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„Eine Analyse der Biodiversität von mit Muschelbänken
assoziiierter permanenter metazoischer Meiofauna der
kalten Tiefseequellen, im Vergleich zu hydrothermalen
Tiefseequellen“

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“Analysis of mussel bed associated permanent metazoan
meiofauna communities from deep sea cold seeps, with a
comparison of deep sea hydrothermal vents”

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INHALTSVERZEICHNIS / INDEX:

1. EINLEITUNG DEUTSCH	3
2. ABSTRACT ENGLISH.....	9
3. INTRODUCTION.....	12
4. MATERIALS AND METHODS.....	17
4.1. SITE DESCRIPTIONS	17
4.2. SAMPLING AND PROCESSING OF SAMPLES.....	18
4.3. STATISTICAL ANALYSIS	19
5. RESULTS.....	21
5.1. ALAMINOS CANYON (AC) COMPARED TO ATWATER VALLEY (AT).....	21
5.1.1 <i>Abundance</i>	21
5.1.2 <i>Higher taxa composition</i>	22
5.1.3 <i>Diversity</i>	22
5.1.4 <i>Genera composition</i>	23
5.2. COLD SEEPS (AC AND AT) COMPARED TO HYDROTHERMAL VENTS (MB AND BF).....	24
5.2.1 <i>Abundance</i>	24
5.2.2 <i>Higher taxa composition</i>	25
5.2.3 <i>Diversity</i>	25
5.2.4 <i>Genera composition</i>	26
6. DISCUSSION	29
6.1. COMPARISON OF THE TWO COLD SEEPS ALAMINOS CANYON (AC) AND ATWATER VALLEY (AT).....	29
6.1.1 <i>Community pattern</i>	29
6.1.2 <i>Clustering</i>	29
6.1.3 <i>Genera composition</i>	30
6.1.4 <i>Comparison of cold seep mussel associated permanent meiofauna with other seep habitats</i>	31
6.2. COMPARISON OF COLD SEEPS AND HYDROTHERMAL VENTS	32
6.2.1 <i>Community pattern</i>	32
6.2.2 <i>Clustering</i>	34
6.2.3 <i>Genera Composition</i>	34
6.2.4 <i>Comparison of cold seep mussel associated permanent meiofauna with other chemosynthetic habitats</i>	37
7. REFERENCES / BIBLIOGRAPHY	37
8. DATA (TABLES + FIGURES).....	44
8.1. TABLES.....	44
8.2. FIGURES	50
9. ZUSAMMENFASSUNG DEUTSCH.....	53
10. DANKSAGUNG.....	55
11. CURRICULUM VITAE	56

1. Einleitung deutsch

Muschelbänke sind Ansammlungen von Muscheln, welche in ihrer Ausdehnung und Erscheinung variieren. So findet man sie entlang der Meeresküsten in den Gezeitenzonen, zahlreiche einzelne Muschelaggregationen in den verschiedensten Größenordnungen kompakt auf einer begrenzten Fläche in der Tiefsee (Bergquist *et al.*, 2005) oder auch als streifenförmige Aggregationen, die Bodenrissen zu folgen scheinen (Turnipseed *et al.*, 2004; Zekely *et al.*, 2006). In der Tiefsee treten viele Muschelaggregationen bei chemosynthetischen Habitaten auf, insbesondere Muscheln der Familie der Mytilidae, eine Gruppe von glattschaligen Meeresmuscheln, die zahlreiche Arten aufweisen. Die Familie der Mytilidae kommt weltweit vor, in Gezeitenzonen, im Sublitoral als auch in der Tiefsee, und sie benutzt ihre Byssusfäden, um sich am Untergrund festzusetzen. In heißen als auch kalten Quellen der Tiefsee ist die Subfamilie Bathymodiolinae (Fam. Mytilidae) dominierend vertreten und weist dort je nach Art Schalengrößen von 3 bis zu 40 cm auf (Duperron *et al.*, 2009). Zu dieser Familie zählt die am häufigsten auftretende Tiefseemuschelgattung *Bathymodiolus*. Muscheln sind generell auch als Makrofauna zu bezeichnen, eine Größenordnungs-kategorie für Organismen über 1mm Körpergröße. Muschelaggregationen können ihrerseits auch andere Makrofaunaorganismen überwachsen, wie z.B. Röhrenwürmer, oder sie überwachsen auch Substrate wie Basalt (Gollner *et al.*, 2010b; Le Bris *et al.*, 2006). Die mosaikartige Zusammensetzung einer Muschelbank durch die einzelnen Muschelschalen führt mit ihrer 3-dimensionalen Struktur zu einer Vergrößerung der Hartsubstratfläche, wobei viele Lücken und Zwischenräume entstehen, welche kleinen Organismen Lebensräume bieten. Diese Lücken und Zwischenräume bieten Schutz vor Fressfeinden und Zugang zu Nahrung, da dort herunter rieselndes Sediment bzw. partikuläres organisches Material akkumuliert werden kann. Meiofauna (das griechische Wort "meio" bedeutet "kleiner") sind Organismen in der Größenordnung zwischen 1mm - 32µm (Giere, 2009). Zur Extraktion der Meiofauna aus den entnommenen Proben wird sie durch ein 1 mm Sieb ausgesondert und mit einem 32µm Sieb aufgefangen. Diese größendefinierte Gruppe an Invertebraten umfasst so gut wie annähernd alle bekannten Tierstämme, nach Flint 2007 sind es 20 von 34 Tierstämme, nach Coull 1988 sind es 22 von 33 Metazoa-Stämme. Innerhalb der Meiofaunagruppe lassen sich zwei Kategorien unterscheiden: die permanente und

die temporäre Meiofauna. Die Gruppe der temporären Meiofauna umfasst Organismen, welche nur als juvenile Tiere dieser Größenklasse zugeordnet werden und später zu größerer Fauna (Makrofauna) heranwachsen, wie zum Beispiel einige juvenile Mollusken und Anneliden (Giere, 2009; Coull, 1988). Die Gruppe der permanenten Meiofauna umfasst Organismen, welche ihren gesamten Lebenszyklus in dieser Größenklasse verbringen (Coull, 1988), wie z.B. die Nematoda, Copepoda, Ostracoda. Der Begriff Meiobenthos wird ebenfalls für die Gruppe der Meiofauna verwendet, um hervorzuheben, dass es sich um Meiofaunaorganismen handelt, welche bodenbezogen leben. Die meisten Meiofaunaorganismen befinden sich auf und/oder zwischen Sandkörnern, aber auch auf Basaltgestein, welches mit einem Biofilm oder einer Detritus-Schicht überzogen ist (Giere, 2009). Diese Studie konzentriert sich auf muschelassoziierte permanente metazoische Meiofauna, welche man zum Epimeiobenthos zählt. Das Meiobenthos stellt eine wichtige Verbindung zwischen dem Mikro- (z.B. chemosynthetische Bakterien) und Makrobenthos (z.B. Muscheln) dar und ist daher von grundlegender Bedeutung für die Nahrungskette (Giere, 2009; Coull, 1988). Die Verbreitung der Meiofauna erstreckt sich vom Süßwasser bis zum Salzwasser in die verschiedensten Tiefen sowie über die verschiedensten Substrate, von weichem Schlamm bis zum groben Muschelkies oder Basalt (Giere, 2009; Coull, 1988). Die Abundanz der Meiofauna reicht von 52 - 3675 Individuen pro 10cm^2 im Süßwasser, bis zu 5 - 11400 Individuen pro 10cm^2 in marinen intertidal Zonen oder 0 - 12 341 Individuen pro 10cm^2 in marinen Subtidalbereichen (Coull, 1988). Nach Giere, 2009 liegt die Meiofaunahäufigkeit in der Tiefsee ($> 200\text{m}$) zwischen 100 - 1500 Individuen pro 10cm^2 und zeigt maximale Werte im Sublitoral (subtidale Zone). In größerer Tiefe finden sich selten Meiofaunaorganismen mit mehr als 2000 Individuen pro 10cm^2 (Giere, 2009). Sedimentinfauna bei chemosynthetischen Habitaten der Tiefsee zeigt Meiobenthosabundanzen von 1 - 11292 Individuen per 10cm^2 in kalten Quellen und 1 - 1075 Individuen per 10cm^2 in heißen Quellen (Bright *et al.*, 2010). Die mit Muscheln oder Röhrenwürmern assoziierte Meiofauna, das Epimeiobenthos, zeigt wesentlich geringere Werte mit 1- 81 Individuen per 10cm^2 bei kalten und 1 - 976 Individuen per 10cm^2 bei heißen Quellen (Bright *et al.*, 2010). Basierend auf der Annahme, dass durchschnittlich über alle Lebensräume gerechnet 1000 - 2000 Meiofauna Individuen pro 10cm^2 vorkommen, berechnete Giere 2009, dass die Meiofauna die Makrofauna mit einem Faktor von etwa 3:1 bezüglich der Anzahl übersteigt. Meiofauna kann

generell als allgegenwärtig und abundant bezeichnet werden. Sie nimmt eine wichtige Rolle im Ökosystem ein, indem sie ein empfindlicher Umweltindikator für Störungen wegen ihrer großen Anzahl und ihre kurzen Generationszeiten ist. Darüber hinaus dient Meiofauna als Nährstoffquelle für höhere trophische Ebenen (Coull, 1988). Die Meiofauna ist dafür bekannt, eine bedeutendere Rolle in der benthischen Energetik der Tiefsee einzunehmen, als die Makrofauna (Coull, 1988). Ein anderer interessanter Gesichtspunkt für die chemosynthetischen Habitate ist, dass Meiofaunaexkretion, genauer gesagt Schleimspuren der Nematoden und auch der harpacticoiden Copepoden, möglicherweise bakterielles Wachstum stimulieren (De Troch et al, 2005; Moens. et al., 2005).

Diese Studie konzentriert sich auf den Vergleich der permanenten metazoischen Meiofaunagattungen, welche mit Muschelbänken in der Tiefsee der kalten Quellen und hydrothermalen Quellen assoziiert sind. Die Umweltbedingungen, welche die Tiefsee (> 200 m) dominieren, sind Dunkelheit, hoher Druck und niedrige Temperaturen von etwa 2 ° C sowie schwache Wasserbewegungen und häufig ein geringes Nahrungsangebot. Die Tiefsee generell ist von der photosynthetischen Primärproduktion der obersten, lichtdurchfluteten Wasserschichten abhängig und auf den organischen Input aus den oberen Wasserschichten angewiesen, dem herunter rieselnden partikulären organischen Material (POM) oder dem Detritus. Hydrothermale und kalte Quellen sind nur indirekt von der Primärproduktion der oberen Wasserschichten abhängig. Bei diesen chemosynthetischen Habitaten bilden chemosynthetische Bakterien, welche zum Microbenthos gezählt werden, die Basis der Nahrungskette und sind somit dort die Primärproduzenten. Sie wandeln mit der gewonnen Energie aus der Sulfidoxidierung anorganischen Kohlenstoff zu organischen Verbindungen um. Solche chemosynthetischen Bakterien leben im Sediment und symbiontisch im Kiemengewebe der dort vorkommenden Muscheln.

Hydrothermale Quellen wurden erstmals 1977 in der Nähe der Galapagos-Inseln entdeckt und zeigen neben den tiefseeüblichen Charakteristika wie Dunkelheit und hohem Druck nach McMullin *et al.*, 2000 Besonderheiten, wie primäre Nährstoffversorgung, Temperaturschwankungen, Sauerstoffkonzentration, pH-Wert und das Vorhandensein von giftigen Chemikalien (z.B. Schwefelwasserstoff und Schwermetalle). Man findet hydrothermale Quellen am mittelozeanischen Rücken und im Back-Arc-Becken (Van Dover, 2000). Die kalten Quellen wurden erstmals 1984 im Golf von Mexiko (GOM) entdeckt (Paull *et al.*, 1984). Sie sind an aktiven

oder passiven Kontinentalrändern zu finden (Levin, 2005; Sibuet and Olu, 1998). Kalte Quellen sind chemosynthetische Lebensräume, bei denen Schwefelwasserstoff, Methan und andere kohlenwasserstoffreiche Flüssigkeiten aus Rissen und Spalten des Meeresbodens heraustreten, ohne einen nennenswerten Temperaturanstieg (Levin, 2005). Hydrothermale Quellen, die auch an Rissen der Planetenoberfläche entstehen, sind häufig in der Nähe vulkanisch aktiver Zentren zu finden, bei denen oft heißes Wasser aus dem Meeresboden tritt. Kalten Quellen werden generell, im Vergleich zu hydrothermalen Quellen, aufgrund ihrer geringeren Umweltfaktorenschwankungen als stabilere und langlebigere Habitate bezeichnet. Die Bedingungen der hydrothermalen Quellen sind wegen der starken Schwankungen betreffend der Temperatur, pH-, Sulfid- und Sauerstoff-Konzentration sehr volatil und auch oft durch unvorhersehbare Ereignisse, wie Vulkanausbrüche, gekennzeichnet.

Hydrothermale und kalte Quellen unterscheiden sich durch die Umgebungstemperatur, die Sulfidkonzentration und die Art der dort auftretenden Toxine (McMullin *et al.*, 2000). Extreme Umweltbedingungen wie Temperaturschwankungen und chemische Emissionen verursachen Stress oder führen zu einer ökologischen Störung (Disturbance) der dort lebenden Organismen. Stress ist eine leichtere, gemäßigte Form der Disturbance, sie ist, genauso wie Disturbance, eine Veränderung der Umweltbedingungen, jedoch lässt Stress noch eine Anpassung zu. Stress ist zum Beispiel eine Änderung des Sauerstoff-Niveaus (O_2), der Temperatur oder des Sulfidgehaltes. Die ökologische Störung (Disturbance) bei Hydrothermalquellen ist hoch und bei kalten Quellen gering. Von den hydrothermalen Quellen des East Pacific Rise ist bekannt, dass 2 vulkanische Eruptionen während der letzten zehn Jahre aufgetreten sind, und zwar etwa 1991 und 2006 (Nees *et al.*, 2009; Shank *et al.*, 1998). Eine solche Art der ökologischen Störung kann zum Aussterben der dortigen Organismen führen und kann der Beginn einer neuen Besiedelungsmeinschaft sein (Qiu, 2010). Hydrothermalquellen am ostpazifischen Rücken werden in der Literatur als kurzlebig angesehen (10-20 Jahre; Fornari & Embley, 1995), während die hydrothermale Quelle des Mittelozeanischen Rückens Snake Pit als ein langlebigere hydrothermale Quelle gilt (8-10 Jahre, Fornari & Embley, 1995; Lalou *et al.*, 1993). Kalte Quellen generell sind, wie bereits erwähnt, als langlebiger Lebensraum im Vergleich zu den allgemein als kurzlebig bezeichneten hydrothermalen Quellen zu bezeichnen (Sibuet and Olu, 1998;

Turnipseed *et al.*, 2004; Turnipseed *et al.*, 2003). Aharon *et al.*, 1997 meint sogar, dass bereits seit der letzten Eiszeit einige der heute bekannten kalten Quellen im Golf von Mexiko aktiv waren und dass es eine versiegte kalte Quelle gibt, welche wahrscheinlich für etwa 200.000 Jahren aktiv gewesen ist (Turnipseed *et al.*, 2003). Die typischen Gründerarten bei der Besiedelung der kalten und hydrothermalen Quellen sind Muscheln und Röhrenwürmer. Bei den kalten Quellen repräsentieren die Muscheln die erste Stufe der Sukzession (Bergquist *et al.*, 2003; Cordes *et al.*, 2005), während bei Hydrothermalquellen die Röhrenwürmer die erste Sukzessionsstufe einnehmen (Van Dover and Lutz, 2004). Muschelbänke bilden ökologische Nischen für Makro- und Meiofaunaorganismen sowohl bei kalten als auch bei hydrothermalen Quellen. Die an den heißen und kalten Quellen weit verbreitete Muschelgattung *Bathymodiolus* (ursprünglich von Kenk & Wilson, 1985 beschrieben) umfasst bis dato 14 pazifische Arten, 7 atlantische und eine Art des Indischen Ozeans (Miyazaki *et al.*, 2010).

