MACROBENTHIC COMMUNITY STRUCTURE AND TOTAL SEDIMENT RESPIRATION AT

COLD HYDROCARBON SEEPS IN THE NORTHERN GULF OF MEXICO

A Thesis

by

CLIFTON CHARLES NUNNALLY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2003

Major Subject: Oceanography

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Major Subject: Oceanography

ABSTRACT

Macrobenthic Community Structure and Total Sediment Respiration at Cold Hydrocarbon Seeps in the
Northern Gulf of Mexico. (August 2003)
Clifton Charles Nunnally, B.S., Abilene Christian University
Chair of Advisory Committee: Dr. Gilbert T. Rowe

Cold seeps are areas of high biomass in the deep-sea, the impacts of these food-rich environments upon the sediment community is unknown in the Gulf of Mexico. The structure and function of benthic communities was investigated at food-rich and food-limited sites on the northern Gulf of Mexico continental slope. Cold seeps were richer in macrofauna densities and total sediment respiration, but were poorer in biomass and taxa diversity than normal slope communities. Decreased diversity is seen at most chemosynthetic communities and suggests a competition for resources. The spatial extent of these results at seeps is unknown and may be a localized, bioenhancement effect caused by seeping fluids.

This thesis is dedicated to Mom and Dad who never limited the scope of things that might be possible for me. My introduction to reading was voracious, I was never without a book and neither were they.   I wandered off to Alaska and the Bering Sea and their encouragement was considerable, even when they might have wished I stayed closer to home and on solid land. I have never had reason to doubt their unconditional love, and that has made all the difference.

ACKNOWLEDGEMENTS

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1. INTRODUCTION

The deep-sea benthos lives in a food-limited environment (Hessler and Sanders, 1967; Sanders and Hessler, 1969) that depends on the slow rain of particulate matter from the surface. The Gulf of Mexico along the slope and abyssal plain is a depauperate area because of low primary production in overlying waters (Rowe, 1996). The discovery of hydrothermal vents and cold seeps in the past 25 years has shown that the deep benthos can be supported by inputs of carbon that are not linked to the surface. In the Gulf of Mexico the discovery of brine seeps (Paull, et al., 1984) and hydrocarbon and methane seeps (Kennicutt, et al., 1985) have shed light on benthic communities that are not food-limited. These cold seeps have a surplus of usable carbon that is chemically derived from methane and hydrocarbons seeping up through fractures in the sediment/salt layer that characterizes much of the Gulf of Mexico basin (Brooks et al., 1987). The ecological forces that this exerts upon sediment infauna, is still not known with any certainty. The chemosynthetic communities that are associated with such seeps have been intensely studied (Kennicutt et al., 1988, Macdonald et al., 1990a, MacDonald et al., 1990b, Rosman et al., 1987, Sassen et al., 1993). Current studies at seeps focus on the larger megafauna such as mussels, clams and tubeworms. In particular they focus on the symbiotic relationship with chemoautotrophic bacteria. The little work on sediment infauna at seeps has shown that meiofauna and macrofauna communities in the western Pacific are greater in abundance than those in the food-limited benthos (Sibuet and Olu, 1998). Further work in shelf and slope settings along the Northern California slope showed only subtle changes between sediment infauna at seeps and those seen at non-seeps (Levin et al., 2000). Stable isotope data has shown that meiofauna and macrofauna at seeps have light $\delta^{13}C$ values (Levin and Michener, 2002; Werne et al. 2002). These same studies have been able to trace the flow of isotopically light carbon from the chemoautotrophs that uptake the seeping methane to the meiofauna and the macrofauna. The infaunal communities of cold seeps have been sampled worldwide but have yielded no definite conclusions as to how sediment communities function as an ecological unit at such an extreme environment. The general tendency has been to regard seeps as isolated fluxes that enhance the local benthic megafauna and the bacterial sediment community.

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This thesis follows the style and format of *Deep-Sea Research I*.

2. BACKGROUND

The ecological influence of cold seeps on the resident soft bottom benthos was compared to the known food-limited benthos in the deep Gulf of Mexico. Seeps outwardly appear to have only isolated impacts in the deep Gulf of Mexico, especially on the megafauna; upon studying the infaunal community composition some ecological impacts seen in the megafauna are present as well. The key faunal patterns associated with seeps are variation in total biomass and the abundance of organisms.

Sampling efforts attempted to determine the ecological impacts of excess available carbon created by a cold seep. The domain of influence is the area that is enriched by the unique properties of seeps. Within this area benthic fauna are hypothesized to be greater in size and number than similar fauna in the food-limited areas of the Gulf of Mexico. Increased particulate organic carbon (POC) flux would enhance local fauna making them distinct from the surrounding deep-sea (Duineveld et al., 2001). The two most noticeable faunistic changes are the high biomass and low diversity at seeps compared to the low biomass and high diversity away from seeps (Agard et al., 1993). Biomass and abundance are greater at seeps because there is more food for local fauna. Diversity is diminished at seeps because of increased competition for resources. The diversity among macrofaunal communities is diminished at seeps in the Pacific (Olu et al., 1996; Sibuet and Olu, 1998). The rates of sediment community oxygen consumption (SCOC) at seeps were measured at seep and non-seeps sites in the Gulf of Mexico. The total respiration of the sediment community is related to the total amount of particulate organic carbon in sediments available as a food source. Increased numbers of sediment metazoans and microbes should cause seep SCOC to be higher than SCOC rates in the food-limited benthos of the Gulf of Mexico.

In the Gulf of Mexico, seeps and their associated communities were first encountered in 1984 when brine seeps were discovered at the base of the Florida Escarpment (Paull et al., 1984). Hydrocarbon and methane seeps were later described in 1985 off the coast of Louisiana (Kennicutt et al., 1985). The seepage of methane and brine in the Gulf are unlike those found on margins of geological activity because they migrate vertically to the surface through salt related fractures in the Louann salt layer.

There are over 30 documented seep sites along the continental slope of the northern Gulf of Mexico that support chemosynthetic communities. The intent of my study was to determine what the structure and function of the macrobenthos was within the domain of influence of a seep, compared to food-limited, benthic communities. Is there a significant difference between population sizes at seeps and away from seeps? Is there a trend of greater biomass per individual at seeps? Are seep communities lower in species diversity? Changes in community structure and increased respiration should signal clear differentiation between macrobenthic communities at seeps and those away from seeps. These changes could possibly be exhibited in a gradient separating seep locales from the background benthic

communities where food is limited. At a seep, the sediment community should be characterized by high biomass and low diversity (Sibuet and Olu, 1998). Away from the seep, in the food-limited areas, biomass should be lower and species diversity higher. This property should be most noticeable in the faunal assemblages of the meiofauna and macrofauna. This property appears as a result of competition for resources. In an environment where sparse levels of food is the norm, an area of intense carbon input will exhibit decreased diversity because organisms that can utilize symbiotic relations will push out less suited species (Hardin, 1960, Haussmann, 1973). This is why animals feeding lower on the food chain, such as mussels and tubeworms (using symbiotic relationships with chemosynthetic bacteria), can out compete organisms adapted for sparse food resources. This competitive pressure for available resources is less in the food-limited benthos, and greater species diversity is seen there.

Increased abundance of meiofauna and macrofauna at seeps is also accompanied by a trend towards gigantism (Grassle and Morse-Porteous, 1987). Larger metazoans respire at a slower rate per unit biomass, while smaller metazoans respire faster per unit biomass. Since seep animals are larger in body size, the individual respiration per unit biomass should be lower than that of non-seep animals. Away from seeps, in food-limited communities, total SCOC should be less, but respiration per unit biomass would be greater.

Studies done in the Indian and Southern Oceans have shown that sediment community oxygen consumption (SCOC) decreases as water depth increases (de Wit et al. 1997; Duineveld et al., 1997; Heip et al., 2001). Here again, seeps mark a discontinuity in the expected characteristics of benthic habitats with depth (Smith 1978, Smith and Hinga 1983). Where respiration should be decreasing, seep areas have increased amounts of sediment respiration. Sediment community oxygen consumption has been shown as a reliable way to determine relative POC flux to the seafloor (Duineveld et al., 1997; Jahnke and Jackson, 1991, Rowe et al., 1997).

2.1. Biogeochemical Attributes

Seeps do not provide instantly usable carbon; food sources, other than the rain of POC, appear as complex, potentially toxic hydrocarbons diffusing up from reservoirs deep under the salt layer. Methane and hydrocarbons are then turned into life nourishing elements by microbial communities that live 1.) free in the water, 2.) in tissues of specialized benthic fauna, 3.) community forming surface mats, and 4.) in the sediment (Aharon, 2000, Brooks, 1987, Sassen, 1993). Four chemical processes are at the core of these changes: 1) methanogenesis (done by methanogens, 2.) anaerobic sulfate reduction (*Desulfavibrio*), 3.) aerobic oxidation of sulfide (*Beggiatoa*), 4.) aerobic oxidation of methane (done by methanotrophs)

(MacDonald et al., 1989; Martens et al., 1991; Sassen et al., 1993). All this is done within anoxic enclaves surrounded by oxygen-rich water (Aharon 2000).

Cold hydrocarbon seeps generate abundant food for benthic organisms because of a bacterial pathway that metabolizes methane and other hydrocarbons results with the production of hydrogen sulfide (Boetius et al., 2000; DeLong, 2000; Hansen et al., 1998; Hoehler et al., 1994). This occurs in a coupled reaction of anaerobic methane oxidation and sulfate reduction. A consortium of archaeobacteria, that oxidize methane, and bacteria, that reduce sulfate, work together to achieve this result.

$$CH_4 + SO_4^{2-} \rightarrow HCO_3^- + HS + H_20$$

These bacterial processes are mediated within the sediments. There are no pathways that can solely utilize methane as a substrate or use sulphate as a terminal electron acceptor. Dissolved inorganic carbon (DIC) in the form of carbon dioxide is then made available when $CaCO_3$ precipitates.

$$Ca^{2+} + 2HCO_3^- \rightarrow H_2O + CO_2 + CaCO_3$$
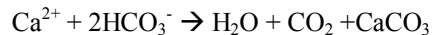
Chemoautotrophic bacteria that live at seeps, either in sediments or as symbionts use the available carbon dioxide as a carbon source for growth and reproduction (Weber and Jorgensen, 2002). This carbon is then converted to bacterial biomass, and from there it can enter the food web as organisms graze on this source of labile carbon within the sediments. Endosymbionts that live within tube worms and clams depend directly upon the oxidation of sulfide that is carried out during these coupled reactions.

