High numbers of nematode genera were found for the deep sea (> 100) (Netto et al. 2005, Renaud et al. 2006) This indicates that surrounding deep-sea sediments and hard substrate communities provide almost same habitat conditions as they are colonized by a similar and a high diverse community.

Although hydrothermal vents and cold seeps are chemosynthetic fueled habitats in the deep sea, both exhibit contrasting diversities and community structures of epizooic meiobenthos in accordance with disturbance and stress levels. Low diversity is found for epizooic meiobenthic mussel and tubeworm communities at hydrothermal vents, where genera richness is low (21 ± 6) (Zekely et al. 2006, Gollner et al. 2007). Vent animals living in mussel beds and tubeworm bushes experience considerable amounts of sulfide emerging from the cracks and crevices of basalt and highly fluctuating sulfide and oxygen concentrations in addition to temperature fluctuations up to 30 degrees. In addition to this environmental stress, disturbances such as waxing and waning of vents and volcanic eruptions are frequent (Scott & Fisher 1995, Fisher et al. 1997). In contrast, such aggregations at seeps are relatively benign and are estimated to exist for several hundreds of years, so that meiobenthic communities rich in species can develop.

Diverse habitats within the cold seep ecosystem are present. Many of them can be considered extreme, at the limits of life for most organisms. However, right in the middle of those, colonized by a few tolerant specialists, we also find benign habitats such as the ones studied here. The impact of foundation species such as tubeworms and mussels leads to habitat amelioration and facilitates colonization of a diverse community, probably equally high in number of species than the clays and oozes of the surrounding deep sea. This study provides a first glimpse into the diversity and community structure of some of these benign seep habitats. Future studies not only should attend to systematically screen the diversity of seep habitats known worldwide, at different depth and geological settings, but also specifically develop and test hypothesis to better understand underlying mechanisms that cause variable responses of these different communities to local conditions.

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Legends

Table 1. Environmental and sample characteristics from all six samples at the two habitats (tubeworm habitat: T-AV1, T-AV2, T-AV3; mussel habitat: M-AV1, M-AV2, M-AV3): listed are geographical location, site, dive number (AD *Alvin* dive, JD *Jason* dive), latitude [°N], longitude [°W], depth [m], total sample area [cm^2], the volume of sediment [ml] (collected between mussels or tubeworms), surface area (total area of tubeworm tubes or mussel shells surfaces calculated per sample), foundation species listed per species (% contributing to total foundation species).

Environmental characteristics	**T-AV1**	**T-AV2**	**T-AV3**	**M-AV1**	**M-AV2**	**M-AV3**
Location	Atwater Valley	Atwater Valley	Atwater Valley	Atwater Valley	Atwater Valley	Atwater Valley
Site	AT 340	AT 340	AT 340	AT 340	AT 340	AT 340
Dive number	JD 277	JD 270	AD 4179	JD 276F	JD 277A	JD 277F
Latitude [°N]	27°38.839	27°38.694	27°38.677	27º25.197	27°38.697	27:38.700
Longitude [°W]	88°22.429	88°21.843	88°21.879	88º21.853	88°21.851	88°21.859
Depth [m]	2175	2192	2185	2190	2190	2190
Sample area [cm^2]	2800	2800	2800	531	531	531
Sediment [ml]	7500	16	301,63	21	3600	390
Surface area [cm^2]	12740	16870	8590	2190	1770	1620
Foundation species:						
Bathymodiolus brooksi (%)				100	100	100
Lamellibrachia ssp. (%)	5.5					
Escarpia laminata (%)	94.5	100	100			

Table 2. Total number of individuals [no. individuals] and standardized abundance [ind. 10 cm^{-2}] are listed for nematodes, copepods, halacarids, ostracods, tanaids, kinorhynchs, isopods and nauplii. (tubeworm habitat: T-AV1, T-AV2, T-AV3; mussel habitat: M-AV1, M-AV2, M-AV3)