Für diese Studie konzentrieren wir uns auf Muschelbänke als Grundlage für permanente Meiofauna. Muschel assoziierte Meiofaunaorganismen wurden bei Hydrothermalquellen (Gollner *et al.*, 2010b; Zekely *et al.*, 2006) sowie bei kalten Quellen (Bright *et al.*, 2010) bereits untersucht. Ein Vergleich der Muschelbank assoziierten Gemeinschaftszusammensetzung zwischen kalten und hydrothermalen Quellen auf permanenter Meiofaunaebene wurde jedoch bisher nicht durchgeführt. Die Kernaufgabe dieser Arbeit ist es, die Gemeinschaftszusammensetzung der Muschelbank assoziierten permanenten metazoischen Meiofauna der untersuchten kalten Quellen zu charakterisieren und sie mit Muschelbank assoziierter permanenter metazoischer Meiofauna von hydrothermalen Quellen zu vergleichen. Dazu wurden die Tiere der Proben gezählt (Gesamtabundanz, Abundanz pro Gattungen), die Gattungen der Tiere bestimmt, sowie deren Verhältnis zueinander (relative Häufigkeit, Dominanz, Diversitätsindizes) berechnet. In diesem Zusammenhang sind folgende Fragen aufgetreten: Wie charakterisiert sich das Gemeinschaftsmuster von Muschelbank assoziierter permanenter metazoischer Meiofauna der verschiedenen chemosynthetischen Habitate? Welche Gattungen sind für die Gemeinschaftszusammensetzung Muschelbank assoziierter permanenter metazoischer Meiofauna der jeweiligen chemosynthetischen Habitate verantwortlich? Gibt es Gattungen Muschelbank assoziierter permanenter metazoischer Meiofauna, die nur bei hydrothermalen oder nur bei kalten Quellen vorkommen? Gibt es

Gattungen der Muschelbank assoziierten permanenten metazoischen Meiofauna, welche sowohl in kalten als auch hydrothermalen Quellen vorkommen? Gibt es einen Zusammenhang zwischen Stress und der Gemeinschaftszusammensetzung von Muschelbank assoziierter permanenter metazoischer Meiofauna?

“Analysis of mussel bed associated permanent metazoan meiofauna communities from deep sea cold seeps, with a comparison of deep sea hydrothermal vents”

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* Extraction and counting of meiofauna, identification of higher taxa and identification of nematodes for the Alaminos Canyon samples. Statistical analysis of all samples, development of manuscript concept with M. Bright¹ and writing of manuscript.

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2. Abstract english

Deep sea cold seeps and hydrothermal vents are chemosynthetic habitats that expose their faunal communities to stressful conditions, such as toxic hydrogen sulfide and high methane levels. While a lot of studies have extensively described macrofaunal communities, little research has focused on the associated epimeiofauna of tubeworms and mussel beds. For the purpose of this study, six samples of permanent metazoan meiofauna, associated with mussel beds from two hydrocarbon cold seeps, were collected in order to identify the genera in the samples and were compared. Three of the samples originated from Alaminos Canyon Block 818 (AC818, ~ 2750 m depth) and three samples from Atwater Valley Block 340 (AT340, ~ 2200 m depth) located in the northern Gulf of Mexico. Six further samples from other studies (Gollner *et al.*, 2010b; Zekely *et al.*, 2006) were used and recalculated, so that a comparison between cold seep and hydrothermal mussel beds could be made. Three samples from 9°50' N EPR Mussel Bed (MB_1, MB_2, MB_3) and three samples from the 11°N EPR Buckfield site (BF_1, BF_2, BF_3), were used and already published by (Gollner *et al.*, 2010b) and (Zekely *et al.*, 2006). The genera of the of the cold seep mussel bed epifauna samples were further compared with an additional hydrothermal vent mussel site in the Atlantic (Mid Atlantic Ridge, MAR) (Zekely *et al.*, 2006) as well as other chemosynthetic sites. A total of 87 genera (AC: 59, AT: 58) were identified at the cold seeps, dominated by nematodes (about 80%) and copepods (about 20%), with minimal others (> 2%). The abundance range of AC varied from 81.35 – 641.89 ind. per 10 cm² and of AT from 57.81 – 1826.48 ind. per 10 cm² and thus showed higher values than in hydrothermal vent sites. There were no statistically significant abundance differences detected between the different chemosynthetic habitat sites. The results of this study propose a correlation of stress and meiofaunal community based on a high similarity of diversity indices between cold seeps and hydrothermal vents. The similarities that were found in the cold seep samples were present at different cold seep sites. The community pattern were similar at the various compared sites, although different genera tended to be responsible for the similar communities. Comparing cold seeps and hydrothermal vents a dominance change of genera in the pattern shifts dramatically from nematodes to copepods as the most dominant taxon. There were no chemosynthetic habitat specific genera found apart from the already known

Dirivultidae. This study gives a consistent overview of permanent mussel bed associated epimeiofauna, describes the abundance and diversity of genera, meiofaunal community patterns and reveals the differences as well as similarities between different cold seep sites and hydrothermal vent locations. Furthermore, it analyses scientific gaps and identifies areas that still require further research efforts, in order to better understand the results and to contextualise the secured knowledge of deep sea epimeiofauna in chemosynthetic habitats.

3. Introduction

Mussel beds are an aggregation of mussels and vary in dimension and appearance. They form big continuous beds along the marine coast in intertidal zones or large areas on the deep ocean floor with numerous beds of ranging size (Bergquist *et al.*, 2005), as well as stripe shaped aggregations with bands of mussels which seem to follow cracks (Turnipseed *et al.*, 2004; Zekely *et al.*, 2006). In the deep sea, mussel aggregations are often present at chemosynthetic habitats such as mussels of the the Mytilidae family. A group of smooth shelled marine mussels, which show many species can be found all over the globe, for example in intertidal zones, subtidal zones as well as in the deep sea. They use their bussal threads to attach to the floor. Some species of the subfamily Bathymodiolinae reach shell lengths of up to 40 cm, at hydrothermal vents and cold seeps. Some smaller species occur at chemosynthetic habitats, such as sunken wood and whale bones, shell lengths of up to 3 cm (Duperron *et al.*, 2009). The most common mussel genera at chemosynthetic habitats are bivalves of the genus *Bathymodiolus*. Mussels are organisms belonging to macrofauna (organisms bigger than 1mm). Such mussel beds can expand and grow over other macrofauna such as tube worms, or substrates like basalt (Gollner *et al.*, 2010b; Le Bris *et al.*, 2006). The mosaic like composition of individual shells of a mussel bed, offers small gaps for the deposit of sediment or refuge for other smaller organisms. The many hollow spaces, which are a result of the aggregation of the individual shells, enable the accumulation of sinking sand or particulate organic matter (pom) in their interstitial spaces. With its 3-dimensional structure, mussel beds enlarge the surface area of hard substrate and contribute to a more complex environment in which small animals find protection against predators while giving access to accumulated organic material. The purpose of this paper is to determine and study permanent, metazoan meiofauna associated with mussel beds at chemosynthetic habitats. Meiofauna, defined by the Greek word meio which means small, are essentially tiny organisms, which range between 1mm – 32µm (Giere, 2009), therefore they pass through a 1mm sieve and retain on a 32µm one. This size defined group are small benthic invertebrates, represented by nearly every known animal phyla (by Flint 2007, 20 of 34 animal phyla; by Coull 1988, 22 of 33 metazoan phyla). There are two categories of meiofauna which can be distinguished, the permanent and the temporary meiofauna. The temporary

meiofauna are organisms which are only of this size for a certain period and develop into macrofauna, such as some juvenile molluscs and annelids for example (Giere, 2009 ; Coull, 1988). The permanent meiofauna, on the other hand, are organisms which are the same size throughout their life cycle (Coull, 1988) such as Nematoda, Copeoda and Ostracoda. The term meiobenthos is used in order to emphasize that all metazoan meiofauna organisms are meant as well as mainly occurring related to the ground. Meiofauna organisms are mostly found on top of and/or inbetween sand grains, as well as on basalt rocks with biofilms or with fine detritus layers. For the purpose of this study we focused on mussel associated metazoan meiofauna, therefore also named epimeiobenthos. Meiobenthos is an important link between the microbenthos, for example chemosynthetic bacteria and macrobenthos, (such as mussels) and are therefore fundamental for the food chain (Giere, 2009 ; Coull, 1988). They can be found in various depths ranging from freshwater to marine habitats as well as from soft muds to coarse shell gravels or basalt (Giere, 2009; Coull, 1988). The abundances of meiofauna generally ranges from 52 – 3675 individuals per 10cm² in fresh water to 5 – 11400 individuals per 10cm² in marine intertidals, or 0 – 12 341 individuals per 10cm² in marine subtidals Coull, 1988. According to Giere 2009, meiofauna abundances ranges in the deep sea (> 200m) between 100 – 1500 individuals per 10cm² (Giere, 2009). Meiofauna abundances are showing maximal values at subtidal (sublittoral) zones but at greater depth meiofauna organisms rarely exceed 2000 ind. per 10cm² (Giere, 2009). Sedimentinfauna of meiobenthos showed abundance ranges of 1 – 11292 ind. per 10cm² at cold seeps and 1 – 1075 ind. per 10cm² at hydrothermal vents (Bright *et al.*, 2010). Mussel and Tubeworm associated epizooic metazoan, epimeiobenthos, showed smaller ranges of 1 – 81 ind. per 10cm² at cold seeps and 1 – 976 ind. per 10cm² at hydrothermal vents (Bright *et al.*, 2010). Based on the assumption of an average 1000 – 2000 meiofaunal ind. per 10cm² integrated over all habitats, (Giere, 2009) calculated that meiofauna exceeds the macrofauna in abundance with a factor of about 3:1. Meiofauna organisms generally could be called omnipresent and abundant. They occupy important roles in the ecosystem, such as being a sensitive environmental indicator of perturbations due to their large numbers and their short generation spans with benthic larvae. Moreover, they serve as a nutrient source for higher trophic levels Coull, 1988. Another interesting aspect for chemosynthetic habitats is that meiofaunal excretion, more specifically secreted mucus trails, produced by nematodes and also harpacticoids,

possibly elevates and stimulates bacterial growth (Moens et al. 2005, De Troch et al. 2005). Meiofauna are known to occupy a more significant role in the deep sea benthic energetics than macrofauna Coull 1988. This study focuses on the comparison of meiofaunal genera associated with mussels in deep sea cold seeps and hydrothermal vent sites. Environmental conditions that dominate the deep sea (>200 m) are darkness, high pressure, low temperatures of about 2°C, poor water movement and mostly poor food availability. Cold seeps and hydrothermal vents are habitats in which organism communities rely on chemosynthesis for food and energy production and not directly on photosynthesis. Hydrothermal vents, which were first discovered in 1977 near the Galapagos, have similar characteristics as deep sea environments. According to McMullin *et al.*, 2000 special differences can be identified such as the nutrient supply, temperature variation, oxygen concentration, pH and the presence of toxic chemicals such as sulfides and heavy metals. Hydrothermal vents appear on mid-ocean ridges and back-arc basins (Van Dover, 2000; Vanreusel *et al.*, 2010). Cold seeps were first discovered in 1984 in the Gulf of Mexico (GOM) (Paull *et al.*, 1984) and appear on active or passive margins (Levin, 2005; Sibuet and Olu, 1998). They are chemosynthetic habitats which have sprouted from cracks and fissures of the ocean floor and issue hydrogen sulfide, methane and other hydrocarbon rich fluid outflow. These ecosystems can be found where reduced sulphur and methane emerges from sea floor sediments without an appreciable temperature rise (Levin, 2005). Hydrothermal vents, which also appear from fissures in the planet's surface, emit heated water and are commonly found near volcanically active sites. They are often characterized by unpredictable conditions such as eruptions and hydrothermal vent environments are highly volatile due to the fluctuating temperature, pH and sulphide and oxygen concentration. Cold seeps are generally defined as longer lived habitats, as compared to hydrothermal vents, due to greater stability of environmental factors. The general differences between hydrothermal vents and cold seep are "fluid temperatures, sulfide concentration and the types of toxin occurring there" (McMullin *et al.*, 2000). Extreme environmental conditions such as temperature fluctuations and chemical emissions cause stress or even disturbance to the organism populations. Stress could be defined as a lighter form of disturbance, which can still be adapted to but also causes an environmental condition change. In other words, stress is a more moderate form of disturbance, for example stress can be variances of oxygen level (O₂), temperature or sulfide.

Disturbance is high at hydrothermal vents and low at cold seeps. At East Pacific Rise hydrothermal vent sites it is known that two volcanic eruptions occurred during small time periods in the last decade. One eruption in 1991 and one in 2006 (Nees *et al.*, 2009; Shank *et al.*, 1998). This kind of disturbance, under such extreme circumstances, can lead to the extinction of organisms and can bring new community compositions (Qiu, 2010). Furthermore, hydrothermal vents at the EPR are considered as short-lived (10-20 years; Fornari & Embley, 1995) hydrothermal vents, whereas the MAR vent site Snake Pit is considered as a longer-lived (80-1000 years, Fornari & Embley, 1995; Lalou *et al.*, 1993) hydrothermal vent site. Cold seep habitats are generally considered as durable habitats compared to the ephemeral hydrothermal vent habitats (Sibuet and Olu, 1998; Turnipseed *et al.*, 2004; Turnipseed *et al.*, 2003). In fact according to Aharon *et al.*, 1997 since the last glaciation period, present seeps from the Gulf of Mexico ought to have been active and maybe some defunct shallow sites could have been seeping for about 200 000 years (Turnipseed *et al.*, 2003). The typical foundation species at cold seeps and hydrothermal vents are macrofaunal mussels and tubeworms. At cold seeps mussels represent the first successional stage (Bergquist *et al.*, 2003; Cordes *et al.*, 2005), while tubeworms represent the first successional stage at hydrothermal vents (Van Dover and Lutz, 2004). Mussel beds offer, at hydrothermal vents and cold seeps, ecological niches for macro and meiofauna organisms. The most abundant deep sea mussels belong to the *Bathymodiolus* genus (originally described by Kenk & Wilson, 1985) and comprise up until now 14 Pacific species, 7 Atlantic species and one species from the Indian Ocean (Miyazaki *et al.*, 2010). For the purpose of this study we will focus on mussel beds as foundation species for permanent meiofauna organisms. The small epimeiofaunal organisms associated with mussel beds were already studied at hydrothermal vents (Gollner *et al.*, 2010b; Zekely *et al.*, 2006) and at cold seeps (Bright *et al.*, 2010), but a comparison of the mussel bed associated permanent metazoan meiofauna communities of cold seeps has not been done. The core task of this study is to investigate the community composition of meiofauna in cold seeps and to compare them to hydrothermal vents. This includes the assessment of their abundance (total abundance, abundance per genera), to specify the genera and to discover how they relate to each other (relative abundance, dominance, diversity indices). In this context the following questions emerged: How are the mussel bed associated permanent metazoan meiofaunal community patterns for the

different chemosynthetic habitats characterised? Which genera are responsible for the mussel bed associated permanent metazoan meiofaunal community compositions at the different chemosynthetic habitats? Are there genera of mussel bed associated permanent metazoan meiofauna that only occur at hydrothermal vent or only at cold seeps? Are there genera of mussel bed associated permanent metazoan meiofauna which occur at both, cold seeps and hydrothermal vents? Is there a connection between stress and mussel bed associated permanent metazoan meiofaunal community compositions?

