

Diversity and composition of the copepod communities associated with megafauna around a cold seep in the Gulf of Mexico with remarks on species biogeography

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Abstract In order to characterize the copepod communities associated with tubeworm and mussel aggregations around a hydrocarbon seep in the Green Canyon of the Gulf of Mexico, diversity, abundance, and community composition were analyzed. Also analyzed were species biogeography and the potential connectivity to other chemosynthesis-based habitats. Copepod abundance and biomass were very low among tubeworms and mussels, with 0.22 to 6.08 individuals per 10 cm² sampled area and 9.02 to 42.43 µg wet weight 10 cm² sampled area, respectively; but, abundance was significantly higher among the mussels. Fifty-five copepod species were identified, of which most were newly discovered and primarily belonging to the Harpacticoida order. Four copepod species were previously recorded from other food-rich and hard-substrata environments, such as hydrothermal vents or wood falls. Another four species showed close morphological proximity to species described from cold seeps, hydrothermal vents, and wood falls. Copepod diversity and community composition showed no significant differences between the foundation species. However, differences in the

relative abundance and dominance of single species indicate a rather homogeneous community in mussel beds and a more heterogeneous community among tubeworms, indicating that foundation species may shape the abundance and community composition of associated copepods at cold seeps.

Keywords Meiofauna · Community structure · Copepod biodiversity · Copepod distribution · Chemosynthesis-based habitats · Deep sea

Introduction

Since their first discovery in the early 1980s, many deep-sea cold seeps have been recorded in various parts of the world's oceans. Most of them occur along geologically passive continental margins, where fluids enriched with methane and other reduced components seep out of the sediment (Levin 2005). Cold seeps are typically characterized by the presence of large megafauna aggregations, such as bathymodiolid mussels and siboglinid tubeworms. These foundation species serve as a habitat for associated macrofauna as well as meiofauna (Levin 2005; Bright et al. 2010; Cordes et al. 2010), and have been shown to influence abundance, diversity, species composition, and community structure of associated organisms (Hacker and Gaines 1997). Especially in the deep-sea, cold seep aggregations of foundation species offer islands of primary production and habitat heterogeneity in an otherwise rather monotonous and nutrient-poor environment (Thistle 1983; Thistle and Eckman 1990; Bergquist et al. 2003).

While the megafauna seep communities are relatively well known (Olu et al. 1996; Barry et al. 1997; Sibuet and Olu 1998; Fujikura et al. 1999; Sibuet and Olu-Le 2003; Cordes

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et al. 2007), information on seep meiofauna has often been restricted to measurements of abundance and biomass of major taxa (Powell et al. 1983, 1986; Buck and Barry 1998; Sibuet and Olu 1998; Robinson et al. 2004). Only a few studies provide information at the genus or species level; however, these studies mainly referred to infaunal communities within sediments underneath bacterial mats or megafauna aggregations (Shirayama and Ohta 1990; Dando et al. 1991; Van Gaever et al. 2006, 2009a). In a recent study, the abundance and higher taxonomic composition of meiobenthos associated with tubeworms and mussels at a cold seep were described, showing extremely low meiofauna abundance as compared to previously reported seep sediment densities (Bright et al. 2010). Similar results have been shown in a comparative study of seep and hydrothermal vent meiobenthos communities associated with foundation species (Degen et al. 2012).

Among the meiofauna, copepods are usually the second most abundant and diverse taxon found at cold seeps and may even exceed nematodes in terms of relative abundance (Bright et al. 2010; Gollner et al. 2010a). Relative abundance of copepods associated with tubeworms ranged between 10 and 34 % and between 17 and 99 % within mussel beds (Bright et al. 2010). Despite their high relative abundance and potential ecological importance, little is known about species diversity and community composition of cold seep copepods associated with foundation species, as well as their connectivity to other chemosynthesis-based habitats.

In contrast to hot vents where a dominance of specialized and endemic siphonostomatoid copepods of the family Dirivultidae can be observed (Humes 1988; Humes and Segonzac 1998; Heptner and Ivanenko 2002; Robinson et al. 2004; Zekely et al. 2006), the investigated cold seeps seem to be dominated by harpacticoid copepods (Degen et al. 2012). Records of copepod diversity from cold seeps are rare in general. Recent investigations of seep sites in the Gulf of Mexico have revealed a copepod genus diversity between 25 and 77 genera (Degen et al. 2012).

Species records from previous studies on copepods around hydrothermal vents, cold seeps, or wood falls indicate a potential overlap of copepod species between different chemosynthesis-based habitats (Heptner and Ivanenko 2002; Gollner et al. 2006; Ivanenko et al. 2012; Cuvelier et al. 2014). Despite the increasing knowledge of meiofauna in these environments, our understanding of the diversity, composition, and biogeography of copepod species from cold seeps and other chemosynthesis-based habitats in general is still very limited. Consequently, investigation of their community structure and distribution patterns is necessary.

The objective of this study was to characterize the species diversity, abundance, and community structure of copepods associated with mussels and tubeworms at a deep-sea cold seep and to compare them according to different foundation species and to other types of chemosynthesis-based

ecosystem. Therefore, copepods from cold seep tubeworm and mussel aggregations were investigated to address the following questions: (1) Do the associated copepod communities differ in diversity and species composition between mussel and tubeworm aggregations?; (2) Are there similarities in copepod species composition between cold seep communities and those from other chemosynthesis-based habitats associated with foundation species?; and (3) Is there a specific copepod community associated with megafauna organisms or other organic substrates such as wood falls?

Material and methods

Samples were taken from natural hydrocarbon seeps of the upper Louisiana slope in the Gulf of Mexico (Green Canyon GC 852) at a depth of 1,400 m with the aid of the DVS *Alvin* and ROV *Jason* submersibles. The habitats sampled included three samples of aggregations of the tubeworms *Lamellibrachia* ssp. (71–85 % rel. abundance) and *Escarpia laminata* (15–29 % rel. ab.) as well as mussel beds of *Bathymodiolus brooksi* (37–100 % rel. ab.) and *Bathymodiolus childressi* (0–63 % rel. ab) (Table 1). A rich and diverse macrofauna is typically associated with these foundation species (Cordes et al. 2010). The faunal aggregations assembled on muddy sediment interspersed with carbonated rocks. Typical geophysical and geochemical conditions amongst seep tubeworms include ambient temperatures of ~2 to 4 °C, a minimum pH of 7.7, and maximal sulfide concentrations of 1 μM (Degen et al. 2012).

