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Diplomarbeit

Community study of tubeworm associated epizooic meiobenthos from deep sea cold seeps and hot vents

Biodiversitätsstudie von Meiofaunagemeinschaften assoziiert mit Röhrenwürmern an kalten und heißen Tiefseequellen

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„Was wir wissen, ist ein Tropfen; was wir nicht wissen, ein Ozean“

Isaak Newton

INHALTSVERZEICHNIS:

EINLEITUNG

Die Basis der meisten marinen Nahrungsketten bilden Primärproduzenten wie Mikro- und Makroalgen und Bakterien, die in den obersten, lichtdurchfluteten Wasserschichten Photosynthese betreiben und somit die Energie des Sonnenlichtes zur Synthese organischer Verbindungen nutzen. Auch jene Organismen, die weit unterhalb der euphotischen Zone (unterhalb von etwa 250 m Wassertiefe) in ewiger Dunkelheit leben, sind auf den organischen Eintrag aus dieser obersten produktiven Schicht angewiesen. Im letzten Drittel des vorigen Jahrhunderts wurden jedoch Lebensräume in der Tiefsee entdeckt, die auch völlig unabhängig von Einträgen aus oberen Wasserschichten existieren können. Basis dieser Ökosysteme ist die Chemosynthese, eine Form der Primärproduktion bei der nicht die Energie der Sonne, sondern die Energie aus chemischen Bindungen anorganischer Stoffe zum Aufbau von organischer Substanz benutzt wird.

Zu diesen Ökosystemen zählen die 1977 am ostpazifischen Rücken erstmals entdeckten hytrothermalen Quellen („hot vents“) (Corliss et al. 1979) und auch die 1985 im Golf von Mexiko entdeckten kalten Quellen („cold seeps“) (Paull et al. 1984). Gemeinsam ist beiden Lebensräumen, dass reduzierte Schwefelverbindungen, die für die meisten Lebewesen toxisch sind (Bagarinao 1992), aus dem Meeresboden sickern und große Röhrenwürmer (Länge > 2 m) an diesen Austrittsstellen siedeln. Diese Röhrenwürmer gehören zu der Familie Vestimentifera (Polychaeta, Siboglinidae) und leben in Symbiose mit schwefeloxidierenden Bakterien, die ihnen auf chemosynthetischem Weg organische Verbindungen liefern (Bright & Lallier 2010). Durch dieses Zusammenleben haben Vestimentifera im Laufe ihrer Evolution ihre Mundöffnung und ihren Darm reduziert und sind bei der Nahrungsaufnahme somit obligat auf ihre Symbionten angewiesen.

Während Röhrenwurmaggregationen an kalten Quellen einen sehr stabilen und moderaten Lebensraum bieten (MacDonald et al. 1989, Roberts & Aharon 1994a, Sassen et al. 1994, Scott & Fisher 1995, Roberts & Carney 1997, Julian et al. 1999, Freytag et al. 2001, Bergquist et al. 2003b, Levin 2005, Cordes et al. 2005a, Cordes et al. 2010b), ist das Habitat an den heißen Quellen wesentlich extremer. Dieser Lebensraum ist durch hohe Temperaturen, hohe Sulfidwerte, niedrige pH-Werte und geringe Sauerstoffkonzentrationen gekennzeichnet und zudem noch ständigen Schwankungen der Fluidaustritte sowie katastrophalen Ereignissen wie Vulkanausbrüchen unterworfen (Van Dover & Trask 2000, Bright & Lallier 2010, Gollner et al. 2010a). Durch diese Umweltfaktoren sind Ökosysteme an heißen Quellen sehr kurzlebig und der Riesenröhrenwurm *Riftiya pachyptila* hat als Anpassung daran eine der

schnellsten Wachstumsraten (> 85 cm pro Jahr) der Tierwelt entwickelt (Fisher et al. 1988, Hessler et al. 1988, Lutz et al. 1994, Shank et al. 1998, Bright & Lallier 2010). Die Lebensräume an kalten Quellen andererseits sind kaum Störungen ausgesetzt und somit konnten sich langlebige Arten wie der Röhrenwurm *Lamellibrachia luymesi* etablieren, die ein Alter von weit über 100 Jahren erreichen können (Fisher et al. 1997, Bergquist et al. 2000, Cordes et al. 2005a).

Die Röhrenwürmer bilden große buschförmige Aggregationen (MacDonald et al. 1989, MacDonald et al. 1990, Bergquist et al. 2002), die zahlreichen Tieren verschiedener Größenordungen und Nahrungsgilden als Rückzugsraum oder Siedlungsfläche dienen. Ökologischen Theorien zufolge sollten diese Provision von Lebensraum sowie die durch chemosynthische Prozesse hohe Produktion zu einer hohen Vielfalt an assozierten Lebewesen führen (Dayton 1972, Tilman 1982, Owen 1988, Huston 1994, Van Dover & Trask 2000, Bruno & Bertness 2001). Während schon einige Studien über röhrenwurmassoziierte Makrofaunaorganismen (Tiere > 1mm) vorliegen (Kennicutt et al. 1988, MacDonald et al. 1990, Carney 1994, Bergquist et al. 2003b, Cordes et al. 2005a, Cordes et al. 2006, Cordes et al. 2010b), ist über Meiofaunagemeinschaften (Tiere die kleiner als 1 mm sind und auf einem Netz von 32 µm zurückbleiben) bis dato noch sehr wenig bekannt (Bright et al. 2010).

In dieser Diversitätsstudie wurden daher alle Meiofaunaorganismen, die auf Röhrenwürmern leben, quantitativ erfasst und auf Gattungsebene bestimmt. Die Probenstellen waren kalte Quellen an seichteren (Green Canyon, ~ 500 m Tiefe) und tieferen Standorten (Atwater Valley, > 2000 m Tiefe) im Golf von Mexico. Im Anschluss wurden die Ergebnisse mit den bereits publizierten Daten (Gollner et al. 2007) einer Meiofaunastudie von heißen Quellen am ostpazifischen Rücken verglichen. Folgende Fragestellungen sollten dabei beantwortet werden: 1) Unterscheiden sich die Meiofaunagemeinschaften von geografisch und bathymetrisch distanzierten kalten Quellen in ihrer Zusammensetzung, Abundanz und Diversität? 2) In wie weit unterscheiden sich die Meiofaunagemeinschaften von kalten und heißen Quellen in Bezug auf Zusammensetzung, Abundanz und Diversität?

Community study of tubeworm associated epizooic meiobenthos from deep sea cold seeps and hot vents

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[13] support in statistical analyses

ABSTRACT

Since the discovery of deep sea cold seeps and hydrothermal vents more than 30 years ago many studies have been conducted about these chemosynthetic environments and their associated macrofauna communities. Although it is commonly accepted that meiofauna plays an important role in marine environments, studies about epizooic meiobenthic communities and their impact in seep and vent ecosystems are still rare.

Four quantitative samples were taken from vestimentiferan aggregations consisting of *Lamellibrachia luymesi* and *Seepiophila jonesi* in the Green Canyon seep site on the upper Louisiana slope in the Gulf of Mexico in depths around 550 m and three samples were obtained from aggregations of *Escarpia laminata* and *Lamellibrachia ssp.* in the Atwater Valley seep site on the lower slope in depths around 2200 m. Abundance, diversity and community composition on genus level was compared between these sites and with the results of a study of epizooic meiobenthos from *Riftia pachyptila* aggregations from the hydrothermal vent sites Tica and Riftia Field in the East Pacific Rise in 2500 m depth (Gollner et al. 2007).

The abundance was not found significantly different between the two seep sites GC (171 to 1 817 ind. 10 cm^{-2}) and AT (7 to 448 ind. 10 cm^{-2}) and also not between the seep and the vents sites that showed an abundance of <1 to 973 ind. 10 cm^{-2}. A total of 150 meiobenthic genera were identified from the cold seep sites GC (25 to 59 genera) and AT (44 to 77 genera), but while no significant difference in genera richness was detected a shift in community composition was found. The hot vent communities included together only 17 genera and the genera richness and Shannon diversity were significantly different between the seep and vent samples. Given that the genera richness was positively correlated with the abiotic factors maximal temperature, maximal sulfide concentration and minimal pH value, it is assumed that these factors explain the high Bray-Curtis dissimilarity of 97% between the meiobenthic communities from seeps and vents.

This study gives an overview of tubeworm associated epizooic meiofauna communities from cold seeps in different depths and reveals the differences between the communities from seeps and vents. Further it is concluded that the extremely harsh conditions found in the hydrothermal vent tubeworm aggregations compared to the moderate habitat at cold seeps are explaining the reported results.

INTRODUCTION

Following Dayton (1972: 81–96) a foundation species is described as "a single species that defines much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes." By providing protection from environmental stress and/or predation, it has been shown that foundation species can often have a positive effect on the local species richness (see Bruno & Bertness 2001). The term has been used for a variety of marine organisms shaping habitats like coral reefs (Bruno et al. 2003, Idjadi et al. 2006), kelp forests (Graham 2004), mussel reefs (Witman 1985, Altieri & Jon 2006), and also for vestimentiferan tubeworm habitats from the chemosynthetic deep-sea environments such as cold seeps (Cordes et al. 2005a, Cordes et al. 2007b, Cordes et al. 2010b) and hydrothermal vents (Gollner et al. 2007, Govenar & Fisher 2007, Bright & Lallier 2010, Gollner et al. 2010a). The tubes of vestimentiferans (Polychaeta, Siboglinidae) create complex secondary structures in form of large aggregations that serve as a living space for a variety of associated species (Bright and Lallier 2010).