Seeps create a gradient between reducing and oxidizing environments within the sediments. This occurs when reduced compounds like sulfides and methane go into oxic waters or where anoxia occurs in the benthic substrate (MacDonald et al., 1989). This is clearly visible in the sediment appearance, when viewed from a submersible, as a distinct change in the color; presumably this is where the sediment anoxia ends (MacDonald, personal communication). Hydrogen sulfide is both produced and consumed by biotic and abiotc processes in the hydrocarbon seep communities at a much higher rate than found in normal sediments (MacDonald et al., 1989).

The chemosynthetic communities associated with the seeps are closely related to the massive seepage of oil and gas through faults in the Louann salt layer (Paull, 1984). The result of this seepage is anaerobic, H_2S-rich sedimentary conditions. The amount of natural seepage of high molecular weight hydrocarbons may be a significant source of carbon to the deep Gulf of Mexico (Kennicutt et al. 1988). Such a contribution could be an important component of slope Ecology, because it means that the Gulf of Mexico benthos is not entirely dependent on the surface layer primary production. If seeps do provide an extra energy source for benthic communities in the Gulf of Mexico, what is the effective domain of influence that seeps have on the bottom surrounding them?

The majority of seep communities, scattered across the Gulf, can be directly related to the sub-bottom source of the hydrocarbons. The ephemeral distribution of fauna around seeps is a function of

variations in the flow of thermogenic and biogenic compounds over space and time (MacDonald et al., 1990). Even though seeps may be long lived (since the late Pleistocene 195-13 ka) (Aharon et al., 1997), their rate of flow and makeup of diffusive hydrocarbons and gases is subject to rise and fall. This can severely affect how the fauna in seep communities survive (as well as background fauna that are benefiting from seeps) (Roberts et al., 1990). Still, the amount of seafloor and benthos influenced by seepage is small in relation to the extent of the subbottom hydrocarbon system (Barry et al., 1996; MacDonald et al., 1998). The richness of sediments can be seen visually at cold seeps and the richness extends only a few meters beyond the seeping fluids (Aharon 2000, Hecker 1985).

2.2. Community Structure

Infaunal community analysis focusing on meiofaunal and macrofaunal abundance is a good tool for looking at the richness of a benthic community because these attributes have a positive linear relationship with the "burial" organic carbon flux (Sibuet et al., 1989). Relationships between abundance and the burial of carbon would be linear if biomass is dependant on POC flux to the sea floor, which decreases with depth (Carney et al., 1983). Increased burial of carbon, like the increased bacterial biomass associated with seeps, will enhance the surrounding fauna.

The faunal aggregations around seep sites are composed of organisms that are endemic to seeps and others drawn strictly because of the available food. Colonies of tube worms (Pogonophora) live around the diffusing gases and assimilate carbon with the help of bacterial symbionts that oxidize H_2S. Seep mussels also form dense patches near the seep efflux, utilizing their methanotrophic bacterial symbionts. Vesicomyid and lucinid clams assimilate carbon through H_2S oxidizing bacterial symbionts in their gills. Also commonly associated with seep communities are bacterial mats of *Beggiatoa* that oxidize H_2S into elemental sulfur granules (Sassen et al., 1993). These fauna flourish because of their tolerance to toxic sulfides, aromatic compounds and hypersaline conditions (MacDonald et al., 1990).

This functional assemblage of organisms is high in biomass, but has low species diversity for the deep-sea. Special adaptations to living in toxic environs, and the ability to harvest resources from normally unusable chemical compounds would give endemic seep fauna a competitive advantage over other species. This kind of competitive exclusion could also been seen in the sediment infauna. High biomass and low species diversity characterize the community structure of the infauna near a seep (Spies and Davis, 1979). Seeps are likely to have a similar macrofaunal community structure in relation to the surrounding benthos, but should have a greater abundance of deposit feeders that can utilize the buried carbon in the sediments better than filter feeders. The abundant carbon in the sediments is largely

composed of the increased numbers of bacteria at the seep site. The remainder is buried carbon that is too great to be utilized by the fauna feeding out of the water column.

Seep populations should be functionally different from those populations that are a part of the surrounding food-limited communities. Shifts in the dominant type of feeders, from filter feeders to infauna that specialize in deposit feeding, are seen at seeps (Davis and Spies, 1980). This functional difference lends to Hypothesis 2, which states "Diversity among macrofaunal taxa at seeps will be less at similar depths than the high levels of diversity seen in the surrounding food-limited benthos away from seep derived carbon input." Since the majority of carbon at seeps is heavily dependant on bacterial processing of raw materials, carbon deposits are greatest in the sediments where the bacteria are most abundant. This gives a functional advantage to deposit feeding meiofauna and macrofauna. The closer to the seep efflux, the greater the amount of carbon buried in the sediments, and this can potentially cause decreased species diversity because filter feeders cannot utilize the resources as well as the deposit feeders. Spies and Davis (1979) showed that seeps have greater abundances of macrofauna than comparable non-seep sites. Their study also showed that deposit feeders, especially oligochaetes and maldainid polychaetes, dominate.

Davis and Spies (1980) in their study of seep and non-seep populations within the Santa Barbara basin found that both groups actually belong to a single community within a defined physical boundary. This is in relation to a definition by Gray, (1974) that communities, especially in soft-bottom marine systems, are "continuously overlapping populations which become more extensive with increased environmental stability." In this case, cold seeps occurring in the Gulf of Mexico have high physical and biological stability, and therefore would be independent populations within the extensive benthic communities in the deep-sea. The challenge then lies in defining the limits of seep populations that coexist within the deep-sea community. These limits should lie within the confines of increased biomass/abundance, greater total respiration, and altered community structure.

2.3. Seeps as Oases

Chemosynthetic communities are commonly thought of as oases in the deep-sea. They are unique communities where increased faunal biomass surrounds large effluxes of inorganic and organic carbon compounds (Carney, 1994). Seeps indeed are anomalies in trends of biomass and SCOC with depth, both higher than the normal observed values for their depth ranges. Most organisms solely related to seeps are spatially restricted to a certain distance from the diffusive carbon media. Seeps provide resources for increased growth and biomass that are the sole reason for any such large numbers of animals to appear in these areas. Tube worms and seep mussels must remain within the defined confines so that

their symbionts can be supplied with materials for reduction and oxidation. Part of the oasis analogy is that the majority of the associated fauna is endemic to chemosynthetic sites. Specifically, they cannot be found in habitats that do not have a direct reducing or oxidizing capacity for their bacterial symbionts. If this were true, it would tend to explain the physical appearance of change in the sediment. It also suggests that any gradient based on faunal abundance, starting from the seep and moving outward, could be very sharp.

Even though seeps provide unusual trends in slope biology, they are also subject to bathymetric and geographic gradients (Carney, 1994; Sibuet and Olu, 1998). Faunal gradients should also be seen within the structure of chemosynthetic fauna as it relates to the oasis analogy, where fauna will be arranged due to a competitive *Nature* because there is a localized abundance of an otherwise rare resource (Carney, 1994). Within seeps, gradients in biomass and species diversity are visible. Tubeworms, clams and mussels tend to utilize the interior of the seep more efficiently than any other animal found at seeps. They are the dominant organisms in terms of biomass, using their decided advantage of having bacterial symbionts to out compete other deep-sea fauna. The extreme advantage that they possess makes the species diversity within the interior of the seep incredibly low.

Even though some fauna are not closely associated with the inner plume of rising methane, this does not refute the oasis analogy. Gradients in faunal biomass would extend the effective range of advantageous carbon flow further out from the "oasis." So in this research, by trying to define an area of seep influence, I am looking for the outer edges of this deep-sea "oasis." Whether or not these domains of influence overlap between seeps is also an important aspect to consider within this research. Areas of increased benthic biomass, that overlap along the slope could significantly impact the perceptions of how rich the benthic communities of the continental slope in the Gulf of Mexico are. These areas of enriched biomass would mean that the background fauna should behave differently than normal isolated, food-limited, benthic communities. As along many continental margins where POC flux is a lateral transport of material, the enhanced community structure associated with seeps may also pass from seeps radially outward to the surrounding benthos.

2.4. Competitive Exclusion

Competitive exclusion occurs where any species is absent due to an advantage gained by another species (Gause, 1934; Hardin, 1960; Volterra, 1931). Seeps are a good example of how species usually absent from the food-limited benthos have gained a competitive advantage when carbon is both abundant and in a complicated form. Being able to withstand toxic and anoxic conditions, and then being able to oxidize methane or sulfur as a food source gives chemosynthetically endemic fauna an advantage over

other benthic organisms that would otherwise occupy their space in the community structure of seeps (Barry et al., 1996). A clear example of exclusion within a seep system due to an advantageous adaptation can be seen in chemosynthetic megafauna. At seeps, mussels and tubeworms are arrayed in a pattern of competition, with tubeworms prevailing in abundance where hydrogen sulfide is present, while mussels tend to cluster in areas of thermogenic methane (Sassen et al., 1993).

Biological demands of seeps are so great that oxidizing agents are depleted when input is high relative to burial, leading to a depleted supply of oxygen to the sediments. These conditions provide an advantage for organisms capable of anaerobic metabolism (Carney 1994). This is where species diversity would decline due to competitive exclusion. Even though there may be plenty of carbon for energy and growth, its unattractive form makes its use rather exclusive.

Species diversity is greater at depth for benthic fauna (Grassle and Maciolek, 1992; Hessler and Sanders 1967; Sanders, 1968), but for chemosynthetic communities, endemic faunal diversity decreases with depth (Sibuet and Olu 1998). This opens up more room for outside organisms to colonize around a seep (Harger, 1972; Hauspie and Polk, 1974, MacArthur and Levins, 1964). Seeps do not lose as much diversity as hydrothermal vent systems, most likely because there is no associated temperature barrier for organisms and the fluid flow of seeps is longer lived and more constant. Since the working hypothesis for diversity in the deep-sea is long, term geologic stability, then the long-lived *Nature* of methane seeps should also provide for greater diversity than that found at relatively short-lived hydrothermal vents (Dayton and Hessler, 1972; Gray, 1977). Is the stability of seeps great enough so that diversity can approach the background benthos? Even though some seep communities can be dated to two hundred years (Bergquist et al., 2000) this time period is not long enough to outlast the results of competitive exclusion pressure.