	T-AV1	**T-AV2**	**T-AV3**	**M-AV1**	**M-AV2**	**M-AV3**
Abundance [no. Individuals]						
Nematoda	103618	1547	1132	2507	87612	16003
Copepoda	20461	755	722	519	8626	2300
Halacaridae	0	6	2	18	71	0
Ostracoda	1002	9	15	17	250	13
Tanaidacea	346	1	6	1	0	0
Kinorhyncha	0	0	1	0	0	0
Isopoda	0	0	1	0	0	0
Nauplii	899	82	24	795	1069	1493
total abundance	126325	2400	1903	3857	97628	19809
Abundance [ind. 10cm^{-2}]						
Nematoda	370.06	5.53	4.04	47.22	1650.16	301.42
Copepoda	73.07	2.70	2.58	9.78	162.47	43.31
Halacaridae	0.00	0.02	0.01	0.34	1.34	0.00
Ostracoda	3.58	0.03	0.05	0.32	4.70	0.25
Tanaidacea	1.23	0.00	0.02	0.02	0.00	0.00
Kynoryhncha	0.00	0.00	0.00	0.00	0.00	0.00
Isopoda	0.00	0.00	0.00	0.00	0.00	0.00
Nauplii	3.21	0.29	0.09	14.97	20.14	28.12
total abundance	451	9	7	73	1839	373

Table 3. Relative abundance of meiobenthic genera for all six samples. Copepodites: all stages of copepodites were found, but identification to genus level was not possible (tubeworm habitat: T-AV1, T-AV2, T-AV3; mussel habitat: M-AV1, M-AV2, M-AV3).

	T-AV1	**T-AV2**	**T-AV3**	**M-AV1**	**M-AV2**	**M-AV3**
Nematoda						
Acantholaimus	<1	0	1.0	<1	0	0
Actinonema	<1	<1	<1	8.2	0	0
aff. Subsphaerolaimus	0	0	0	0	0	<1
Alaimella	0	0	<1	0	0	0
Amphimonhystera	0	0	<1	0	0	0
Amphimonhystrella	0	0	0	<1	0	0
Anticyatus	0	0	<1	0	0	0
Antimicron	0	0	<1	0	0	0
Axonolaimus	0	0	<1	0	0	0
Calyptronema	0	8.5	5.6	0	0	0
Camacolaimus	<1	0	2.3	1.4	3.6	1.2
Cervonema	0	0	2.7	0	0	0
Chromadora	2.5	<1	0	<1	0	<1
Chromadorella	0	0	0	<1	<1	0
Chromadorina	<1	<1	1	1.6	0	2.3
Chromadorita	<1	3.9	<1	4.9	1.5	2.9
Comesa	18	<1	0	<1	0	0
Cyartonema	<1	0	0	0	0	0
Daptonema	8.0	<1	1.3	2.2	0	0
Daptonema cfr	0	<1	0	0	0	0
Desmodora	32.6	12.6	2.5	16.6	<1	<1
Desmolorenzenia	0	<1	<1	0	0	0
Desmoscolex	<1	<1	1.3	<1	<1	0
Dichromadora	1.1	0	<1	<1	0	0
Diplopeltoides	0	0	<1	0	0	0
Dorolaimidae	0	0	<1	0	0	0
Eumorpholaimus	0	0	0	0	0	<1
Halalaimus	0	0	<1	0	0	0
Halichoanolaimus	<1	0	4	0	0	0
Halomonhystera	0	0	<1	<1	5.5	6.1
Leptolaimoides	0	0	<1	0	0	0
Leptolaimus	7.2	4.1	1.0	7.9	14.0	13.7
Linhomoeus	2.5	<1	0	2.2	22.4	7.0
Metacyatholaimus	1.7	0	0	<1	0	0
Metacylicolaimus	0	0	1.9	0	1.8	<1
Metadesmoliamus	1.4	<1	0	0	0	0
Metalinhomoeus	1.4	0	0	0	<1	0
Microlaimus	<1	2.4	3.5	0	<1	<1
Molgolaimus	<1	<1	1.5	<1	0	0
Nemanema	0	0	0	<1	0	0
Neochromadora	<1	0	<1	<1	7.0	1.8
Notochaetosoma	0	<1	0	0	0	0
Odontanticoma	0	8.9	3.1	2.2	<1	0
Oncholaimus	0	8.7	0	3.5	0	0
Oxystomina	0	0	<1	0	0	0
Paracanthonchus	<1	<1	<1	2.7	20.6	27.5
Pareudesmoscolex	0	<1	0	0	0	0
Platycomopsis	0	0	<1	0	0	0
Prochaetosoma	0	1.1	2.1	<1	<1	0
Prochromadora	0	0	<1	0	0	0
Prochromadorella	<1	6.5	0	3.5	0	<1
Pseudodesmodora	<1	0	<1	<1	0	0