Tubeworm samples were taken using a hydraulically actuated collection net called a “bushmaster” (2,828 cm² sampling area, see Govenar et al. 2005). The mussel samples were collected with a “mussel pot” sampling device (531 cm² sampling area, see Van Dover 2002). On board, the megafauna organisms were immediately disassembled and rinsed with

Table 1 Sample information on sampling gear, dive number, date, location, and bathymetry

Sample name	Sampling gear	Dive	Date	Location	Depth (m)
M-GC1	Mussel pot	AD4186	22.05.2006	27°06.357 N, 91°09.974 W	1,410
M-GC2	Mussel pot	AD4187	23.05.2006	27°06.656 N, 91°09.937 W	1,406
M-GC3	Mussel pot	J278	24.05.2006	27°06.380 N, 91°09.953 W	1,408
T-GC1	Bushmaster	AD4186	22.05.2006	27°06.371 N, 91°09.968 W	1,409
T-GC2	Bushmaster	AD4187	24.05.2006	27°06.676 N, 91°09.932 W	1,406
T-GC3	Bushmaster	J273	15.05.2006	27°06.370 N, 91°09.967 W	1,410

Abbreviations: *M* mussel, *T* tubeworm, *GC* Green Canyon

filtered seawater to wash off the associated fauna. The meiofauna organisms were retained on a 32- μm sieve, passing through a 1-mm net, and fixed in 4 % formalin. In the laboratory, the samples were washed with tap water through a 40- μm sieve. Meiofauna were extracted from sediments and other remaining particles by centrifugation with a colloidal silica polymer (H.C. Stark, Levasil 200/40 %, $\rho=1.17$) as a flotation medium. Kaolin was used to cover heavier particles and retain those at the bottom of the centrifuge beaker while decanting the supernatant containing the meiofauna specimens (McIntyre and Warwick 1984). Centrifugation was repeated 3 times at 400 rpm for 6 min. After centrifugation, the supernatant was decanted and rinsed with tap water.

Copepods were sorted, counted, and transferred to glycerine. For species identification, individuals were transferred onto glass slides using glycerine as an embedding medium and observed with a Leitz microscope with phase contrast. A total of 1,718 specimens were identified to a species level.

Total copepod biomass in μg wet weight (ww) was estimated according to Warwick and Gee (1984). The total length and width of up to 30 specimens for each species were measured and multiplied with the specific conversion factor to determine the specific volume ($V[nl]=L \times W^2 \times C$; V =volume, L =length in mm, W =width in mm, c =conversion factor). To estimate the wet weight (μg), the calculated volume was multiplied by 1.13, the specific weight for meiofauna organisms (Wieser 1960). From these data, a mean male and female size for each species was calculated. Total copepod biomass was estimated by calculating the mean biomass of each species multiplied by its total abundance per sample. Due to the different sizes of the sampled area and in order to compare the results to other meiofauna studies, we standardized copepod abundance and biomass to a 10 cm^2 sampling area. However, the sampled area that was covered by the tubeworm or mussel aggregations can significantly differ from the three-dimensional surface area provided by the biogenic structure of foundation species which is inhabited by associated copepods. To consider these differences, we additionally calculated copepod abundance and biomass per surface area of the foundation species. The surfaces of mussels and tubeworms were estimated by measuring length and widths of each individual of the collected assemblage (Bright et al. 2010).

Additionally, we calculated the relative abundance of all copepod species for each sample. All species with >5 % of the total abundance were displayed in a pie chart in order to show differences in community composition. To determine the diversity of copepod communities, we calculated species richness (S), Shannon-Wiener diversity (H'_{\log_e}), Pielou's evenness index (J'), and the expected number of species [ES(14)] from quantitative species-abundance data by using the DIVERSE subroutine in PRIMER v6 package (Clarke and Gorley 2006). We performed a Mann–Whitney U -test to test for significant differences in copepod abundance, biomass,

and diversity between mussel and tubeworm aggregations. All data were square-root transformed (except for H'_{\log_e} and J').

Hierarchical clustering techniques were used to compare the copepod communities between the different foundation species aggregations. The similarity matrices for the cluster analysis were generated using Bray–Curtis similarity (Bray and Curtis 1957) calculated from standardized and square-root transformed data. The square-root transformation ensures that highly abundant species do not dominate the analysis and that both very abundant and less common species contribute to the similarity matrix (Clarke and Gorley 2006). Similarity percentage (SIMPER) analyses were used in order to test for similarities between the communities and to investigate which copepod species were responsible for similarities/dissimilarities between tubeworm and mussel samples. We additionally conducted an analysis of similarity (ANOSIM) to test for significant differences in copepod community composition between mussel beds and tubeworm fields. All univariate indices and multivariate measures were performed using the PRIMER v6 package (Clarke and Gorley 2006).