Bacterial mats of *Beggiatoa* spp. are a component that allows the sediment infauna to benefit from the chemical energy generated at hydrocarbon seeps. *Beggiatoa* is a sulphide oxidizer that utilizes the high levels of H_2S created at seeps as a chemical precursor for energetic reactions. A trophic pathway linking these bacterial mats with nematodes and thus other infauna has been shown in studies done with seeps along the California coast (Spies and DesMarais, 1983). *Beggiatoa* forms dense mats near seeps and provides an abundant source of food for deposit-feeding sediment infauna. These bacterial mats are integral in the trophic enrichment of seeps since they can degrade hydrocarbons and oxidize sulphide (Spies and DesMarais, 1983).

Meiofauna communities have rarely been studied at seeps, and as of yet no persistent evidence can determine how they benefit from seep resources. One important function that meiofauna may serve at seeps is the trophic link that makes bacteria available to the larger food web (Montagna and Spies 1985, Montagna et al., 1989). Research outside Sagami Bay at cold seep sites has shown no change in

meiofaunal abundance between seep and control sites (Shirayama and Ohta, 1990). Meiofauna densities are also found with some variance within bacterial mats at seeps (Montagna and Spies, 1985). Parallel research done in the northern Barbados prism has shown increases in meiofaunal abundance by two orders of magnitude from control to seeps (Olu et al., 1997). Meiofauna communities dominated by deposit feeders have been found to be denser than those at nearby non-seep sites (Montagna et al., 1989).

2.5. Sediment Community Oxygen Consumption

Another indicator of seep influence on the surrounding benthic food-limited community should be found in the respiration of the infauna or the sediment community oxygen consumption (SCOC). Oxygen consumption increases as usable carbon input increases (Hansen and Blackburn, 1992). This is because the input of usable carbon also increases the biomass, and with a larger total biomass a larger total respiration is also expected. Bacterial respiration as a percent of total SCOC should be greater at seep sites than non-seep sites. This is because the presence of methane and hydrocarbon based communities are dependant on bacterial consumption and production. Bacterial respiration will also be greater in anoxic conditions that occur within the sediments of seeps (Brooks et al., 1987, Sassen et al., 1993).

The most telltale gradient to evaluate would be increase or decrease in respiration per individual (Childress and Mickel, 1985). Macrofauna increase not only in abundance but also in mean size close to seeps (Olu et al., 1997). Macrofauna mean size correlates to proximity to a seep when compared to macrofauna from control sites (Sibuet and Olu, 1998). Meiofauna mean size has also shown the same correlation (Powell et al., 1986). As the size of an organism increases, the respiration rate decreases. Thus, greater size per individual at seeps in meiofauna and macrofauna would also lead to a decreased respiration rate per individual. A gradient along these lines would have the largest total infaunal respiration and lowest respiration per individual at the seep, and total respiration would decrease with distance, while respiration per individual would increase with distance.

3. HYPOTHESES TESTED

3.1. Abundance

Hypothesis 1: Total abundance of macrofauna should be greater at seeps than in the food-limited benthos away from seep derived carbon input.

Null Hypothesis 1: Total abundance of macrofauna at seeps will be the same at similar depths as the food-limited benthos.

The total number of organisms near a seep should be elevated because there is an increased supply of carbon that can be used as a food source. This increased supply is primarily due to the chemoautotrophic bacteria that live in association with some of the larger megafauna and within the sediments. These bacteria can utilize the carbon from methane and other hydrocarbons to provide energy for growth and respiration. The increased amount of bacteria in the sediments and the water column provide an additional source of food for the benthos. Increased food should lead to a greater amount of macrofauna in the sediment. The background food-limited benthos does not have access to a secondary carbon source and cannot support an increased number of organisms.

3.2. Biomass

Hypothesis 2: Biomass at seeps should be greater than in the food-limited benthos away from seep derived carbon input.

Null Hypothesis 2: Biomass of the macrobenthos at seeps will be the same at similar depths in the food-limited benthos.

Just as the total number of macrofauna in the sediments surrounding seeps should be greater, so should the biomass incorporated in the macrobenthos be larger than that of the food-limited benthos. Since these organisms have access to a larger food supply, they should be able to grow larger than their food-limited counterparts. Since the abundance of macrofauna should be larger at seeps; more, larger organisms will cause the total carbon per square meter to be greater than that of the food-limited benthos.

3.2. Diversity

Hypothesis 3: Diversity among macrofaunal taxa at seeps will be less at similar depths than the high levels of diversity seen in the surrounding food-limited benthos.

Null Hypothesis 3: Species diversity at seeps will be the same at similar depths in the food-limited

benthos.

Species diversity in the deep-sea is high, but at chemosynthetic communities it is diminished due to competitive exclusion. Animals that are better suited to living in a slightly toxic, but food rich environment, will be able to out-compete other animals for space and food. Animals that can utilize symbiotic relationships with bacteria have a further advantage because the bacteria with which they live with can more effectively use the methane and other form of inorganic carbon found at seeps. This property depends upon competitive pressure as a driving force. Where fluid flow is the greatest and the highest levels of chemical material seeps out, animals especially adapted for such extreme situations will be the most dominant. Many times only a single species will be found near the most active seepage. Away from a seep these competitive pressures will lessen, and the benthos will regain its high species diversity.

The deep benthos is food-limited, but it also is characterized by high species diversity (Hessler and Sanders, 1967). This diversity is a result of low competitive pressure that is associated with being food-limited. Chemosynthetic communities do not have as much diversity because their surplus of carbon sources makes competitive pressure greater (Hardin, 1960).

3.3. Sediment Community Oxygen Consumption

Hypothesis 4: Sediment community oxygen consumption (SCOC) will be higher at seeps at similar depths than the food-limited benthos away from seep derived carbon input.
Null Hypothesis 4: Sediment community oxygen consumption (SCOC) at seeps will be the same at similar depths in the food-limited benthos.

Ecological differences that exist based on sediment community oxygen consumption (SCOC) occur both when looking at total respiration rates and also in individual respiration rates per unit body mass. Greater values of respiration near the seep are directly related to higher biomass. SCOC can be used to estimate what is occurring within a benthic community. SCOC is a measure of the total remineralization rate of organic carbon in sediments (Pamatmat, 1971; Piepenburg et al., 1995). SCOC can also be used to measure and compare fluxes of POC to the seafloor in different areas. Seeps are areas of increased organic carbon flux, so the total respiration within the sediment is an excellent proxy of the total supply of organic substances. Intense mineralization of carbon also occurs at seeps, both by aerobic and anaerobic pathways. Using SCOC rates to determine the ecological properties of seeps on the benthos is useful because it not only relates the activity of sediment infauna but also the relative carbon flux to a defined area.

4. METHODS

4.1. Selection of Seep and Non-Seep Sites

This research tests ecological parameters of the cold hydrocarbon seep macrobenthos against those of the food-limited benthos in the northern Gulf of Mexico. The community structure and function of cold seep and food-limited communities was sampled within similar depth ranges. Two seep sites, Garden Banks 425 (GB 425) and Green Canyon 234 (GC 234), were sampled during the deployment of the Johnson Sea-Link in association with the Shelf and Slope Experimental Taphonomic Initiative (SSETI). Information about the food-limited macrobenthos was gained during the Deep Gulf of Mexico Benthos project, which sampled benthic communities in the Gulf of Mexico from 300 to 3700, meters water depth. Seeps GB 425 and GC 234 lie at 570 and 549 meters, water depth, respectively. DGOMB sites similar in depth to these seep sites were used to compare ecological parameters of the macrobenthos, and are referred to as "non-seep" sites. Most of these sites are extremely food-limited and thus provide data as control sites to test the hypotheses that are outlined in this proposal. A map of all DGoMB sites, Garden Banks 425 and Green Canyon 234 is shown in Figure 1.
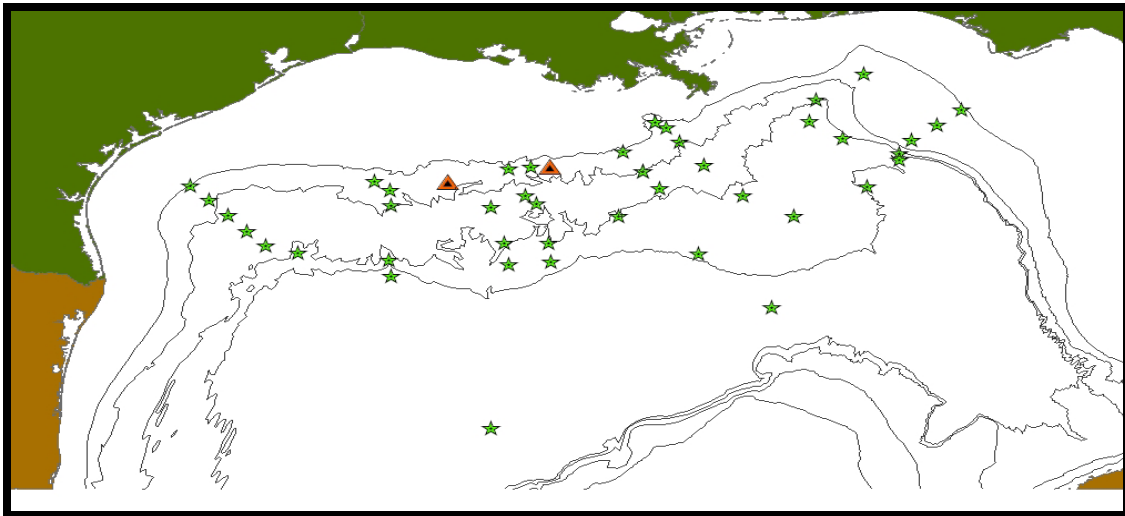

Fig. 1. Map of study sites

A map of the Northern Gulf of Mexico showing DGoMB sites (stars) and seep sites (triangles).

4.2. Sampling Strategy

Data for the evaluation of community structure came from two primary sources: ship-based box cores taken during the DGoMB project and submersible push cores taken during the SSETI 1995 cruise. Cores taken from Cruise 1 of DGoMB will be used to evaluate the food-limited benthos in the Gulf of Mexico (Rowe et al., 1999). Sites sampled with the GOMEX box core were done in replicate, with each station sampled five times. Cores taken during Cruise 2 of DGoMB approximately two miles from the Bush Hill seep were also used to try and set a limit on the distance of Bush Hill's trophic enrichment. Push cores taken in 1995 by the Johnson Sea-Link (JSL) research submersible while deployed at two seeps, GC 234 and GB 425, during the SSETI Gulf of Mexico cruise, were used to evaluate the macrofaunal abundance at seep sites.