4. Materials and Methods

4.1. Site descriptions

The two hydrocarbon cold seep sites Alaminos Canyon Block 818 (AC 818, ~ 2750 m depth) and Atwater Valley Block 340 (AT 340, ~ 2200 m depth) are located in the northern Gulf of Mexico (GOM) at the deep continental slope (Table 1) (Roberts *et al.*, 2007a). The Alaminos Canyon is situated in the north-western Gulf of Mexico at the base of the continental slope south of the Louisiana/Texas border. AC818 is about 322 km, south of Galveston in Texas, near the edge of the Sigsbee Escarpment and hydrocarbon seepage occurs there along a well defined linear fault. Atwater Valley is located along the eastern extension of the Mississippi at the transitions from a canyon to a submarine fan. The AT340 dive site is characterized with three mounded areas on top of the geologically bathymethric high position of this site (Roberts *et al.*, 2007b). Both, AC 818 and AT 340 cold seep sites had diverse and densely populated seep communities and a topograhphically complex seafloor geology (Roberts *et al.*, 2007a). Mussel beds at AC 818 were either exclusively built of *Bathymodiolus brooksi* or a mixture of *B. brooksi* and *Bathymodiolus heckerae*, while at AT 340 only *B. brooksi* was present Table 1. Echinoderms like brittle stars, sea cucumbers and heart urchins occurred at both locations as well as Decapod shrimps and Galatheid crabs, which had been closely associated with mussel beds (Roberts *et al.*, 2007a).

Meiofauna collections associated with mussel beds from two hydrothermal vent sites of the East Pacific Rise (EPR) used for this study were previously published (Table 1) (Gollner *et al.*, 2010b; Zekely *et al.*, 2006). The site Mussel Bed is located within the axial summit trough (AST) at the EPR 9°50' N region in about 2500 m depth. During the time of sampling the mussel *Bathymodiolus thermophilus* was present (Gollner *et al.*, 2010b). The maximum measured temperature among mussels growing on basalt was 10°C. *In situ* analysis of vent fluid at this site showed a minimal pH of 6.7 and maximal sulfide concentrations of 151µM Σ H₂S (Gollner *et al.*, 2010b; Le Bris *et al.*, 2006). The Buckfield site is situated in the AST of the EPR 11°N region in about 2500 m depth. The mussels there also grew on basalt, had a maximal dimension of ~20 - 30 m and were formed by *B. thermophilus* bands (Zekely *et al.*, 2006). The maximum temperature at Buckfield ranged approximately between

2 – 10°C and pH or sulfide concentration were not measured at this site (Gollner *et al.*, 2006).

4.2. Sampling and processing of samples

The seep samples used for this study were collected during cruises in 2006 and 2007. Three quantitative samples had been taken from AC 818 (AC_1, AC_2, AC_3) and three samples from AT 340 (AT_1, AT_2, AT_3) (Table 1). For a comparison between cold seep and hydrothermal mussel beds, we used three samples from 9°50' N EPR Mussel Bed (MB_1, MB_2, MB_3), and three from the 11°N EPR Buckfield site (BF_1, BF_2, BF_3), both already published by (Gollner *et al.*, 2010b) and (Zekely *et al.*, 2006). The quantitative seep samples were taken with the “mussel pot” collection device with the DSV ALVIN accommodated at the research vessel *Atlantis* in 2006, and with the ROV JASON and the NOAA ship *Ronald H. Brown* in 2007. The mussel pot had a diameter of 26 cm with a sample area of 531 cm² (Bright *et al.*, 2010). To avoid sampling of sediment containing infauna at seeps, we paid attention to collect as little sediment as possible from underneath the mussel beds. After sampling, mussel pots were temporarily stored in priorly cleaned plastic boxes fixated to platforms of ALVIN and JASON until they were transported to the surface. The samples consisted of mussels, their associated fauna, and sediment, mainly particulate organic material trapped between mussels.

Onboard the ship mussels were carefully taken out of the sample by rinsing them with 32µm filtered cold seawater. Macrofauna was extracted by rinsing the sample through a net of 1 mm mesh size. Then the volume of sediment was measured and after these procedures the meiofauna was extracted by rinsing the samples through a net of 32 µm mesh size. The macrofauna was studied by collaborators (Cordes *et al.*, 2010a).

The meiofauna fraction was fixed in 4% buffered formalin and later transported to the lab for further progressing. In case of very large samples, only a small portion of the entire sample was processed and the total number of meiofauna was estimated by measures of the sediment volume. AC_1 and AT_1 were totally processed the other samples (AC_2, AC_3, AT_2, AT_3) were subsampled for counting. The density centrifugation technique using the silicapolymer Levasil ® mixed with kaolin was performed to separate meiofauna from the sediment (McIntyre

and Warwick, 1984; Veit-Koehler et al., 2008). By using a dissecting microscope all metazoan meiofauna animals in the size class between 1 mm and 32 μ m were counted and sorted according to higher taxa, including temporary, permanent and pelagic meiofauna.

For this study only the permanent metazoan meiofauna (animals which remain small during their entire life) was used. The temporary meiofauna (animals which are only small during larval/juvenile development), the benthic and pelagic protists and other pelagic meiofauna were only recorded. If present, 300 individuals of each higher taxon were taken out randomly for further identification to genus level.

Nematodes were slowly transferred into glycerine for making whole mount slides. Identification was done using standard literature (Platt & Warwick, 1983; Platt & Warwick, 1988; Warwick et al., 1998). The other taxa were identified by the following taxonomists: Christoph Plum: copepods; Rosalie F. Maddocks and Louis S. Kornicker: ostracods; Ilse Bartsch: halacarids and Kim Larsen: the tanaid. The single Tardigrad was not sent to a specialist. The number of identified individuals per higher taxon was then estimated for the entire sample. For comparisons, the total number of metazoan meiofauna individuals from 531 cm² sample area was standardized to a 10 cm² area (Table 1).

Sampling and processing of hydrothermal vent samples are published in detail in Gollner *et al.*, 2010b and Zekely *et al.*, 2006. For this comparison, data of hydrothermal vent sites were recalculated because identification was done on species level and protists were included in these previous studies.

4.3. Statistical analysis

In order to compare the meiofauna communities from the seeps of AT and AC with each other and with those of the hydrothermal vents (MB and BF), several analyses were performed. Genera richness (G), estimated genera richness (EG(n)), Shannon diversity index ($H' \log e$), and Pielou's evenness index (J') were calculated (Table 2) by using Primer Version 6 package (Clarke and Gorley, 2006: PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth). Due to missing raw data of the Buckfield vent site the EG(n) for this site could not be calculated. To explore the dominance ratios, cumulative k-dominance curves were generated with Primer v6 (Fig. 3). After the basic data had been standardized and square-root transformed to

downweight high abundant genera without disregarding the rare ones, and after Bray-Curtis similarity was created, several community analysis like SIMPER (similarity percentage analysis), ANOSIM (analysis of similarity), MDS (multi dimensional scaling), and Hierarchical Cluster Analysis were performed also using the Primer v6 package. Between sites (AC,AT, MB, BF) and between habitats (cold seeps = AC+AT; hydrothermal vents = MB+BF) the 1-way SIMPER analysis and the 1-way ANOSIM analysis were calculated. Two-way crossed ANOSIM and SIMPER analysis were performed in order to test the null hypothesis that there are no differences between treatments (seep and vent), allowing for the possibility that there may be site differences.

Student's t-tests were carried out with the program "Statistica" to detect significant differences in univariate indices between the two cold seep sites as well as between seep and hydrothermal vent sites. In addition we also used a bootstrapping method (2-sided t-test with 10 000 resamplings each, using the "FTBOOT" routine from the "computer intensive statistics" package by Nemeschkal; see Nemeschkal 1999) because we worked with a relatively low number of samples and high variances. The tested univariate indices were the diversity indices G, H'log e, and J', abundances, sediment volume, surface area, and depth. To ensure a normal distribution, the data had to be transformed. The genera richness, the estimated genera richness, and abundances were square-root transformed, the sediment volume, the surface area and the depth were ln transformed, the relative abundances were arcsine transformed, and the remaining data [H'log e, J'] were not transformed.

To detect possible correlations between AC and AT and between cold seeps (AC, AT) and hydrothermal vents (MB,BF) the Pearson's r were calculated from transformed data for the same comparisons as done for the t-tests using again the Programm Statistica. The comparisons were done on the total permanent meiofauna level (T) as well as on the Nematoda (N) and Copepoda level (C), and the other remaining permanent meiofauna (O), for example ostracods and halacarids. All these calculations were done with nauplii excluded but they were also calculated with nauplii included. All results were classical bonferroni corrected ($p = \alpha/n$; $\alpha = 0,05$; n = Number of realized tests).

5. Results

5.1. Alaminos Canyon (AC) compared to Atwater Valley (AT)

5.1.1 Abundance

The mussel beds of both investigated cold seep sites AC and AT were mainly built of *Bathymodiolus brooksi* and only in two samples at AC, *Bathymodiolus heckerae* co-occurred but contributed to a minor degree to the total mussel individuals (AC_2: 6.2%, AC_3: 12.5%). The surface area of mussel shells of total AC samples ranged from 1310 to 2900 cm² while AT showed a range of 1620 to 2190 cm² (Table 1). Thus, the potential living space for the epizooic meiofauna provided by the foundation species increased, comparing the mussel pot area (531 cm²) with the mussel surface areas, between 2 to 5 times. The sediment trapped between mussel shells per sample was between 21 and 3600 ml and did not correlate with the surface area of mussels (Spearman correlation, $r = -0.53$; $p = 0.28$).

Both investigated seep sites at AC and AT revealed total abundances of mussel associated permanent meiofauna between 57.81 and 1826.48 ind. per 10 cm². Although the total abundances were not statistically discernable, the three samples from AC showed smaller variations (81.35 – 641.89 ind. per 10 cm²) than those of AT (57.81 – 1826.48 ind. per 10 cm²) (Table 1). When standardized to volume of sediment (ml) the mean and deviation of abundance for AC was 131.37 ± 25.39 and for AT was 73.48 ± 63.76 but when standardized to 10cm² mussel surface area the mean and deviation of abundance for AC was 134.31 ± 122.76 and for AT 225.3 ± 283.8 .

Positive but no significant correlations were shown for total abundance per sample and total sediment of cold seeps (Spearman correlation, $r = 0.96$; $p = 0.003$; not significant) as well as for the abundance per 10cm² mussel surface and total sediment (Spearman correlation, $r = 0.94$; $p = 0.005$; not significant). The correlation of animals per 10cm² sample area and Sediment per 10cm² sample area (Spearman correlation, $r = 0.96$; $p = 0.002$; significant) as well as the correlation of animals per 10cm² mussel surface area and Sediment per 10cm² sample area (Spearman correlation, $r = 0.91$; $p = 0.011$; not significant), showed the same trends.

5.1.2 Higher taxa composition

The epizooic, metazoan meiofauna community was composed of Nematoda, Copepoda, Ostracoda, and Halacaridae. Additionally, at AC Tardigrada and at AT Tanaidacea were found, although they were represented with less than 1% of higher taxa (Fig. 1). The most prominent higher taxon of all samples were the nematodes with a relative abundance between 72% and 93% at AC and between 82% and 91% at AT (Table 3). The second most abundant taxon was the copepods with 7% to 28% at AC and 9% to 17% at AT, followed by ostracods and halacarids. Also nauplii were found but they were not included in these analyses because they cannot be identified to higher crustacean taxa level. We note that protists, such as foraminiferans were present but they were excluded in this study of metazoan meiofauna.

5.1.3 Diversity

All univariate measures of diversity on genus level were similar between sites (Table 2). The genera richness (G) was 31 ± 4 at AC and 33 ± 15 of AT, with slightly higher variations at AT than at AC. The estimated genera richness EG (300) was 30 ± 4 at AC and 28 ± 12 at AT. The Shannon diversity indices ($H' \log_e$) were similar (AC 2.34 ± 0.51 , AT 2.43 ± 0.47). The Pielou's evenness index (J') revealed relatively even distributed genera (AC is 0.68 ± 0.13 , AT 0.71 ± 0.05). In all samples the first 10 genera showed total dominance of about 68% to 93% (Fig. 3). The three most dominant genera together showed a dominance over 50% in every sample except AT_1, where five genera summed up to a dominance over 50%. In sample AC_2 the most dominant genus, *Leptolaimus*, occupied a dominance of 56% alone. AT_1 needed therefore 5 genera, while the genus *Leptolaimus* in AC_2 occupied a dominance over 50% alone.

Taking into account the 3 most abundant genera of each sample, *Leptolaimus* occurred in 5 of all 6 cold seep samples (Table 3). The AC location showed in 2 of his 3 samples the nematode genera *Methalinhomoeus* and also *Paralinhomoeus* but they were not present in AT except *Metalinhomoeus* in one sample (AT_2). The AT location showed in 2 of his 3 samples the nematode *Paracanthorchus* and also in 2 of 3 *Thalassomonhystera* but they were not dominant in the AC location.

Measures of diversity for nematodes were also similar between sites (Table 2). The mean genera richness at AC was 20 ± 5 and for AT 21 ± 8 , $EG_{(300)}$ was 20 ± 4 for AC and 21 ± 8 for AT. Their evenness (J') was 0.61 ± 0.07 for AC and 0.74 ± 0.04 for AT (these differences were first significant concerning the statistical t-test calculation but after the bonferroni correction not anymore.) Their mean diversity ($H' \log_e$) differed higher with 1.81 ± 0.33 for AC and 2.21 ± 0.4 for AT higher than the Pielou's evenness between the sites.

The mean copepod evenness (J') and the mean diversity ($H' \log_e$) differed more than on total or nematode level but the mean genera richness were again close to the other sites value. The mean copepoda genera richness for AC is 9 ± 2 and for AT 9 ± 5 , the mean copepoda evenness (J') showed for AC 0.99 ± 0.01 and for AT 0.42 ± 0.02 . The highest difference between AC and AT indices showed the different mean values for diversity ($H' \log_e$) of copepods with 2.2 ± 0.18 for AC and 0.95 ± 0.7 for AT.

The Shannon index and the evenness of copepods were in statistical t-test calculation at first significant but after the bonferroni correction not significant.

All diversity information in detail, including the fractionation on taxa level (Nematoda, Copepoda), are shown in Table 2.

5.1.4 Community composition

Hierarchical cluster analysis based on Bray Curtis community similarity values showed that the samples clustered according to sites (Fig. 4). SIMPER analysis revealed a similarity of 44% among AC samples, and 57% similarity among AT samples. At AC the nematodes *Leptolaimus*, *Halomonhystera* and *Paralinhomoeus* contributed with 21%, 10%, and 10%, respectively to the similarity of samples. The most important copepod and the fourth important species was *Ameira*, with a contribution of 7%. For AT, the contribution to the similarity of samples were 15%, 14%, and 12%, for the nematodes *Thalassomonhystera*, *Leptolaimus*, and *Paracanthonchus* and 10% for the copepod *Ameira*. SIMPER analysis revealed a 62% dissimilarity between sites were the nematodes *Paracanthonchus*, *Thalassomonhystera* and *Paralinhomoeus* contribute with 7%, 6% and 6%. ANOSIM analysis did not detect significant differences (Global R = 0.704, p = 0.1, number of permutations = 10). The 2-D multidimensional scaling analysis showed a clear grouping of samples according to sites Fig. 5.

5.2. Cold seeps (AC and AT) compared to hydrothermal vents (MB and BF)

5.2.1 Abundance

The mussel beds of the East Pacific Rise hydrothermal vents were entirely built of *Bathymodiolus thermophilus* (Table 1). The sediment per sample trapped between mussels at the hydrothermal vents was between 7.4 – 25 ml. For cold seeps it was 21 – 3600 ml per sample.