Since their discovery less than 30 years ago in the Gulf of Mexico (Paull et al. 1984), cold seeps and their associated symbiont-housing foundation species have been studied extensively (Levin 2005, Cordes et al. 2005a, Cordes et al. 2005b, Cordes et al. 2006, Fisher et al. 2007, Cordes et al. 2007a, Cordes et al. 2007b, Cordes et al. 2009, Cordes et al. 2010b). The cold seep sites on the upper Louisiana slope (< 1000 m depth) of the Gulf of Mexico are colonized by three species of vestimentiferan tubeworms (Black et al. 1997, McHugh 1997, Rouse 2001, Bergquist et al. 2002, Rouse et al. 2004, Cordes et al. 2006, Cordes et al. 2009). One species of lamellibrachid, *Lamellibrachia luymesi* van der Land and Nørrevang, 1975 is described, beneath two species of escarpids, *Seepiophila jonesi* Gardiner, McMullin and Fischer, 2001 and a still undescribed species (McMullin 2003). On the lower slope (> 1000 m depth) *Escarpia laminata* Jones, 1985 and two still undescribed species of lamellibrachids (Brooks et al. 1990, Nelson & Fisher 2000, Roberts 2007, Cordes et al. 2007a, Cordes et al. 2009) are found.

Hundreds to thousands of individuals of *Seepiophila jone*si co-occurring with *Lamellibrachia luymesi* form bush-like aggregations of several meters in diameter and sometimes over 2 m in height on the upper slope (MacDonald et al. 1989, MacDonald et al. 1990, Bergquist et al. 2002). Conservative age estimates of *Lamellibrachia* are over 100 years or even far more, with the upper limit of age still being unknown (Fisher et al. 1997, Bergquist et al. 2000, Cordes et al. 2005a). Vestimentiferan tubeworms with sulfide-oxidizing

symbionts settle on a seepage site as soon as suitable carbonate substrata and sulfide at the substrate/water interface are present (Bergquist et al. 2002, Bergquist et al. 2003a). Since fluid flow is continuous and may last over thousand years or more (Levin 2005) and due to the ability of tubeworms to reduce the amount of sulfide or methane within or around their aggregations (Cordes et al. 2009) a relatively stable and stressless environment for associated organisms is created. This stability favored the evolution of longevity in these tubeworm species that stands in contrast to the relatively short-lived and fast growing vestimentiferan species from the unstable ecosystem at hydrothermal vents (Cordes et al. 2007).

Hydrothermal vents on the other hand are a highly disturbed and stressful environment (Van Dover & Trask 2000). The vent foundation species *Riftia pachyptila* and organisms associated with it have to deal with variable physico-chemical conditions like high temperature and pH gradients, high levels of sulfide, intermittent availability of oxygen or changes in vent fluid composition or flux (Bright & Lallier 2010, Gollner et al. 2010a). As it was shown that the habitat provision by foundation species can increase the diversity in associated communities (Bruno & Bertness 2001, Bergquist et al. 2003a, Govenar et al. 2005, Govenar & Fisher 2007), it is still required to be tested to what extend diversity is influenced by the stability or instability of these extreme habitats .

Several macrofaunal community studies from the upper (Kennicutt et al. 1988, MacDonald et al. 1990, Carney 1994, Bergquist et al. 2003b, Cordes et al. 2005a, Cordes et al. 2006) and lower slope (Cordes et al. 2007a, Cordes et al. 2010b) seep communities have been conducted so far. The density and biomass of tubeworm associated macrofauna was found similar regardless of depth (Cordes 2005a, 2007a). These communities are initially dominated by species obligatorily associated with seeps (and in the community of seep and vent researchers commonly called endemic), but proceed through a series of successional stages where overall biomass declines and the proportion of non-endemic species in upper trophic levels increases as water column sulfide concentrations near the sediment surface decline (Bergquist et al. 2003b, Cordes et al. 2006). Overall, the densities of associated macrofauna where found relatively high, whereas the diversity seemed to be rather low, with highest levels at aggregations in mid-age successional stages (Cordes et al. 2005a). A significant bathymetric zone of transition around 1000 m depth is emphasized by Cordes et al. (2010), due to the fact that only a low degree of species overlap was observed with species from the upper slope (Carney 2005).

Vent macrofauna communities are as well characterized by low diversity and low species richness, but high abundances due to *in situ* chemosynthetic primary production

(Govenar et al. 2005). A shift between endemic and non-endemic macrofauna species was not found at hot vents, where the majority of macrofauna species is endemic to this permanently extreme environment (Tunnicliffe et al. 1998). In general it appears that the abundance of associated macrofauna is lower but the species richness is higher at seeps compared with vents (Bright and Lallier 2010).

In contrast to macrofauna only little information is available on the epizooic meiofauna communities associated with cold seep or hydrothermal vent foundation species (Govenar et al. 2005, Gollner et al. 2007, Van Gaever et al. 2009a, Van Gaever et al. 2009b, Bright et al. 2010). Low abundances were reported for seep and hydrothermal vent epizooic meiofauna (Bright et al. 2010, Gollner et al. 2010a) compared to the background deep-sea meiofauna.

Contradictory to the theory of habitat provision and therefore higher diversities, the diversity of epizooic meiofauna at hydrothermal vents was found lower than in the close by basalt area that harboured no foundation fauna and was thus less heterogeneous (Gollner et al 2010a)**.** No data are yet available on the total meiofauna communities on genus- or species level, but the nematode fauna from highly sulfidic and oxygen depleted sediments from cold seep bacterial mats (De Beer et al. 2006) was found significantly less diverse compared to deep-sea sediments, whereas the diversity of nematodes from well-oxygenated surface sediments from siboglinid fields (De Beer et al. 2006) was found to be similarly high (Van Gaever et al. 2009a, Van Gaever et al. 2009b, Van Gaever et al. 2010, Vanreusel et al. 2010b). On higher taxa level, the community composition of seep meiofauna was found different from those of the adjacent non-seep sediments so it was assumed that meiofauna from cold seeps forms a distinct group (Bright et al. 2010). Contrary, at hydrothermal vents the epizooic meiofauna seems to be a subset of the surrounding fauna inhabiting the non-vent basalt of the axial summit collapse trough (Gollner et al. 2010a).

In this study we investigates the abundance, diversity, and genera composition of epizooic, permanent, metazoan meiobenthos associated with vestimentiferan tubeworm aggregations from two different cold seep sites from the upper and lower Louisiana slope of the Gulf of Mexico. Further, the results of this study where compared with published data from tubeworm associated permanent meiobenthos from hydrothermal vent sites on the East Pacific Rise (Gollner et al. 2007). The questions addressed were: 1) Do seep meiofauna communities in the Gulf of Mexico separated in distance and depth show differences in their abundance, diversity and composition? 2) Do meiofauna communities from cold seeps and hydrothermal vents show differences in their abundance, diversity and composition?

MATERIALS AND METHODS

Collection sites

Four vestimentiferan aggregations from the Green Canyon (GC) seep sites were collected during a cruise with the RV Seward Johnson II and the Johnson Sea-Link I and II submersibles on the upper Louisiana slope of the Gulf of Mexico in 2003. Two collections each came from the sites GC 232 (27°44.5'N, 91°19.1'W) and GC 234 (27°44.7´N, 91°13.3'W), which were about 10 km apart, in depth ranges from 538 to 571 m (Cordes et al. 2005a, Cordes et al 2006). They were similar in their geophysical and geochemical conditions (maximal temperature 4°C; min. pH 7.7; maximal sulfide concentration 1 µM). Three collections were obtained from Atwater Valley (AT 340) (sample AT 1: 27°38.8'N, 88°22.4'W, sample AT 2 27°38.694'N, 88°21.843'W and sample AT 3 27°38.677' N, 88°21.879'W), previously abundance data published by Bright et al. (2010b). They were sampled during cruises with the RV Atlantis and DSV Alvin in 2006 and the NOAA ship Ronald Brown and ROV Jason in 2007 in depths from 2175 to 2192 m (maximal temperature 2°C; min. pH 7.7; maximal sulfide concentration 1 µM).

For comparisons between epizooic seep and hydrothermal vent meiobenthos, we used six vestimentiferan aggregations from the East Pacific Rise (EPR) 9° 50 N regions, previously published by Gollner et al. (2007). They were collected during cruises in 2001 and 2002 at the vent sites Tica (T 1 - 3: 9°50.447' N, 104°17.493' W) and Riftia Field (R 1 - 3: 9°50.705' N, 104°17.493' W) in 2500 m depth (Tica: maximal temperature 18°C, maximal sulfide concentration 176 µM, minimal pH 7; Rifitia field: maximal temperature 23°C, maximal sulfide concentration 35 µM, minimal pH 5; for details see Govenar et al 2005, Le Bris et al. 2006, Gollner et al. 2007).

Sample collections and processing

All vestimentiferan aggregations were obtained using the Bushmaster Jr. collection device with an maximal surface area of 2800 cm^2 sampled (see Bergquist et al. 2003a, Cordes et al. 2005a, Gollner et al. 2007 for further details). Whereas for seep samples this maximal surface area was obtained and used for calculations of abundance at the seep samples (GC and AT), for the aggregations at the hot vent sites Tica and Riftia field a smaller surface area between 300 and 1300 cm^2 was obtained (Gollner et al. 2007).

The sampled aggregations from GC region consisted of *Lamellibrachia luymesi* van der Land & Nørrevang, 1975 and *Seepiophila jonesi* Gardiner, McMullin & Fisher, 2001, the

aggregations from AT of *Escarpia laminata* Jones, 1985 and *Lamellibrachia ssp.* and the dominant vent vestimentiferan species was *Riftia pachyptila* Jones, 1981.