The large box core deployed from the deck of the R/V Gyre covers an area of 0.1725 m^2 and the macrofauna and overlying water are washed on a 300μm sieve and then sorted to major taxonomic group. The taxonomic groups are then classified to the species level when possible and evaluated for biomass. The push cores taken by the JSL have an area of 0.0053 m^2 and are also sieved on a 300μm sieve and sorted into major taxonomic groups. From these samples, biomass, abundance, species diversity, richness and other measures of community structure are gained. Batch Micro Incubation Chambers (BMIC's) were taken from six DGoMB sites and were used to determine abundance and diversity. The BMIC's were also used to determine macrobenthic biomass from food-limited sites. DGoMB study sites were sampled by the box core five times. SSETI push cores were taken in pairs.

4.3. Sediment Biological Samples

Density, biomass, abundance and general sediment community structure were determined using box cores, BMIC's and push cores. The samples came from the GOMEX box corer with macrofauna samples taken from the top 15 centimeters within the core. Each box core was also subsampled for meiofauna, bacteria, heavy metals, biogeochemistry and *Geology*. These were taken primarily as a structure-sampling tool for the MMS funded DGoMB project. The subsamples are used to provide background data for food-limited benthic communities at all depths in the Gulf of Mexico. Push cores taken using the Johnson Sea-Link submersible while deployed at sites during the SSETI project in 1995 are the basis of the sediment community seep samples. These small push cores were sampled for macrofauna only. All samples were sieved on a 300 μ sieve and sorted to major taxonomic groups, which will eventually be identified to the species level.

Biomass for food-limited sites was determined by measuring the volumetric dimensions of the macrofauna sorted from sediment used in BMIC's (Batch Micro Incubation Chambers). These biovolumes were then converted to wet weights using a factor of 1.2 for seawater density. The wet weights were then converted to carbon weights by applying taxa-dependent conversion factors that were determined by Rowe et al. 1993.

4.4. Sediment Community Oxygen Consumption

Sediment community oxygen consumption data were gained from *in situ* benthic flux chambers, deployed from a benthic lander and from historical data from the Gulf of Mexico. The deploys benthic respiration chambers are capable of measuring oxygen consumption within the sediment while on the sea floor. The benthic lander was deployed in the Gulf of Mexico during the DGoMB project process cruises of 2001 and 2002.

SCOC measurements at seep sites were *in situ*, using a set of benthic respiration chambers deployed by the Johnson Sea-Link manned submersible. The benthic chambers are designed to be set firmly into the bottom sediment by the submersible and left to measure the flux in the sediment-water interface using syringe samples and a SeaBird® oxygen sensors and a Sealogger® system. The syringe samples are used in Winkler titrations to determine O_2 concentration and were also sampled for DIC (dissolved inorganic carbon) and nutrients. SCOC measurements incorporate data taken during four cruises (1993, 1995, and 2001) in collaboration with the research submersible Johnson Sea Link from sites visited by SSETI.

4.5 Statistical Analysis

Statistical analysis of macrofauna community structure and function parameters sought to prove seep and non-seep communities, as defined in this research, are separate populations of the benthos in the northern Gulf of Mexico. Community structure parameters of abundance and biomass were evaluated for seep and non-seep samples using a single factor analysis of variance to test for significant differences in the means of the two community variables. A single factor analysis of variance was also be used to test for statistical differences in the mean values of SCOC rates from seep and non-seep sites. Diversity of macrofauna taxa between seep and non-seep sites was evaluated to determine if the mean number of taxa between seep and non-seep communities is statistically different.

These statistical tests were used to look for a statistical difference in mean values of seep community and non-seep community attributes. Mean values from cold seeps were compared to non-seeps between 200 to 1000 meters. Macrofauna abundance and diversity of taxa were tested against 16 stations that fit these criteria. The food-limited stations were divided into three ranged depth-groups to test against the effects of shallower, comparable and deeper macrofauna communities. Group A has six sites and a mean depth of 308 meters. Group B has five sites and a mean depth of 600 meters. Group C has five sites and a mean depth of 926 meters.

4.6 Model of Macrobenthic Communities Influenced by Seeps

A normal benthic community in the deep sea depends solely on the input of organic matter, either from falling particles or lateral transport. These communities can be modeled using simple trophodynamic principles (Lindeman, 1942) and combining standing stock data with known patterns of feeding, predation, reproduction and respiration. Communities at seep sites should be modeled differently since they are not totally dependent on POC flux from the surface. Macrofaunal communities influenced by seeps are unlike the surrounding deep-sea sediments because they are not carbon limited.

A vertical model of seep communities would have two inputs of carbon into the system, one for overhead POC flux and another for seep-originated carbon via a microbial pathway. This second input of carbon within the domain of influence is the driving force behind increased biomass, density and total sediment community oxygen consumption. The model in Figure 2 can be run to demonstrate the mechanisms that affect biomass and respiration, as outlined in the above hypotheses. Slight manipulations in the values of standing stocks, fluxes, imports and exports can be used to determine the sensitivity of factors that affect the trophodynamics of seeps. Once the fluxes of carbon within the system and the biomass of standing stocks are determined, the model can be run using Stella 7.2 software. Stella 7.2 allows for the dynamics of the community to be simulated over time using differential equations that conserve energy and matter.

Increased abundance, biomass and SCOC due to added carbon input to a macrobenthic ecosystem can be shown as a cumulative process when viewed in a flow model. Standing stocks and fluxes are directly related to the additional source of carbon into the system and can be seen as the red lines, which denote relationships that affect these variables. This research will provide a standing stock value for the macrobenthos at seeps sites in the Gulf of Mexico. Reverse calculation of fluxes and standing stocks for the meiobenthos and bacterial populations at seeps can be made with reasonable certainty to show what kinds of ecosystem parameters are needed to support the known values determined in this research.

Results on macrofauna community structure taken from seeps and non-seeps should provide a general idea of how these habitats differ in their faunal assemblages of animals. Total community respiration values will also determine if the differences in communities causes a change in the community functioning. Standing stocks for macrofauna communities and SCOC rates can then be incorporated into simpler models of seep and food-limited communities. Using STELLA to model (Figure 2) these communities based on actual data can show how other parts of the community, namely the bacteria and meiofauna, also react to changes in the amount of food available.
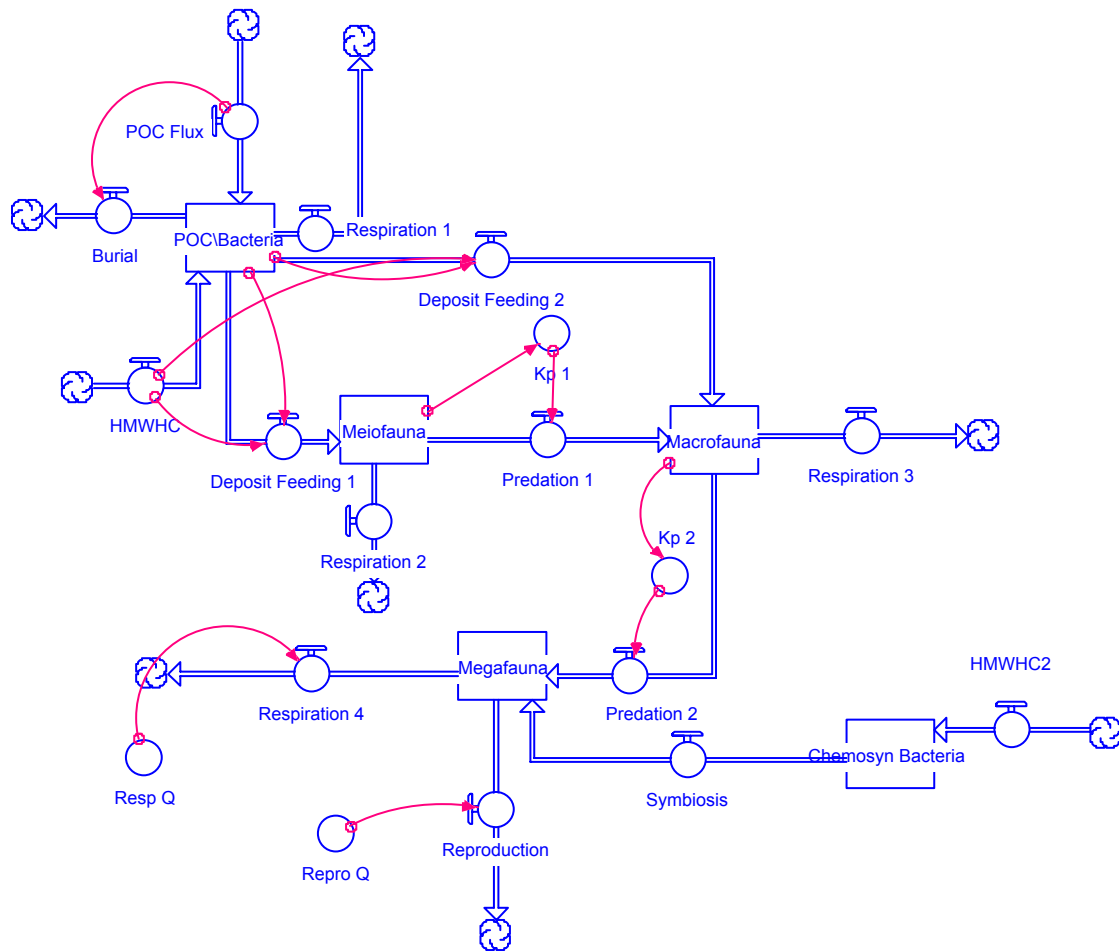
Fig. 2. Trophodynamic Model of al Cold Seep

This represents a conceptual flow model that accounts for input and output sources for standing stocks of benthic community groups. High Molecular Weight Hydrocarbons (HMWHC) is the input of carbon to the system from seeps. The rectangular blocks represent standing stocks of biomass. The arrows between boxes represent flow of carbon within the system. Gains or inputs into the system are shown as arrows that enter the system directly through a standing stock. Losses or outputs from the system are seen as arrows leaving standing stocks ending in small clouds. Small free, standing circles contain constants and are connected to various fluxes by the red arrows.