Sabatieria	<1	<1	4.2	2.7	0	0
Southerniella	0	<1	4.0	0	0	0
Sphaerolaimus	<1	<1	<1	0	0	0
Thalassomonhystera	<1	4.8	3.3	13.4	11.8	21.1
Tricoma	0	<1	<1	<1	0	0
Trileptium	0	0	<1	0	0	0
Trophomera	0	0	2.1	0	0	0
Viscosia	0	0	3.3	2.7	0	0
Copepoda						
Ameira	<1	1.7	1.0	4.7	5.3	7.9
Ameiridae	0	0	<1	0	0	0
Ameiropsis	0	1.2	1.1	0	0	0
Amphiascella	<1	14.6	8.4	0	0	0
Amphiascus	<1	2.4	2.2	0	0	0
Ancorabolidae .	<1	0	0	0	0	0
Archesola	<1	<1	0	<1	<1	<1
Aregstes .	0	<1	<1	0	0	0
Argesthidae	0	0	0	<1	0	0
Bradya	<1	0	<1	0	0	0
Calanoida spec.1	0	0	<1	<1	0	<1
Calanoida spec. 2	<1	0	0	0	0	0
Canthocamptidae	0	0	<1	0	0	0
Cletodidae	<1	0	0	0	0	0
Cyclopina	<1	1.6	0	<1	0	0
Cyclopoida spec. 1	0	0	<1	0	0	0
Cyclopoida spec. 2	0	0	<1	0	0	0
Delavalia	1.4	0	<1	0	0	0
Enalcyonium	<1	<1	<1	0	<1	0
Erebonaster	<1	0	0	0	0	0
Eurycletodes	0	0	<1	0	0	0
Fultonia	<1	<1	<1	0	0	0
Halectinosoma	<1	0	0	0	0	0
Haloschizopera	0	0	<1	0	0	0
Heteropsyllus	<1	0	1.3	0	0	0
Laophontidae spec.1	0	0	0	<1	0	0
Laophontidae spec.2	0	0	0	<1	0	0
Mesochra	<1	<1	1.1	1.5	<1	<1
Mesocletodes	<1	0	0	0	0	0
Metahuntemannia	<1	0	0	0	0	0
Metis	0	0	0	0	<1	0
Microsetella	0	0	<1	0	0	0
Miraciidae spec.	<1	0	0	<1	0	0
Miraciidae spec. 2	0	0	<1	0	0	0
Miraciidae spec. 4	0	0	<1	0	0	0
Oncaea	0	0	<1	0	0	0
Paraleptopseudomesochra	0	0	<1	0	0	0
Proameira	<1	0	0	0	0	0
Psammis	<1	0	<1	<1	0	0
Pseudameira	<1	0	0	0	0	0
Pseudobradya	<1	<1	1.0	2.2	<1	0
Pseudomesochra	<1	0	0	0	0	0
Sarsameira	<1	0	0	0	0	0
Smacigastes	<1	0	0	0	0	0
Strongylacron	<1	0	0	<1	0	0
Tisbe	<1	1.6	<1	<1	<1	<1
Uptionyx	1	0	0	<1	0	0
Xylora	<1	<1	0	<1	0	0
Copepodites	8,2	6,7	18,6	6,2	2,5	4,1
Tanaidacea						
Pseudotanais	<1	<1	<1	<1	0	0
Isopoda						

Isopoda spec.	0	0	<1	0	0	0
Kinorhyncha						
Echinoderes	0	0	<1	0	0	0
Halacaridae						
Copidognathus	0	<1	<1	<1	<1	0
Ostracoda						
Ambocythere	0	0	0	<1	0	0
Argilloecia	<1	0	0	0	0	0
Krithe	<1	0	<1	0	<1	0
Paradoxostoma	<1	0	<1	0	0	0
Thomontocypris	<1	0	<1	0	0	0
Typhlocythere	0	0	0	<1	0	0
Xylocythere	<1	<1	<1	<1	<1	<1

Table 4. Genera richness (G), Pielou’s evenness index (J’) and Shannon-Wiener diversity index ($H'_{\log e}$) for total meiobenthos, nematoda, and copepoda calculated for all six samples and estimated genera richness (EG(n)) is shown for total meiobenthos (tubeworm habitat: T-AV1, T-AV2, T-AV3; mussel habitat: M-AV1, M-AV2, M-AV3).