On board, the macro- and megafauna of all seep samples was rinsed with cold, 32µm filtered seawater into a tub and afterwards removed for further processing (see Bergquist et al. 2003a, Cordes et al. 2005a). All remaining contents in the tub were sieved through a 2 mm, 1 mm and finally 32 µm mesh to separate the macro- from the meiofauna. The retained meiofauna was fixed and stored in 4% buffered formalin. The tubeworms were identified, counted and measured onboard. The GC samples were composed of *Lamellibrachia luymesi* and *Seepiophila jonesi* (percentages *L. luymesi*: GC 1a 69.1%, GC 1b 48.7%, GC 2a 61.2%, GC 2b 76%). The samples AT 1 and AT 2 consisted exclusively of *Escarpia laminata* and sample AT 3 included *Escarpia laminata* (94. 5 %) as well as *Lamellibrachia ssp*. (4.5 %). The vent samples were treated slightly different. In brief, tubes were washed with filtered seawater into a large container and samples were afterwards sieved through a 1mm and 63µm mesh to extract the meiofauna community. Samples were fixed in 4% buffered formalin for 24 h and stored in 70% Ethanol (Gollner et al. 2007).

The length of the cold seep tubeworms was measured to a standardized posterior outer tube diameter (see Bergquist et al. 2000, Cordes et al. 2005a) and surface area was calculated as for a cone frustrum (see Bergquist et al. 2003a, Cordes et al. 2005a). To obtain the surface area of each *Riftia pachyptila* aggregation the length and the anterior diameter of each tube was measured (Govenar et al. 2005, Gollner et al. 2007).

Sulfide concentration at the cold seep sites was measured using the enzymatic assay of Singh et al. (1993) as modified by Freytag et al. (2001) (for details see Cordes et al. 2005a) and at hydrothermal vent sites the *in situ* flow analyzer, 'ALCHIMIST' was used (Le Bris et al. 2000, for details see Govenar et al. 2005).

Identification and Quantification

In the lab meiofauna was extracted from the sediment using a density centrifugation technique with a medium consisting of a Silicapolymer (Fa. Levasil®) mixed with Kaolin (McIntyre & Warwick 1984, Veit-Köhler et al. 2008). Either the meiofauna of the entire samples was counted (GC 1a, GC 1b, GC 2a, GC 2b, AT 2, AT 3, T 1-3, R 1-3) or a subsample was taken (AT 1) and the total abundance was finally extrapolated to the total volume of the original sample.

All animals belonging to meiobenthos (permanent and temporary) were sorted, counted and identified to a higher taxon level under a dissecting microscope. Temporary

meiobenthos, protists, and crustacean nauplii were also recorded, but not further included in this study. The community in the study from the EPR (Gollner et al. 2007) was identified on species level and included foraminiferans as well and therefore abundance data were recalculated.

If present in the sample, 300 individuals of each taxon of permanent, metazoan meiobenthos were picked out for identification on genus level; the remaining individuals were only counted. Nematodes were mounted on slides using glycerine (Higgins & Thiel 1988) and identified following mainly Platt & Warwick (1983), Platt & Warwick (1988) and Warwick et al. (1998). All specimens of other taxa were sent to experts for further identification. C. Plum identified all copepods; M. Bright identified kinorhynchs, L.S. Kornicker and R. F. Maddocks identified ostracodes, K. Larsen identified the tanaids, and I. Bartsch identified the halacarids. The abundance was standardized to 10cm² sample area.

Diversity indices and statistical analyses

For description of the community diversity the genera richness (G) and the diversity indices Shannon diversity ($H'_{\log e}$), Pielou's evenness (J') and estimated genera richness (EG (n)) were calculated using Primer v6 package (Clarke, KR, Gorley, RN, 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth13). Cumulative k-dominance curves were generated to determine the dominance of the most common genera.

Similarity and differences in the community structure between the samples were examined by multidimensional scaling (MDS), Similarity percentage (SIMPER) and Analysis of similarity (ANOSIM) using again Primer Version 6. Similarity between genera distributions was assessed by constructing cluster dendrograms from Bray-Curtis similarity values (Bray & Curtis 1957). The abundance of genera was beforehand standardized and square-root transformed to down-weigh the importance of very abundant genera without loosing the influence of rarer genera (Clarke & Gorley 2001). Primer Version 6 was also used to test the impact of abiotic factors on the community composition with the BIO-ENV procedure.

Student's t-tests were carried out using STATISTICA to test for differences in abundance (square-root transformed), relative abundance of nematodes and copepods (arc sin transformed), genera richness (square-root transformed), sediment volume (ln transformed), tube surface area (ln transformed), and the diversity indices $H'_{\log e}$, J', and EG (n) (no transformation) between GC and AT samples as well as between seep and vent samples. Bootstrapping was used because of the 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). Significance levels were Bonferroni corrected ($p = \alpha/n$; $\alpha = 0.05$). Significance of correlations was tested among abundance, relative abundance, genera richness, sediment volume, abiotic factors, and tube surface area using Pearson's r and STATISTICA.

RESULTS

Abundances

A total of more than 800 000 epizooic, meiobenthic individuals was estimated for the four samples from Green Canyon GC 1a, b and GC 2a, b and the three samples from Atwater Valley AT 1 – 3 with a total surface area of 19 600 cm^2 (Table 1, see also Bright et al. 2010b for data on two samples of AT included in this study). Standardized to 10 cm^2, the number of animals ranged between 171 to 1 817 ind. 10 cm^{-2} at GC and between 7 and 448 ind. 10 cm^{-2} at AT (Table 1). No significant differences in abundance between sites was detected (bootstrapping, $p = 0.1898$). Also when standardized to the tube surface area of foundation species, no differences were found (bootstrapping, $p = 0.4339$).

A total of seven higher taxa was identified, but only two of them, nematodes and copepodes, were present in all samples. Ostracods and tanaids were found in all samples except GC 2b; halacarids were only detected in low numbers in samples GC 1b, AT2, AT3. In contrast to GC samples, also kinoryhnchs and isopods were found in AT samples, but only in small numbers in sample AT 3. Nematodes were always the most abundant taxon with ranges from 4 to 1602 ind. 10 cm^{-2}. The next prevalent taxon was copepods in abundances between 3 to 203 ind. 10 cm^{-2}. Where present, the numbers of ostracods ranged from <1 to 9 ind. 10 cm^{-2}, tanaids from 1 to 3 ind. 10 cm^{-2}, and halacarids, kinoryhnchs, and isopods were <1 ind. 10 cm^{-2}.

The relative abundances of nematodes and copepods were highly variable and no significant differences were detected between GC and AT. Nematodes contributed with more than 56% up to 93% to the total community, while copepods ranged between 3% and 41%. The relative abundance of other higher taxa ranged from <1 to 2% at GC but were around or below < 1% at AT (Fig. 1).

Diversity on genus level

A total of 150 meiobenthic genera were identified from all samples. Whereas at GC only 93 genera were found, AT samples contained 119 genera (Table 3). At GC genera richness ranged between 25 and 59 genera, while at AT a range between 44 and 77 was found. Accordingly also the number of expected genera EG (100) was between 16.01 and 30.83 at GC, and between 24.96 and 40.71 at AT. Both univariate measures of diversity were not significantly different between sites (bootstrapping, $H'_{\log e}$, $p = 0.57$; EG (100), $p = 0.36$). GC and AT samples had 53 genera in common (26 nematodes, 22 copepods, 3 ostracodes, 1

halacarid and 1 tanaid). At GC 42 genera (29 nematodes, 6 copepodes, 6 ostracodes and 1 tanaid) and at AT 57 genera (32 nematodes, 21 copepods, 2 ostracods, 1 isopod and 1 kinoryhnch) were exclusively found, respectively. The Pilou's evenness values were similar between sites (bootstrapping, $p = 0.98$) and ranged between 0.59 to 0.84 (Table 3). The k-dominance curves shows that the communities of all samples were quite evenly distributed with a cumulative dominance below 40% (Fig. 2). The Shannon diversity index ranged from 2.15 to 3.29 at GC and between 2.46 and 3.66 at AT, and were similar between sites (bootstrapping, $H'_{\log e,}$ $p = 0.57$) (Table 3).

The relative abundances of all genera is shown in Table 4. At the site GC 1a the nematode *Sabatieria* showed the highest relative abundance of 17%, followed by the nematodes *Desmodora* (15%) and *Dorylaimopsis* (14%). The nematode genera *Desmodora* (20%) and *Marylynia* (16%) dominated the community at GC 1b and the nematode genus *Daptonema* showed the highest relative abundance at GC 2b (35%). These nematode genera have been found in all four samples. GC 2a was the only sample where a copepod genus (*Dactylopodopsis*, 10%) showed the highest relative abundance. This genus was found at both sites, but not in all samples. Like in GC 1b *Desmodora* showed the highest relative abundance in AT 1 (33%). This genus was also found in high percentage in all other AT samples. The copepod *Amphiascella* (that occurred in lower abundance in GC samples) was the most abundant genus in AT 2 and 3 sample (15% and 8%, respectively), but showed a relative abundance below 1% at AT 1.

Community patterns

The hierarchical cluster diagram based on Bray-Curtis similarity values grouped the samples by site (Fig. 4). ANOSIM detected a significant difference between the two seep locations (Global R=0.981; p= 0.029; number of permutations 35). The SIMPER analysis showed an average dissimilarity of 72% between the two seep locations. The AT samples showed a little lower average similarity (40%) than the GC samples (44%).

GC samples from location 1 and 2 only about 10 km apart, were not grouped according to these locations, but GC 1a and GC 2a were closer together than GC 1 and GC 2 samples, respectively (Fig. 3). ANOSIM did not detect any differences in the community structure between the two GC locations (Global R=0; p=1; number of permutations 3).