Results

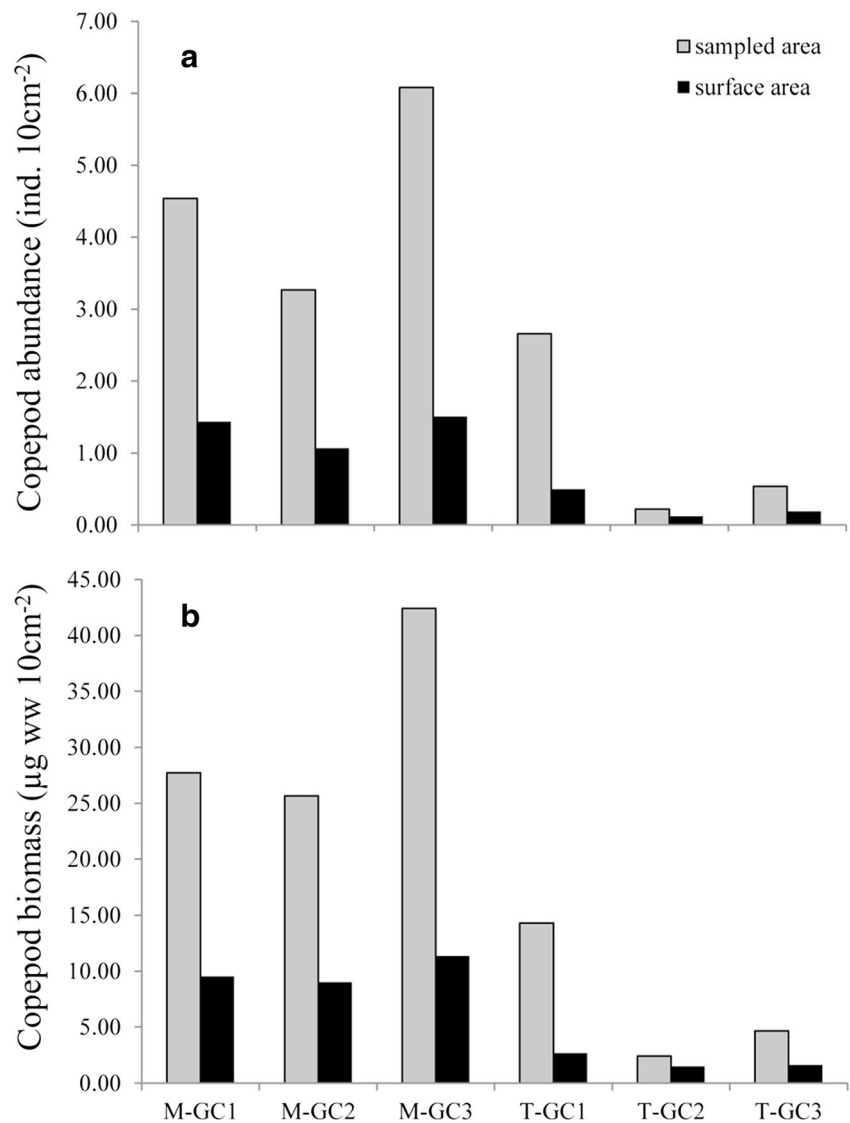
Copepod abundance and biomass

The total copepod abundance per sample area was generally very low, ranging from 0.22 to 6.08 ind. per 10 cm^2 (Fig. 1a). Copepod abundance in mussel beds ranged from 3.27 to 6.08 ind. 10 cm^2 while the tubeworm aggregations harboured even lower abundance (0.22 to 2.66 ind. 10 cm^2), resulting in significantly higher copepod abundance in the mussel beds (Mann–Whitney U -test, $p=0.049$). Total abundance per surface area revealed even lower numbers (Fig. 1a). As a consequence of the higher surface area of tubeworms compared to mussels, copepod densities were significantly lower in tubeworm aggregations (0.12 to 0.50 ind. 10 cm^2) compared to mussel beds (1.07 to 1.51 ind. 10 cm^2 ; Mann–Whitney U -test, $p=0.049$). Accordingly, the copepod biomasses per sample area and per surface area (Fig. 1b) were also significantly higher in mussel beds (sample area: 25.67 to 42.43 μg ww per 10 cm^2 ; surface area: 9.02 to 11.36 μg ww per 10 cm^2) compared to tubeworm aggregations (sample area: 2.42 to 14.31 μg ww per 10 cm^2 ; surface area: 1.64 to 2.69 μg ww per 10 cm^2 ; Mann–Whitney U -test, $p=0.049$).

Diversity and community patterns

The adults obtained from all 6 samples were assigned to 16 families, 29 genera, and 55 species (Table 2). The most species-rich family was the Miraciidae with 10 species, followed by the Ameiridae and the Ectinosomatidae with 9

Fig. 1 Copepod abundance (a) and biomass (b) per 10 cm² sample area and surface area, respectively, of three mussel (M-GC1, M-GC2, M-GC-3) and three tubeworm samples (T-GC1, T-GC2, T-GC3) at Green Canyon in the Gulf of Mexico



and 8 species, respectively. The highest copepod species richness (S) was found among the tubeworms ($S=27$) and the lowest among mussel assemblages ($S=5$). Species richness ranged from 12 to 27 in tubeworm fields and from 5 to 24 in mussel aggregations, but showed no significant differences between mussels and tubeworms (Table 3, Mann–Whitney U -test, $p=0.51$). The Shannon–Wiener Indices (H'_{\log_e}) of the entire copepod community ranged from 1.49 to 2.99 in the mussel fields and from 2.21 to 2.95 in tubeworm aggregations (Table 3). However, H'_{\log_e} showed no significant differences between tubeworm aggregations and mussel fields (Mann–Whitney U -test, $p=0.82$). Pielou's evenness (J') of the mussel fields was relatively high and ranged from 0.89 to 0.94 and showed no significant difference from the tubeworm aggregations (Table 3, Mann–Whitney U -test, $p=0.82$).

Of the 1,718 identified specimens, 599 (35 %) individuals were copepodids and 1,119 (65 %) were adults. The most

species-rich families (Miraciidae, Ameiridae, and Ectinosomatidae) comprise 49 % of all species found in the samples. Most of the detected species ($S=43$, i.e., 78 %) have not been reported. Only 12 species were already known to science (Table 2). Four of them, the species *Tychidion guyanense*, *Xylora bathyalis*, *Delavalia gundulae*, and the undescribed species *Mesochra* sp. have been previously reported from other chemosynthetic ecosystems (Table 4A). Another four species, *Erebonaster* sp., *Uptionyx* sp., *Tisbe* sp. 1, and *Smacigastes methanophilus*, showed close morphological proximity to species described from cold seeps, hydrothermal vents, and wood falls (Table 4B).

Among the 55 species, not a single one co-occurred in all samples. The species *Ameira parvula*, *Mesochra* sp., and *Oncaea* sp. showed the widest distribution within the studied area with an occurrence in five of six samples. All other species were patchily distributed among the different samples.

Table 2 Species-Station-Matrix for all copepods found in six samples from three sites and two different foundation species