Due to the Mussel Bed site being scooped with a net, Sediment standardizations were also done for additional calculations. The sediment was standardized to a 10cm² sample area and showed a range of 0.40 – 67.80 ml per 10cm² sample area for cold seeps and a range of 0.14 – 0.30 ml per 10cm² sample area for hydrothermal vents. Furthermore, cold seeps showed a larger sediment fraction than the hydrothermal vents, which was more obvious in a standardization of sediment to 10cm².

Sediment calculated per 10cm² mussel surface could only be done for cold seeps (0.10 – 20.34 ml per 10cm² mussel surface area) because of the missing hydrothermal vent mussel surfaces.

The East Pacific Rise hydrothermal vent samples of Mussel Bed and Buckfield showed an abundance range of 24.39 – 86.36 individuals per 10cm². This was a smaller range than the cold seep samples (Table 1). When standardized to volume of sediment (ml) the mean and deviation of abundance for CS was 102 ± 54 and for HV was 258 ± 114. The mean, when standardized to a 10cm² sample area, was for CS 561 ± 657 and HV 50 ± 25.

The correlation of cold seep samples and hydrothermal vent samples for total abundance with total sediment (Spearman correlation, $r = 0.95$; $p \leq 0.000$; significant) showed a significant positive effect (Fig. 2). The correlation of abundance per 10cm² sample area and sediment per 10cm² sample for both habitats together (Spearman correlation, $r = 0.95$; $p \leq 0.000$; significant) also showed a significant positive correlation.

5.2.2 Higher taxa composition

The epizooic metazoan meiofauna community of the hydrothermal vent samples were composed of Copepoda, Nematoda and Ostracoda (Table 2). It was determined that Halacarids were only found at the Mussel Bed location and that Nauplii were not found at the hydrothermal vent samples. The hydrothermal vent samples showed a shifted order of dominance compared to cold seep samples (Fig. 1). The main group at this chemosynthetic habitat were the copepods with a range from 50% to 96%, followed by the nematodes with 4% to 50%. The other permanent meiofauna taxa (ostracods, halacarids) exhibited less than 1%.

The student's t-test showed significant differences between cold seep and hydrothermal vent samples, such as the relative abundances on nematode and on copepod level. Whereas the bootstrapping t-test didn't show any significant difference.

Without being statistically relevant, the relative abundance between the hydrothermal vent locations also varied. The Mussel Bed samples showed a copepod range of 50% to 69% and a nematode range of 31% to 50% while the Buckfield samples showed a range of 94% to 96% copepods and 4% to 5% nematodes, with a larger difference between Copepoda and Nematoda occurrence (Table 3).

5.2.3 Diversity

In the case of the habitat comparison the univariate measures showed differences but statistically they were not significant differences (Table 3). Cold seeps showed larger genus richness stretching (G: 22 – 50) than the hydrothermal vents (G: 18 – 25). Mean and deviation for cold seeps genus richness were 32 ± 10 and for hydrothermal vents 20 ± 3 . Estimated genera richness could not be calculated for HV sites due to the lack of data.

The student's t-test showed, after the bonferroni correction, a significant difference between cold seep and hydrothermal vent samples concerning the genus richness of Nematoda. The bootstrapping t-test didn't show any significant differences.

The mean and deviation of the evenness (J') for cold seep samples were 0.69 ± 0.09 and for hydrothermal vents 0.72 ± 0.03 , therefore a slight difference of approximately 0.03. The mean Shannon diversity ($H' \log_e$) is 2.38 ± 0.44 for cold seeps and 2.28 ± 0.34 for hydrothermal vents, which made a difference of about 0.1. The t-test showed no significant difference between the Pielou's evenness and the shannon indexes. Only the Pielou's evenness of nematodes showed a difference between the two habitats but not after the bonferroni correction was made. The Nemeschkal calculations did not show any significant differences.

In all cold seep samples the first 10 genera showed totalized dominance of about 68 to 93%, the hydrothermal vent samples showed 69 to 98%. (Fig. 3) The most prominent taxa, which was in every hydrothermal vent sample, a Dirivultidae copepod had a dominance of about 18% to 30%. The second and third dominant taxa followed with dominance of about 10% or 20% steps. These steps got smaller the more the taxa followed the hierarchy down. Further, it was observed that the Dirivultidae copepod is known to be a hydrothermal vent-specific group (Gollner *et al.*, 2010a).

The two chemosynthetic habitats (CS and HV) showed together that for genera counts 26 ± 9 (mean \pm deviation), for the evenness 0.71 ± 0.06 and for Shannon diversity 2.28 ± 0.34 . Diversity information in detail included the mean and deviation of locations (AC, AT, MB, BF) as well as habitats (CS, HV) in Table 2.

5.2.4 Community composition

The hierarchical cluster analysis showed, based on the Bray Curtis, similarity values clustering according to sites (Fig. 4). The Graph exhibited that the hydrothermal vent sites had similarity between them, as compared to the cold seep site Alaminos Canyon (AC_1, AC_2, AC_3) amongst the related sites. The similarity between the two cold seep sites was not much higher than the Alaminos Canyon.

According to one Way SIMPER analysis, sites showed a similarity between the mussel bed samples of 69%, whereby the nematodes *Thalassomonhystera*, *Halomonhystera* and *Chromadorita* contributed 11%, 9% and 9% to this similarity. For the Buckfield site a similarity of 88% was calculated and the three most important permanent meiofaunal animals were from the copepod Dirivultidae group the *Aphotopontius* with 16%, *Rhogobius* with 15% and *Scotoecetes* with 12%.

Between both hydrothermal vent sites exhibited a dissimilarity of 60%. The Dirivultidae copepod *Rhogobius* (8%), *Scotocetes* (7%) and the copepod *Halectinosoma* (7%) were the three most important genera, which contributing to this dissimilarity.

According to one Way SIMPER analysis for habitats, a similarity of 55% for hydrothermal vents was revealed. The two-way SIMPER, which examines the habitat groups across all site groups, showed a larger similarity of 78%.

For cold seeps a one-way SIMPER similarity of 43% and a two-way SIMPER of 51% were calculated. The dissimilarity of 81% between both habitats was calculated by using the one-way SIMPER analysis, whereby the Dirivultidae copepod *Aphotopontius* contributed 6%, the nematode *Leptolaimus* contributed 6% and the Dirivultidae *Rhogobius* 5% , to the dissimilarity. Consequently, the SIMPER analysis showed that the Dirivultidae group was important for similarities and dissimilarities between the hydrothermal vent sites as well as between the habitats of cold seeps and hydrothermal vents. The two way SIMPER analysis showed closer similarities than the one way SIMPER analysis for the purpose of habitat comparison.

The ANOSIM calculated an insignificant Global R of 1 ($p = 0.1$; number of permutations = 10) for the MB and BF hydrothermal vent sites. The same significance level and number of permutations, a Global R of 0.704, showed the calculation for the similarity of the two cold seep sites AC and AT. The ANOSIM calculated, for all sites (AC, AT, MB, BF), a significant Global R of 0.938 ($p = 0.001$; number of permutations = 999) and predicated that the groups were well separated and therefore dissimilar. On the habitat level (CS, HV) the ANOSIM Global R was significant and calculated with 0.972 ($p = 0.002$; number of permutations = 462), which were also interpreted as dissimilar. The two-way crossed ANOSIM, which would show differences between sites across all habitats (CS, HV), calculated a Global R of 0.852 ($p = 0.01$; number of permutations = 100). The calculation between habitats across all sites did not show a value because the groups were too small. The two-way nested ANOSIM, where the sites were nested in the habitats, the Global R for differences between Sites across all habitat groups was 0.833 ($p = 0.01$; number of permutations = 100). For the two-way calculation of differences between Habitat Groups using Site Groups as samples the Global R showed an insignificant value of 1 ($p = 0.333$; number of permutations = 3), which exhibited a clear difference between the habitats.

The Multidimensional scale (MDS) analysis formed separate groups for all locations with a stress of 0.06 in the 2-dimensional view (Fig. 5) and a lower stress of 0.01 in the 3-dimensional imaging. The MB, BF and AT samples formed, with their site relatives, closer group than the AC site where the AC_1 sample located beside their site relatives.

6. Discussion

6.1. Comparison of the two cold seeps Alaminos Canyon (AC) and Atwater Valley (AT)

6.1.1 Community pattern

Independent of their location, nearly equal community patterns of cold seeps were observed, despite their community compositions being different. Based on the gathered data we can assume that permanent meiofauna community patterns associated with mussel beds in Alaminos Canyon and at Atwater Valley are alike. Differences were consistent in genus composition (for further details refer to 6.1.3. Genera composition). By reference to all the calculated diversity indices [genus richness (G), estimated genus richness for 300 individuals ($EG_{(300)}$), Pielou's evenness (J'), Shannon Index ($H' \log_e$)] it was revealed that the two cold seep samples AC and AT showed equal community patterns (Table 2). Even though the two permanent meiofauna communities have a geographical distance of approximately 640km [In Google Earth (~640 km), measured on a map published by (Roberts *et al.*, 2007b) (~ 635 km)], the small differences between the AC and AT diversity indices as well as mean relative abundance (Table 2, Table 3) were not large enough to affect the statistical analysis.

6.1.2 Clustering

Samples with similar foundation species compounds (*Bathymodiolus brooksi*, *Bathymodiolus heckerae*) clustered close and site samples clustered even closer. Both cold seep sample sites had mussels as their foundation species, while all samples of AT mussel aggregations were composed of 100% *Bathymodiolus brooksi*. The AC site exhibited one sample with 100% *B. brooksi* and the other two samples were mixtures of *B. brooksi* and *B. heckerae* (Table 1). The Hierarchical Cluster Analysis showed that AC_1, composed of 100% *B. brooksi*, clustered closer with three 100% *B. brooksi* samples of AT, than with their site relatives, which had a mixture of *B. brooksi* and *B. heckerae* (Fig. 4). This leads to the assumption that the species type, of the foundation species, could be important for the meiofaunal community. *Bathymodiolus brooksi* is a mussel with two symbionts, one

methanotrophic and one thiotrophic symbiont (Duperron *et al.*, 2009; Fisher *et al.*, 2007), while *Bathymodiolus heckerae* (also *Bathymodiolus heckeri*) is a mussel with four different species of symbionts, two sulfur-oxidizers, one methane-oxidizer and one methylotroph. In other words, two of them had been recognised as sulfur reducing species and the other two species use methane, and possibly methanol, as their energy source (Duperron *et al.*, 2009; Fisher *et al.*, 2007). Due to the fact of having 4 symbionts, we can assume that *B. heckerae* is more flexible to environmental changes and therefore it may lead indirectly to different mussel associated meiofaunal communities. However, the permanent meiofauna samples of the cold seeps clustered site adequately and predicated that samples of site relatives are more similar than samples of Mussel species relatives to each other (Fig. 4). But overall the data set was too small to make testimonial evidence for this observance.

6.1.3 Genera composition

The identified genera are already known from most intertidal habitats. There were no new genera discovered except *aff. Subspheerolaimus*. The two cold seeps sites showed similar community pattern, as well as heterogeneities. The same community pattern was composed of different genera (Table 4). The dissimilarity (SIMPER) between AC and AT was quite significant at 62%. The three most important genera for the AC samples were the Nematoda *Leptolaimus*, *Halomonhystera* and *Paralinhomoeus*. For AT the three most important Genera were also Nematoda, apart from *Leptolaimus* two different genera like *Thalassomonhystera* and *Paracanthochus* occurred (Table 3). *Leptolaimus* is a widespread nematode, other than the two cold seep locations, also occurred as epifauna in a shallow cold seep site (Degen, 2010), as well as in a tubeworm field at the AT site (Degen, 2010). Beside these habitats, *Leptolaimus* is also known from intertidal sands and mud, subtidal fine sand and mud as well as from intertidal seaweeds. The genera which are mainly responsible for the AC – AT dissimilarity of 62% were the three nematode Genera *Paracanthochus*, *Thalassomonhystera* and *Paralinhomoeus*. Also *Paracanthochus* and *Thalassomonhystera* occurred as epifauna at a AT tubeworm field (Degen, 2010) while *Paralinhomoeus* did not occur at all as Epifauna at cold seep site of AT, nor on mussel beds nor on tubeworms.

This genus also did not appear as Epifauna in shallow seeps (Degen, 2010) whereas it occurs as infauna in the Portuguese Mondego estuary southern arm (Adão *et al.*, 2009).

6.1.4 Comparison of cold seep mussel associated permanent meiofauna with other seep habitats

6.1.4.1 Comparison with mussel associated macrofauna

Mussel associated meiofauna occupies a bigger part of the associated metazoan fauna than associated macrofauna. The total permanent mussel associated meiofauna (without nauplii) had a mean and deviation for AC of 134313 ± 122756 Ind. per m^2 mussel surface area and for AT of 225295 ± 283797 Ind. per m^2 mussel surface area. In contrast, the associated macrofauna data of the same locations in the GOM (Cordes *et al.*, 2010a) showed much lower mean and deviation values for the mussel associated macrofauna data (AC: 127 ± 38 Ind. per m^2 mussel surface area and AT: 329 ± 355 Ind. per m^2 mussel surface area). Meiofauna data for AC is about 1055 times higher, and AT is about 684 times higher than the published associated macrofauna from Cordes *et al.*, 2010a concerning the same sites. This leads to the assumption that meiofauna occupies a much larger part of associated metazoan fauna than macrofauna. Mussel associated permanent metazoan meiofauna also showed at cold seeps a higher diversity than mussel associated macrofauna (H' : AC: 1.12 ± 0.11 , AT: 0.87 ± 0.16) with a more even distribution of genera (Macrofauna J' : AC: 0.49 ± 0 , AT: 0.43 ± 0.15). Although Cordes *et al.* 2010a's calculations were done on species level, the results can still be compared because only one species occurred per each genus.

6.1.4.2 Comparison with permanent meiofauna associated with tubeworms

The mussel associated permanent meiofauna was larger than the tubeworm associated permanent meiofauna (Degen, 2010). A comparison of the permanent meiofauna communities associated with a different foundation species (Tubeworms) at the AT site showed smaller abundance values for tubeworm associated permanent meiofauna (AT_deep tubeworms (Degen, 2010): 154 ± 254 Ind. per 10cm^2 ; AT_deep mussels: 744 ± 949 Ind. per 10cm^2). The same tendency is present for a different

cold seep site at a similar depth (AC_deep mussels: 378 ± 282 Ind. per 10cm^2). These trends also correspond to nematodes as they are the dominant group for the mentioned samples.

The cold seep (AC and AT) range of mussel associated nematodes (561 ± 657 Ind. per 10cm^2) from our study falls inbetween the general 10 – 8300 range for bivalve habitats of nematodes per 10cm^2 (Vanreusel *et al.*, 2010), as well as between the means of the two siboglinidae fields for nematodes which are sediment infauna at the Nyegga area (6591 ± 1099 Ind. per 10cm^2) and Storegga slide (39 ± 21 Ind. per 10cm^2) (Van Gaever *et al.*, 2009b). The meiobenthos abundances showed a high variability within the same habitat types, which is a general trend in literature (Van Gaever *et al.*, 2009b; Vanreusel *et al.*, 2010). As also shown in (Bright *et al.*, 2010) the general trend of meiofaunal abundance associated with foundation species is that associated meiofauna abundance is much lower than the sediment infaunal abundance.

