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

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

Keywords: Meiobenthic copepods ● Hydrothermal vent ● *Bathymodiolus thermophilus* ● *Riftia pachyptila* ● East Pacific Rise ● Community structure

Introduction

Copepoda is one of the largest and most diversified taxa at hydrothermal vents. They are estimated to contribute more than 15% of the total species described from vents worldwide (Tunnicliffe et al., 1998). The most important order is the Siphonostomatoida, with more than 50 described species including the families Dirivultidae and Ecbathyriontidae, which are largely endemic to vents (Humes, 1988; Heptner & Ivanenko, 2002). Even with the large number of described species, our knowledge of the variability in copepod community structure, as well as the geographic distribution and habitat selection of individual species is limited.

In this study, we focused on the identification and quantification of the meiobenthic copepod communities from three sites on the northern East Pacific Rise. We also

explored the influence of the dominant megafaunal species *Riftia pachyptila* Jones, 1981 and *Bathymodiolus thermophilus* Kenk & Wilson, 1985 and hydrothermal fluid flux on the structure of the copepod communities.

Materials and Methods

In December 2001 and December 2002, quantitative collections of either mussel-dominated or tubeworm-dominated communities were made at three hydrothermal vent sites on East Pacific Rise at ~ 2500 meters depth: Tica (9°50.447´N, 104°17.493´W), Riftia Field (9°50.705´N, 104°17.393´W), and Buckfield (11°24.90´N, 103°47.20´W). At Tica, large aggregations of the tubeworm *Riftia pachyptila* were visibly dominant, but the mussel *Bathymodiolus thermophilus* was also present. At the time of sampling in 2002, this site was characterized by warm fluids with maximum temperatures of 18°C, maximum sulfide concentrations of 176 µM ΣH_2S, and slightly acidic pH. The more sparse and patchy aggregations of tubeworms at Riftia Field lacked mussels and in 2002 exhibited similar maximum temperatures of 23°C but maximum sulfide concentrations were 35 µM ΣH_2S and minimal pH was below 5 (see Le Bris et al., 2006). At Buckfield, mussels formed a dense bed, and temperatures ranged between ~2 and 10°C (Van Dover pers. obs.) (Table 1). No data on sulfide concentrations and pH were available for this site. Both, *R. pachyptila* and *B. thermophilus* formed aggregations on hard substrate, and small amounts of sediment, consisting primarily of particulate organic matter and a few mineral grains, accumulated between the tubes and between the shells and byssal threads of the mussels.

Three quantitative samples were taken at each of the three sites, Tica (TC1, TC2 in 2001 and TC3 in 2002), Riftia Field (RF1, RF2 in 2001 and RF3 in 2002) and Buckfield (BF1, BF2 and BF3 in 2001) using two collection devices. The tubeworm aggregations were sampled with the "Bushmaster Jr." (300-1300 cm² sample area) (Govenar et al., 2005), and mussel aggregations were sampled with the "mussel pot" (531 cm² sample area) (Van Dover, 2002). Meiofauna was retained on 63 µm mesh-sized net, passing through a 1 mm net, fixed in 4% buffered formalin for 24 h, and stored in 70% ethanol. In order to compare these large sample areas to other meiofauna studies, we standardized all samples to 10 cm². All copepods were counted, and at least 300 individuals per sample were identified to species level, until an asymptote was obtained for the cumulative species effort curve constructed for each sample (Fig. 1). Planktonic species were excluded in this study because this community, albeit closely related to the benthic environment, is not part of the meiobenthos (Giere, 1993). Biomass of the vent endemic
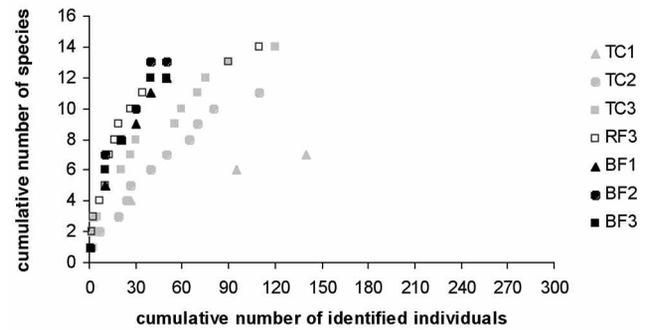
Figure 1. Cumulative species-effort curves for copepods based on cumulative number of species for samples with > 300 individuals (Tica: TC1, TC2, TC3; Riftia Field: RF3; Buckfield: BF1, BF2, BF3).