Comparison of communities between cold seeps and hydrothermal vents

The obtained data from cold seeps above were compared with the data of a study of tubeworm associated meiobenthos from two hydrothermal vent sites Tica (T 1 - 3) and Riftia Field (R 1 - 3) on the East Pacific Rise (EPR) 9º 50'N region (Gollner et al. 2007).

The abundances in the vent samples ranged from 45 individuals (T 4) to 29 180 individuals (T 1) and were not found significantly different from the seep samples (Table 1; Table 3). The abundances standardized to an area of 10 cm² ranged between <1 to 973 ind. 10 cm^{-2}. No significant correlation could be detected between abundance and the tube surface area. Nematodes and copepods occurred in all vent samples, whereas ostracods were missing in the samples T 1, R 1 and R 2. Nematodes were the most abundant taxon (<1 - 746 ind. 10 cm^{-2}), except in the samples with the lowest overall abundance R 1 and R 2, where copepods have been found most abundant (values <1). The relative abundance ranged between 18 and 97% for nematodes and between 3 and 82% for copepods. Also the relative abundance between seeps and vents was not found significantly different (Table 2).

The vent communities included only 17 genera and were therefore significantly different from the total number of genera found in seep communities (test, $p < 0.001$). The genera richness was altogether low and ranged from 5 to 12 genera per sample, the number of expected genera EG (100) ranged from 4.06 to 9.17 (Table 3). There was a significant correlation of genera richness and tube surface area ($r=0.63$; $p=0.02$) (Table 2).

Four genera only where shared between vents and both seep sites (the nematod genera *Chromadorita* and *Daptonema* and the copepod genera *Halectinosoma* and *Xylora*). Further, four genera where shared between the vent sites and the deeper seep sites at AT (the nematode genera *Halomonhystera* and *Thalassomonhystera* and the ostracode genera *Thomontocypris* and *Xylocythere*). The vent communities included nine genera that lacked at any of the seep sites (8 copepod genera, 1 ostracod genus). No genus was detected that occurred only at vents and the shallower seep site GC.

The Pilou's evenness values ranged from 0.47 to 0.89 and were not significantly different to values calculated for the seep samples (Table 2b and 3). The k-dominance curve shows that the vent communities were far less evenly distributed than the seep communities with a cumulative dominance up to 90% (Fig. 2). The Shannon diversity indices were significantly lower at vents (0.37 – 1.75) than at the seep sites (bootstrapping, $p < 0.001$) (Table 2b).

The nematode genus *Thalassomonhystera* had the highest relative abundance in the vent samples T1 – R 1 (27 to 91%) and contributed therefore to the low evenness. The most

abundant genus of R 3 was the nematode *Halomonhystera* (55%) and the sample R 2 was dominated by the copepod genus *Benthoxynus* (51%), which was not present in any of the seep samples. The nematodes *Thalassomonhystera* and *Halomonhystera* also occurred in lower abundances at AT seep samples, but were absent in GC samples.

The SIMPER analysis showed an average dissimilarity between communities of seeps and vents of 97.10%. The vent group had an average similarity of 52%, whereas the seep group showed only 34% average similarity. The nematode genera *Thalassomonhystera* and *Halomonhystera* contributed on average most to the similarity within the vent sites (33 and 29 %, respectively). The hierarchical cluster diagram based on Bray-Curtis similarity values clearly grouped the vent and the seep sites (Fig. 3). ANOSIM showed a significant difference between the communities of the vent and seep sites (Global R=1; p=0.002; number of permutations 999) and the MDS plot based on Bray-Curtis similarities (2D Stress 0.01) clearly separated the communities (Fig. 6).

Meiobenthic vent and seep communities and their environment

The total meiobenthic abundance did not significantly correlate with the abiotic factors maximal temperature, maximal sulfide concentration, and minimal pH. In contrast, the genera richness was positively correlated with the maximal temperature ($r=0.92$; $p<0.001$), with maximal sulfide concentration ($r=0.89$; $p<0.001$) and with minimal pH value ($r=0.71$; $p<0.001$).

The relation of tubeworm surface to sample area showed that the *Riftia pachyptila* aggregations at the vent sites were ~22 times more structured than the tubeworm aggregations formed by *Lamellibrachia luymesi*, *Seepiophila jonesi* and *Escarpia laminata* from the seeps. The seep aggregations from the upper slope showed a mean abundance of more than 300 ind. per 10 cm² tube surface area, the aggregations from the lower slope around 30 ind. per 10 cm² tube surface area and in the *Riftia* aggregations from the hot vent sites only ~ 1 epibenthic meiofauna ind. per 10 cm² was detected.

DISCUSSION

Long-term stability of hydrocarbon seeps in the Gulf of Mexico, longevity and amelioration environmental conditions by tubeworms of potentially stressful abiotic factors for animals living associated with these foundation species and *in situ* chemosynthetic primary production are features creating a benign, food enriched seep habitat. According to general ecological theory diversity is expected to be high in such low disturbed, relatively stressless, and productive environments (Connell 1978, Menge & Sutherland 1987, Huston 1994, Hacker 1997, Sousa 2001, Scrosati & Heaven 2007). Consistent with these predictions, our study shows that the epizooic, meiobenthic community is indeed diverse. Although the associated meiofauna is composed of the same major taxa in similar proportions and exhibits similar univariate measures of diversity, the tubeworm aggregations from shallow GC and deep AT seep sites are nevertheless inhabited by communities rather different in genera composition. Epizooic meiobenthos associated with tubeworms occurs at cold seeps and hydrothermal vents, but despite their chemosynthetic foundation and the rather low, similar abundances we found no further similarities between these communities. Due to the strikingly different environmental conditions and stress regimes, the metazoan meiofauna from the hydrothermal vent sites is composed only of half of the major taxa and is far less diverse in terms of genera richness than those at seeps. The few genera found at both environments comprise cosmopolitans as well as deep-sea genera, but no specific genera restricted to chemosynthesis-based ecosystems.

Seeping processes in the Gulf of Mexico can last for hundreds to thousands of years with a constant flow of reduced chemicals of relatively high concentrations and occasional fluid and gas expulsions (Roberts & Aharon 1994b, Sassen et al. 1994, Roberts & Carney 1997, Levin 2005). In some areas seeping considerable amounts of biogenic produced sulfide, toxic to animals (Bagarinao 1992) in conjunction with low oxygen concentrations are the reasons for depicting this ecosystem as extreme (Sibuet & Olu 1998, Levin 2005). However, overall environmental conditions among tubeworms in mid-successional stages are quite the opposite and consistent with these benign conditions we found at diverse and evenly distributed community. Such bushes, e.g. those we studied at GC on the upper slope were composed of up to 1500 individuals of *L. luymesi* and *S. jonesi* and estimated to be between 20 and 150 years old (Cordes et al. 2005a). These aggregations of vestimentiferans have a high demand of reduced sulfur species for energy generation used for carbon fixation (Cordes et al. 2005a). Uptake of sulfide seeping from the sediment into the water column and uptake

of considerable amounts already within the sediments by their roots (Julian et al. 1999, Freytag et al. 2001, Cordes et al. 2005a, Cordes et al. 2009) results in very low or undetectable sulfide concentrations and ambient deep-sea oxygen levels among tubeworms. 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 (MacDonald et al. 1989, Scott & Fisher 1995, Julian et al. 1999, Freytag et al. 2001, Bergquist et al. 2003b, Cordes et al. 2005a, Cordes et al. 2009).

In addition to amelioration of environmental conditions, the habitat increases in size considerably and provides large surfaces of tubes for colonization of associated animals. Although the tubeworm aggregations we studied were composed of different vestimentiferan species, the shallow located GC sites of *Lamellibrachia luymesi* and *Seepiophila jonesi* and the deeper located AT of *Escarpia laminata* and *Lamellibrachia ssp*., both showed a similar degree of surface increase of between 2.3 and 4.5. Further, habitat complexity also increases by tubeworms creating a three-dimensional structure (Hacker & Gaines 1997, Sarrazin & Juniper 1999, Bruno et al. 2003, Bergquist et al. 2003a, Cordes et al. 2005a, Cordes et al. 2010b), and both factors are expected to facilitate an increase in diversity in general (Van Dover 2000, Bruno & Bertness 2001).

In situ primary production by free-living bacteria and foundation species like Vestimentiferans living in symbiosis with chemoautotrophic sulfide-oxidizing bacteria (Fisher 1990, Childress & Fisher 1992, Gardiner & Jones 1993, Fisher et al. 1997) is much higher than productivity of the surrounding deep sea, even comparable to the most productive marine systems (Bergquist et al. 2003b). Following succession studies of tubeworm aggregations from the upper slope, the earliest successional stages are characterized by active seepage and enhanced chemoautotrophic production, which decline in middle and finally cease in the latest successional stages (Bergquist et al. 2002, Bergquist et al. 2003b, Cordes et al. 2005b, Cordes et al. 2006). Ecological theory depicts a unimodal relationship between productivity and diversity (Tilman 1982, Owen 1988, Huston 1994). The macrofauna communities indeed appear to follow this pattern, as in early successional stages very species poor communities are found while highest diversity levels develop in mid-successional stages (Cordes et al. 2005a). Also our results for the epizooic meiofauna are in accordance with these predictions that lower productivity in mid-successional stages creates higher diversity than those in early and late stages. However, overall meiofauna diversity is higher (H' GC 2.77 ± 0.47, AT 2.99

± 0.61) than of macrofauna (H' GC 2.23 ± 0.54, AT 1.08 ± 0.46) in similar stages when comparing the same aggregations (Cordes et al. 2005a, Cordes et al. 2010b).