5.   RESULTS

5.1 Macrofauna Community Structure

5.1.1   Abundance

The average macrofaunal abundance of cores taken for the DGoMB project taken between 200 and 1,000 meters was 8,499 individuals per square meter with a standard deviation of 5,616. The seep site Green Canyon 234 had a mean abundance of 21,888 individuals per square meter, and the seep site Garden Banks 425 had a mean abundance of 35,660 individuals per square meter. The mean value of seep macrofaunal abundance was 28,774 individuals per square meter with a standard deviation of 9,739 (Table 1). Food-limited sites between 200 and 100 meters were subdivided into three groups based on depths and frequency distributions. Group A consisted of sites in the depth range of 200 to 420 meters. The mean abundance for group A was 7,467 individuals per square meter $\pm$ 3,607. Group B consisted of sites between 420 and 700 meters. The mean abundance for group B was 12,364 individuals per square meter $\pm$ 8,792. Group C consists of sites between 700 and 1000 meters. The mean abundance for group C was 6,300 individuals per square meter $\pm$ 4,030. The mean abundances of the three groups were not significantly different as tested using a single factor analysis of variance, showing that depth was not a significant factor in determining macrofaunal abundance within this 200 to 1,000 meter depth range. A single factor analysis of variance indicated that the mean values for abundance of seeps and non-seeps are significantly different ($F = 23.038$, 1, 47 df, $p < 0.01$).

Table 1. Mean Abundance Values

Statistical mean and standard deviation for macrofauna abundance at the seep and non-seep sites studied.

	Mean Abundance	Standard Deviation	n
SEEPS	28,774	9739	4
NON-SEEPS	8,883	5616	92

5.1.2   Biomass

Total macrofauna biomass at seep and non-seep sites are quantified as the total amount of carbon per square meter. For DGoMB sites MT3, S36, S42 and C7, the average amount of carbon per square meter was 0.91mg ± .102. The Green Canyon 234 seep site macrofaunal biomass was 0.032 mg-C per square meter. Garden Banks 425 seep site had a macrofaunal biomass of 0.11 mg-C per square meter. The mean seep macrofaunal biomass was 0.072 mg-C per square meter ± 0.056 (Table 2). A single factor analysis of variance indicated that the mean values for total biomass of seeps and non-seeps were significantly different ($F = 108.410$, 1, 5 df, $p < 0.01$).

Nine major macrofauna taxa were measured for biomass at seep and non-seep sites. The results were that the average size of the macrofauna was greater at non-seep sites than at the two seeps studied (Table 3). Table 2 shows the comparison of average size of the macrofaunal groups at seeps compared to the DGoMB, non-seep sites. The mean size of individual macrofauna from DGoMB sites MT3, S36, S42 and C7 was 12.29 µg of carbon ± 0.53. The mean size at seeps GC 234 and GB 425 was 0.00363 and 0.00185 µg of carbon, respectively, with a combined mean 0.0027 µg of carbon ± 0.0013. A single factor analysis of variance indicated that the mean values for individual biomass of seeps and non-seeps are significantly different ($F = 957.768$, 1, 5 df, $p < 0.01$).

Table 2. Mean Biomass Values
Statistical means and standard deviation values for total macrofauna biomass and individual biomass from the seep and non-seep sites studied.

	Mean Individual Biomass	Standard Deviation	Mean Total Biomass	Standard Deviation	n
SEEP	0.0027	0.0013	0.072	0.05	4
NON-SEEP	12.29	0.53	0.91	0.10	92

Table 3. Mean Taxon Biomass Values

Average biomass for major macrofauna taxa as measured from sediment core samples taken at cold hydrocarbon seep sites and non-seep sites from the northern Gulf of Mexico continental slope. All weights are in µg-carbon.

Taxa Group	Seeps (SSETI)	n	Non-Seep (DGoMB)	n
Amphipoda	0.0063	7	4.85	38
Aplacophora	0.0390	3	0.39	44
Bivalvia	0.0290	5	65.30	29
Harpacticoida	0.0002	43	0.11	40
Isopoda	0.0006	7	1.34	25
Nematoda	0.0005	35	0.14	230
Ostracoda	0.0410	5	7.22	316
Polychaeta	0.0031	38	15.30	105
Tanaidacea	0.0015	95	0.68	70
Mean	0.0027	238	12.29	897

5.1.3   Diversity

At this point, biodiversity can only be based on the major macrofaunal groups into which the sediment cores were originally sorted. Both seep and non-seep sediment cores have been sorted into these major groups which include Amphipoda, Anthozoa, Aplacophora, Ascidiacea, Asteroidea, Bivalvia, Brachiopoda, Bryozoa, Copepoda [non-Harpacticoida], Cumacea, Decapoda, Echinoidea, Echiura, Gastropoda, Harpacticoida, Holothuroidea, Hydrozoa, Isopoda, Kinorhyncha, Mysidacea, Nematoda, Nemertini, Oligochaeta, Ophiuroidea, Ostracoda, Polychaeta, Porifera, Priapulida, Pycnogonida, Scaphopoda, Scyphozoa, Sipunculida, Tanaidacea, Turbellaria, Unknown, Pogonophora, Chaetognatha, Halacaridae, Crinoidea , Hemichordata, and Cladocera. The median number of macrofauna taxa at GB 425 was 10. The median number of macrofauna taxa at GC 234 was 9. The median number of taxa found

among macrofauna at DGoMB sites between 200 and 1000 meters was 21. The mean number of taxa found at seeps was 9.5 and the mean number of taxa found at non-seep sites (200-1000m) was 21.4. A single factor analysis of variance indicated that the mean values for taxa of seeps and non-seeps were significantly different (F = 18.839, 1, 47 df, p < 0.01). Table 4 shows the median, mean, Shannon-Weiner (H') and Eveness values for seep and non-seep sites.

Food-limited (non-seep) sites between 200 and 100 meters were subdivided into three groups based on depths and frequency distributions. Group A consisted of sites in the depth range of 200 to 420 meters, with a median number of taxa of 22. Group B consisted of sites between 420 and 700 meters, with a median number of taxa of 18. Group C consists of sites between 700 and 1000 meters, with a median number of taxa for group C was 23. The mean number of taxa, for the three groups are not significantly different as tested using a single factor analysis of variance, showing that depth is not a significant factor in determining number of macrofauna taxa within this 200 to 1000 meter depth range.
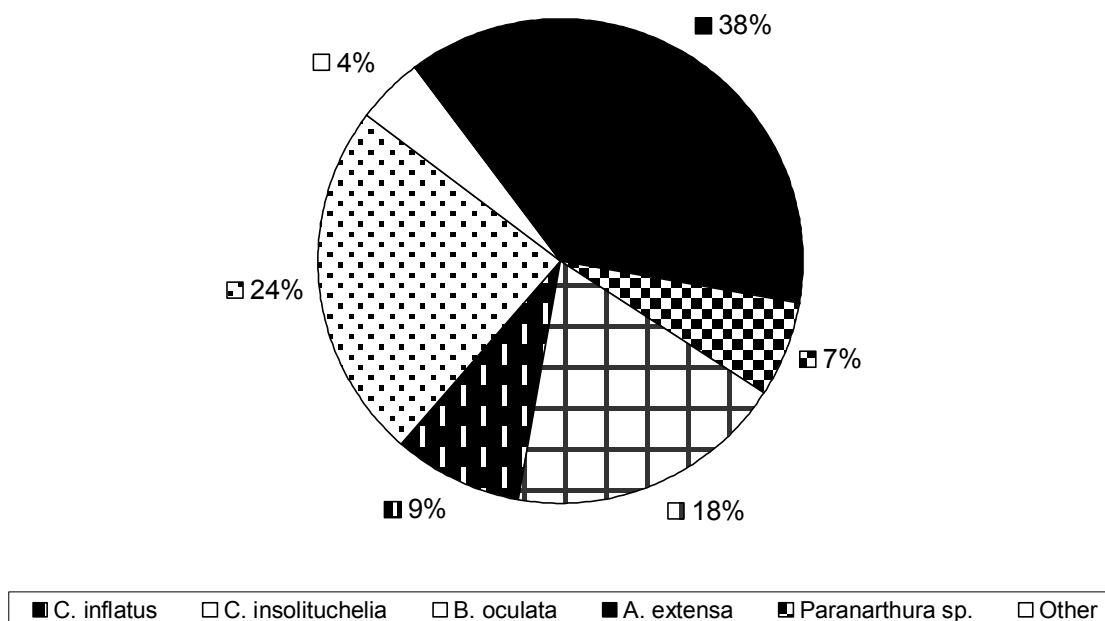
Complete species data for the macrofauna Tanaidaceans at Garden Banks 425 showed a low amount of diversity, with only five species being found in 72 identified individuals (Larsen, 2003). Tanaidaceans were the dominant taxon group at Garden Banks 425 accounting for 49 % of the total number of individuals present. Within the 72 tanaids found in the cores from GB 425, three new genera and four new species were described (Larsen, 2003). The individuals were sorted into five genera and from these groups five species emerged. Two of the new species, *Coalecerotanais inflatus* and *Crurispina insolituchelia*, comprise two new genera and do not belong to any recognized families (Larsen, 2003). *Bathyleptochelia oculata*, a new species similar to species usually found on the continental shelf, has well-developed eyes and may be a recent inhabitant to the mid-slope of the northern Gulf of Mexico. The remaining two species, *Araphura extensa* and *Paranarthura* spp., are exclusively found in the deep-sea. The descriptions of morphological features for these five species indicate an interesting relationship based on mouth morphology (Larsen, 2003). *Coalecerotanais inflatus* and *Crurispina insolituchelia* have a reduced mandible size and accounted for 33% of the tanaidaceans identified. *Bathyleptochelia oculata* that had large mouthparts, well suited for larger food particles typical of the continental shelf, accounted for only 4% of the tanaid sample. *Araphura extensa* and *Paranarthura* spp., which are common to the deep-sea, accounted for 45% of the tanaids, and the remaining 18% of the tanaids collected could not be placed into definite groups (Other, Figure 3).

Table 4. Mean Diversity Values

The mean value of major macrofaunal taxa, the median value of taxa, the Shannon-Weiner index of diversity, and the Eveness value of taxa is shown compared between the seeps GB 425 and GC 234 and the non-seep sites analyzed.

Sites	Mean value of taxa	Median value of taxa	Shannon-Weiner (H')	Eveness	n
GC 234	9.5	9	1.33	0.64	2
GB 425	10.5	10	1.38	0.63	2
Non-Seeps	21.4	21	1.79	0.584	92

Population Structure of GB 425 Tanaidaceans

■38%

□4%

■24%

■7%

■9%

□18%

| ■ C. inflatus | □ C. insolituchelia | □ B. oculata | ■ A. extensa | ■ Paranarthura sp. | □ Other |

Fig. 3. Population Structure of GB 425 Tanaidaceans

Percent makeup of Tanaidacean fauna at Garden Banks 425.