6.2. Comparison of cold seeps and hydrothermal vents

6.2.1 Community pattern

Similar Stress, in terms of environmental factors like temp. and sulfide concentrations, between cold seeps and hydrothermal vents do create a similar permanent meiofaunal community pattern. Several diversity Indices had been very similar between cold seeps and hydrothermal vents used for this study (Table 2). Statistically no significant differences for the total meiofaunal community were shown between these two chemosynthetic habitats. Hydrothermal vents and cold seeps share high pressure and constant darkness with the surrounding deep sea but they showed special characteristics which both chemosynthetic habitats do or do not share. The fundamental differences between hydrocarbon seeps of the GOM and hydrothermal vents, McMullin *et al.*, 2000 listed, were temperature, sulfide concentrations and types of toxin occurring there. Cold seep habitats are generally considered as durable habitats (Sibuet and Olu, 1998; Turnipseed *et al.*, 2004; Turnipseed *et al.*, 2003), compared to the ephemeral hydrothermal vent habitats. They exhibited relatively constant environmental conditions with temperatures equal to the surrounding ocean water and generally characterised, compared to hydrothermal vents, as habitats with a relatively low stress level. Hydrothermal vents

are generally considered as ephemeral and highly stressful habitats, disturbed by volcanic eruptions and tectonic influences and with fast changes in vent fluid compositions as well as changes in environmental conditions. (Childress and Fisher, 1992; Fornari *et al.*, 1998; Gollner *et al.*, 2010b; Van Dover, 2000). This stress classification is mostly used on a comparison of hydrothermal vents against cold seeps. When the stress classification is done between the foundation species, for example mussel beds and tubeworms, for one chemosynthetic habitat the level of stress can shift additionally. Mussel beds are the first stage of succession at cold seeps and therefore they are dealing with relatively high levels of methane and sulfide (Bergquist *et al.*, 2003; Cordes *et al.*, 2005). The cold seep locations Alaminos Canyon and Atwater Valley had extremely sulfidic sediments (Roberts *et al.*, 2007a) with assumingly high methane concentrations (Roberts *et al.*, 2007a) in the sediment. Although these characteristics correspond to measures done in the sediment, it shows also the general characteristics of these sites. Even on low concentrations Sulfide is extremely toxic to most animals (Bagabarinao, 1992; Somero *et al.*, 1989; (Levin, 2005). Therefore, mussel beds can be rated between other cold seep habitats like tubeworm fields as a stressful habitat. Organisms at hydrothermal vents are exposed to even higher delivery rates of sulphide than those of cold seeps (Scott and Fisher, 1995; Turnipseed *et al.*, 2003). Hydrothermal vents generally are considered as stressful habitats, but mussel beds, compared to other hydrothermal vent habitats (pompei worm fields, tubeworm fields), are hydrothermal vent habitats with a low stress level (Gollner *et al.*, 2010b). They occur in diffuse-flow zones with low temperatures (2-10°C; Van Dover, 2000) which is a big difference to the elevated temperatures (up to 400°C; Von Damm, 1995) characteristic for hydrothermal vents (Turnipseed *et al.*, 2004). Vent mussel beds are habitats with temperatures about 2-10°C (Van Dover, 2000), therefore temperatures comparable with them from seeps 2-4°C (Sibuet and Olu, 1998; Turnipseed *et al.*, 2003). So the organisms living there do have experience with comparable temperatures (Turnipseed *et al.*, 2003). The first two fundamental factors McMullin *et al.*, 2000 listed as differences between hydrothermal vents and cold seeps are more or less equalized because the moderate temperatures where hydrothermal vent mussel beds used in this study are found and the extreme levels of sulfide cold seep mussel beds occurred. It could be assumed that both chemosynthetic habitats (Cold seep: AC + AT, Hydrothermal vents: MB+BF) used in this study had similar stress levels due to the neutralization of the

fundamental differences and the similar community pattern of mussel associated permanent metazoan meiofauna.

6.2.2 Clustering

The variance of similarity between the samples of the hydrothermal vents was smaller than the variance within the cold seep samples. The hierarchical cluster analysis based on the Bray Curtis similarity matrix showed a strong similarity of genera at the sites within their own chemosynthetic habitat (Fig. 4). As stated by Cordes *et al.*, 2010b there are geological as well as biological sources for habitat heterogeneity. The difference in determining the sole effect of a single one of these factors lies in the numerous types of intercorrelations between environmental factors such as the intensity and volume of fluid flow, the occurrence of gas hydrates, the methane and sulfide concentrations and their fluxes through the underlying sediment (Henry *et al.*, 1992; Cordes *et al.*, 2010b). All these factors are manifested as differences among sites and even areas of sites. For future research purposes it would be beneficial to have a closer look at the influence of environmental factors as compared to the influence of the foundation species on the composition of associated meiofauna.

6.2.3 Genera Composition

Cold seeps and hydrothermal vents showed similar mussel bed associated permanent metazoan meiofaunal community patterns but simultaneously different genus compositions. Between these chemosynthetic habitats there was a high dissimilarity, even though their same similarity community patterns are made of different genera. At cold seeps nematodes were the most important group while at hydrothermal vents the copepods, more precisely the Dirivultidae were occupying this status. The Dirivultidae is a vent specific family belonging to the siphonostomatoid copepods (Gollner *et al.*, 2010b). The dominance for the most important taxon showed at both chemosynthetic habitats equal relative abundances but the dominance shifted from one taxon to another taxon (Fig. 1).

The dominant higher taxon at cold seep were the nematodes with a mean relative abundance of $77 \pm 13\%$ (Copepoda $14 \pm 6\%$), while copepods showed at

hydrothermal vents a similar relative abundance mean of 77 ± 21 % (Nematoda 23 ± 21 %) and were therefore the dominant higher taxon at hydrothermal vents. The t-test from programm statistica showed significant differences for the relative abundances of Nematoda and Copepoda as well as for the genus richness of Nematoda, but the bootstrapping Nemeschkal calculation could not confirm this difference.

6.2.3.1 Genera that occur at mussel beds at vents and seeps

The most important cold seep genera were the nematodes *Leptolaimus* and *Halamonhystera* and the Copepod *Ameira*. The three most important genera for hydrothermal vents are the hydrothermal vent Dirivultidae copepods *Aphotopontius*, *Ceuthocetes* and *Rhogobius*. Apart from their different genera occurrences and dominances (Table 3), both chemosynthetic habitats also share some genera. Altogether 15 Genera (of all 105 genera) were shared between cold seeps (AC or AT) and hydrothermal vents (MB or BF) mussel associated permanent metazoan meiofauna. Eleven of them were nematodes, 3 were copepods (*Ameira*, *Bradya*, *Xylora*) and one Ostracod (*Xylocythere*). Interestingly every nematode which occurred at the EPR hydrothermal vents (MB or BF) also occurred in the GOM cold seeps (AC or AT) (Table 4).

In order to contextualize the data and to exclude the possible ocean variance between the GOM seeps and the EPR hydrothermal vents, we compared another hydrothermal vent field named Snake Pit (SP), located at the Moose Site at the Mid Atlantic Ridge (MAR) in the Atlantic ocean (Zekely et al., 2006), against the AC, AT samples. As the hydrothermal vent chosen did not have the data available in the necessary granularity for extensive comparison, the decision was made to compare data concerning genera appearance.

Five nematode genera are shared between GOM cold seeps, and the EPR hydrothermal vents as well as the MAR hydrothermal vent field Snake Pit (Zekely et al., 2006). Two additional nematodes (*Araeolaimus*, *Diplopeltula*) are not shared between them (Table 4). These two nematodes are neither shared with other hydrothermal vent locations of the East Pacific Rise (Copley et al., 2007; Gollner et al., 2010b; Gollner et al., 2007; Zekely et al., 2006) or with other cold seep sites (Degen, 2010; Shirayama and Ohta, 1990; Van Gaever et al., 2009a; Van Gaever et

al., 2006; Van Gaever et al., 2009b), but these nematodes are known from intertidal sands and some species of *Aerolaimus* additionally are known from intertidal seaweeds and kelp holdfasts. A comparison with a hydrothermal vent site from the North Fiji Basin shared only *Diplopeltula* with less than 1% relative abundance (Vanreusel et al., 1997) while at MAR site showed about 2.6 % relative abundance (Zekely et al., 2006). Interestingly *Paralinhomoeus* did occur at AC with a mean relative abundance of 12 ± 12 , but at no other cold seep location (Degen, 2010; Shirayama and Ohta, 1990; Van Gaever et al., 2009a; Van Gaever et al., 2006; Van Gaever et al., 2009b), while it occurred at some hydrothermal vent sites (Copley et al., 2007; Vanreusel et al., 1997; Zekely et al., 2006) and in intertidal sands (Platt & Warwick, 1983; Platt & Warwick, 1988; Warwick et al., 1998).

As cold seeps and hydrothermal vents showed similar community patterns with different genera. The cold seep samples had a larger variety regarding the appearance and composition of genera, while hydrothermal vent samples showed a vent specific copepoda group (Dirivultidae). Of all 105 genera of our study, 75 genera were only found at the GOM cold seeps (AC or AT) and did not occur at the EPR hydrothermal vents (MB or BF) (Table 3). Of the 75 genera 42 were nematodes, which are already known (Platt & Warwick, 1983; Platt & Warwick, 1988; Warwick et al., 1998) except the aff. *Subsphaerolaimus*. Comparing these 42 cold seep nematodes to other hydrothermal vent sites (Copley et al., 2007; Gollner et al., 2010b; Gollner et al., 2007; Vanreusel et al., 1997; Zekely et al., 2006), only 31 nematodes are not shared with hydrothermal vents. All of the 42 cold seep nematodes did not show high relative abundances. Out of the 105 genera 26 copepods, 4 ostracods and 1 genus each of halacarids, tanaids and tardigrads were only found at the AC, AT cold seeps. The copepod *Ameira* is the only copepod genus which did not verify the general trend of the overall higher relative abundances at hydrothermal vents compared to cold seeps. Apart from the copepods, at the hydrothermal vent sites (MB+BF), the most important nematode Genera were represented by *Thalassomonhystera*, *Halamonhystera* and *Chromadorita*. The three nematodes *Anticoma*, *Chromadorita* and *Microlaimus* showed a similar phenomenon like the copepod *Ameira* as they had higher relative abundances at hydrothermal vents than at cold seeps of our study. There are 17 Genera which only occur at the hydrothermal vents MB or BF and not at the GOM sites AC or AT. Certainly the 7 Dirivultidae copepod Genera are included, as well as 6 Copepods 3 Ostracods and a

single Halacarid genus. As already mentioned except aff. *Subsphaerolaimus* our study did not discover any new nematode genera, but it is expected that based on the study of the samples new species will be included in these known genera and be open for further studies.

6.2.4 Comparison of cold seep mussel associated permanent meiofauna with other chemosynthetic habitats

Nearly all associated nematode genera found in cold seeps and hydrothermal vents are already known mainly from intertidal sands. We were able to identify 11 Nematoda and 7 Copepoda that appeared in various cold seep habitats, ranging from shallow to deep level and associated with mussels (this study) as well as tubeworms (Degen, 2010). Drawing conclusions from the samples, it can be assumed that different foundation species host different genera in cold seeps. Associated tubeworm meiofauna genera for instance seem to outnumber associated mussel meiofauna. The main part of all found genera were already known from intertidal sands while some genera also occurred for example in intertidal seaweeds, such as the genus *Leptolaimus*, *Paralinhomoeus* or *Chromadorina*, or in kelp holdfasts like *Paracanthochus*, *Chromadorita* or *Sabatieria*.

The nematode *Chromadorita* is a cross-habitat (chemosynthetic) generalist. It appeared to be associated with both foundation species (mussel and tubeworms), whether hydrothermal vents or cold seeps, or generally in intertidal sand. It also appeared to be associated with tubeworms in deep and shallow cold seeps (Degen, 2010).

In conclusion, both studied chemosynthetic habitats showed a different dominant taxon. Every site and sample had its own special genera compositions but overall a comparison of cold seeps from different sites or with another chemosynthetic habitat, like hydrothermal vents, showed similar community patterns for mussel associated permanent metazoan meiofauna. There is still insufficient knowledge about these deep-sea chemosynthetic habitats. Due to this study field more investigation still has to be done to better understand this fascinating area.

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8. Data (Tables + Figures)

8.1. Tables

Table 1

Detailed sample informations of the six cold seep samples (AC_1-3; AT_1-3) and the six hydrothermal vent samples (MB_1-3; BF_1-3) including site, mussel, environmental informations and abundances. [AST...axial summit trough; AD#...Alvin Dive Number; JD#...Jason Dive Number; n.d....no data]

	COLD SEEPS:						HYDROTHERMAL VENTS:					
Sample Informations:	AC_1	AC_2	AC_3	AT_1	AT_2	AT_3	MB_1	MB_2	MB_3	BF_1	BF_2	BF_3
Geographic region	Gulf of Mexico	Gulf of Mexico	Gulf of Mexico	Gulf of Mexico	Gulf of Mexico	Gulf of Mexico	East Pacific Rise	East Pacific Rise	East Pacific Rise	East Pacific Rise	East Pacific Rise	East Pacific Rise
location	Alaminos Canyon	Alaminos Canyon	Alaminos Canyon	Atwater Valley	Atwater Valley	Atwater Valley	within the AST	within the AST	within the AST	within the AST	within the AST	within the AST
site	AC818	AC818	AC818	AT340	AT340	AT340	Mussel Bed	Mussel Bed	Mussel Bed	Buckfield	Buckfield	Buckfield
latitude [°N]	26°10.819	26°10.847	26°10.843	27°25.197	27°38.697	27°38.700	9°50.615'N	9°50.613'N	9°50.629'N	11°24.90'N	11°24.90'N	11°24.90'N
longitude [°W]	94°37.380	94°37.463	94°37.377	88°21.853	88°21.859	88°21.852	104°17.509'W	104°17.504'W	104°17.512'W	103°47.20'W	103°47.20'W	103°47.20'W
depth (m)	2744	2745	2745,3	2190	2190	2190	2503	2503	2503	2480	2480	2480
sample area (cm ²)	531	531	531	531	531	531	1370	770	630	531	531	531
sediment (ml)	42	225	155,5	21	3600	390	25	15	19	7,50	7,40	9,70
dive number	AD#4192	JD#282B	JD#284D	JD#276F	JD#277A	JD#277F	AD#3845	AD#3847	AD#3852	AD#3742	AD#3742	AD#3742
sampling device	Musselpot	Musselpot	Musselpot	Musselpot	Musselpot	Musselpot	Scooped with 63µm linen bag	Scooped with 63µm linen bag	Scooped with 63µm linen bag	Musselpot	Musselpot	Musselpot
Date of collection:	24.05.2006	01.07.2007	04.07.2007	20.06.2007	23.06.2007	24.06.2007	2002	2002	2002	2001	2001	2001
Mussels: <i>Bathymodiolus</i>												
surface area (cm ²)	2900	1310	1700	2190	1770	1620	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
<i>B. brooksi</i> (%)	100	93,8	87,5	100	100	100	-	-	-	-	-	-
<i>B. heckeræen</i> (%)	-	6,2	12,5	-	-	-	100	100	100	100	100	100
<i>B. thermophilus</i> (%)	-	-	-	-	-	-						
Environmental characteristics												
Temperature Mussel Bed: °C	about 4°C	about 4°C	about 4°C	about 4°C	about 4°C	about 4°C	max.10°C	max.10°C	max.10°C	2-10°C	2-10°C	2-10°C
pH:	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	min. 6,7	min. 6,7	min. 6,7	n.d.	n.d.	n.d.
sulfide:	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	max.151µM	max.151µM	max.151µM	n.d.	n.d.	n.d.
Abundances												
Ind. per 10cm²												
Nematoda (+unknown)	58,14	593,77	324,92	47,37	1655,66	303,44	42,77	25,39	21,24	1,32	1,48	1,36
Copepoda (+unknown, +Copepodites ¹)	23,15	47,65	84,14	9,75	164,77	44,15	43,50	30,94	47,41	23,01	27,68	30,56
Ostracoda (+unknown, unidentifiable)	0,06	0,19	0,27	0,34	4,70	0,25	0,09	0,19	0,30	0,06	0,06	0,04
Halacarida	0,00	0,19	0,18	0,34	1,34	0,00	0,00	0,06	0,00	0,00	0,00	0,00
Tanaidacea	0,00	0,00	0,00	0,02	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Tardigrada	0,00	0,09	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
total abundance	81,35	641,89	409,50	57,81	1826,48	347,84	86,36	56,58	68,95	24,39	29,22	31,96
Nauplii	21,08	23,26	0,00	14,97	20,14	28,12	0,00	0,00	0,00	0,00	0,00	0,00
Copepodites ¹	0,02	0,00	0,00	3,59	44,66	14,09	6,85	10,69	14,78	0,00	0,00	0,00

Table 2

Diversity informations (G...genus richness; J'...Pielou's evenness; H'log_e...Shannon Index; Estimated genus richness for 300 Individuals...EG₍₃₀₀₎) and relative abundances (without Nauplii) of the cold seep (CS: AC_1-3 and AT_1-3) and hydrothermal vent samples (HV: MB_1-3 and BF_1-3), with their mean values and standard deviations (MV±SD) [n.d....no data]. In cases where no data for the Buckfield (BF) site was present the mean for HV was calculated by using only with the the MB samples and the mean for CS plus HV was calculated by using the cold seep samples with only the Mussel Bed (MB) samples.