Whereas the high productive system in early successional stages is capable of carrying a highly abundant associated macrofauna community, the abundance of associated species declines with less and less sulfide in the older aggregations (Bergquist et al. 2003b, Cordes et al. 2005a, Cordes et al. 2006). Generally we found rather low meiofauna abundances in this study of tubeworm aggregations in mid-successional stages. Although a general trend of decrease in abundance with productivity declining with depth is reported worldwide in the deep sea (Soltwedel 2000, Carney 2005, Giere 2009) we did not find any significant differences between the sites from the upper and lower slope. This was also not expected owing to *in situ* primary production and the independence of organisms from organic influx of upper layers production. The food supply of organisms living in chemosynthetic symbioses does not decrease with depth like for the background fauna (Carney 2005, Cordes 2007) and abundance of associated heterotrophs should be similar independent (Carney 2005).

Another bottom up control mechanism that determines the low abundances is competition, as different meiofauna (and also macrofauna genera that in juvenile stages temporarily belong to the size class of meiofauna) compete for the same resources. In addition, another factor shaping the abundance of the community is the top down control mechanism predation. Meiofauna serves as food for other meiofauna genera and for macrofauna (Bell & Coull 1978, Coull & Bell 1979, Bell 1980, Coull 1990, Giere 2009) and two recent studies of seep infauna emphasize this argument as they indicated an inverse correlation between macrofauna and meiofauna respectively nematode densities (Debenham et al. 2004, Van Gaever et al. 2009b).

As one studied seep site was located at the upper slope in the Green Canyon at depths of less than 600 m and the other one at the lower slope in the Atwater Valley, south in the continuation of the Mississippi Canyon at about 2200 m depth, they were about 300 km apart from each other with a depth difference of about 1600 m. Nevertheless, the associated meiofauna communities in principal were similar in univariate measures of diversity and abundance. This is in contrast to associated macrofauna communities, which show a clear pattern of decline of diversity with depth (Cordes et al. 2010b). However, the multivariate community analyses of the two cold seep sites showed that not only within site similarities each were relatively low (GC 44% and AT 40% SIMPER similarity), also between site dissimilarity was high (SIMPER dissimilarity 72%). This points to a large heterogeneity within and among sites of varying genera creating a similar community pattern.

The two sites shared about half of the genera (53 genera) from five higher taxa, whereas kinoryhnchs and isopods occurred in low numbers only in AT samples from lower slope. The other half of genera was found exclusively on the GC upper slope (42 genera) and on the AT deeper site (57 genera), respectively. Although the majority of the surveyed meiofauna genera are cosmopolitan found in several marine ecosystems, some genera like the nematode genus *Thalassomonhystera*, the ostracod genus *Xylocythere* or all genera belonging to the copopod family Argestidae (e.g. *Argestes, Mesocletodes* and *Fultonia*) are reported as typical deep-sea inhabitants and were accordingly present only on the lower slope.

Our results therefore support studies for cold seep macrofauna that emphasize a bathymetric zone of transition around 1000 m (Carney 2005, Cordes et al. 2007, Cordes et al. 2010b) like it has been reported for adjacent deep sea sediments (Pequegnat et al. 1990). We note that our work was carried out on genus level only and as most genera include cosmopolitans as well as specialists, e.g. from the deep-sea, a clear evidence for bathymetric trends can not be given with this study. For tubeworm associated macrofauna it was found that communities were significantly different among depth ranges whereas no significant difference was discovered among communities separated by geographic distance in the Gulf of Mexico (Cordes et al. 2010b). We assume that this could be as well valid for the meiofauna communities, though community studies on species level in similar depth but separated by distance have to be conducted to affirm this assumption.

Although both seep and vent ecosystems are based on chemosynthetic *in situ* primary production (Childress and Fisher 1992, Levin 2005) and harbour vestimentiferan foundation species (Bright & Lallier 2010), they exhibit fundamentally different disturbance and stress regimes. According to the different environmental conditions and the resulting different life strategies of the foundation species the associated meiobenthic communities are strikingly different in terms of genera richness and community composition.

Hydrothermal vents are highly unstable and short-lived environments with a life span confined by large-scale disturbances like catastrophic volcanic eruptions and tectonic events and small-scale disturbances when vent flow ceases. The vent sites Tica and Riftia field on the East Pacific Rise (EPR) 9°50 N region (Gollner et al. 2007), we took for our comparison with the seep sites, were struck by volcanic eruptions in 1991 and 2006 (Shank et al. 1998, Tolstoy et al. 2006). In both events, most of the communities were destroyed and some newly formed vents were colonized rapidly by the tubeworm *Tevnia jerichonana* (Shank et al. 1998, pers. obs. M.B.). Within 32 months post 1991 eruption *Riftia pachypitla* replaced the primary colonist (Shank et al. 1998). *R. pachypila* is extremely fast growing (> 85 cm per yr) and

short-lived (Fisher et al. 1988, Hessler et al. 1988, Lutz et al. 1994, Shank et al. 1998, Bright & Lallier 2010).

The tubeworms themselves and associated communities are exposed to high stress levels induced by extreme and fluctuating physico-chemical conditions comprising relatively high temperature and pH gradients, high sulfide and low oxygen concentrations as well as rapid changes in vent fluid composition. As already pointed out by Gollner et al (2010) these factors may be the driving forces behind the low meiofauna diversity at hydrothermal vent tubeworm aggregations. Compared to the environmental conditions and high diversity of meiofauna from tubeworm aggregations at cold seeps we studied, it is not surprising that genera richness was positively correlated with the abiotic factors maximal temperature ($r=0.92$; $p<0.001$), maximal sulfide concentration ($r=0.89$; $p<0.001$) and with minimal pH value ($r=0.71$; $p<0.001$). Also the results of the Bio-ENV procedure indicate that these abiotic factors explain the community patterns to a high grade with rank correlations over 0.75. The low genera richness and the cumulative dominance from up to 90% at vents (Fig.2) point out that only a few meiofauna genera are able to tolerate the extreme conditions in this habitat, whereas high genera richness and the cumulative dominance below 40 % at seeps indicate benign conditions favouring many genera with more even distribution.

Only three (Nematoda, Copepoda, Ostracoda) of the seven major metazoan meiofauna taxa found at cold seep sites were also found at the vent sites. Whereas a total of 150 genera were identified from only seven samples from two different seep sites, only a total of 17 genera occurred in six samples of two vent sites. Clearly all univariate measures of diversity were different as well as the community separated well in multivariate analyses. From the total of 17 genera found at the vent sites, nine where restricted to this habitat, and the other eight were found also at our seep locations. From the nine genera exclusively occurring at Tica and Riftia Field, six belong to the copepod family Dirivultidae, which is reported to be endemic to deep-sea hydrothermal vent habitats (Gollner et al. 2006, Gollner et al. 2007, Ivanenko et al. 2007, Gollner et al. 2010a, Gollner et al. 2010b). The two remaining copepod genera belong to the order Harpacticoida, whereof the genus *Bathylaophonte* is so far also only described from hydrothermal vents (Lee et al. 1999) and the other one is yet unidentified. The only ostracod genus *Polycopetta* exclusively found at the vent sites includes one species which is only described from Riftia field (Kornicker & Harrison-Nelson 2005).

Our study on meiofauna from seeps as well as other studies from vents (Van Gaever et al. 2009a, Vanreusel et al. 2010a, Vanreusel et al. 2010b, Gollner et al. 2010a) revealed no genera typical for chemosynthesis-based environments. Half of the eight vent genera co-

occurring also at cold seeps are known as cosmopolitan genera and were detected in the shallow GC as well as at the deeper AT seep samples. The other four genera, the ostracod genera *Thomontocypris* and *Xylocythere* and the nematod genera *Halomonhystera* and *Thalassomonhystera* are mainly reported from the deep sea and especially from hydrothermal vent habitats, but several species are also known from other ecosystems.

Our results show that tubeworm associated meiobenthos from two different cold seep sites shows similar abundances and relatively high and similar diversities on higher taxa and on genus level. The community composition on genus level however is rather heterogeneous. Whether this is due to biogeographic patterns in the Gulf of Mexico or a depth gradient needs to be studied in future. In contrast, epizooic communities associated with tubeworms from hydrothermal vents, are strikingly different to those at seeps. They are composed of a rather limited number of higher taxa and are also far less diverse on genus level. While only a few genera are adapted to the extreme and unstable environmental conditions at hydrothermal vents, a far more diverse and evenly distributed meiofauna community thrives at a moderate and far more stable cold seep environment. Despite cosmopolitan and deep-sea genera inhabiting both chemosynthesis-based ecosystems, tubeworm associated communities at vents exhibit some specializations whereas no seep specialists were detected in this study.

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LEGENDS

Table 1. Environmental characteristics and abundances (total and standardized to 10 cm²) for the Green Canyon seep sites (GC), the Atwater Valley seep sites (AT) and the vent sites Tica (T) and Riftia Field (R).