Taxa	Stations					
	M-GC1	M-GC2	M-GC3	T-GC1	T-GC2	T-GC3
Ord. HARPACTICOIDA						
Fam. Ameiridae						
Ameiridae sp.	0.0000	0.0000	0.0188	0.0000	0.0000	0.0035
Gen. Ameira						
<i>Ameira parvula</i>	0.0000	0.0377	0.1318	0.1839	0.0354	0.0495
<i>Ameira longipes</i>	0.0000	0.0000	0.0188	0.0000	0.0000	0.0000
Gen. Ameiropsis						
<i>Ameiropsis mixta</i>	0.0000	0.0000	0.0000	0.1273	0.0000	0.0000
<i>Ameiropsis</i> sp.	0.0000	0.0000	0.0000	0.0813	0.0000	0.0000
Gen. Pseudameira						
<i>Pseudameira</i> sp. 1	0.0000	0.0000	0.0000	0.0035	0.0000	0.0000
<i>Pseudameira</i> sp. 2	0.0000	0.0000	0.0000	0.0035	0.0000	0.0000
Gen. Proameira						
<i>Proameira dubial/simplex</i>	0.0000	0.0000	0.1695	0.0000	0.0000	0.0000
Gen. Sarsameira						
<i>Sarsameira</i> sp.	0.0188	0.0000	0.0000	0.0071	0.0000	0.0000
Fam. Ancorabolidae						
Ancorabolidae sp.	0.0000	0.0000	0.0000	0.0035	0.0000	0.0000
Gen. Uptionyx						
<i>Uptionyx</i> sp.	0.0000	0.0000	0.0753	0.0106	0.0000	0.0000
Fam. Argestidae						
Argestidae sp. 1	0.0000	0.0000	0.0000	0.0071	0.0000	0.0000
Argestidae sp. 2	0.0000	0.0000	0.0000	0.0071	0.0000	0.0000
Gen. Argestes						
<i>Argestes</i> sp.	0.0000	0.0000	0.0000	0.0000	0.0354	0.0000
Fam. Canthocamptidae						
Gen. Heteropsyllus						
<i>Heteropsyllus</i> sp.	0.0000	0.0000	0.0753	0.0141	0.0000	0.0000
Gen. Mesochra						
<i>Mesochra</i> sp.	0.0000	0.7156	0.2825	0.3926	0.0141	0.0106
Gen. Psammocamptus						
<i>Psammocamptus</i> sp.	0.0000	0.0188	0.0000	0.0000	0.0000	0.0000
Fam. Cletodidae						
<i>Cletodidae</i> sp.	0.0000	0.0000	0.0377	0.0000	0.0000	0.0000
Gen. Cletodes						
<i>Cletodes longicaudatus</i>	0.0000	0.0000	0.0000	0.0000	0.0071	0.0000
Gen. Strongylacron						
<i>Strongylacron</i> sp.	0.0000	0.0000	0.0188	0.0071	0.0000	0.0000
Fam. Ectinosomatidae						
Ectinosomatidae sp. 1	0.0000	0.0000	0.1883	0.0000	0.0035	0.0000
Ectinosomatidae sp. 2	0.0000	0.0000	0.0377	0.0000	0.0000	0.0000
Ectinosomatidae sp. 3	0.0000	0.0000	0.0188	0.0000	0.0000	0.0000
Gen. Halectinosoma						
<i>Halectinosoma</i> sp. 1	0.0000	0.0000	0.0000	0.0000	0.0071	0.0000
<i>Halectinosoma</i> sp. 2	0.0000	0.0000	0.0942	0.0000	0.0000	0.0000
Gen. Pseudobradya						
<i>Pseudobradya</i> sp.. 1	0.0188	0.2072	0.0000	0.0000	0.0071	0.0000

Table 2 (continued)

Taxa	Stations					
	M-GC1	M-GC2	M-GC3	T-GC1	T-GC2	T-GC3
<i>Pseudobradya</i> sp. 2	0.0000	0.0000	0.1507	0.0035	0.0000	0.0000
<i>Pseudobradya</i> sp. 3	0.0000	0.0000	0.0000	0.0000	0.0000	0.0071
Fam. Laophontidae						
Gen. <i>Archesola</i>						
<i>Archesola typhlops</i>	0.0000	0.0942	0.0753	0.0884	0.0035	0.0000
Fam. Miraciidae						
Miraciidae sp. 1	0.0000	0.0000	0.0377	0.0000	0.0000	0.0000
Miraciidae sp. 2	0.0000	0.0000	0.0377	0.0000	0.0000	0.0000
Miraciidae sp. 3	0.0000	0.0000	0.0000	0.0212	0.0000	0.0000
Miraciidae sp. 4	0.0000	0.0000	0.0377	0.0000	0.0000	0.0000
Gen. <i>Amphiascella</i>						
<i>Amphiascella neglecta</i>	0.0000	0.0000	0.0000	0.2051	0.0141	0.1309
Gen. <i>Amphiascus</i>						
<i>Amphiascus</i> sp. 1	0.0000	0.0000	0.0000	0.0283	0.0035	0.0000
<i>Amphiascus</i> sp. 2	0.0000	0.0000	0.0188	0.3148	0.0000	0.0141
<i>Amphiascus</i> sp. 3	0.0000	0.0000	0.0000	0.3607	0.0000	0.0035
Gen. <i>Delavalia</i>						
<i>Delavalia gundulae</i>	0.0000	0.0188	0.2072	0.0071	0.0000	0.0000
<i>Delavalia</i> sp.	0.0000	0.0000	0.0000	0.0071	0.0000	0.0000
Fam. Pseudotachidiidae						
Gen. <i>Pseudomesochra</i>						
<i>Pseudomesochra</i> sp. 1	0.0000	0.0000	0.0000	0.0035	0.0000	0.0000
<i>Pseudomesochra</i> sp. 2	0.0000	0.0188	0.0000	0.0000	0.0000	0.0000
<i>Pseudomesochra</i> sp. 3	0.0000	0.0188	0.0000	0.0000	0.0000	0.0000
Gen. <i>Xylora</i>						
<i>Xylora bathyalis</i>	0.0000	0.0565	0.4520	0.0000	0.0071	0.0000
Gen. <i>Psammis</i>						
<i>Psammis longipes</i>	0.0000	0.0000	0.0942	0.0000	0.0000	0.0000
Fam. Tegastidae						
Gen. <i>Smacigastes</i>						
<i>Smacigastes methanophilus</i>	0.0000	0.0000	0.0000	0.1556	0.0000	0.0000
Fam. Tisbidae						
Gen. <i>Tisbe</i>						
<i>Tisbe</i> sp. 1	0.1695	1.2241	1.1676	0.0000	0.0000	0.0035
<i>Tisbe</i> sp. 2	0.0000	0.2825	0.0000	0.0000	0.0000	0.0035
Ord. CYCLOPOIDA						
Fam. Cyclopinidae						
Cyclopinidae sp.	0.0000	0.0000	0.0000	0.0106	0.0000	0.0071
Gen. <i>Cyclopina</i>						
<i>Cyclopina</i> sp.	0.0377	0.1695	0.5273	0.0000	0.0000	0.1273
Gen. <i>Pterinopsyllotus</i>						
<i>Pterinopsyllotus</i> sp.	0.0000	0.0000	0.0000	0.0000	0.0035	0.0000
Fam. Erebonasteridae						
Gen. <i>Erebonaster</i>						
<i>Erebonaster</i> sp.	0.0000	0.0000	0.0000	0.0000	0.0035	0.0000
Gen. <i>Tychidion</i>						

Table 2 (continued)

Taxa	Stations					
	M-GC1	M-GC2	M-GC3	T-GC1	T-GC2	T-GC3
<i>Tychidion guyanense</i>	0.0000	0.0000	0.0000	0.0000	0.0035	0.0000
Fam. Oncaeidae						
Gen. Oncaea						
<i>Oncaea</i> sp.	0.0188	0.0188	0.0000	0.0106	0.0177	0.0035
Fam. Poecilostomatoidae						
Poecilostomatoidae sp.	0.0000	0.0188	0.0000	0.0071	0.0141	0.0000
Fam. Sapphirinidae						
Gen. Sapphirina						
<i>Sapphirina</i> sp.	0.0000	0.0000	0.0000	0.0000	0.0188	0.0000
N/station	0.2637	2.9002	3.9736	2.0725	0.1992	0.3607
S/station	5	14	24	27	17	12