5.2 *Sediment Community Oxygen Consumption*

Below are rates of sediment community oxygen consumption measured using *in situ* benthic flux chambers. Rates were determined by measuring the change in dissolved oxygen over time. Reported values are in milligrams of carbon per meter squared per day or mg-C m^{-2} d^{-1} (Table 5). Green Canyon 234 had a mean SCOC value of 76.1 mg-C m^{-2} d^{-1} ± 13.8 (n=7), and Garden Banks 425 had a mean of 95.3 mg-C m^{-2} d^{-1} ± 6.3 (n=2), with a mean of 80.3 mg-C m^{-2} d^{-1} ± 15.8 (n=9). Non-seep SCOC rates had a value of 36.1 mg-C m^{-2} d^{-1} ± 18.3 (n=7). A single factor analysis of variance indicated that the mean values for sediment community oxygen consumption of seeps and non-seeps were significantly different ($F = 28.885$, 1, 15 df, $p < 0.01$). Non-seep SCOC values were taken from the four sites in the Northern Gulf of Mexico between depths of 755 and 1845 meters. The values from these sites were not significantly different from each other when the means were tested using a single factor analysis of variance, showing that differences in depth for these values do contribute in the significantly different values between seeps and non-seeps.

Table 5. Mean SCOC Values

Statistical mean and standard deviation for sediment community oxygen consumption (mg-carbon m^{-2} d^{-1}) at the seep and non-seep sites studied.

	Mean SCOC	Standard Deviation	n
Seep	80.3	15.8	9
Non-seep	34.4	18.4	7

6. DISCUSSION

6.1 Hypotheses Tested

The direct comparison of seep and non-seep communities presented in this study proved Hypotheses 1, 3 and 4 and disproved Hypotheses 2. The seeps evaluated for community structure in this study were statistically proven to be separate populations of macrofauna by statistical differences in the mean values of their community attributes. This statistical qualifier only helps to prove a significant difference in the structural components for which macrofaunal communities were evaluated and they provide no quantitative answers to the ecological forces that make the hydrocarbon seep and the food-limited macrobenthos different. The only conclusion that can be drawn directly from supporting evidence is the ability to accept or reject the four initial hypotheses. The first three hypotheses addressed the community structure of macrofauna assemblages in the two defined benthic habitats. The fourth hypothesis addressed the community function of the two defined benthic habitats.

Hypothesis 1 theorized that seep sites studied in the Northern Gulf of Mexico will have elevated levels of macrofaunal abundance when compared to food-limited sites in the same study area. A significantly greater abundance of macrofauna at seeps supports Hypothesis 1. This significant association in macrofaunal abundance suggests that seep macrofauna were not food-limited. The mean abundance at seeps GB 425 and GC 234 was greater by approximately 20,000 individuals than the mean abundance of benthic communities in the food-limited benthos.

Hypothesis 2 theorized that seep macrofauna individuals will be greater in biomass than those individuals from the food-limited benthos. Hypothesis 2 also theorizes that the total biomass of macrofauna per square meter of habitat area will be greater at seeps than in the food-limited benthos. A significant difference in both individual macrofaunal biomass and total community macrofauna biomass was found for seep and non-seep communities. Contrary to this hypothesis non-seep communities had larger animals and a greater total biomass. These parameters of community structure indicated that macrofauna communities at seeps were different from those found in the food-limited benthos. Seep macroinvertebrates were smaller in size than non-seep macroinvertebrates by almost four orders of magnitude. Not only was the individual size of organisms larger at non-seeps, but the total amount of carbon stored in the sediment macrofauna at seeps was twelve times less than carbon standing stocks in the food-limited benthos.

Hypothesis 3 was designed to show loss of taxonomic diversity at seeps compared to the generally high diversity of macrofauna in the food-limited deep-sea. The taxa diversity at these seeps was diminished when compared to non-seep sites. The mean number of taxa found at seeps was

approximately half of the mean number of taxa found at non-seeps. Once again this represents a significant difference in community structure between the two environments.

Hypothesis 4 was designed to test whether total sediment community respiration at seeps was different from non-seeps. Mean sediment community oxygen consumption rates from seeps GB 425 and GC 234 was approximately twice that of non-seep sites along the Northern Gulf of Mexico continental slope. The rationale for testing sediment community oxygen consumption is that SCOC is also a measure of the rate of organic carbon turnover, which is dependent on the amount of POC in the sediment. A community with an elevated amount of SCOC can be said to have a greater amount of organic carbon within the system. The increased SCOC seen at seep sites can easily be explained then by the abundance of labile organic carbon generated by microbial mediation of seeping hydrocarbons.

A summary of the conclusions reached by the statistical testing of the first three primary hypotheses show that these seeps proved to have distinct macrofauna populations that were larger in abundance, smaller in individual size, diminished in total carbon per meter square and decreased in taxonomic diversity. The fourth hypothesis tested lead to a conclusion that total sediment respiration was elevated at seeps. This indicated a functional change in sediment community dynamics from the food-limited benthos. The four primary hypotheses and the associated conclusions discussed above show that there are significant differences in macrofauna community structure between cold hydrocarbon seeps and the food-limited benthos in the northern Gulf of Mexico. It should also be noted that the increased rate of remineralization of POC is an indicator of changes in benthic sediment community function. It is not assumed that the structural differences were responsible for the functional difference in the different communities.

6.2 Total Abundance and Biomass of Macrofauna

Cold hydrocarbon seeps are environments that have an enriched pool of particulate organic carbon within the sediments. At Garden Banks 425 and Green Canyon 234 this increased supply of food has altered the general Ecology of the macrofauna population and thus the entire community. Seeps had a greater abundance of individuals per square meter than is normally found in the food-limited benthos. The two paradoxes of this structural change are the individual size of macrofauna is decreased and the total macrofaunal carbon pool is diminished. These changes in the structural assemblage of macrofauna could be important to ecosystem function. First, the increased number of macrofauna individuals could increase SCOC. Second, the smaller size of seep macrofauna means that the respiration rate per individual would be greater than larger animals. Third, the decreased importance of macrofauna to the total sediment community means that meiofauna and bacteria now account for a greater percentage of the

total sediment biomass. The increased importance of these smaller organisms would lead to increased sediment community oxygen consumption as well.

Increased numbers of macrofauna at seeps is not unexpected since continental slope habitats that accumulate enhanced carbon supplies have greater faunal densities. An unknown ecological force, which may be intrinsic to extreme environments, causes the large disparity in the individual sizes of the macrofauna. However, the adaptation for smaller size may be a product of enhanced competition for resources or a survival strategy that puts reproduction above growth.

A detailed comparison of macrofauna communities at hydrocarbon seeps and away from seeps indicated that the seep environment caused a change in the structure of the macrofauna communities in the deep Gulf of Mexico. Seep communities have total particulate organic carbon concentrations within the sediment that are greater than the surrounding food-limited communities, but the macrofauna carbon pool was decreased. This could be due to increased importance of microbial producers and consumers in the ecosystem. More carbon is stored in bacteria at seeps because they are best equipped to utilize the available carbon. Since the structure of the sediment community has changed, the function of the ecosystem should also show a change in its rates of carbon consumption and remineralization.

The natural assemblage of macrofauna at seeps has changed from that found in the food-limited benthos. This change means that the sediment community has also shifted its ratios of biomass between the three main components, bacteria, meiofauna and macrofauna. This change impacts not only the density and individual size of the macrofauna but also the carbon pool of macrofauna. Since we know that POC in seep sediments is far greater than concentrations in the food-limited benthos, it is reasonable to assume that this carbon is going to increase the standing stocks of bacteria and meiofauna. Knowing that seep macrofauna populations are structurally different form other sediment communities in the Gulf of Mexico, the next question to answer is, how do changes to community structure affect community function?

6.3 Implications of Increased Sediment Community Oxygen Consumption

Structural shifts of the infaunal community at cold hydrocarbon seeps brought on by excess food cause the functioning of these ecosystems to change as well. Macrofauna has become a less influential player in the cycling of carbon within the food rich environments of cold seep ecosystems. Since bacteria are the gatekeepers of carbon flow via methane and hydrocarbons into the ecosystem, they have a competitive advantage over the meiofauna and the macrofauna. Since the majority of the food available to sediment infauna at seeps is either bacteria or byproducts of bacterial activity, being small enough to ingest these food particles is another competitive advantage. Hence, the larger size of macrofauna works

to its disadvantage, and thus makes it a less able to compete for food in the seep ecosystem. Even the diminutive macrofauna found at seeps GB 425 and GC 234 are not small enough to outcompete bacteria at seeps.

Macrofauna found at seeps, GB 425 and GC 234 are reduced in size. This decreased size may be caused by a number of environmental or ecological factors. Chemical toxicity of hydrocarbons has been shown to limit growth in certain types of sediment infauna such as crustaceans and benefit others such as polychaetes and nematodes (Jensen, 1986; Montagna and Harper, 1996; Peterson et al., 1996). The ecosystem is balanced between intense organic enrichment and various levels of anoxia/hypoxia coupled with chemical toxicity. The importance of crustaceans, namely the large proportion of tanaidaceans at GB 425 (49% of total macrofauna samples), suggests that seep environment's areas of toxicity are spatially or temporally patchy. Therefore, the reason(s) for the diminished individual size of macrofauna are more likely to be due to ecological factors. Factors that are related to the competition for resources, niches utilization, scope of growth and reproductive survival strategies.

6.4 Competition for Resources and Niche Spaces

The shift in the relative sizes of standing stocks of bacteria, meiofauna and macrofauna may be the cause for a significant increase in the rate of respiration by the sediment community. Bacteria at seeps have an abundant supply of carbon resources to utilize for metabolic respiration, so that the only limitations on their rates of respiration are environmental factors. For this reason, a shift in community structure toward increased bacterial importance may be one cause for the increased sediment community respiration. Decreased body size of the macrofauna can also be a factor affecting community function. For metazoan fauna, decreased size leads to increased respiration rates because of a greater surface area-to-volume ratio (Mahaut et al., 1995). Decreases in average body size of the macrofauna may be related to the size and availability of food.

In an environment where bacteria dominate the cycling of carbon through the food web, food particles available to deposit feeders should be small in size. In this instance the competitive advantage would shift towards smaller fauna that can process food more easily and quickly. Bacteria and meiofauna are better suited to accumulate food where the available particles are small and the dispersal of particles is homogeneous. Peterson (1979) noted that in low food environments cold-blooded marine invertebrates adapt to conditions by having low metabolic rates and an ability to restrict growth. This ability to partition food sources into growth, respiration and reproduction could also be used in high food environments by the macrofauna to compete for the same food resources used by the meiofauna and bacteria.