		Environmental characteristics			**Abundance (no. individuals)**							
Parameter		Sample area (cm²)	Tube surface area (cm²)	Sediment (ml)	Nematoda	Copepoda	Ostracoda	Tanaidaceae	Halacarida	Kynoryhncha	Isopoda	Total abundance
GC 1a	total	2800	8990.00	4937.64	448619.97	56782.87	2645.16	705.38	0.00	0.00	0.00	508753.39
	10 cm^2		32.11	17.63	1602.21	202.80	9.45	2.52	0.00	0.00	0.00	1816.98
GC 1b	total	2800	5910.00	4565.99	40467.21	5998.46	537.18	805.76	89.53	0.00	0.00	47898.14
	10 cm^2		21.11	16.31	144.53	21.42	1.92	2.88	0.32	0.00	0.00	171.06
GC 2a	total	2800	9850.00	5671.22	36394.46	26728.72	1479.45	295.89	0.00	0.00	0.00	64898.52
	10 cm^2		35.18	20.25	129.98	95.46	5.28	1.06	0.00	0.00	0.00	231.78
GC 2b	total	2800	600.00	4632.90	47992.07	1663.09	0.00	0.00	0.00	0.00	0.00	49655.16
	10 cm^2		2.14	16.55	171.40	5.94	0.00	0.00	0.00	0.00	0.00	177.34
AT 1	total	2800	12740	7500.00	103617.51	20460.83	1002.00	345.62	0.00	0.00	0.00	125425.96
	10 cm^2		45.5	26.79	370.06	73.07	3.58	1.23	0.00	0.00	0.00	447.95
AT 2	total	2800	16870	16.00	1547.00	755.00	9.00	1.00	6.00	0.00	0.00	2318.00
	10 cm^2		60.25	0.06	5.53	2.70	0.03	0.00	0.02	0.00	0.00	8.28
AT 3	total	2800	8590	301.63	1132.00	722.00	15.00	6.00	2.00	1.00	1.00	1879.00
	10 cm^2		30.68	1.08	4.04	2.58	0.05	0.02	0.01	0.00	0.00	6.71
T 1	total	600	52300	88.00	951.00	217.00	0.00	0.00	0.00	0.00	0.00	1168.00
	10 cm^2		872	1.47	15.85	3.62	0.00	0.00	0.00	0.00	0.00	19.47
T 2	total	300	65500	165.00	28369.00	807.00	4.00	0.00	0.00	0.00	0.00	29180.00
	10 cm^2		2183	5.50	945.63	26.90	0.13	0.00	0.00	0.00	0.00	972.66
T 3	total	700	38000	133.00	3237.00	983.00	1.00	0.00	0.00	0.00	0.00	4221.00
	10 cm^2		543	1.90	46.24	14.04	0.01	0.00	0.00	0.00	0.00	60.29
R 1	total	1300	9600	40.00	20.00	25.00	0.00	0.00	0.00	0.00	0.00	45.00
	10 cm^2		74	0.31	0.15	0.19	0.00	0.00	0.00	0.00	0.00	0.34
R 2	total	600	18300	37.00	11.00	48.00	0.00	0.00	0.00	0.00	0.00	59.00
	10 cm^2		305	0.62	0.18	0.80	0.00	0.00	0.00	0.00	0.00	0.98
R 3	total	800	26600	85.00	573.00	342.00	15.00	0.00	0.00	0.00	0.00	930.00
	10 cm^2		333	1.06	7.16	4.27	0.19	0.00	0.00	0.00	0.00	11.62

Table 2. Results of student's t-test (p) for tube surface area standardized to 10 cm² surface area, total abundance and abundance of nematodes and copepods standardized to 10 cm² surface area, genera richness (G), Shannon diversity (H' loge), Pilou's evenness (J') as well as the Global R and p value of ANOSIM for the comparison of the two seep sites Green Canyon (GC) and Atwater Valley (AT) and the comparison of these seep sites with the vent sites Tica (T) and Riftia Field (R).

	seeps (GC, AT)	**seeps-vents (GC, AT – T, R)**
p (tube surface area / 10cm²)	0.24	<0.01
p (abundance)		
total [ind. / 10 cm²]	0.28	0.29
Nematoda [/ 10 cm²]	0.29	0.34
Copepoda [/ 10 cm²]	0.34	0.10
p (G)	0.27	<0.01
p (H' log e)	0.62	<0.01
p (J')	0.98	0.17
dissimilarity (%) Global R	0.981	1
p (Anosim)	0.029	0.002

Table 3. Genus richness (G), Shannon diversity (H' log e) , Pilou's evenness (J') and estimated genera richness (EG(100)) of the seep samples from Green Canyon (GC) and Atwater Valley (AT) and the vent samples Tica (T) and Riftia Field (R).

Sample	**G**	**J'**	**H'(loge)**	**EG(100)**
GC 1a	59	0.67	2.73	30.15
GC 1b	50	0.75	2.92	30.61
GC 2a	50	0.84	3.29	30.83
GC 2b	25	0.67	2.15	16.01
AT 1	63	0.59	2.46	32.91
AT 2	44	0.75	2.84	24.96
AT 3	77	0.84	3.66	40.71
T1	5	0.47	0.76	4.06
T2	11	0.16	0.37	8.72
T3	12	0.44	1.09	7.74
R1	7	0.90	1.75	7.00
R2	7	0.86	1.68	7.00
R3	12	0.57	1.43	9.17

Table 4. Relative abundance of meiofauna genera from the cold seep sites Green Canyon (GC) and Atwater Valley (AT) and the hot vent sites from Tica (T) and Riftia Field (R). Relative abundances above 5% are marked in bold.

Genus	**GC 1a**	**GC 1b**	**GC 2a**	**GC 2b**	**AT 1**	**AT 2**	**AT 3**	**T 1**	**T 2**	**T 3**	**R1**	**R2**	**R3**
Nematoda													
Acantholaimus	0.0	0.0	0.0	0.0	<1	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Actinonema	0.0	0.0	0.0	0.0	<1	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0
Alaimella	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Amphimonhystera	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Anoplostoma	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anticoma	0.0	1.1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anticyathus	0.0	0.0	<1	<1	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Antimicron	0.0	<1	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Axonolaimus	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Belbolla	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calyptronema	0.0	0.0	0.0	0.0	0.0	**8.5**	**5.6**	0.0	0.0	0.0	0.0	0.0	0.0
Camacolaimus	0.0	0.0	0.0	0.0	<1	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0
Campylaimus	<1	**7.4**	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cervonema	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0
Chromadora	0.0	0.0	0.0	0.0	2.5	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chromadorella	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chromadoridae gen. 1	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Chromadorina	1.0	0.0	2.4	0.0	<1	<1	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Chromadorita	1.6	<1	**6.6**	4.9	<1	3.9	<1	0.0	0.0	<1	0.0	0.0	0.0
Cobbia	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Comesa	0.0	<1	<1	0.0	**17.9**	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyartonema	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Daptonema	2.9	4.1	**5.3**	**35.4**	8.0	<1	1.2	0.0	0.0	0.0	0.0	0.0	<1
Daptonema ***cfr***	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Desmodora	**14.9**	**19.7**	**7.7**	**8.9**	**32.6**	**12.6**	2.5	0.0	0.0	0.0	0.0	0.0	0.0
Desmolaimus	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Desmolorenzenia	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Desmoscolex	<1	<1	0.0	0.0	<1	<1	1.3	0.0	0.0	0.0	0.0	0.0	0.0
Dichromadora	0.0	0.0	0.0	0.0	1.1	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Diplopeltoides	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Dorolaimidae!	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Dorylaimopsis	**14.0**	6.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Elzalia	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Enoplus	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epsilonema	0.0	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyatholaimidae gen. 1	1.0	2.2	2.6	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Linhomoeidae Genus 1	2.9	1.1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fam X Genus 1	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fam Y Genus 1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Graphonema	<1	0.0	3.1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halalaimus	<1	<1	<1	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Halichoanolaimus	1.0	1.5	<1	0.0	<1	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0
Halomonhystera	0.0	0.0	0.0	0.0	0.0	0.0	<1	**10.0**	**5.8**	**12.0**	**18.1**	**18.7**	**55.0**
Innocuonema	<1	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Laimella	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Leptolaimoides	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Leptolaimus	3.2	0.0	<1	3.1	**7.2**	4.1	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Linhomoeus	0.0	0.0	0.0	0.0	2.5	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Marylynia	0.0	**15.6**	**5.5**	5.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Megadesmolaimus	1.3	0.0	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metacyatholaimus	<1	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metacylicolaimus	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0
Metadesmoliamus	0.0	0.0	0.0	0.0	1.4	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metalinhomoeus	1.9	0.0	0.0	<1	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microlaimus	0.0	0.0	0.0	0.0	<1	2.4	3.5	0.0	0.0	0.0	0.0	0.0	0.0
Molgolaimus	**12.4**	<1	1.1	<1	<1	<1	1.5	0.0	0.0	0.0	0.0	0.0	0.0
Neochromadora	0.0	0.0	0.0	**13.5**	<1	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Notochaetosoma	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Odontanticoma	0.0	<1	2.6	0.0	0.0	**8.9**	3.1	0.0	0.0	0.0	0.0	0.0	0.0
Oncholaimellus	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oncholaimus	<1	0.0	<1	0.0	0.0	**8.7**	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oxystomina	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Paracanthonchus	0.0	0.0	0.0	0.0	<1	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0
Paramonhystera	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parasphaerolaimus	<1	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pareudesmoscolex	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Platycomopsis	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Pontonema	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prochaetosoma	0.0	0.0	0.0	0.0	0.0	1.1	2.1	0.0	0.0	0.0	0.0	0.0	0.0
Prochromadora	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Prochromadorella	0.0	0.0	3.5	0.0	<1	**6.5**	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudodesmodora	0.0	0.0	0.0	0.0	<1	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Quadricoma	<1	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Sabatieria	**17.1**	7.8	2.6	5.8	<1	<1	4.2	0.0	0.0	0.0	0.0	0.0	0.0
Southerniella	<1	<1	1.3	0.0	0.0	<1	4.0	0.0	0.0	0.0	0.0	0.0	0.0
Sphaerolaimus	0.0	1.5	<1	0.0	<1	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0
Spirinia	0.0	0.0	0.0	**13.9**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Synonchiella	0.0	<1	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terschellingia	**6.3**	4.1	1.1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thalassomonhystera	0.0	0.0	0.0	0.0	<1	4.8	3.3	**71.4**	**91.4**	**64.4**	**27.1**	0.0	**6.2**
Tricoma	<1	0.0	1.1	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Trileptium	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Trophomera	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0
Viscosia	1.0	<1	<1	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0
Copepoda													
Ameira	<1	3.8	4.0	1.2	<1	1.7	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Ameiridae spec.	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Ameiropsis spec. 4	0.0	0.0	0.0	0.0	0.0	1.2	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Amphiascella	<1	0.0	0.0	0.0	<1	**14.6**	**8.4**	0.0	0.0	0.0	0.0	0.0	0.0
Amphiascus	<1	0.0	0.0	<1	<1	2.4	2.2	0.0	0.0	0.0	0.0	0.0	0.0
Ancorabolidae spec.	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aphotopontius	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	**7.9**	**6.8**	0.0	2.2
Archesola	<1	<1	0.0	0.0	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aregstes spec.	0.0	0.0	0.0	0.0	0.0	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0
Bathylaophonte	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	0.0
Benthoxynus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<1	<1	0.0	**25.5**	0.0
Bradya	0.0	<1	0.0	0.0	<1	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Calanoida Genus 2	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calanoida Genus 1	0.0	<1	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Canthocamptidae spec.	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Ceuthocetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**13.1**	<1	**9.0**	0.0	**17.0**	4.5
Cletodidae spec. 1	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Corbulaseta	<1	0.0	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyclopina	<1	0.0	<1	0.0	<1	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyclopoida Genus 2	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Cyclopoida Genus 1	<1	<1	<1	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Dactylopodopsis	<1	<1	**9.8**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Delavalia	0.0	<1	0.0	0.0	1.4	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Enalcyonium	0.0	0.0	0.0	0.0	<1	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0
Erebonaster sp. nov.	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eurycletodes spec.	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Fultonia spec.	0.0	0.0	0.0	0.0	<1	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0
Halectinosoma	0.0	<1	0.0	0.0	<1	0.0	0.0	0.0	<1	<1	2.3	0.0	0.0
Haloschizopera	<1	0.0	<1	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Harpacticoida genus 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<1
Heteropsyllus	0.0	<1	0.0	0.0	<1	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0
Mesochra	<1	0.0	1.2	<1	<1	<1	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Mesocletodes sp. nov.	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metahuntemannia spec.	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microsetella norvegica	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Miraciidae Genus 1	2.5	<1	**6.3**	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Miraciidae Genus 2	<1	0.0	0.3	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Miraciidae Genus 4	0.0	<1	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Miraciidae Genus 5	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oncaea spec.	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Paraleptopseudomesochra sp. nov.	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Paraschizopera	0.0	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Proameira dubia	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Psammis	0.0	<1	0.0	0.0	<1	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0