Figure 1. Courbes d'espèces cumulées en fonction de l'effort d'échantillonnage basé sur le nombre cumulé d'espèces des échantillons contenant plus de 300 individus (Tica: TC1, TC2, TC3; Riftia Field: RF3; Buckfield: BF1, BF2, BF3).

siphonostomatoid copepods was calculated according to their body form (see Heptner & Ivanenko, 2002). Body volume of harpacticoid copepods was estimated (Volume = Length x Width² x Conversion factor corresponding to body form) and was then multiplied by the specific gravity of 1.13 (for meiobenthos in general) to obtain wet mass in mg (see Feller & Warwick, 1979). The trophic status of each species was determined according to the mouth structure of copepods, according to the classification determined by Heptner & Ivanenko (2002). Univariate (S, $H´_{\log e}$, J´) and multivariate measurements (cluster-analysis, SIMPER, ANOSIM; data were standardized and square-root transformed) were calculated using PRIMER v5 Package (Plymouth Marine Laboratory; Clarke & Gorley, 2001). Student´s t-tests were used to test significant differences in abundance and species richness. Due to the relatively small number of samples, bootstrapping (1000 resamplings each, two-sided test; routine "FTBOOT" from the package "computerintensive statistics" by Nemeschkal, 1999) was used to test for significant differences in abundance, species richness, and Shannon-Wiener diversity indices among the three sites. Results from statistical analysis were classical Bonferrroni-corrected (p = a/n; a = 0.05).

Results and Discussion

Hydrothermal vents on the East Pacific Rise are highly variable habitats inhabited by distinct mega- and macrofaunal communities dominated by the tubeworm *Riftia pachyptila* or the mussel *Bathymodiolus thermophilus* found in vigorous to moderate diffuse flow areas (Shank et al., 1998). Since at the time of sampling, the tubeworm-

Table 1. Characteristics of collection sites and benthic copepod communities according to sites.
Tableau 1. Caractéristiques des sites de prélèvement et des communautés de copépodes selon les sites.

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

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

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

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

dominated sites Tica and Riftia Field were known to exhibit higher overall maximum temperatures than the mussel site Buckfield, but differed in their maximum sulfide concentrations and minimum pH (Le Bris et al., 2006; Table 1), we expected a divergence in copepod community structure among the three different sites. Our findings showed that despite differences in environmental characteristics and dominant megafauna, univariate and multivariate analyses revealed that the meiobenthic copepod community composition (e.g. abundance, S, H´$_{\log e}$) and trophic structure were similar among the tubeworm dominated sites. The mussel dominated site Buckfield and the tubeworm dominated site Riftia Field showed differences in abundance and Shannon-Wiener diversity index, but were similar in species richness and trophic structure. Differences in the distribution and relative abundance of species among samples reflect a relative homogenous mussel bed community and a highly heterogeneous tubeworm community.

We identified a total of 27 species from all three sites. Similar to other studies from the Mid-Atlantic Ridge (Zekely et al., 2006) and the Juan de Fuca Ridge (Tsurumi et al., 2003), vent endemic siphonostomatoid copepods dominated the communities on the East Pacific Rise. The highest relative abundance of siphonostomatoids with little variation among samples occurred at the mussel bed

Buckfield (96-97%). At the tubeworm-dominated site Tica, siphonostomatoid relative abundance was also high, but the intra-site variation was larger (87-97%), while the lowest relative abundance was found at Riftia Field (75-86%) (Table 1). Harpacticoid copepods, known form a variety of shallow-water and deep-sea habitats, apparently play a minor role at vents with the exception of one senescent vent site at the Juan de Fuca Ridge (Tsurumi et al., 2003).

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

All univariate measures of community structure (S, H'$_{\log e}$, J', abundance, biomass) were quite similar among sites (Table 1). Species richness (S) varied from 6 to 14

Table 2. Bootstrapping and student´s t-test (two-sided, t_{4df} = 2.776, p-value in parentheses) was used to test for differences in abundance (Ab, ind. 10 cm^{-2}) and species richness (S) between the three sites (Tica versus Riftia Field, Tica versus Buckfield, Riftia Field versus Buckfield). Bootstrapping was used to test for differences in Shannon-Wiener diversity (H´$_{log\ e}$). Results are given prior Bonferroni corrections.

Tableau 2. Bootstrap et test t de Student (bilatéral, t_{4df} = 2,776, p associée entre parenthèses) utilisés pour tester les différences d'abondance (Ab, ind. 10 cm^{-2}) et la richesse spécifique entre les trois sites (Tica *vs* Riftia Field, Tica *vs* Buckfield, Riftia Field *vs* Buckfield). Le bootstrap est utilisé pour tester les différences entre les indices de diversité de Shannon-Wiener (H´$_{log\ e}$). Les résultats sont donnés avant d'effectuer la correction de Bonferroni.