Invertebrates under high food conditions have a higher feeding rate, which tends to lower the absorption efficiency leading to an increased metabolic rate (Ahn, 1997). Ahn (1997) also noted that the potential scope for growth decreased in invertebrates despite the increase in total ingestion. This creates a negative feedback as growth is hindered since smaller sized invertebrates would have an even higher respiration rate. Figures 4 and 5 show how different ecological factors affecting metabolic rates and food intake lead to feedback loops within low-food and high-food environments.

In each figure a feedback loop created by physiological effects of body size and uptake kinetics of the available food source positively enhances the processes at work. If indeed, smaller animals are the outcome of such processes at seeps, then the smaller animals will have a higher metabolic rate so that the cycle of decreased growth will influence the factors that lead to small body size. In the case of low food environments the animals grow larger because of more efficient uptake and food processing and have more resources to allocate to growth. The larger size of the macrofauna seen at non-seep sites is a mechanism for conserving energy in an environment where the fauna are limited by the scarcity of food (Ahn, 1997). The ability to restrict growth as an adaptation to environmental conditions can be beneficial in both high and low food environments (Peterson, 1979).

The unexpectedly small size of macrofauna at seeps GB 425 and GC 234 could then be considered a result of physiological characteristics of cold blooded marine invertebrates, but the shift in the macrofauna community could also have advantages as a survival strategy for the macrofauna. Seeps are food rich environments with tiny particles available for consumption these characteristics put the macrofauna at a disadvantage in competing for resources. If the size distinction between the meiofauna and macrofauna is negated by the decreased size of the macrofauna then the odds of macrofauna success increases (Rowe, 1997). However, the impact upon meiofauna size can only be speculated about. The impact on macrofauna population structure and diversity can be seen from the cores taken from the seeps. Greater densities and smaller body size of macrofauna at seeps could also be seen as a selection of reproduction over growth.
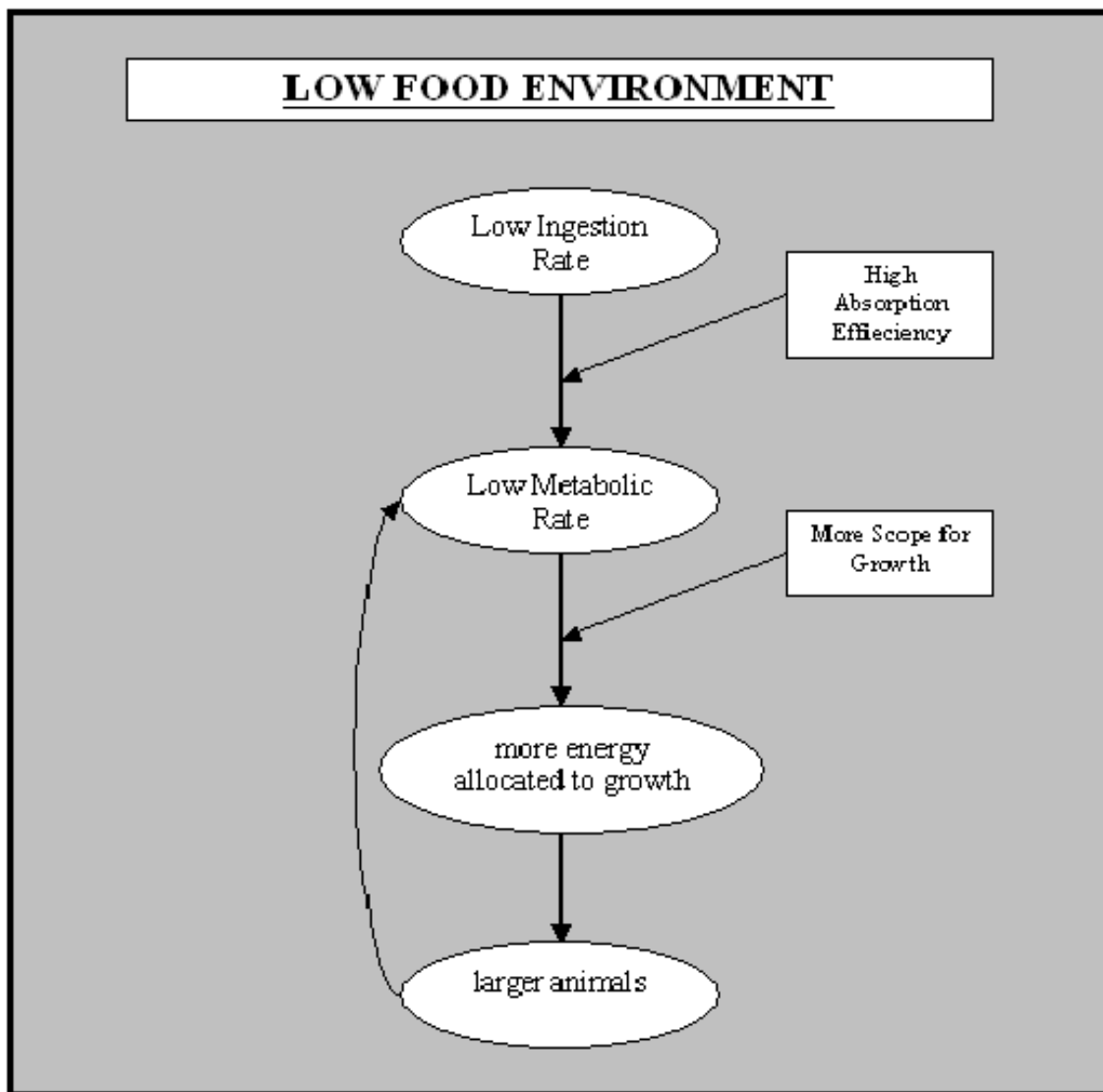
Fig. 4. Low Food Environment

A conceptual flow diagram of ecological forces combining to influence the size of invertebrates, in a low-food benthic settings in the deep-sea.
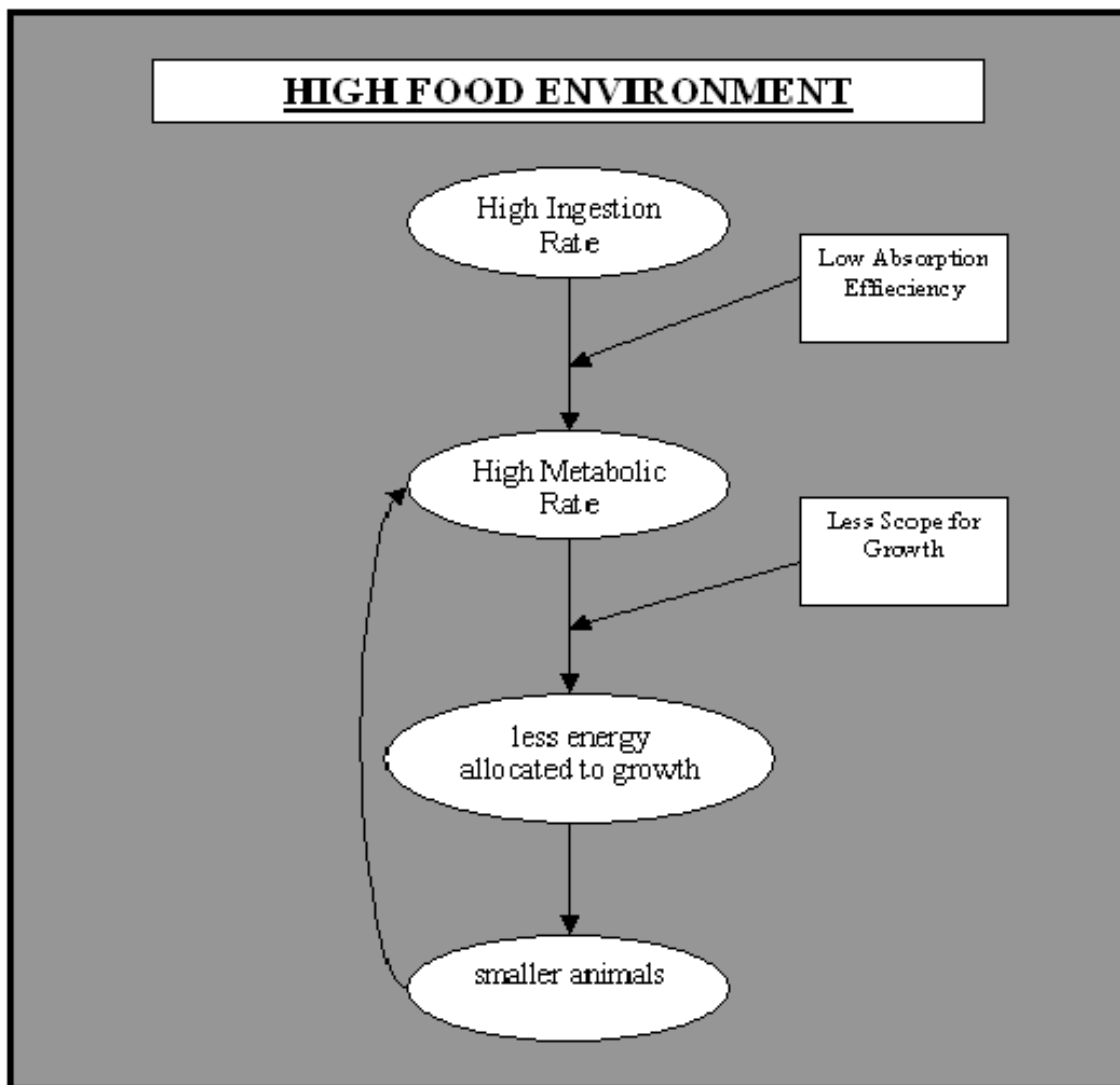
Fig. 5. High Food Environment

A conceptual flow diagram of ecological forces, combining to influence the size of invertebrates, in high-food benthic settings in the deep-sea.