Copepod orders are given in capital and bold, followed by families in bold and species in italic. Total abundance (N) of adults per 10 cm² sample area and number of species (S) per sample, respectively, are given at the bottom

Overall, 18 species with a proportion >5 % dominated the copepod fauna. However, the relative abundance was remarkably different between the two habitats of foundation mega-fauna species (Fig. 2). *Tisbe* sp. 1 appeared to be the most characteristic and abundant species in the mussel beds, contributing between 29 and 64 % of the total abundance, while this species was either absent or only present in very low abundance (< 5 %) in the tubeworm samples (Fig. 2). In contrast, the tubeworm aggregations were dominated by the species *Ameira parvula*, *Amphiascella neglecta*, *Mesochra* sp., *Amphiascus* sp. 3, and *Argestes* sp.1. Interestingly, the species *Mesochra* sp. was also very abundant among the mussel samples M-GC1 (25 %) and M-GC3 (8 %) and can be considered as a more generalist species.

The SIMPER analyses demonstrated a dissimilarity of copepod communities between tubeworm and mussel aggregations of 77 %. Similarities within groups were relatively low with only 33 % among the tubeworm-associated copepod communities and 42 % for the mussel bed communities. Cluster-analyses (Fig. 3) showed that mussel and tubeworm samples cluster, however, SIMPROF revealed that this was not significant ($p > 0.05$). Similarly, ANOSIM detected no

significant differences in copepod communities associated with the different habitats ($p > 0.05$), although global R was relatively high (R=0.963).

Discussion

Abundance

Although the few available datasets on seep meiofauna may limit our ability to predict a trend in copepod abundance concerning different habitat types, at our current state of knowledge, the total abundance of copepods associated with foundation species found at Green Canyon (GC) are apparently lower than those from infaunal communities of seep sediments (reviewed in Bright et al. 2010), but are similar to the abundance of associated communities from hydrothermal vents (Gollner et al. 2006). Relatively low copepod abundance from seep sediments has only been described for anoxic sediments of the Black Sea and for a brine seep located at the East Flower Garden Banks in the Gulf of Mexico (Powell et al. 1983; Sergeeva and Gulin 2007).

The generally low densities observed for copepods at GC are counterintuitive considering the generally known high productivity of seep systems, making bottom-up control rather unlikely. Previous studies suggested competition among organisms of the same size class, including juvenile macrofauna organisms, as one possible explanation for the low abundance observed for permanent meiofauna (Bright et al. 2010; Degen et al. 2012). In addition, foundation species at seeps harbour a wide range of highly abundant macrofauna organisms that may feed on the same resources, and thereby out-compete the smaller meiobenthic animals, or prey upon them (Bright

Table 3 Diversity indices for all samples, including species number (S), estimated species number (ES), Shannon-Wiener diversity ($H'_{\log e}$), and Pielous evenness (J')

Sample	S	ES (14)	$H'_{\log e}$	J'
M-GC1	5	4.94	1.49	0.92
M-GC2	14	9.06	2.35	0.89
M-GC3	24	11.61	2.99	0.94
T-GC1	27	11.24	2.95	0.89
T-GC2	16	9.57	2.68	0.96
T-GC3	12	8.13	2.21	0.89

Table 4 References for geographical and bathymetrical distribution as well as preferred substrata of A) known species found at Green Canyon (GC) and other chemosynthesis-based habitats, and B) species found solely at GC and morphologically related to previously described species from other chemosynthesis-based habitats

No.	Species	Reference	Location/Records	Substratum	Depth (m)	Geographic region
A 1	<i>Delavalia gundulae</i>	Willen 2003	hot vent, Indonesia	mussels	1,440	West Pacific
2	<i>Tychidion guyanense</i>	Humes 1973	hot vent, Guyana, Continental Slope	tubeworms	500	West Atlantic
3	<i>Xylora bathyalis</i>	Hicks 1988	wood falls, New Zealand	wood	1,514	West Pacific
		Gollner et al. 2006	hot vent, East Pacific Rise	tubeworms	2,500	East Pacific
		Cuvelier et al. 2014	hot vent, Mid Atlantic Ridge	mussels	~1,700	North Atlantic
4	<i>Mesochra</i> sp.	Martinez-Arbizu pers. comm.	hot vent, Mid Atlantic Ridge	mussels	2,996	South Atlantic
B 5	<i>Smacigastes methanophilus</i>	Plum and Martinez-Arbizu 2009	cold seep, GC, Louisiana Lower Slope	tubeworms	1,400	Gulf of Mexico
6	<i>Smacigastes micheli</i>	Ivanenko and Defaye 2004	hot vent, Mid Atlantic Ridge	artificial substratum	1,698	North Atlantic
		Ivanenko et al. 2012	hot vent, Mid Atlantic Ridge	mussels	~1,700	North Atlantic
		Cuvelier et al. 2014	hot vent, Mid Atlantic Ridge	wood, slate	~1,700	North Atlantic
7	<i>Smacigastes barti</i>	Gollner et al. 2008	hot vent, East Pacific Rise	artificial substratum	2,500	East Pacific
8	<i>Tisbe</i> sp.	this study	cold seep, GC, Louisiana Lower Slope	mussels	1,400	Gulf of Mexico
9	<i>Tisbe dahmsi</i>	Ivanenko et al. 2011	hot vent, Mid Atlantic Ridge	mussels	~1,700	North Atlantic
10	<i>Uptoniynx spec.</i>	this study	cold seep, GC, Louisiana Lower Slope	mussels/tubeworms	1,490	Gulf of Mexico
11	<i>Uptoniynx verenae</i>	Conroy-Dalton and Huys 2000	hot vent, Juan de Fuca Ridge	macroinvertebrates	2,417	East Pacific
12	<i>Erebonaster</i> sp.	this study	cold seep, GC, Louisiana Lower Slope	tubeworms	1,490	Gulf of Mexico
13	<i>Erebonaster prontentipes</i>	Humes 1987	hot vent, Gulf of California	mussels	2,000	East Pacific
14	<i>Erebonaster spinulosus</i>	Humes 1989	cold seep, Florida Escarpement	bacterial mats	3,266	Gulf of Mexico

This list just gives references of species found in the investigated area and their closest related species within genus level. It is not an overview of all known copepods from chemosynthetic systems

et al. 2010; Degen et al. 2012). Previous studies from other ecosystems have suggested that macrofauna organisms may shape meiofauna communities by processes such as competition, predation, and physical disturbance (reviewed by Olafsson 2003). More recently, meiofauna abundance has been shown to be negatively correlated with macrofauna abundance, suggesting predation pressure as the underlying mechanism for this relation (Debenham et al. 2004; Van Gaever et al. 2009b).