Total	**G**	**J'**	**$H'_{\log e}$**	**EG(300)**
T-AV1	63	0.59	2.46	53.08
T-AV2	44	0.75	2.84	36.47
T-AV3	77	0.84	3.66	64.58
M-AV1	50	0.76	2.97	41.63
M-AV2	26	0.67	2.20	21.99
M-AV3	22	0.68	2.11	19.88
Nematoda				
T-AV1	27	0.62	2.03	
T-AV2	28	0.74	2.45	
T-AV3	43	0.88	3.30	
M-AV1	30	0.79	2.67	
M-AV2	16	0.73	2.02	
M-AV3	16	0.70	1.94	
Copepoda				
T-AV1	30	0.86	2.94	
T-AV2	13	0.64	1.63	
T-AV3	26	0.69	2.26	
M-AV1	15	0.64	1.74	
M-AV2	7	0.35	0.68	
M-AV3	5	0.26	0.42	

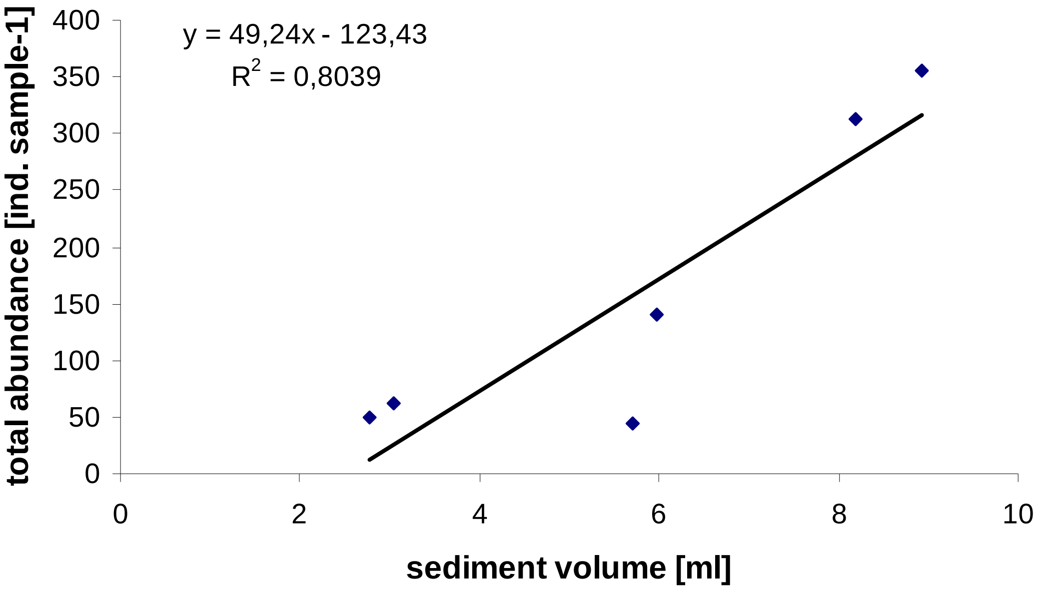

Fig. 1. Correlation of total abundance [ind. sample^{-1}] and sediment volume [ml] of all six samples.