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

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

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

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

Out of 16 species found at Tica and 17 species found at Riftia Field, the majority of 13 species (76% of total species
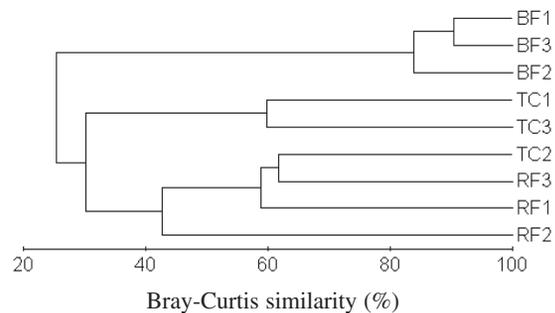
Figure 2. Hierarchical cluster diagram for group average linking, based on Bray-Curtis community similarity values from the nine samples (Tica samples: TC1, TC2, TC3; Riftia Field samples: RF1, RF2, RF3; Buckfield samples: BF1, BF2, BF3).

Figure 2. Dendrogramme hiérarchique par groupement moyen, fondé sur les valeurs de similarité de l'indice de Bray-Curtis des neuf prélèvements (Tica samples: TC1, TC2, TC3; Riftia Field samples: RF1, RF2, RF3; Buckfield samples: BF1, BF2, BF3).

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

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

Copepods are usually a very abundant part of the benthos in a variety of habitats, and play an important role in the food web by linking the microbial community and the macrofauna (Giere, 1993). Although copepods are known to have representatives at all trophic levels, from primary consumers to secondary and tertiary predators and parasites, at the hydrothermal vents sites in this study, deposit feeders dominated the copepod community, with a total of 24 of 27 total species. Parasites were represented by

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

Tableau 3. Abondance relative (%) des espèces de copépodes issues des 9 prélèvements (Tica: TC1, TC2, TC3; Riftia Field: RF1, RF2, RF3; Buckfield: BF1, BF2, BF3). Les abondances relatives > 10% sont indiquées en gras.

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

[a]Harpacticoid copepods

the three species of *Ceuthocetes*, and predators were absent. Trophic status can be inferred from mouth structures (Heptner & Ivanenko, 2002). While direct feeding observations have yet to be conducted, the mouthparts of many vent siphonostomatoids appear to be suitable for feeding on finely grained particles. Furthermore, bacteria embedded in mucus were found in the foreguts of such copepod species (Dinet et al., 1988). The dominance of primary consumers in the meiobenthic copepod community could be important for the transfer of organic matter at hydrothermal vents.

The role of parasitic copepods at hydrothermal vents is less understood. For example, *Ceuthocetes* species are thought either to feed on mucus and/or cut round holes into the host tissue and obtain their food through these holes (Heptner & Ivanenko, 2002; Ivanenko & Defaye, 2006). So

far, they have been found associated with tubeworms or the clam *Calyptogena magnifica* Boss & Turner, 1980 (Ivanenko & Defaye, 2006). In our samples they were also associated with the mussel *Bathymodiolus thermophilus*.

Little is known about the population structure, reproduction, and dispersal of vent copepods. Female dominated copepod communities are often found in diverse shallow-water habitats (Giere, 1993) and were also reported from a vent site at Juan the Fuca Ridge (Tsurumi et al., 2003). Also, the majority of species in our samples showed a female bias or completely lacked males (*Aphotopontius hydronauticus* Humes, 1989, *A. probolus*, *A. acanthinus* Humes & Lutz, 1994). On the other hand, some parasitic species, such as *Ceuthocetes acanthothrix* Humes, 1987, *C. aliger* Humes & Dojiri, 1980, and *C. introversus* Humes,

1987 and the primary consumer *Scotocetes introrsus* Humes, 1987 were male dominated. While underlying mechanisms of population and community dynamics of female or male dominated species cannot be fully understood when samples are collected at a single time point, the occurrence of certain larval stages in benthic samples at least points to specific life history traits and dispersal capabilities. Copepodite stages from I to V were found at the two tubeworm-dominated sites, and a particularly high number of copepodites was present at Tica. At the mussel-dominated site Buckfield, copepodites from stage III to V were found, but in lower overall abundance than the tubeworm-dominated sites (Table 1). The differences in occurrence of copepodite stages between tubeworm and mussel communities cannot be explained by possible seasonality in reproduction cycles since all samples were taken in the same month of the year. Early copepodite stages have not been found previously in vent samples, suggesting pelagic dispersal (Tsurumi et al., 2003; Ivanenko, 1998). However, from our findings we infer that at least in some species living among tubeworm aggregations, development through copepodite stages I to V occurs in the benthic environment. It has to be kept in mind, however, that many copepods, adults or larvae, are known to frequently migrate from the benthic to the pelagic environment in order to disperse, reproduce, search for food, or escape predators (Giere, 1993).

Acknowledgments

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