Despite the overall low copepod abundance at GC, our results revealed significantly higher copepod abundance and biomass in mussel beds compared to tubeworms. While detailed information about abundance and biomass of copepods associated with foundation species from seeps is rare, comparable differences in meiofauna densities and biomass have been previously reported for nematode and copepod communities at hydrothermal vents (Gollner et al. 2006; Zekely et al. 2006). Predation by macrofauna organisms may provide a potential explanation for the observed differences in copepod abundance. Additionally, the seep megafauna organisms (i.e., vestimentiferan tubeworms and bathymodiolin mussels) may influence the local biogeochemistry and reduce the environmental stress within an aggregation by consuming considerable amounts of sulfide and/or methane from the sediments

(Cordes et al. 2009; Degen et al. 2012), thereby shaping the associated copepod community.

Diversity and community patterns

Our results show that copepod diversity was similar between mussel and tubeworm aggregations. However, their community composition was homogenic among mussels, but rather heterogenic among tubeworms, as has been previously shown for vent copepod communities (Gollner et al. 2006). Underlying reasons could be the different body structure of mussels and tubeworms. Tubeworms are longer and extend the habitat with their tubes up to 1.5 m above the bottom, creating many potential micro-niches for the associated fauna (Govenar et al. 2005). In contrast, the mussel shape is more uniform, although its byssus threads might also offer additional habitat structure. Another potential explanation might be the habitat preferences of *Tisbe* sp. 1, which was very dominant among seep mussels, causing high homogeneity. Previous studies on copepod communities at the hydrothermal vent site Lucky Strike (Mid-Atlantic Ridge) demonstrated high natural abundance of the species *Tisbe dahmsi* within mussel fields and in a colonization experiment (Ivanenko et al. 2011).