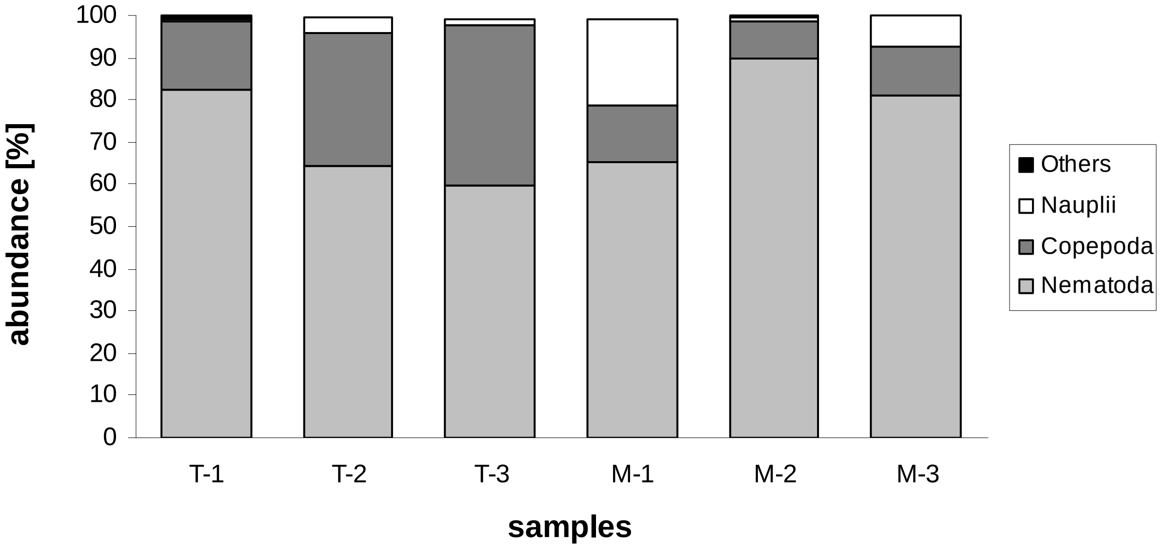

Fig. 2. Meiofaunal community. Reported are nematodes, copepods, nauplii and others and their relative abundance [%] at all samples of the tubeworm- and mussel habitats (tubeworm-habitat: T-AV1, T-AV2, T-AV3; mussel habitat: M-AV1, M-AV2, M-AV3).

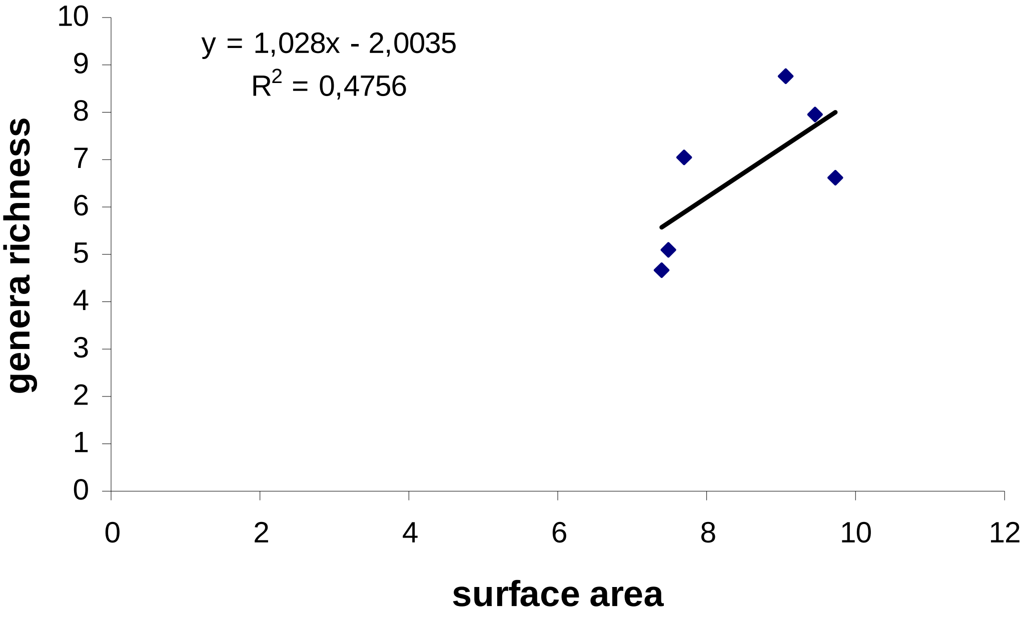

Fig. 3. Correlation of genera richness and surface area built by tubeworms and mussels [10 cm^2 surface area] of all six samples.