Pseudameira	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudobradya	<1	0.0	<1	0.0	<1	<1	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudomesochra sp. nov.	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhogobius	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	<1	0.0	0.0	0.0
Robertgurneya	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sarsameira	0.0	0.0	1.2	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scotoecetes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	<1	**24.9**	**10.2**	**11.5**
Siphonostomatoidae Genus 1	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Smacigastes	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Strongylacron sp. nov.	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stygiopontius	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<1	<1	9.0	1.7	5.2
Tisbe	0.0	<1	0.0	0.0	<1	1.6	<1	0.0	0.0	0.0	0.0	0.0	0.0
Uptionyx	<1	0.0	<1	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Xylora	0.0	0.0	0.0	0.0	<1	<1	0.0	0.0	<1	<1	**11.3**	**5.1**	**5.4**
copepodits	**5.6**	5.0	**14.5**	<1	**8.2**	**6.7**	**18.6**	4.8	<1	4.4	2.3	**18.7**	**7.6**
Ostracoda													
Argilloecia	<1	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eucytherura	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fam Polycopidae Genus 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Krithe	0.0	0.0	<1	0.0	<1	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Legitimocythere	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Palmoconcha	0.0	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paradoxostoma	0.0	0.0	0.0	0.0	<1	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Polycopetta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<1
Superfam Cytheroidea Genus 1	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thomontocypris	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	1.1
Van Harten's N.Gen. N.Sp.	<1	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Xylocythere sp. C	0.0	0.0	0.0	0.0	<1	<1	<1	0.0	0.0	0.0	0.0	0.0	<1
Halacarida													
Copidognathus	0.0	0.0	0.0	0.0	0.0	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0
Tanaidacea													
Bathyleptochelia	<1	<1	<1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pseudotanais	0.0	<1	0.0	0.0	<1	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Isopoda													
Isopod gen. 1	0.0	0.0	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0
Kinorhyncha													
Echinoderes	0.0	<1	0.0	0.0	0.0	0.0	<1	0.0	0.0	0.0	0.0	0.0	0.0

Fig. 1. Relative abundance of Nematoda, Copepoda and others (including Ostracoda, Tanaidacea, Halacarida, Kinorhyncha and Isopoda) from the cold seep sites Green Canyon (GC) and Atwater Valley (AT) and the hot vent sites Tica (T) and Riftia Field (R).

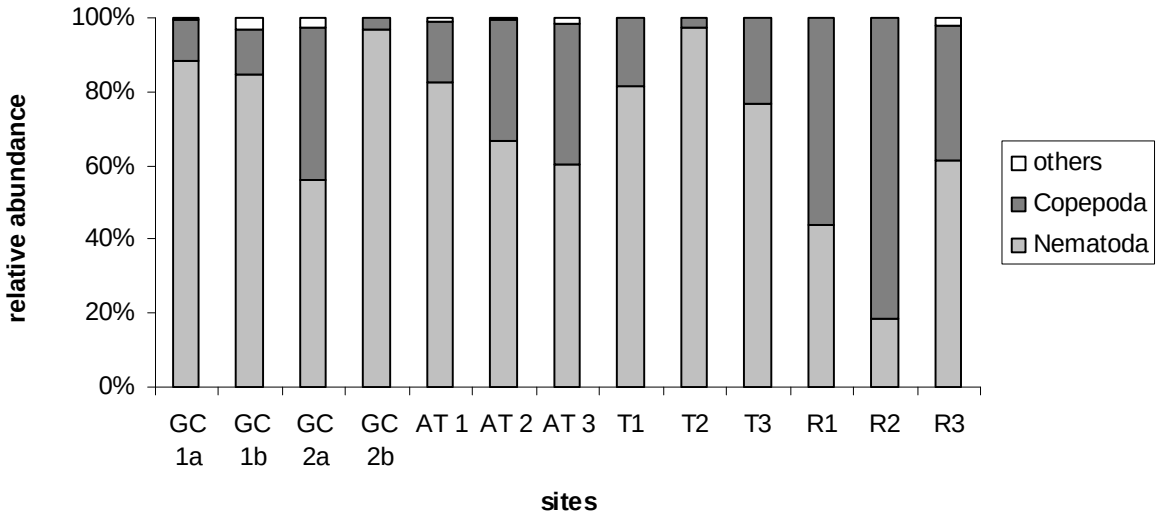


Fig. 2. Cumulative k-dominance curves of the cold seep samples from Green Canyon (GC) and Atwater Valley (AT) and the hot vent samples from Tica (T) and Riftia Field (R) with relative abundance of genera being plotted against genus ranks.

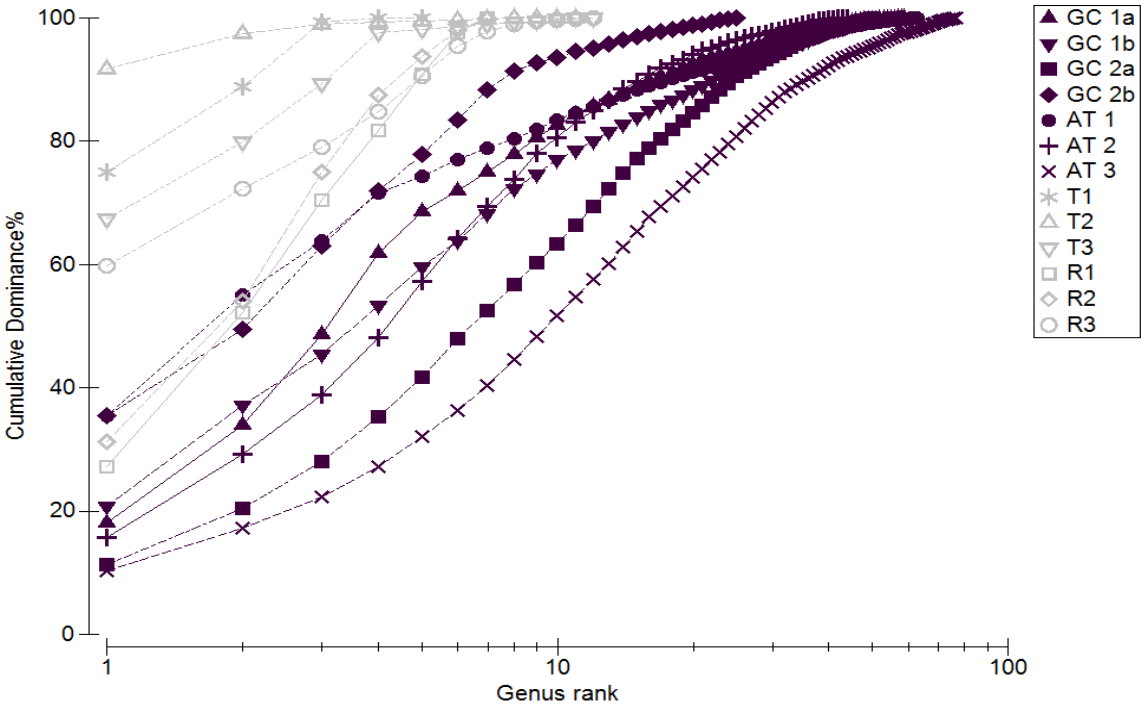


Fig. 3. Hierarchical cluster diagram based on Bray-Curtis community similarity from the cold seep samples Green Canyon (GC) and Atwater Valley (AT) and the hot vent samples Tica (T) and Riftia Field (R).