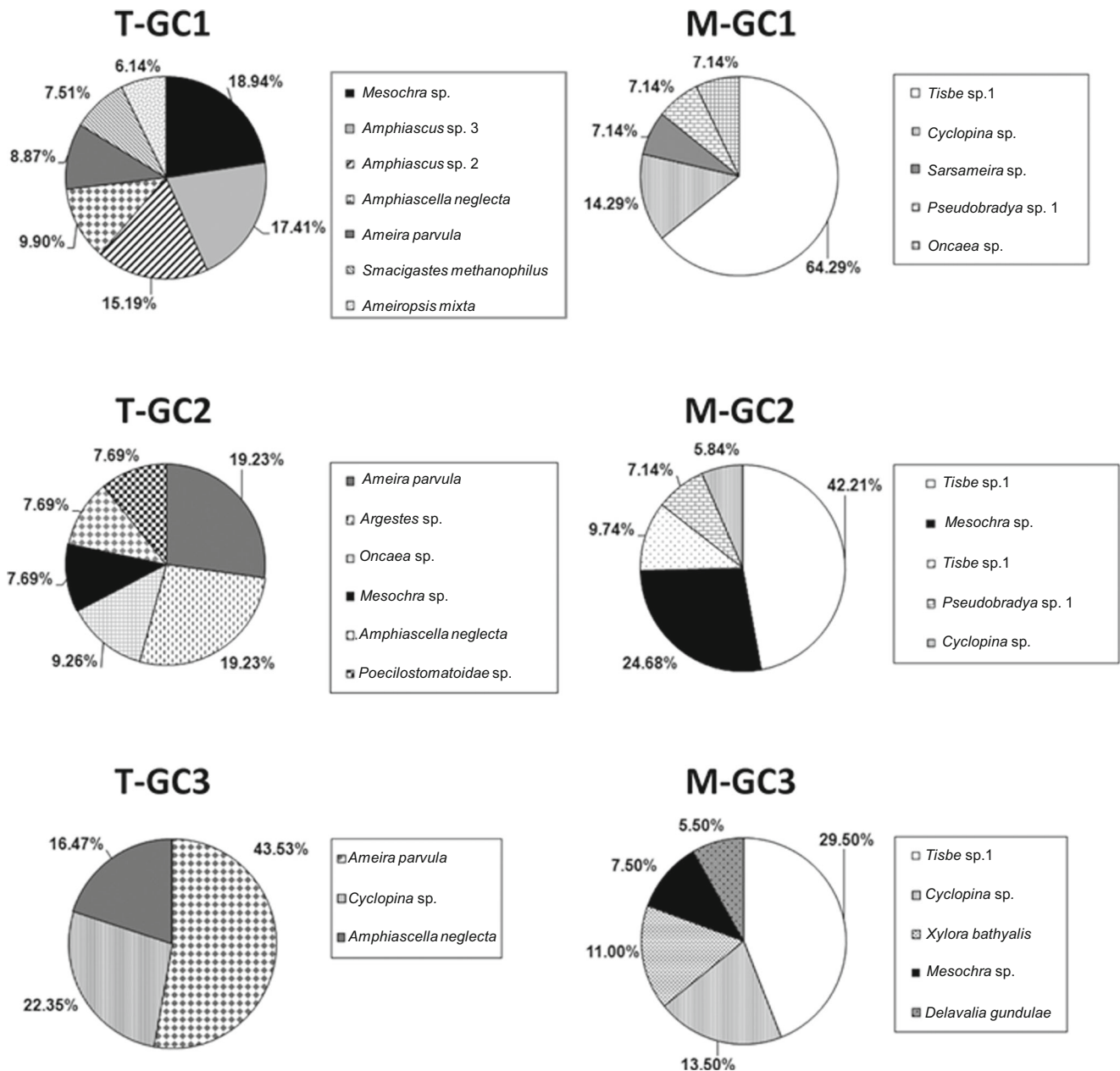


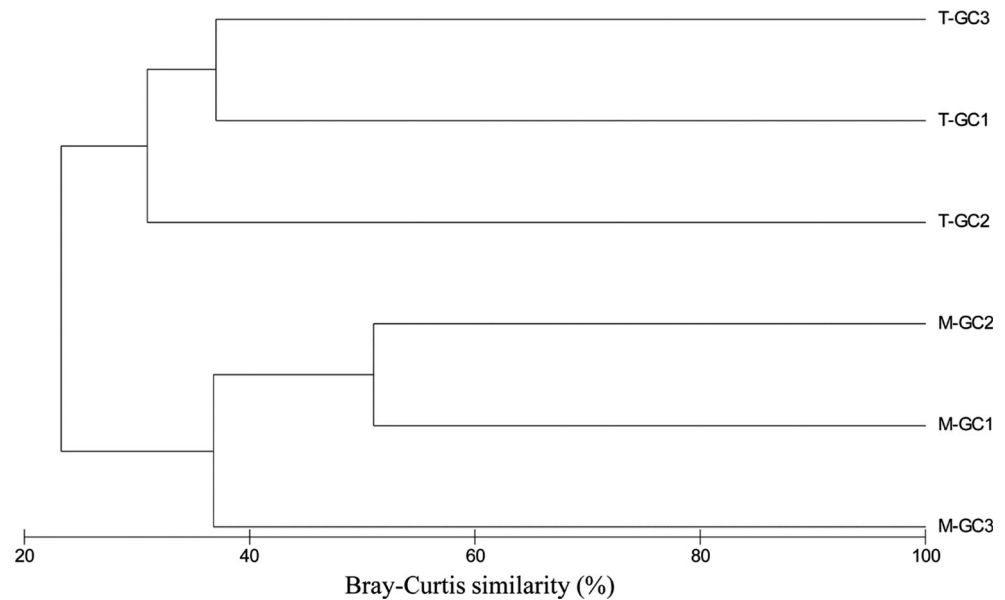
Fig. 2 Frequency (> 5 %) of copepod species within the communities associated with tubeworm aggregations (left column) and mussel beds (right column) for each sample

The observed species richness (S: 12–27) within the copepod communities associated with the foundation species is similar (S: 6 – 30) to previously described copepod communities associated with tubeworms from the same seep area (Green Canyon) but from shallower depth and from Atwater Valley seeps (Degen et al. 2012). In contrast, it is relatively low compared to data reported for surrounding deep-sea sediments at the northern Gulf of Mexico continental slope and abyssal plain (S: 30–104; Baguley et al. 2006). More stable physico-chemical conditions, non-toxic levels of sulphide, potentially lower predation pressure by lower abundant macrofauna, or the different nature of the substrate (sediment versus

hard substrate) may cause higher diversity in the adjacent areas of the Gulf of Mexico.

Seep copepod richness was similarly low to the copepod richness reported for tubeworms and mussels at hydrothermal vents (S: 7–14) on the East Pacific Rise (Gollner et al. 2006, 2010a), although environmental conditions, such as high and varying temperatures, are more extreme at vents than at seeps. Degen et al. (2012) found that total meiofauna diversity was higher at seeps than at vents and explained this by the more moderate environmental conditions at seeps. At first glance, this contradictory result of similar copepod richness but different total meiofauna richness can be explained by the unique

Fig. 3 Hierarchical cluster diagram of group-average linking based on a Bray-Curtis community similarity value from three mussel (M-GC1, M-GC2, M-GC-3) and three tubeworm samples (T-GC1, T-GC2, T-GC3) at Green Canyon in the Gulf of Mexico



presence of a diverse copepod family at hydrothermal vents. Dirivultidae are very abundant and diverse at hydrothermal vents and have developed numerous adaptations to deal with toxic and hot hydrothermal fluids, but have not been reported from other habitats (reviewed in Gollner et al. 2010b). The addition of dirivultid copepod species to total copepod diversity at hydrothermal vents compensates for the low diversity of other copepod species and leads to similar copepod diversity at vents and seeps.

Biogeography of copepods at chemosynthesis-based ecosystems

While harpacticoid copepods seem to play a minor role at hydrothermal vents, which are typically dominated by dirivultids, the communities of the investigated cold seeps mainly include species belonging to harpacticoid families. Among these, the Ameiridae, Argestidae, Ancorabolidae, Miraciidae, and Ectinosomatidae generally show a broad geographical, as well as bathymetrical, distribution and are typically found in almost all marine habitats, including shallow coastal waters, deep-sea sediments, and chemosynthesis-based systems (Heptner and Ivanenko 2002; Tsurumi et al. 2003; George 2005; Baguley et al. 2006; Gheerardyn et al. 2009; Veit-Köhler et al. 2010).

Although chemosynthesis-based habitats in general are often isolated from each other by several hundreds of metres to thousands of kilometres and may substantially differ in their physico-chemical settings, our results indicate that certain harpacticoid and epibenthic cyclopoid species may be strongly associated with, or even restricted to, megafauna organisms at chemosynthesis-based habitats or organic substrata such as wood and whale bones that have been shown to support

chemosynthesis-based communities (Smith and Bacon 2003; Bienhold et al. 2013). The co-occurrence of copepod species associated with foundation species at different reduced ecosystems, as well as the findings of species known from coastal and deep-sea sediments, poses questions regarding the mechanism of global copepod distribution, the colonization of chemosynthesis-based habitats, and their connectivity on a larger scale. Several hypotheses have been previously suggested in order to explain the broad distribution of benthic copepods and the colonization of organic structures in the deep sea (Gheerardyn et al. 2009; Veit-Köhler et al. 2010). Analogous to an investigation of a deep-sea coral degradation system (Gheerardyn et al. 2009), we discuss the biogeography of the identified species and consider different possibilities for the colonisation of the investigated area.

- 1) *Colonisation from shallow-water systems*: Of the few already known copepod species found among the foundation species, eight (*Ameira parvula*, *Ameira longipes*, *Ameiropsis mixta*, *Proameira dubia*, *Cletodes longicaudatus*, *Amphiascella neglecta*, *Psammis longipes*, *Archesola typhlops*) have only been reported from shallow-water habitats. The species *Ameiropsis mixta*, *Amphiascella neglecta*, and *Archesola typhlops* have only been reported from European coasts so far. In turn, *Ameira parvula* shows a wide global and bathymetrical distribution with records from the coasts of northern Europe, the Mediterranean Sea, the Black Sea, and the east coast of North America, but also along the coast off New Caledonia, New Zealand, and in arctic waters (Lang 1948; Wells and Rao 1987). More recently, this species has been reported in the northern Gulf of Mexico continental slope (Baguley et al. 2006), indicating that there

might have been an exchange between the investigated cold-seep and shallow-water areas of the Gulf of Mexico. However, investigations of the northern Gulf of Mexico continental slopes suggest rather small distribution ranges and low dispersal rates on a spatial scale of less than 50 km (Baguley et al. 2006).

The Tisbidae and Tegastidae species are very rare in the deep sea and are usually considered typical epiphytic species in shallow waters (Lang 1948). More recent findings, however, have demonstrated the existence of deep-sea Tegastidae and Tisbidae associated with foundation species at chemosynthesis-based habitats (Ivanenko and Defaye 2004; Gollner et al. 2008; Plum and George 2009; Back et al. 2010; Ivanenko et al. 2011; Cuvelier et al. 2014). The occurrence of shallow-water species within the studied area indicates that an appropriate habitat structure and other favourable environmental conditions are more important than water depth.