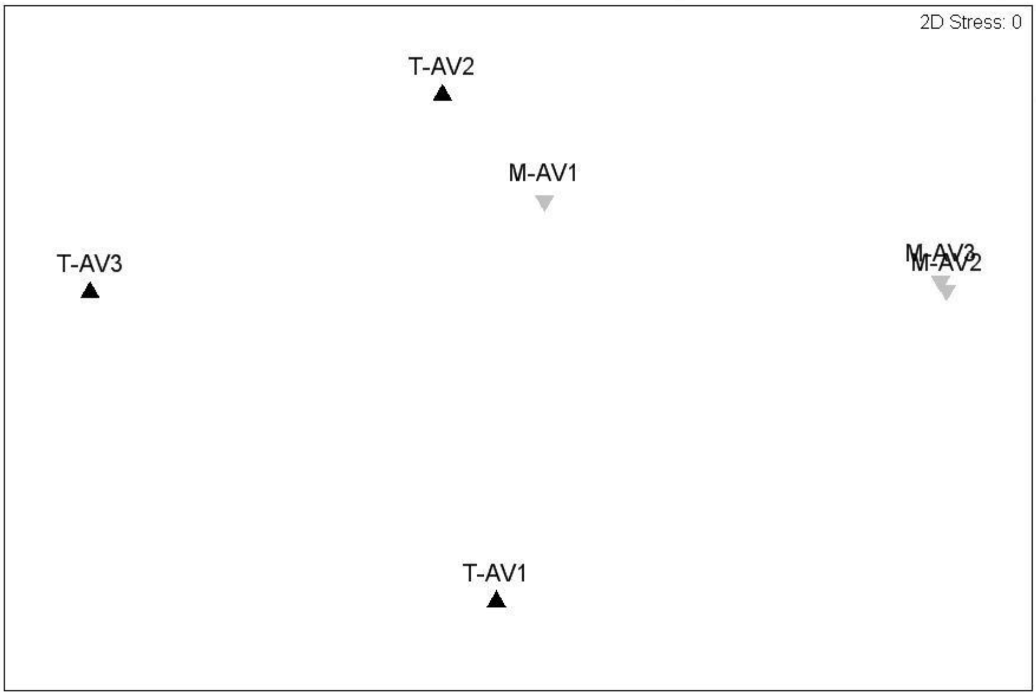

Fig. 4. Multidimensional scaling analyses performed using genera composition for all six samples. (tubeworm habitat: T-AV1, T-AV2, T-AV3; mussel habitat: M-AV1, M-AV2, M-AV3).

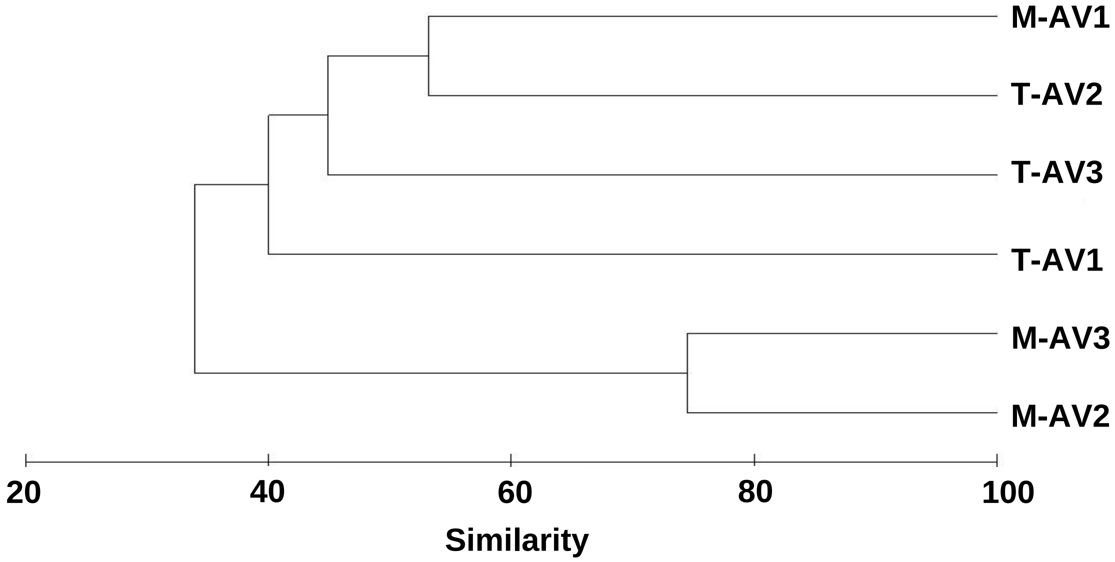

Fig. 5. Cluster analyses (group average linkage) based on Bray-Curtis similarity of standardized abundances of genera among all six samples. (tubeworm- habitat: T-AV1, T-AV2, T-AV3; mussel habitat: M-AV1, M-AV2, M-AV3).