	AC_1	AC_2	AC_3	AC (MV±SD)	AT_1	AT_2	AT_3	AT (MV±SD)	CS (MV±SD)	MB_1	MB_2	MB_3	MB (MV±SD)	BF_1	BF_2	BF_3	BF (MV±SD)	HV (MV±SD)	CS+HV (MV±SD)
Total																			
G_Total	32	26	34	31 ± 4	50	26	22	33 ± 15	32 ± 10	22	25	20	22 ± 3	18	19	18	18 ± 1	20 ± 3	26 ± 9
J'_TOTAL	0.77	0.54	0.73	0.68 ± 0.13	0.76	0.67	0.68	0.71 ± 0.05	0.69 ± 0.09	0.71	0.76	0.74	0.74 ± 0.03	0.72	0.74	0.68	0.71 ± 0.03	0.72 ± 0.03	0.71 ± 0.06
H'log _e _TOTAL	2.68	1.76	2.59	2.34 ± 0.51	2.97	2.20	2.11	2.43 ± 0.47	2.38 ± 0.44	2.19	2.45	2.23	2.29 ± 0.14	2.07	2.18	1.96	2.07 ± 0.11	2.18 ± 0.17	2.28 ± 0.34
EG(300)_Total	32	25	32	30 ± 4	42	22	20	28 ± 12	29 ± 8	22	24	20	22 ± 2	n.d.	n.d.	n.d.	n.d.	22 ± 2	26 ± 7
Nematoda																			
G_Nematoda	21	15	24	20 ± 5	30	16	16	21 ± 8	20 ± 6	7	9	8	8 ± 1	8	9	8	8 ± 1	8 ± 1	14 ± 8
J'_Nematoda	0.64	0.53	0.64	0.61 ± 0.07	0.79	0.73	0.70	0.74 ± 0.04	0.67 ± 0.09	0.79	0.80	0.85	0.81 ± 0.03	0.75	0.80	0.73	0.76 ± 0.03	0.79 ± 0.04	0.73 ± 0.09
H'log _e _Nematoda	1.96	1.44	2.05	1.81 ± 0.33	2.67	2.02	1.94	2.21 ± 0.4	2.01 ± 0.39	1.53	1.76	1.77	1.69 ± 0.14	1.56	1.76	1.53	1.61 ± 0.13	1.65 ± 0.12	1.83 ± 0.34
EG(300)_Nematoda	21	15	23	20 ± 4	30	16	16	21 ± 8	20 ± 6	7	9	8	8 ± 1	n.d.	n.d.	n.d.	n.d.	8 ± 1	16 ± 8
%Nematoda (NoNauplii)	56,77%	89,27%	79,35%	75 ± 17	65,08%	89,66%	80,71%	78 ± 12	77 ± 13	49,52%	44,87%	30,80%	42 ± 10	5,41%	5,07%	4,25%	5 ± 1	23 ± 21	50 ± 33
Copepoda																			
G_Copepoda	11	8	9	9 ± 2	15	7	5	9 ± 5	9 ± 3	12	12	10	11 ± 1	9	9	9	9 ± 0	10 ± 1	10 ± 3
J'_Copepoda	1.00	0.98	0.98	0.99 ± 0.01	0.64	0.35	0.26	0.42 ± 0.2	0.7 ± 0.34	0.58	0.69	0.60	0.62 ± 0.06	0.85	0.90	0.82	0.85 ± 0.04	0.74 ± 0.14	0.72 ± 0.25
H'log _e _Copepoda	2.40	2.04	2.16	2.2 ± 0.18	1.74	0.68	0.42	0.95 ± 0.7	1.57 ± 0.82	1.44	1.71	1.38	1.51 ± 0.18	1.87	1.98	1.79	1.88 ± 0.09	1.69 ± 0.24	1.63 ± 0.58
EG(300)_Copepoda	11	8	9	9 ± 2	15	7	5	9 ± 5	9 ± 3	12	12	10	11 ± 1	n.d.	n.d.	n.d.	n.d.	11 ± 1	10 ± 3
%Copepoda (NoNauplii)	22,60%	7,16%	20,55%	17 ± 8	13,39%	8,92%	11,74%	11 ± 2	14 ± 6	50,37%	54,67%	68,76%	58 ± 10	94,36%	94,74%	95,63%	95 ± 1	76 ± 21	45 ± 36

Table 3

Relative abundances of all permanent meiobenthic genera of the cold seep samples (AC_1-3; AT_1-3) and hydrothermal vent samples (MB_1-3; BF_1-3). The relative abundances >10% are bold marked. Dirivultidae genera are underlined.

	COLD SEEPS:						HYDROTHERMAL VENTS:					
	AC_1	AC_2	AC_3	AT_1	AT_2	AT_3	MB_1	MB_2	MB_3	BF_1	BF_2	BF_3
Nematoda												
<i>Acantholaimus</i>	0	0	0.24	0.27	0	0	0	0	0	0	0	0
<i>Actinonema</i>	0	0	0.24	8.15	0	0	0	0	0	0	0	0
<i>aff. Subspheerolaimus</i>	0	0	0	0	0	0.87	0	0	0	0	0	0
<i>Amphimonhystrella</i>	0	0	0	0.27	0	0	0	0	0	0	0	0
<i>Anticoma</i>	0	0	0.24	0	0	0	4.95	4.02	11.20	0.08	0.14	0
<i>Camacolaimus</i>	1.16	0	0	1.36	3.62	1.16	0	0	0	0	0	0
<i>Chromadora</i>	0	0	0	0.82	0	0.29	0	0	0	0	0	0
<i>Chromadorella</i>	0	0	0	0.54	0.30	0	0	0	0	0	0	0
<i>Chromadorina</i>	0	0.56	0	1.63	0	2.33	0	0	0	0	0	0
<i>Chromadorita</i>	5.50	1.69	1.68	4.89	1.51	2.91	8.00	9.71	3.03	0.37	0.27	0.06
<i>Cobbia</i>	0.58	0	0	0	0	0	0	0	0	0	0	0
<i>Comesa</i>	0.29	0	0	0.27	0	0	0	0	0	0	0	0
<i>Comesoma</i>	0.29	0	0	0	0	0	0	0	0	0	0	0
<i>Crenopharynx</i>	0	0	0.24	0	0	0	0	0	0	0	0	0
<i>Daptonema</i>	2.60	0	1.20	2.17	0	0	0	0.67	1.17	0	0	0
<i>Desmodora</i>	0	1.13	5.05	16.58	0.60	0.58	0	0	0	0	0	0
<i>Desmolaimus</i>	0	1.41	0	0	0	0	0	0	0	0	0	0
<i>Desmolorenzenia</i>	0	0	0.96	0	0	0	0	0	0	0	0	0
<i>Desmoscolex</i>	0	2.26	0	0.27	0.04	0	0	0	0	0	0	0
<i>Dichromadora</i>	0	0	0	0.27	0	0	0	0	0	0	0	0
<i>Elzalia</i>	0.29	0	0	0	0	0	0	0	0	0	0	0
<i>Eumorpholaimus</i>	2.60	0	0	0	0	0.58	0	0	0	0	0	0
<i>Halaphanolaimus</i>	0	0.28	0.24	0	0	0	0	0	0	0	0	0
<i>Halomonhystera</i>	30.09	4.23	3.37	0.54	5.44	6.11	11.81	10.05	2.33	1.15	0.65	0.34
<i>Leptolaimus</i>	12.44	55.56	21.40	7.88	13.89	13.67	0	0.67	1.17	0.33	0.14	0.28
<i>Linhomoeus</i>	0.29	1.69	5.53	2.17	22.35	6.98	0	0	0	0	0	0
<i>Marylynna</i>	0.29	0	0.24	0	0	0	0	0	0	0	0	0
<i>Megadesmolaimus</i>	0	0	0.48	0	0	0	0	0	0	0.33	0.27	0.25
<i>Metacatholaimus</i>	0	0	0	0.27	0	0	0	0	0	0	0	0
<i>Metacycolaimus</i>	0	0	0	0	1.81	0.29	0	0	0	0	0	0
<i>Metalinhomoeus</i>	0.29	9.02	7.45	0	0.60	0	0	0	0	0	0	0
<i>Microlaimus</i>	1.45	0	0.24	0	0.30	0.29	1.90	0.67	0	0	0	0
<i>Molgolaimus</i>	8.68	0	0.24	0.82	0	0	0	0	0	0	0	0
<i>Nemanema</i>	0	0	0	0.54	0	0	0	0	0	0	0	0
<i>Neochromadora</i>	0	0	0	0.82	6.95	1.74	0	0	0	0	0	0
<i>Odontantocoma</i>	0	0	0.48	2.17	0.30	0	0	0	0	0	0	0
<i>Oncholaimus</i>	0	0	0	3.53	0	0	0	0	0	0	0	0
<i>Paracanthonchus</i>	0.87	0	0.24	2.72	20.54	27.33	0.76	6.36	6.07	0.16	0.27	0.25
<i>Paracantholaimus</i>	0.29	0	0	0	0	0	0	0	0	0	0	0
<i>Paralinhomoeus</i>	0.87	11.28	24.04	0	0	0	1.52	0.67	1.17	0	0.38	0.06
<i>Prochaetosoma</i>	0	0.28	0	0.10	0.30	0	0	0	0	0	0	0
<i>Prochromadorella</i>	0	0	0	3.53	0	0.58	0	0	0	0	0	0
<i>Pseudodesmodora</i>	0	0	0	0.27	0	0	0	0	0	0	0	0
<i>Sabatieria</i>	0	0.28	0.48	2.72	0	0	0	0	0	0	0	0
<i>Setoplectus</i>	0	0	0.24	0	0	0	0	0	0	0	0	0
<i>Sphaerolaimus</i>	0.29	0	0	0	0	0	0	0	0	0	0	0
<i>Spilophorella</i>	0	0.28	0	0	0	0	0	0	0	0	0	0
<i>Thalassomonhystera</i>	0.87	0.85	0.24	13.32	11.78	20.94	20.57	12.05	4.67	2.62	2.26	2.06
<i>Theristus</i>	1.16	0	2.16	0	0	0	0	0	0	0.37	0.68	0.94
<i>Tricoma</i>	0	0	0	0.03	0	0	0	0	0	0	0	0
<i>Viscosia</i>	0	0	0	2.72	0	0	0	0	0	0	0	0
Copepoda												
<i>Copepodites</i>	0.02	0	0	6.21	2.45	4.05	7.93	18.89	21.44	0	0	0
<i>Ameira</i>	2.58	1.65	2.05	4.68	5.27	7.83	0.47	2.58	2.22	0	0	0
<i>Ameiridae</i>	0	0	2.05	0	0	0	0	0	0	0	0	0
<i>Amphiascella</i>	2.58	0	0	0	0	0	0	0	0	0	0	0
<i>Amphiascus</i>	0	0	0	0	0	0	1.17	1.59	1.97	0	0	0
<u><i>Aphotopontius</i></u>	0	0	0	0	0	0	23.09	1.79	3.70	19.74	22.13	29.76
<i>Archsola</i>	2.58	0.82	0	0.28	0.04	0.09	0	0	0	0	0	0
<i>Argesthidae</i>	0	0	0	0.06	0	0	0	0	0	0	0	0
<i>Bathylaophonte</i>	0	0	0	0	0	0	0	0	0	0.87	0	0.87
<i>Bradya</i>	0	0.82	0	0	0	0	8.86	0.40	1.48	0	0	0
<i>Breviconia</i>	0	0	2.05	0	0	0	0	0	0	0	0	0
<i>Calanoida spec.1</i>	0	0	2.05	0.06	0	0.09	0	0	0	0	0	0
<i>Calanoida spec.2</i>	0	0	0	0	0	0	0	0	0	0	0	0
<u><i>Ceuthocetes</i></u>	0	0	0	0	0	0	4.90	3.18	3.94	15.39	8.10	11.85
<i>Cletodidae</i>	2.58	0	0	0	0	0	0	0	0	0	0	0
<i>Cycloplina</i>	0	0	0	0.06	0	0	0	0	0	0	0	0
<i>Delavalia</i>	0	0.82	0	0	0	0	0	0	0	0	0	0
<i>Diosaccinae</i>	0	0	0	0	0	0	0	0.40	0	0	0	0
<i>Ecbathyron</i>	0	0	0	0	0	0	0.70	0.60	0	8.13	16.83	4.91
<i>Enalcyonium</i>	0	0	0	0	0.04	0	0	0	0	0	0	0
<i>Erebionaster</i>	0	0.82	0	0	0	0	0	0	0	0	0	0
<u><i>Exrima</i></u>	0	0	0	0	0	0	0	0	0	2.03	4.99	1.73
<i>Halectinosoma</i>	0	0	0	0	0	0	0.23	18.49	30.31	1.74	4.05	3.18
<i>Laophontidae spec.1</i>	0	0	0	0.11	0	0	0	0	0	0	0	0
<i>Laophontidae spec.2</i>	0	0	0	0.11	0	0	0	0	0	0	0	0
<i>Mesochra</i>	2.58	0.82	2.05	1.52	0.04	0.18	0	0	0	0	0	0
<i>Metis</i>	0	0	0	0	0.08	0	0	0	0	0	0	0
<i>Microsetella</i>	2.58	0	0	0	0	0	0	0	0	0	0	0
<i>Miracidae gen.</i>	0	0	0	0.17	0	0	0	0	0	0	0	0
<i>Miracidae spec.4</i>	2.58	0	0	0	0	0	0	0	0	0	0	0
<i>Miracidae spec.5</i>	0	0	2.05	0	0	0	0	0	0	0	0	0
<i>Miracidae spec.6</i>	0	0.82	0	0	0	0	0	0	0	0	0	0
<i>Nilva</i>	0	0	0	0	0	0	1.40	1.19	0.49	9.29	9.04	6.07
<i>Psammis</i>	0	0	0	0.06	0	0	0	0	0	0	0	0
<i>Pseudobryadia</i>	2.58	0	2.05	2.20	0.21	0	0	0	0	0	0	0
<u><i>Rhogobius</i></u>	0	0	0	0	0	0	0.47	4.37	1.23	26.42	16.21	25.13
<u><i>Scotoecetes</i></u>	0	0	0	0	0	0	0.23	0.80	0	10.74	12.78	12.13
<i>Strongylacron</i>	0	0	0	0.06	0	0	0	0	0	0	0	0
<u><i>Stylogopontius</i></u>	0	0	0	0	0	0	0.23	0	0	0	0.62	0
<i>Tetragoniceps</i>	0	0	0	0	0	0	0	0	0.74	0	0	0
<i>Tisbe</i>	2.58	0.82	2.05	0.73	0.76	0.45	0	0	0	0	0	0
<i>Uptonyx</i>	2.58	0	4.11	0.34	0	0	0	0	0	0	0	0
<i>Xylora</i>	2.58	0	0	0.23	0	0	0.70	0.40	1.23	0	0	0