- 2) *Colonisation from adjacent areas*: The majority of the detected species are unknown but belong to families that are frequently found in deep-sea sediments (Argestidae, Ancorabolidae, Miraciidae, and Ectinosomatidae). This indicates that these species may have colonized the investigated mussel beds and tubeworm aggregations from adjacent deep-sea sediments. Species from a background community may represent facultative inhabitants of habitats provided with organic structures (Gheerardyn et al. 2009).
- 3) *Colonisation from chemosynthetic habitats*: Among the species already known to science, *Xylora bathyalis*, *Delavalia gundulae*, and *Tychidion guyanense* have been exclusively described from reduced ecosystems in association with epibenthic, organic substrata. The first record of *X. bathyalis* stems from a wood fall near New Zealand's coast (Humes 1973). In addition, this species has been found in association with vent vestimentiferan tubeworms and in close proximity to hydrothermal vents located at the East Pacific Rise (Gollner et al. 2006, 2010a) as well as at the Mid-Atlantic Ridge (Lucky Strike vent field) on deployed wood and slate substrata in the frame of a colonization experiment (Cuvelier et al. 2014). With these findings, *X. bathyalis* shows the widest distribution of the herein described copepods. The harpacticoid species *Delavalia gundulae* was described from a mussel field of a hydrothermal vent located at a submarine volcano off the Indonesian coast (Willen 2003), while *T. guyanense* was found in association with vestimentiferan tubeworms at a hydrothermal vent site located at the continental slope off Guyana (Humes 1973).

Relatives of the four undescribed species *Erebonaster* sp., *Uptionyx* sp., *Mesochra* sp. and *Tisbe* sp. 1 have been

previously reported from cold seeps and hydrothermal vents. So far, the genus *Erebonaster* contains the species *E. spinolosus* and *E. protentipes*. The latter was first described from a hydrothermal vent site in the Gulf of California associated with mussel aggregations (Humes 1987). *E. spinolosus* has been reported from a cold seep located in the Gulf of Mexico in association with bacterial mats (Humes 1989). The genus *Uptionyx* was established with the description of *Uptionyx veranae* found at the East Pacific Rise in association with foundation species (Conroy-Dalton and Huys 2000). The undescribed species of the recent study shows the morphological features of the genus *Uptionyx*, but clearly differs from *U. veranae*. The third undescribed species, *Mesochra* sp., has already been found in samples taken at a hydrothermal vent at the Mid-Atlantic Ridge (pers. obs. Martinez-Arbizu). Based on its morphological features, the undescribed species *Tisbe* sp. 1 belongs to the *T. gracilis* group. Recently, the closely related species *Tisbe dahmsi* has been described from the Lucky Strike hydrothermal vent field at the Mid-Atlantic Ridge, where it has been found in an in situ colonization experiment deployed on *Bathymodiolus azoricus* mussel assemblages (Ivanenko et al. 2011).

Relatives of the seep species *Smacigastes methanophilus* were also recorded from vents and whale falls (Plum and Martinez Arbizu 2009). The genus *Smacigastes* was established by Ivanenko and Defaye in 2004 with the description of *Smacigastes micheli*. At that time, it was the first record of a tegastid species from the deep sea. A few years later the second species of this genus, *Smacigastes barti* was described from the East Pacific Rise (Gollner et al. 2008). Both species were first described from artificial substrata deployed directly at or near foundation species at hydrothermal vents in colonization experiments (Ivanenko and Defaye 2004; Gollner et al. 2008). More recent investigations have revealed the existence of *S. micheli* in mussel beds and on organic substrata (wood) at the Lucky Strike vent field (Ivanenko et al. 2012; Cuvelier et al. 2014). At the time of its description, however, *S. methanophilus* was the first tegastid species found among natural megafauna aggregations at a cold seep. Shortly thereafter, the new tegastid species *Tegastes okinawensis* was described from the Okinawa Trench at a depth of 580 m as the first species from the genus *Tegastes* found at a hydrothermal vent (Back et al. 2010). Another species of the genus *Tegastes*, the already known *Tegastes satyrus*, was found associated with bacterial mats on a whale bone during a shallow-water whale-fall experiment in the north Atlantic (Dahlgren et al. 2006; Willems et al. 2009).

Several potential mechanisms may be responsible for the wide distribution range of the above-described epibenthic harpacticoid and cyclopoid species exclusively known from chemosynthesis-based habitats. One theory that has been frequently discussed as a potential distribution mechanism for meiofauna organisms such as copepods is the source-sink

hypothesis that originally refers to the maintenance of macrofaunal abyssal biodiversity by immigrating larval stages from reproductively stable populations (Rex et al. 2005). However, many benthic copepods (including harpacticoids) lack such planktonic larval stages (Thistle 1988; Baguley et al. 2006). In contrast to macrofauna, with larval dispersal in the pelagial, benthic copepod dispersal strongly depends on resuspension and subsequent passive transportation of adults by benthic currents (Thistle 1988).

Further hypotheses have considered paleotectonic history, such as altered sea levels, plate tectonics, and continental drift, as potential explanations for the distribution of small-size organisms on a larger scale (Rao 1972; Westheide 1977). Taking into account the biogeographically and evolutionary history of species, geographical separation followed by speciation may be responsible for the occurrence of closely related species, such as those of the genus *Smacigastes*, at different chemosynthesis-based habitats and geographic areas. Observations of shared and related species at hydrothermal vents, cold seeps, and large organic falls such as whale carcasses and wood have led to the hypothesis that organic substrata may serve as stepping stones in the dispersal of organisms found in deep-sea chemosynthesis-based habitats, including associated meiofauna taxa with limited dispersal such as copepods (Distel et al. 2000; Bienhold et al. 2013). The “stepping stone” hypothesis, or “isolation distance model,” may apply to cosmopolitan copepods such as *Xylora bathyalis*, *Delavalia gundulae*, or *Tychidion guyanense* that apparently are specialized to vents and seeps as well to organic substrata such as wood or whale bones found in the deep sea.

To conclude, our analyses of the copepod communities from a hydrocarbon seep site revealed low densities and differences in relative abundance of copepod species between tubeworm and mussel aggregations, indicating that the distribution pattern of megafauna organisms at seeps may have an effect on associated copepod communities. Copepod communities within the mussel fields showed a higher similarity, potentially due to the dominance and the restricted occurrence of *Tisbe* sp. 1 in the mussel beds, while the tubeworm aggregations harboured a more heterogeneous copepod community. Most of the species identified herein have not yet been reported elsewhere. The majority belong to genera generally found in coastal waters or deep-sea sediments. Whether the high number of undescribed species reflects the specificity of the copepod community at the investigated cold seeps should be considered after further investigation of the surrounding areas. However, our results indicate the existence of some characteristic epibenthic copepod species exclusively associated with organic substrata at chemosynthesis-based ecosystems.

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