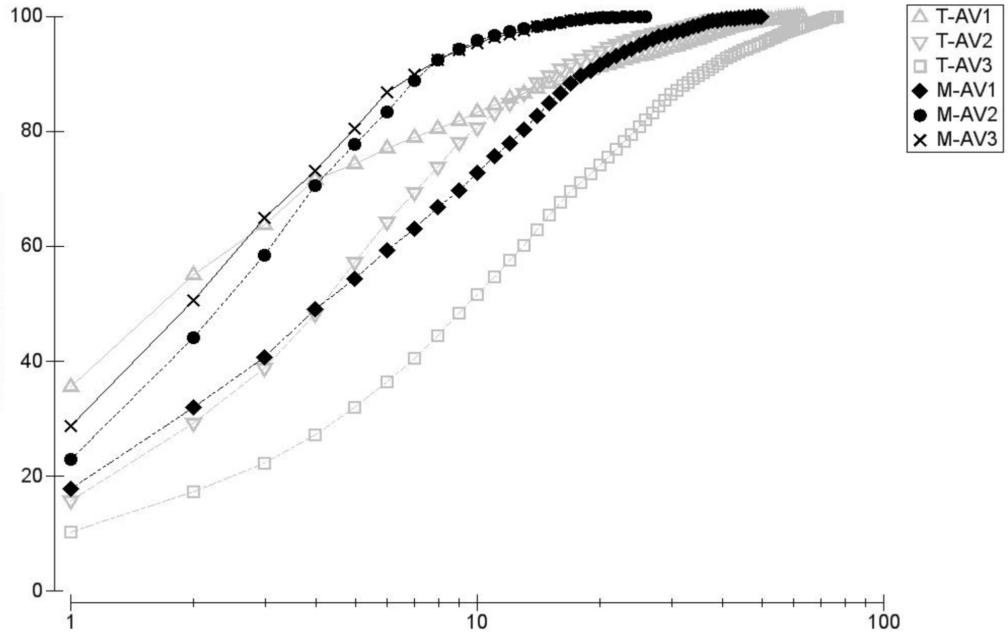

Fig. 6. k- dominance curves based on genus level for all six samples (tubeworm- habitat: T-AV1, T-AV2, T-AV3; mussel habitat: M-AV1, M-AV2, M-AV3). Relative abundance of genera was plotted against genus ranks.

ZUSAMMENFASSUNG

Diese Studie ist die erste, die quantitative Analysen über das assoziierte Meiobenthos in Muscheln- und Röhrenwürmerhabitaten vorgenommen hat. Biogene Strukturen, die von Muscheln und Röhrenwürmern gebildet werden, bieten an den Kalten Quellen der Tiefsee ein optimales Habitat für assoziierte Faunagemeinschaften unterschiedlicher Größenklassen. Da es bis heute noch keine vergleichbare Studie gibt, sondern alle bisherigen Untersuchungen des Meiobenthos der *cold seeps* sich mit der Sedimentinfauna beschäftigten, wurden diese biogenen Habitate gewählt, um deren Einfluss auf die Meiobenthosgemeinschaften in diesem einzigartigen Ökosystem festzustellen. Sowohl die Muschel- als auch die Röhrenwurmaggregationen wurden an derselben Stelle (Atwater Valley, AV) in derselben Tiefe (~2200 m) im nördlichen Golf von Mexiko entnommen.

Um einen Vergleich mit anderen Studien über die Meiofauna vorzunehmen, wurden die Abundanzen auf eine Fläche von 10 cm^2 standardisiert. Die Abundanz des assoziierten Meiobenthos war generell sehr niedrig. In den Röhrenwurmaggregationen variierte sie zwischen 7 und 451 Ind. 10 cm^{-2} und in den Muschelaggregationen zwischen 73 und 1839 Ind. 10 cm^{-2}. Der Abundanzunterschied zwischen diesen beiden Habitaten war nicht signifikant. Eine relativ niedrige Abundanz wurde in einer erst jüngst durchgeführten Studie im Golf von Mexiko festgestellt, in der die Abundanz des mit Muschel- und Röhrenwurmaggregationen assoziierten Meiobenthos zwischen < 1 bis 447 Ind. pro 10 cm^{-2} (Bright et al. submitted) lag. Auch an den Hydrothermalquellen wurde eine niedrige Abundanz von assoziierten Meiobenthosgemeinschaften beobachtet (Zekely et al. 2006: 32 bis 43 Ind. 10 cm^{-2} in Muschelaggregationen; Gollner et al. 2007: < 1 bis 976 Ind. 10 cm^{-2} in Röhrenwurmaggregationen). Im Vergleich zu Sedimenthabitaten von Kalten Quellen, wo Abundanzen von meist über 1000 Ind. 10 cm^{-2} üblich sind (Montagna & Spies 1985, Montagna et al. 1987, Palmer et al. 1988, Olu et al. 1997, Soltwedel et al. 2004, Sommer et al. 2007, Van Gaever et al. 2006, Van Gaever 2009a), sind diese Abundanzen sehr niedrig.