	COLD SEEPS:						HYDROTHERMAL VENTS:					
	AC_1	AC_2	AC_3	AT_1	AT_2	AT_3	MB_1	MB_2	MB_3	BF_1	BF_2	BF_3
Ostracoda												
<i>Ambocythere</i>	0	0	0	0.03	0	0	0	0	0	0	0	0
<i>Krithe</i>	0	0	0	0	0.04	0	0	0	0	0	0	0
<i>Ostracoda</i> Buckfield	0	0	0	0	0	0	0	0	0	0.23	0.19	0.12
<i>Polycopetta</i>	0	0	0	0	0	0	0.01	0.05	0	0	0	0
<i>Thomontocypris</i>	0	0	0	0	0	0	0.05	0.14	0.23	0	0	0
<i>Typhlocythere</i>	0	0	0	0.03	0	0	0	0	0	0	0	0
<i>Xestoleberis</i>	0	0.01	0	0	0	0	0	0	0	0	0	0
<i>Xylocythere</i>	0	0	0	0.52	0.22	0.07	0.05	0.16	0.21	0	0	0
Halacarida												
<i>Copidognathus</i>	0	0.03	0.04	0.59	0.07	0	0	0	0	0	0	0
<i>Lohmannella</i>	0	0	0	0	0	0	0	0.11	0	0	0	0
Tanaidacea												
<i>Pseudotanaids</i>	0	0	0	0.03	0	0	0	0	0	0	0	0
Tardigrada												
<i>Tardigrada</i>	0	0.01	0	0	0	0	0	0	0	0	0	0
Totals:												
Nematoda	71.19	90.81	76.94	81.68	90.35	86.66	49.52	44.87	30.80	5.41	5.07	4.25
Copepoda	28.43	7.42	20.55	10.65	6.45	8.64	42.44	35.78	47.32	94.36	94.74	95.63
Others												
(Ostracoda, Halacarida, Tanaidacea, Tardigrada)	0.00	0.06	0.04	1.21	0.33	0.07	0.11	0.46	0.44	0.23	0.19	0.12

Table 4

Genera comparison of the cold seep sites (AC, AT) from the Gulf of Mexico, East Pacific Rise hydrothermal vent sites (MB, BF) and Mid Atlantic Ridge (MAR) hydrothermal vent Snake Pit (SP) site. Dirivultidae genera are underlined. [X... Genus was present; - ... Genus was not present]

	COLD SEEPS:		HYDROTHERMAL VENTS:		
	AC	AT	MB	BF	SP (MAR)
Nematoda					
<i>Acantholaimus</i>	X	X	-	-	-
<i>Actinonema</i>	X	X	-	-	-
<i>aff. Subspheerolaimus</i>	-	X	-	-	-
<i>Amphimonhystrella</i>	-	X	-	-	-
<i>Anticoma</i>	X	-	X	X	X
<i>Araeolaimus</i>	-	-	-	-	X
<i>Camacolaimus</i>	X	X	-	-	-
<i>Chromadora</i>	-	X	-	-	-
<i>Chromadorella</i>	-	X	-	-	-
<i>Chromadorina</i>	X	X	-	-	-
<i>Chromadorita</i>	X	X	X	X	X
<i>Cobbia</i>	X	-	-	-	-
<i>Comesa</i>	X	X	-	-	-
<i>Comesoma</i>	X	-	-	-	-
<i>Crenopharynx</i>	X	-	-	-	-
<i>Daptonema</i>	X	X	X	-	-
<i>Desmodora</i>	X	X	-	-	-
<i>Desmolaimus</i>	X	-	-	-	-
<i>Desmolorenzenia</i>	X	-	-	-	-
<i>Desmoscolex</i>	X	X	-	-	-
<i>Dichromadora</i>	-	X	-	-	-
<i>Diplopeltula</i>	-	-	-	-	X
<i>Elzalia</i>	X	-	-	-	-
<i>Eumorpholaimus</i>	X	X	-	-	-
<i>Halaphanolaimus</i>	X	-	-	-	-
<i>Halomonhystera</i>	X	X	X	X	-
<i>Leptolaimus</i>	X	X	X	X	X
<i>Linhomoeus</i>	X	X	-	-	-
<i>Marylynnia</i>	X	-	-	-	-
<i>Megadesmolaimus</i>	X	-	-	X	X
<i>Metacyatholaimus</i>	-	X	-	-	-
<i>Metacylicolaimus</i>	-	X	-	-	-
<i>Metalinhomoeus</i>	X	X	-	-	-
<i>Microlaimus</i>	X	X	X	-	-
<i>Molgolaimus</i>	X	X	-	-	-
<i>Nemanema</i>	-	X	-	-	-
<i>Neochromadora</i>	-	X	-	-	-
<i>Odontanticoma</i>	X	X	-	-	-
<i>Oncholaimus</i>	-	X	-	-	-
<i>Paracanthonchus</i>	X	X	X	X	-
<i>Paracyantholaimus</i>	X	-	-	-	-
<i>Paralinhomoeus</i>	X	-	X	X	-
<i>Prochaetosoma</i>	X	X	-	-	-
<i>Prochromadorella</i>	-	X	-	-	-
<i>Pseudodesmodora</i>	-	X	-	-	-
<i>Sabatieria</i>	X	X	-	-	-
<i>Setoplectus</i>	X	-	-	-	-
<i>Sphaerolaimus</i>	X	-	-	-	-
<i>Spilophorella</i>	X	-	-	-	-
<i>Thalassomonhystera</i>	X	X	X	X	X
<i>Theristus</i>	X	-	-	X	-
<i>Tricoma</i>	-	X	-	-	-
<i>Viscosia</i>	-	X	-	-	-

	COLD SEEPS:		HYDROTHERMAL VENTS:		
	AC	AT	MB	BF	SP (MAR)
Copepoda					
<i>Ameira</i>	X	X	X	-	-
<i>Ameiridae spec.</i>	X	-	-	-	-
<i>Amphiascella</i>	X	-	-	-	-
<i>Amphiascus</i>	-	-	X	-	-
<i>Aphotopontius</i>	-	-	X	X	X
<i>Archesola</i>	X	X	-	-	-
<i>Argesthidae spec.</i>	-	X	-	-	-
<i>Bathylaophonte</i>	-	-	-	X	X
<i>Bradya</i>	X	-	X	-	-
<i>Breviconia</i>	X	-	-	-	-
<i>Calanoida gen. 1</i>	X	X	-	-	-
<i>Ceuthocetes</i>	-	-	X	X	-
<i>Cletodidae spec. 2</i>	X	-	-	-	-
<i>Cyclopina spec.</i>	-	X	-	-	-
<i>Delavalia</i>	X	-	-	-	-
<i>Diosaccinae</i>	-	-	X	-	-
<i>Ecbathyrion</i>	-	-	X	X	-
<i>Enalcyonium</i>	-	X	-	-	-
<i>Erebonaster</i>	X	-	-	-	-
<i>Exrima</i>	-	-	-	X	-
<i>Halectinosoma</i>	-	-	X	X	X
<i>Laophontidae gen. 1</i>	-	X	-	-	-
<i>Laophontidae gen. 2</i>	-	X	-	-	-
<i>Mesochra sp. nov.</i>	X	X	-	-	-
<i>Metis ignea</i>	-	X	-	-	-
<i>Microsetella</i>	X	-	-	-	-
<i>Miraciidae gen.</i>	-	X	-	-	-
<i>Miraciidae spec. 4</i>	X	-	-	-	-
<i>Miraciidae spec. 5</i>	X	-	-	-	-
<i>Miraciidae spec. 6</i>	X	-	-	-	-
<i>Nilva</i>	-	-	X	X	-
<i>Psammis longipes</i>	-	X	-	-	-
<i>Pseudobradya</i>	X	X	-	-	-
<i>Rhogobius</i>	-	-	X	X	-
<i>Rimipontius</i>	-	-	-	-	X
<i>Scotoecetes</i>	-	-	X	X	-
<i>Strongylacron sp. nov.</i>	-	X	-	-	-
<i>Stygiopontius</i>	-	-	X	X	-
<i>Tetragoniceps</i>	-	-	X	-	-
<i>Tisbe spec. 1</i>	X	X	-	-	-
<i>Uptionyx</i>	X	X	-	-	-
<i>Xylora bathyalis</i>	X	X	X	-	-
Ostracoda					
<i>Ambocythere</i>	-	X	-	-	-
<i>Krithe</i>	-	X	-	-	-
<i>OstracodaBuckfield</i>	-	-	-	X	-
<i>Polycopetta</i>	-	-	X	-	-
<i>Thomontocypris</i>	-	-	X	-	-
<i>Typhlocythere sp.</i>	-	X	-	-	-
<i>Xestoleberis sp.</i>	X	-	-	-	-
<i>Xylocythere</i>	-	X	X	-	-
Halacarida					
<i>Copidognathus sp.A</i>	X	X	-	-	-
<i>Lohmannella</i>	-	-	X	-	-
unidentifiable Halacarid	-	-	-	-	X
Tanaidacea					
<i>Pseudotanaids</i>	-	X	-	-	-
Tardigrada					
<i>Tardigrada</i>	X	-	-	-	-
Total	59	58	27	20	12

8.2. Figures

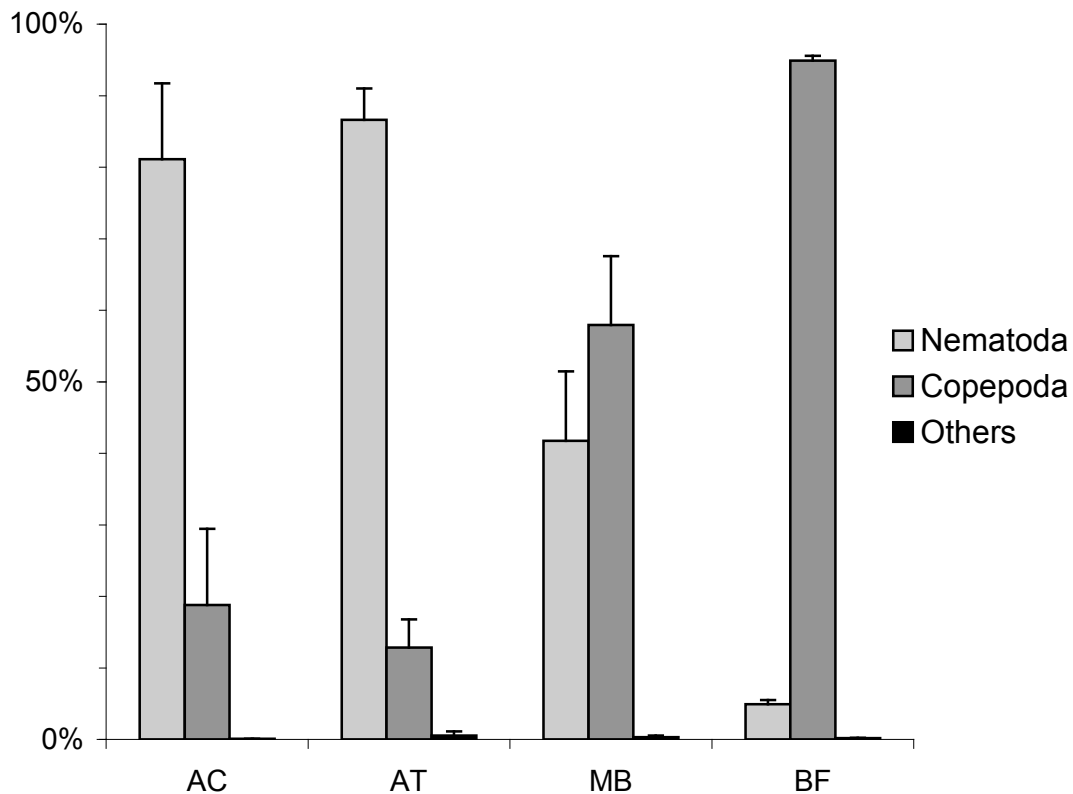


Fig. 1. Mean relative abundances of the meiobenthic community main taxa without nauplii larvae. Cold seep samples, Alaminos Canyon (AC_1-3), and Atwater Valley (AT_1-3) and hydrothermal vent samples, Mussel Bed (MB_1-3) and Buckfield (BF_1-3).

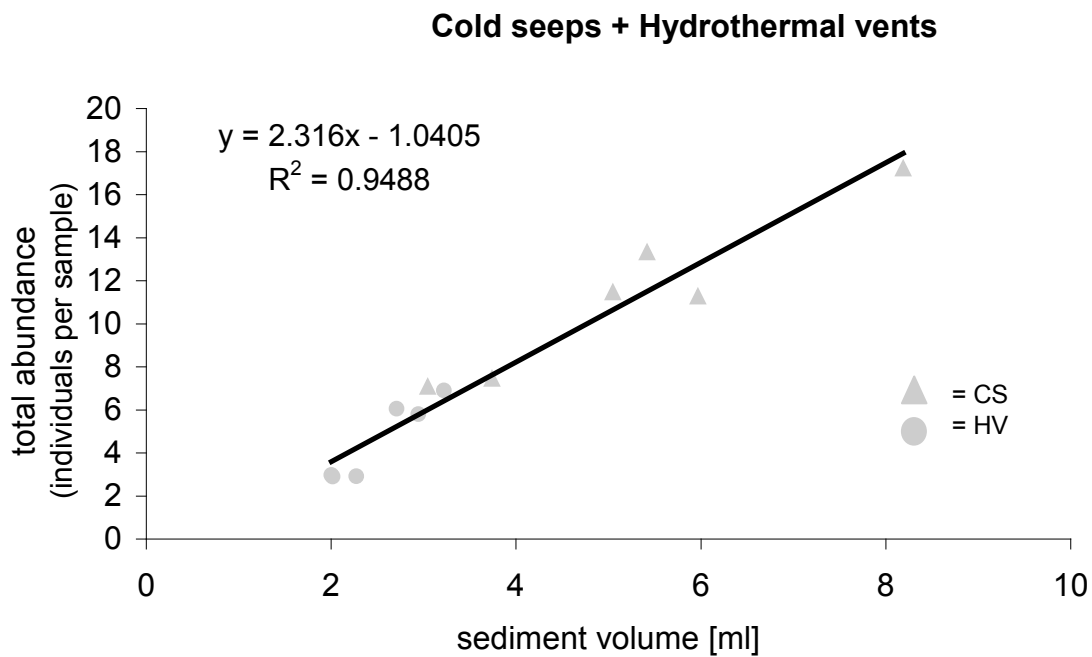


Fig. 2. Spearman correlation of sediment volume [ml] and total abundance [Individuals per sample] of six cold seep (AC_1-3; AT_1-3) and six hydrothermal vent samples (MB_1-3; BF_1-3).