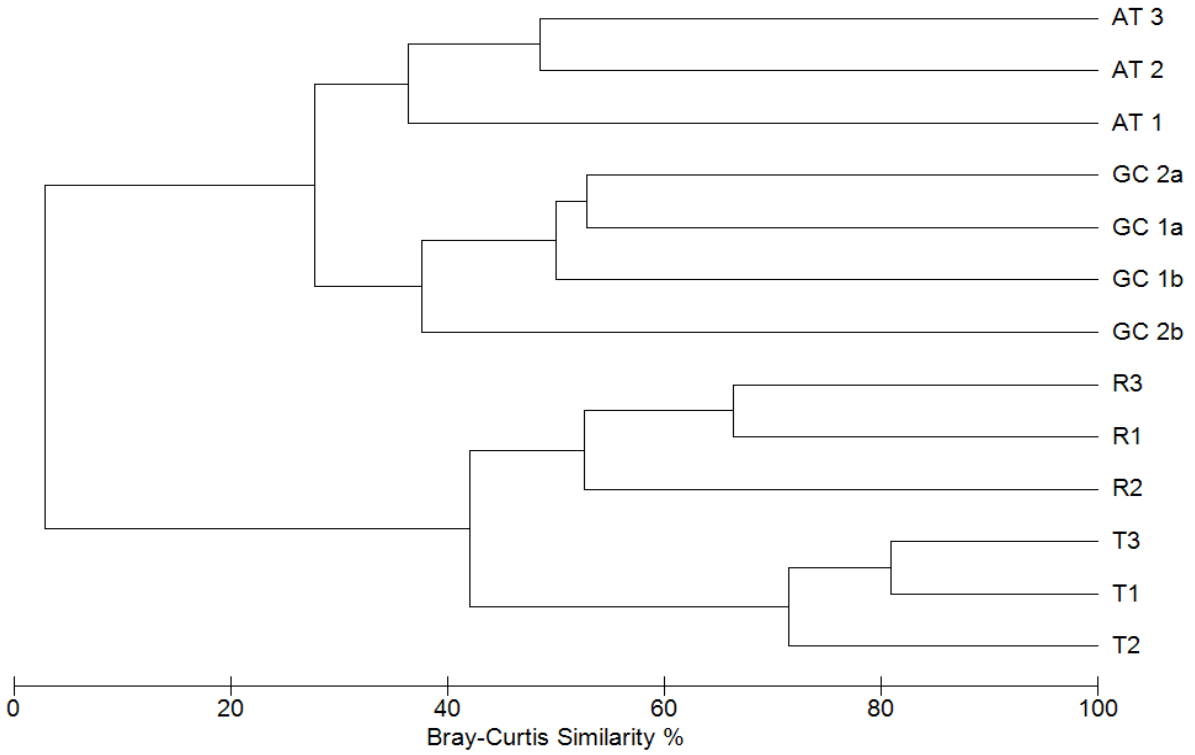
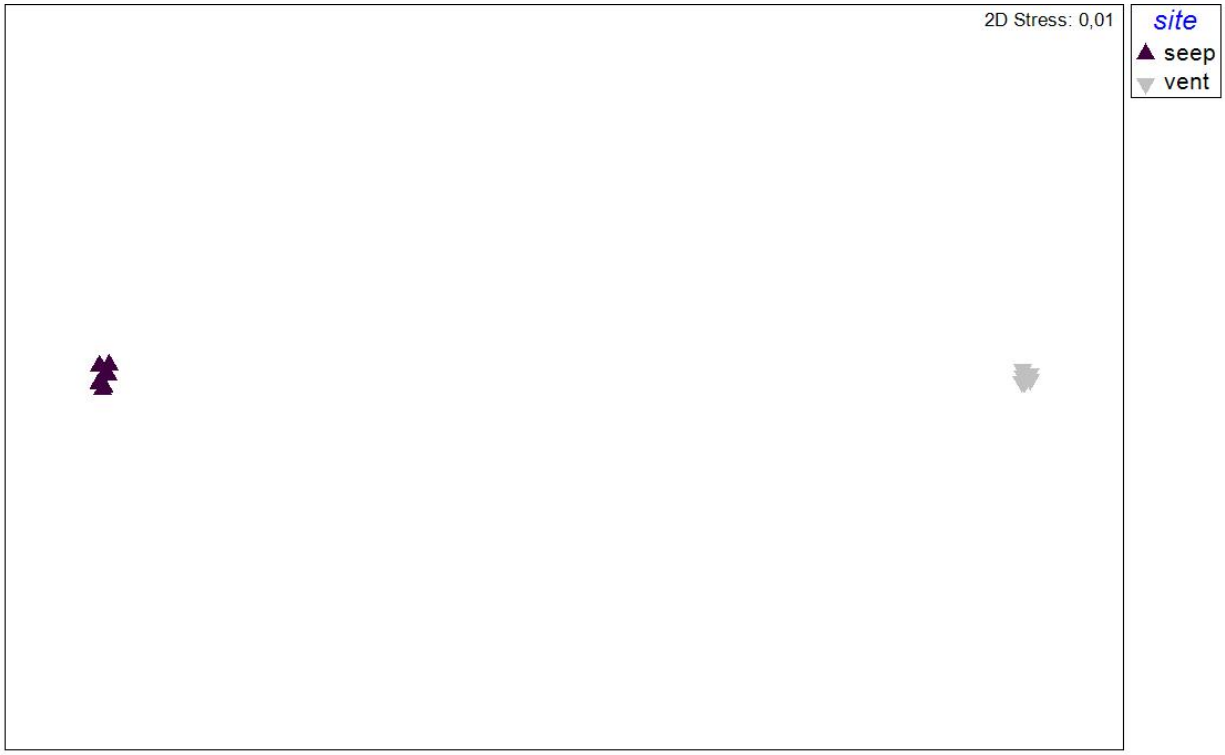


Fig. 4. MDS plot based on Bray-Curtix similarity values of the seep samples Green Canyon (GC) and Atwater Valley (AT) (both black) and the vent samples from Tica (T) and Riftia Field (R) (both grey).



ZUSAMMENFASSUNG

Röhrenwurmaggregationen an kalten Quellen sind durch Stabilität, Langlebigkeit, Strukturiertheit und ihre Fähigkeit die Umweltbedingungen moderat zu gestalten charakterisiert und bieten daher einen geeigneten Lebensraum für eine Vielzahl assoziierter Organismen. Diese Voraussetzungen sowie die hohe chemosynthetische Primärproduktion erklären die in dieser Studie gefundene hohe Diversität (Shannon index H' log e 2.87 ± 0.47) und geringe Dominanz einzelner Genera innerhalb der meiobenthischen Gemeinschaften. Obwohl sich die Populationen der seichten und tieferen Standorte in Abundanz, Diversität und Großtaxazusammensetzung sehr ähnlich waren, wiesen sie doch eine sehr unterschiedliche Zusammensetzung auf Genus-Ebene auf. Die beiden Standorte GC und AV hatten 53 Genera gemeinsam, während 43 Genera nur an den seichten Probenstellen vorkamen und 57 ausschließlich an den Tieferen. Obschon es sich bei den meisten untersuchten Gruppen um Generalisten handelte, wurden an den tieferen Probenstellen Genera gefunden zu denen typische Tiefsee-Spezialisten gehören wie der Nematoden Genus *Thalassomonhystera* sowie sämtliche Vertreter der Copepoden-Familie Argestidae. Diese Ergebnisse ähneln Makrofaunastudien, die eine bathymetrische Übergangszone bei etwa 1000 m Tiefe vermuten (Carney 2005, Cordes et al. 2007, 2010), wobei die Meiofaunagemeinschaften für eine eindeutige Aussage in mehreren Tiefenzonen sowie auch auf Spezies-Ebene untersucht werden müssten.

Im Gegensatz zu den moderaten Umweltbedingungen an kalten Quellen sind die Röhrenwurmaggregationen an hydrothermalen Quellen ein instabiler und extremer Lebensraum. Der ermittelte niedrige Generareichtum – nur 17 Genera aus drei Großtaxen an den sechs Standorten der heißen Quellen versus 150 Genera aus sieben Großtaxen an den sieben Standorten an kalten Quellen – korrelierte mit den abiotischen Faktoren pH-Wert, Temperatur und Sulfid- und Sauerstoffkonzentration. Wir vermuten daher, dass genau diese Faktoren die Ursache für die geringe Vielfalt der epizooischen meiobenthischen Gemeinschaft innerhalb der *Riftia*-Aggregationen an Vents sind. Während an den kalten Quellen keine auf chemosynthetische Habitate spezialisierten Meiofaunagenera gefunden wurden, befanden sich unter den neun Genera die ausschließlich an den heißen Quellen vorkamen einige wie jene zur Copepodenfamilie Dirrivultidae gehörenden Genera, die Spezialisierungen für dieses extreme Ökosystem aufweisen (Heptner et al. 2006, Ivanenko et al 2007, Gollner et al. 2006, 2007, 2010a, 2010b).

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