Da man weiß, dass Makrofauna in biogenen Strukturen sehr häufig vorkommt geht man davon aus, dass ein hoher Fraßdruck innerhalb dieser Aggregationen herrscht. Organismen des Meiobenthos könnten direkte Beute von Makrofauna sein und juvenile Makrofauna könnte sowohl als Räuber als auch Konkurrenz fungieren (Ólafsson, 2003). Außerdem bietet das Sediment eine weitaus größere Fläche und daher mehr Lebensraum (Donavaro & Fraschetti 2002) als die Oberflächen von den Röhrenwürmern oder Muscheln.

Das assoziierte Meiobenthos lässt sich durch sieben höhere Taxa, deren relative Häufigkeiten unterschiedlich verteilt sind, charakterisieren. Nematoden und Copepoden dominierten in allen Proben beider Habitate, gefolgt von Ostracoden. Weiters wurden Halacariden, Tanaiden, Isopoden und Kinorhynchen gefunden. Auch Nauplienlarven wurden in relativ hoher Abundanz beobachtet, wurden allerdings aus den Analysen über die Diversität ausgeschlossen, da sie in diesem Stadium schwer zu bestimmen sind. Die relative Häufigkeit der Nematoden betrug in allen Proben mehr als 60 % der Gemeinschaft, die der Copepoden zwischen 9 und 38 %. Alle anderen Taxa machten zusammengenommen weniger als 1% des gesamten Meiobenthos in allen Proben aus.

Obwohl die Anzahl der Individuen relativ gering war, wurden insgesamt 119 Gattungen identifiziert. 108 Gattungen kamen insgesamt im Habitat der Röhrenwürmer vor und 58 in dem der Muscheln. Dieser Unterschied war allerdings nicht signifikant. Die Anzahl der Gattungen variierte innerhalb der einzelnen Aggregationen und reichte von 44 bis 77 Gattungen in den Röhrenwurmaggregationen und von 22 bis 50 Gattungen in den Aggregationen der Muscheln.

Die Nematoden war die Gruppe mit der höchsten Anzahl an Gattungen, insgesamt wurden 60 von ihnen identifiziert. Die Copepoden waren mit 48 Gattungen vertreten. Die restlichen Taxa bestanden zusammengefasst aus lediglich 11 Gattungen.

Die Diversität des Meiobenthos war in beiden Habitaten relativ hoch ($H'_{\log e} \geq 2$), genauso wie die Gleichheit der Gattungen (Pielou’s evenness: $J' \geq 0.6$), kaum eine Gattung dominiert alleine eine Probe oder ein Habitat. Diese hohe Diversität des assoziierten Meiobenthos steht im Gegensatz zur Diversität der Sedimentinfauna an den Kalten Quellen, die durch die hohe Dominanz einzelner Gattungen meistens eine geringere Artenvielfalt aufweisen. Grund für die hohe Diversität innerhalb der Aggregationen sind die milderen Bedingungen in dem eigentlich sonst sehr toxischen Ökosystem. Die Meiobenthosgemeinschaften, die sich in den Muschel- und Röhrenwürmerhabitaten angesiedelt haben, sind wesentlich weniger gestresst auf Grund erheblich geringerer Sulfid- und höherer Sauerstoffkonzentrationen. Die Röhrenwürmer nehmen das Sulfid bereits innerhalb des Sediments auf, durch „wurzelähnliche“ Verlängerung ihrer Körper ins Sediment (Julian et al. 1999, Freytag et al. 2001). Die Muscheln absorbieren das Sulfid durch ihre Kiemen aus dem umgebenden Wasser (Cordes et al. submitted). Diese Habitate liefern daher eine stabile Umgebung mit geringem Stress, die es ermöglicht von weniger gut spezialisierten Gattungen genutzt zu werden.

In der vorliegenden Arbeit wurde zum ersten Mal die Meiobenthosgemeinschaft, assoziiert mit Muschel- und Röhrenwurmaggregationen an den Kalten Quellen ausführlich beschrieben und analysiert. Es konnte festgestellt werden, dass die Aggregationen ein ungestörtes Habitat mit niedrigem Stress in einer sonst sehr rauen Umgebung mit hohen Sulfidkonzentrationen und geringer Sauerstoffverfügbarkeit, bieten. Die vergleichsweise geschützten Habitate werden daher von einer breiten Meiobenthosgemeinschaft besiedelt.

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