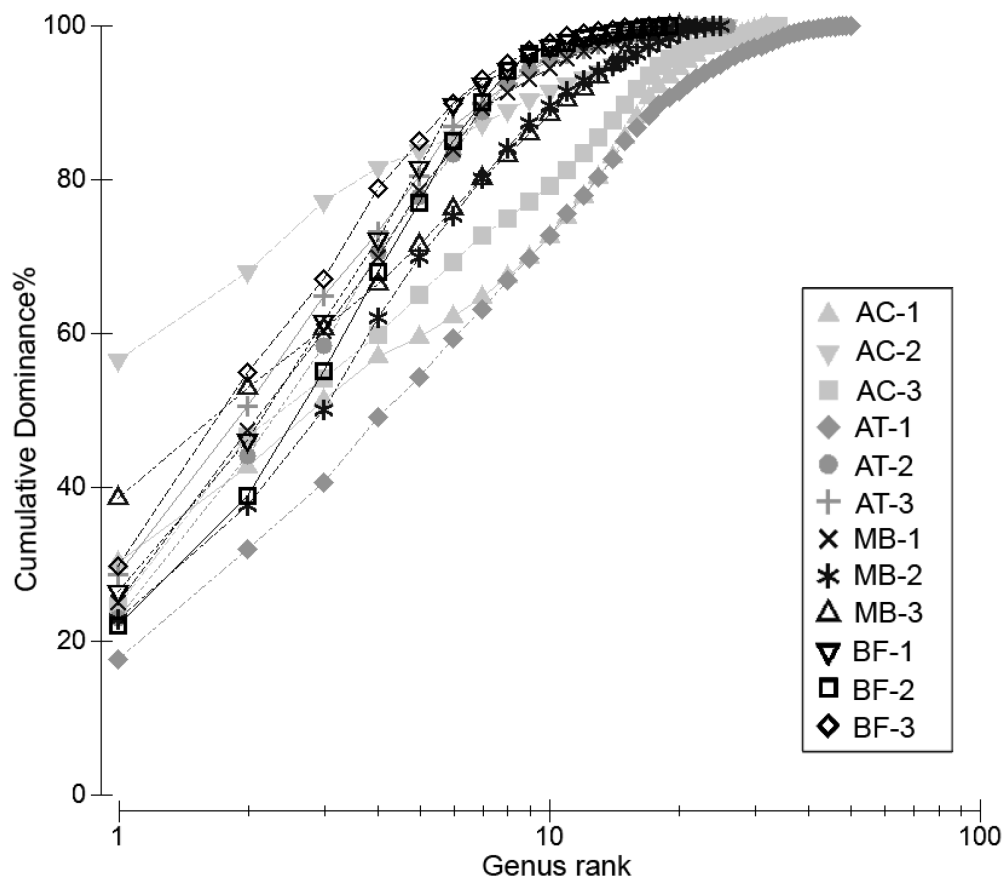


Fig. 3. K-dominance curves for six cold seep (AC_1-3; AT_1-3) and six hydrothermal vent samples (MB_1-3; BF_1-3).

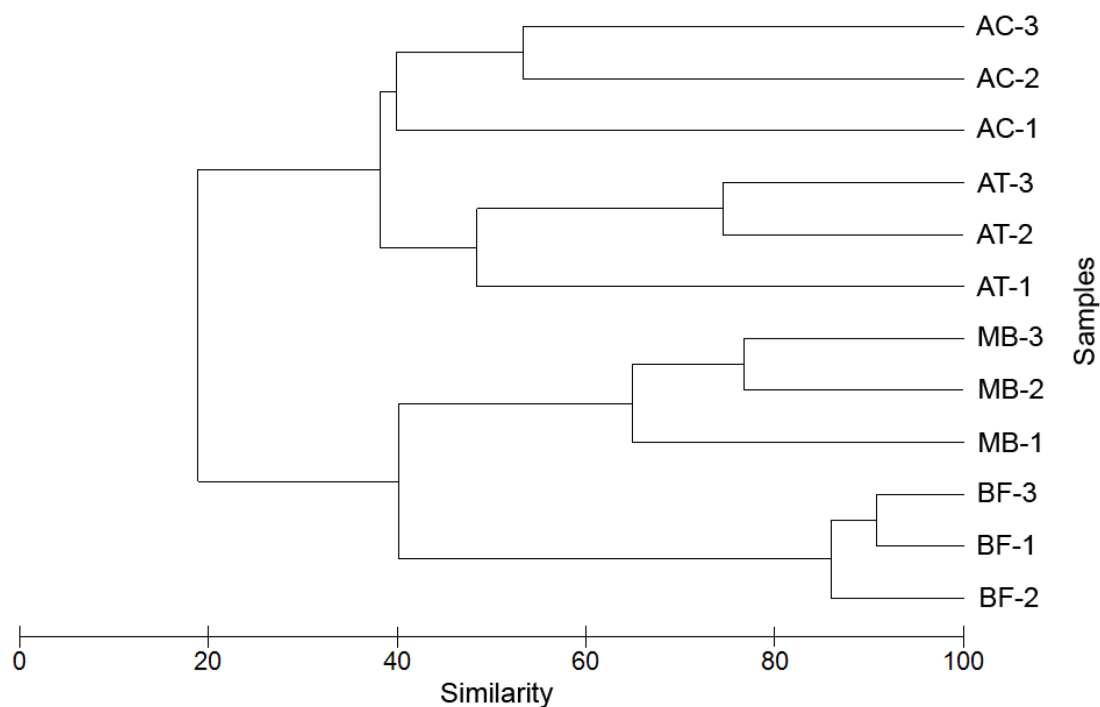


Fig. 4. Hierarchical Cluster Analysis based on Bray Curtis similarity values of six cold seep (CS) samples, three of Alaminos Canyon (AC_1-3) and three of Atwater Valley (AT_1-3), and six hydrothermal vent (HV) samples, three of Mussel Bed (MB_1-3) and three of Buckfield (BF_1-3).

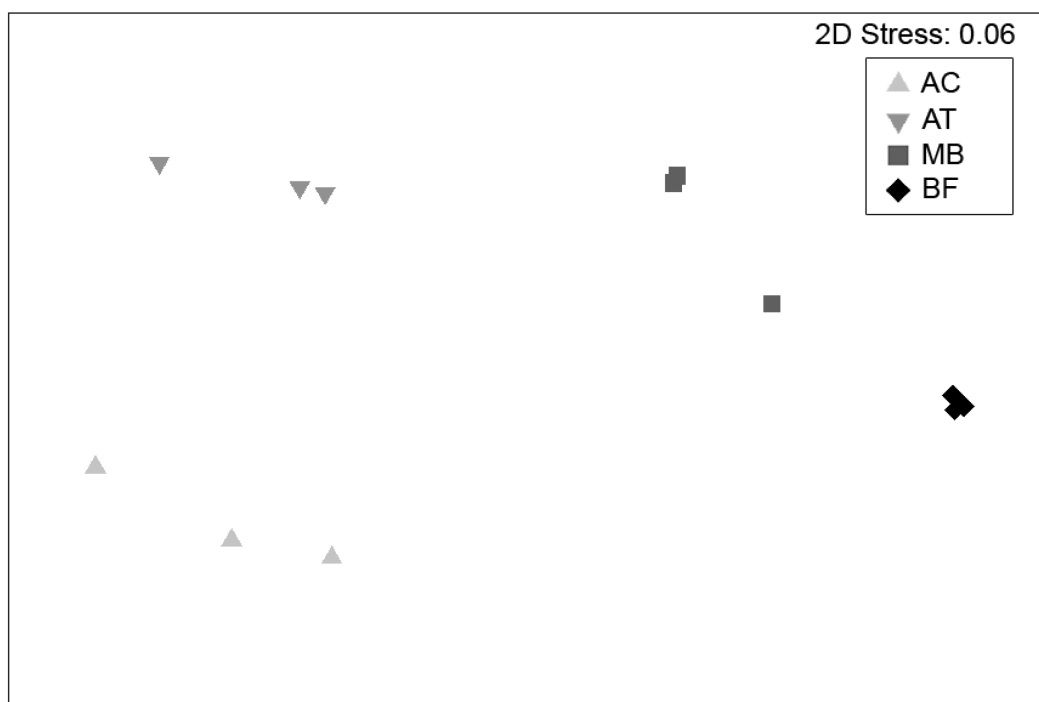


Fig. 5. Multidimensional scales (MDS) on site level for cold seep sites (AC_1-3; AT_1-3) and hydrothermal vent sites (MB_1-3; BF_1-3) in a 2-dimensional view.

9. Zusammenfassung deutsch

Für diese Studie der mit Muschelbänken assoziierten permanenten metazoischen Meiofauna wurden insgesamt 6 Proben, je 3 Proben zweier verschiedener Standorte der kalten Quellen in einer Tiefe von ca. 2100 m bis 2700 m (Alaminos Canyon und Atwater Valley) im Golf von Mexiko gesammelt. Die Muscheln der beiden Standorte waren Arten der Gattung *Bathymodiolus*. Die Untersuchung der Proben hat ergeben, dass das Gemeinschaftsmuster der Meiofauna an beiden Standorten trotz ihrer geografischen Distanz von ca. 635 km in Bezug auf ihre Diversitätsindizes und ihre relativen Abundanzen gleich war. Auch die verschiedenen Abundanzen zeigten statistisch keinen Unterschied. Das gleiche Gemeinschaftsmuster der Meiofauna beider Standorte, setzt sich jedoch je Standort aus verschiedenen Gattungen zusammen. Die Proben zeigen standortadäquate hierarchische Clusterbildungen. Auch die vorkommenden Muschelgattungen mit ihren artspezifischen Bakteriensymbiosen können Rückschlüsse auf hierarchische Clusterbildung der Meiofauna zulassen. Desweiteren wurden beide Standorte der kalten Quellen mit 2 Standorten der heißen Quellen des ostpazifischen Rückens verglichen. Die Daten der bereits publizierten Arbeiten (Gollner *et al.*, 2010b; Zekely *et al.*, 2006) wurden für diese Studie neu berechnet, um einen Vergleich auf Muschel assoziierter permanenter Meiofaunaebene durchzuführen. An den Standorten der heißen Quellen kamen ebenfalls Muscheln der Gattung *Bathymodiolus* vor. Festzustellen war, dass sich auch zwischen kalten und heißen Quellen ein gleiches Gemeinschaftsmuster zeigte. Zusätzlich zur standardadäquaten hierarchischen Clusterung zeigten sich zwischen den Proben innerhalb eines jeden Standortes bei den kalten Quellen weniger Ähnlichkeiten verglichen zu heißen Quellen. Betrachtete man beide Standorte der kalten Quellen zueinander, zeigte sich hingegen der gleiche Grad an Ähnlichkeit wie beide Standorte der heißen Quellen zueinander. Beim Vergleich zwischen kalten und heißen Quellen zeigte sich, dass das gleiche Gemeinschaftsmuster, aus verschiedenen Gattungen zusammensetzt war, was sogar eine Dominanzverschiebung auf Großtaxaebene zur Folge hatte. Denn bei heißen Quellen dominierten die Copepoden vor den Nematoden. Insgesamt wurden bei den kalten Quellen 87 Gattungen gefunden, jedoch neue Gattungen bis auf den Nematoden aff. *Subsphaerolaimus* wurden nicht entdeckt. Bei den heißen Quellen fand man nur 32 Gattungen, bei denen die ventspezifische Copepodengattung der

Dirivultidae die dominierende war. Aufgrund der ähnlichen Gemeinschaftsmuster der Muschel assoziierten permanenten Meiofauna, kann man davon ausgehen, dass gleiche Umweltbedingungen zwischen Muschelbänken der kalten und heißen Quellen vorherrschen. Dies bedarf jedoch künftig eingehenderer Untersuchungen.

10. Danksagung

Meiner Diplomarbeitsbetreuerin Monika Bright möchte ich danken, da sie mir den Blick für das Wesentliche geschärft, mir die Charakteristika des wissenschaftlichen Arbeitens nahe gebracht und mir die Teilnahme an einer außergewöhnlichen und faszinierenden Forschungsreise ermöglicht hat. Ebenso an Scott Nooner einen Dank, der mir die Möglichkeit gegeben hat, an einem U-Boot Tauchgang teilzunehmen und an Horst Felbeck, der auf seinen Tauchgang-Platz verzichtet hat, um mir diese phantastische Erfahrung zu schenken. Außerdem möchte ich meinen lieben Studienkollegen und -kolleginnen danken, besonders Laura, Renate und Tina, welche mir durch ihre fröhliche Art die Diplomarbeitszeit versüßt haben, und all den guten Seelchen der neuen und alten Meeresbiologieabteilung. Des Weiteren danke ich meinen Chorfreunden für die verbrachte fröhliche Zeit, die mich auch über schwierige Phasen hinweggetröstet hat. Allen, die mir sonst geholfen haben, danke ich von ganzem Herzen. Mein größter Dank jedoch gilt meiner Familie und meinem Freund Harald, welche alles getan haben und tun, um mich zu unterstützen, mir den Rücken zu stärken und mir Kraft zu geben. Jeder von euch hilft mir auf seine ganz besondere Weise. Ohne euch hätte ich das nicht geschafft!

11. Curriculum Vitae

Personal Information:

Name: Nora Nikolov
Date of Birth: 8th of May 1980
Place of Birth: Blagoevgrad / Bulgaria
Nationality: Austrian
Family status: Single



Education:

- 1999 – date: Study of Biology (Zoology), University Vienna
with main focus on Marine Biology
- Master thesis: “Community analysis of permanent metazoan meiofauna associated with mussel beds – a comparison of deep sea cold seeps and hydrothermal vents”
- 1994 – 1999: High school (BRG) Unterberggasse, Vienna
- High school certificate of Unterberggasse, Vienna (5-year special class for serious athletes)
- 1990 – 1994: High school (BRG) Vereinsgasse, Vienna

Scientific Expedition:

Dez.2009/Jän.2010 – Expedition with the research vessel *R/V Atlantis* along the East Pacific Rise from Mexico to Costa Rica. To explore hydrothermal vents, and having a submersible (Alvin) dive to the deep ocean floor in about 2600 m.

Publication:

2010 – Bright M., Plum C., Riavitz L.A., Nikolov N., Martinez Arbizu P., Cordes E.E., Gollner S. 2010. Epizooic metazoan meiobenthos associated with tubeworm and mussel aggregations from cold seeps of the northern Gulf of Mexico. *Deep-Sea Research II*: 57: 1982-1989

Poster presentation:

2009 – Bright M., Plum C., Riavitz L.A., Nikolov N., Martinez Arbizu P., Cordes E.E., Gollner S., 4th International Symposium on Chemosynthesis Based Ecosystems – Hydrothermal vents, seeps and other reducing habitats, 2009 Okinawa, Japan

Special Skills:

- Language: German - Native proficiency (written and spoken),
Bulgarian - Native proficiency (spoken, cyrillic reading),
Englisch - Fluent (written and spoken),
French and Spanish - Basic knowledge
- EDV: Windows 98 til windows 7 inkl. Microsoft-Office-Package
Adobe Photoshop + Illustrator, Corel Draw,
HTML+CSS basic knowledge
Various specialized software,
GIS basic knowledge
- Other: Typewriting (Touch typing), Driving licence (B),
Diving licence (Paddy + SSI), SCUBA diving, underwater
fieldwork
On shipboard labwork
Aerobic Trainer Diploma
Swim coach

Biological Practice:

- 2009 – Expedition along the East Pacific Rise from Mexico to Costa Rica, on shipboard labwork and submersible dive
- 2009 – Training to determine nematodes in Belgium at the University of Ghent /Belgium
- 2008 – Coral reef course in Dahab, Sinai /Egypt
- 2007 – Marine biological field course on the Mediterranean fauna and flora, Center for Marine Research, Rovinj, Croatia
- 2006 – Muselatechnics, University of Vienna
- 2005 – Histology special practical course, Medical Univ. of Vienna
- 2004 – Electron microscopy and preparation technics, Univ. of Vienna
- 2003 – Identification course for stony Corals, Univ. of Vienna
- 2001 – Identification course for Water beetles, Museum of Natural History, Vienna
- 2000 – Insect preparation course, Natural History Museum of Blagoevgrad /Bulgaria

Athletic Achievements:

- Multit-national swim champion (Child-, Junior-, General-)
- Summer 1993 athlete at the children's olympic games in Eindhoven (Holland), Swimming

Vienna, March 2011