Glimpses of strategies ranging from decreased size to specialized feeding appendages were evident in the Tanaidacea fauna found in cores from the Garden Banks 425 seep site. Two of the newly identified species were indeterminate in family membership, the other new species, B*athyleptochelia oculata*, belongs to the family Leptocheliidae, a family with only one other group found in the deep-sea. B*athyleptochelia oculata* is indicative of its membership to a shallow water family because of its well, developed eyes. It mandibles are large in size, as expected of a newcomer to deep water habitats that are food-limited, so its relatively low occurrence (3 % of Tanaidacean population, 1.5 % of total population) within the food rich seep community, may be a result of its inability to effectively compete for small food particles. The other newly described species *Coalecerotanais inflatus* and *Crurispina insolituchelia* have mandibles reduced in size, and account for 33% of the Tanaidacean population (19% of total population). *Araphura extensa* and *Paranarthura* spp. Are cosmopolitan species in the deep-sea and account for 45% of the population (21% of total population). Since there are no other tanaidaceans that are closely related to *Coalecerotanais inflatus* and *Crurispina insolituchelia* their morphologically diminished mouthparts suggest that they are adapted to eating smaller food particles than *Araphura extensa* and *Paranarthura* spp. Other unusual features as described by Larsen (2003) make it possible that *C. inflatus* and *C. insolituchelia* have evolved toward their present states in the absence of other Tanaidacean fauna.

Ecological research at cold seeps attempts to categorize local fauna into three groups of habitat users. The first category is endemic, which are animals that exclusively inhabit seeps because of a competitive advantage over other animals. Examples of this would be tube worms and clams that use chemosynthetic bacteria that live in their gut or gills. The second category is transient, which may be animals that appear at seeps on a regular basis but come only to feed or scavenge, and do not spend a large amount of time within the seep environment. The third category is visitor, which are animals that in their trek across the sea-floor pass through the seep environment. These classifications are more useful for large fauna that are mobile and can make decisions about appropriate habitat usage (MacAvoy et al., 2002).

The sediment infauna do not have these options so they must either conform to a very, specific niche or utilize a competitive advantage to push out other species. Within the Tanaidacean fauna three groups appear to exist, first the endemics, second the locals and third the immigrants. Endemics would be inhabitants that live only at seeps because of unique adaptations or competitive advantages. *C. inflatus* and *C. insolituchelia* are probably endemic to Garden Banks 425. Morphological adaptations in the mouthparts of these species provide a competitive advantage over other macrofauna deposit feeders. It is even possible that *C. inflatus* and *C. insolituchelia* are found exclusively near GB 425 if they did indeed evolve in isolation from other tanaidaceans. No tanaidaceans were found at the other seep site studied, Green Canyon 234, and the Tanaidacean fauna may not be an influential competitor in all seep

communities, as these two species have been found nowhere else. Locals are likely to be fairly common over the entire slope and end up at seeps purely by accident. *Araphura extensa* and *Paranarthura* spp. (cosmopolitan across the northern Gulf of Mexico continental slope) are likely just local members of the fauna. Immigrants are animals that have moved either up-slope or down-slope in search of food finding seep communities by accident. B*athyleptochelia oculata* is an immigrant from the continental shelf and still retains morphological features of shallow water communities, like the enlarged mouthparts and well developed eyes. Since it was only at GB 425 where tanaids were found within the sediment samples it cannot be said that they are indicator species for seeps unlike Vestimentiferan and Pogonophoran tubeworms and Lucinid and Vesicomyid clams.

It is also important to note that the Tanaidacean fauna found at Garden Banks 425 are not only curious for their morphological features, but also for the lack of diversity within the population. Tanaidaceans are one of the more diverse groups among the sediment macrofauna, yet at Garden Banks 425 only five species were found out of 72 identifiable individuals. This low diversity within the Tanaidacean fauna is evident in species rarefaction curves, for Tanaidaceans, when other slope habitats are compared to that of GB 425 in Figure 6. Non-seep Tanaidacean species and individual number data comes from the Northern Gulf of Mexico Continental Slope Study (Galloway, 1987). Rarefaction curves for deep-sea macroinvertebrate fauna usually need large numbers of individuals before the number of species found begins to even out. As seen in rarefaction curves the non-seep Tanaidacean populations continue to show room for additional species even after 150 individuals (Figure 6). However the number of seep Tanaidacean species reaches a plateau after only 30 individuals. Sample size of cores used between the NGMCSS and the SSETI study may contribute to this disparity in deep-sea diversity, but until more sampling is done of seep Tanaidaceans there is still a greater number of species per square meter sampled at Garden Banks 425 than in the extensive sampling done along the slope in the NGMCSS populations.

The disparity in the size of cores evaluated may have had an effect upon abundance and diversity values reported in the results. The smaller SSETI push cores ($0.0053 \ m^2$) compared to the DGoMB GOMEX box core ($0.1725 \ m^2$) may create artifacts in the abundance and diversity values. Push cores taken during the SSETI project along the continental slope and shelf yield the similar numbers of taxa as the larger GOMEX corer. From these same push cores it is evident that they slightly underestimate macrofauna abundance. So it may be that the sampled abundance values reported from seeps are lower than the in-situ
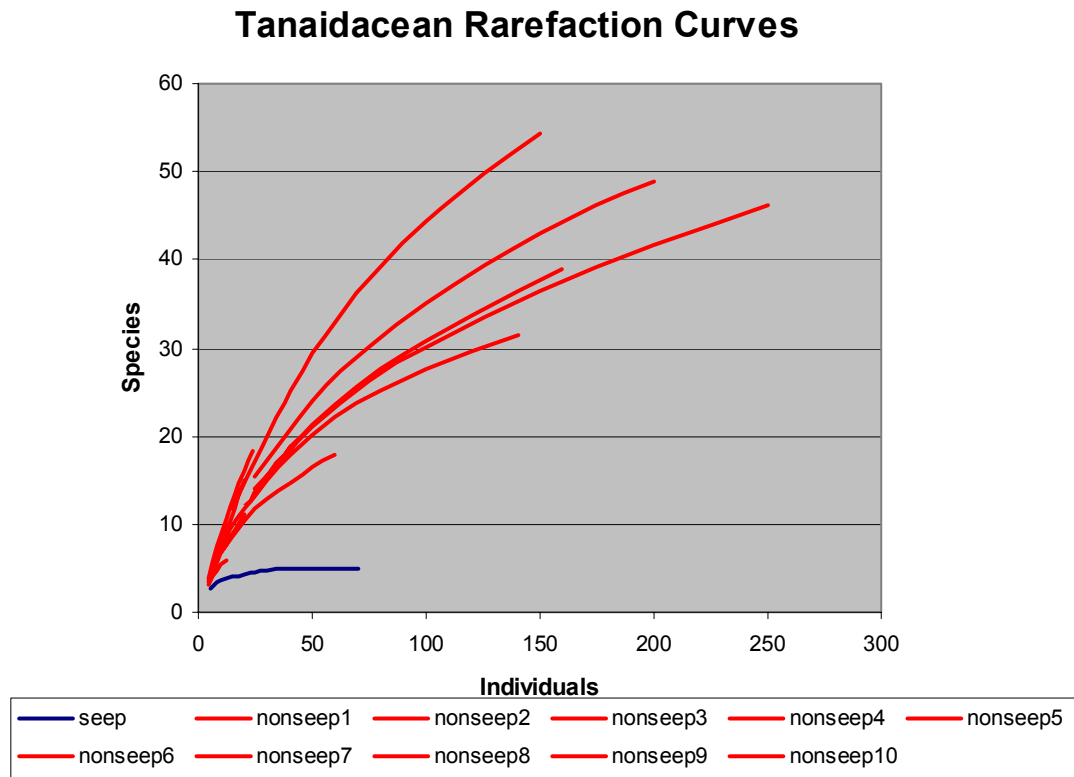population.

Fig. 6. Tanaidacean Rarefaction Curves

Tanaidacean rarefaction curves for slope sites less than 1000 meters water depth compared to the rarefaction curve from GB 425. Tanaidacean species and individuals data for non-seep slope sites was taken from the Northern Gulf of Mexico Continental Slope Study.

6.5 Model Perturbations of Steady State Systems

Models of steady state seep and non-seep communities were designed using reported values of macrofauna standing stocks and total sediment community oxygen consumption. Figure 7 illustrates the simplified sediment community structure for non-seep slope sites, using the mean values for total macrofauna biomass, 0.91 mg-Cm^{-2} and the using the SCOC rate of 34.4 mg-Cm^{-2} d^{-1} as the total input of organic matter to the system. Model results of steady state conditions (Figure 8) showed a total sediment respiration value of 31 mg-Cm^{-2} d^{-1}. Bacterial respiration accounts for 55%, meiofauna respiration accounts for 32% and macrofauna respiration accounts for 13% of the SCOC.

A second model was also created to simulate the affects of additional carbon input into a continental slope sediment community using known community attributes for cold seep infaunal communities (Figure 10). Total macrofauna biomass for seeps, 0.072 mg-Cm^{-2}, was used to simulate the known community change within the macrofauna. An increased respiration coefficient was incorporated into the model for macrofauna to simulate the change in metabolic rate due to decreased body size. The same value of POC flux was used for the seep model as the non-seep model. However the seep model seen in Figure 9 also incorporates an additional input from High Molecular Weight Hydrocarbons (HMWHC) that accounts for the difference in mean SCOC values between seep and non-seep communities, which is 45.9 mg-Cm^{-2} d^{-1}. The remainder of community attributes in both models stayed constant to try and detect what changes in additional input and decreased macrofauna biomass will have on the total sediment community. Model results show a steady state condition respiration value of 80 mg-C m^{-2} d^{-1} (Figure 11). Bacterial respiration accounts for 50%, meiofauna respiration accounts for 20% and macrofauna respiration accounts for 30% of total sediment respiration.

Since not all ecological parameters have been thoroughly measured for deep-sea sediment communities, these steady state models presented do not completely represent the entire interaction of biological, physical and chemical processes at work at seep and non-seep sites. The purpose however of such modeling is being able to control these unknown factors of a community, while being able to manipulate known standing stocks and fluxes to gain a better understanding of how changes in community structure affect the total community functioning. The results of both models provide a total respiration value for the community that is within one standard deviation of the measured mean values. A change in standing stock size and metabolic rates for the macrofauna make a large difference in the percent of total sediment respiration that macrofauna is responsible for. A jump from 13% to 30% of the total oxygen consumption by the macrofauna can be seen in the differences of results from the two models. Additional carbon input modeled as HMWHC in the seep model also ramped up the bacterial and meiofauna components of the community. As more studies are done in the deep-sea additional

community parameters such as trophic transfer efficiency, grazing and predation rates, and metabolic consequences of community change will allow these types of model to be more comprehensive and more accurate (Figures 9 and 12) (Rowe et al., 1997).
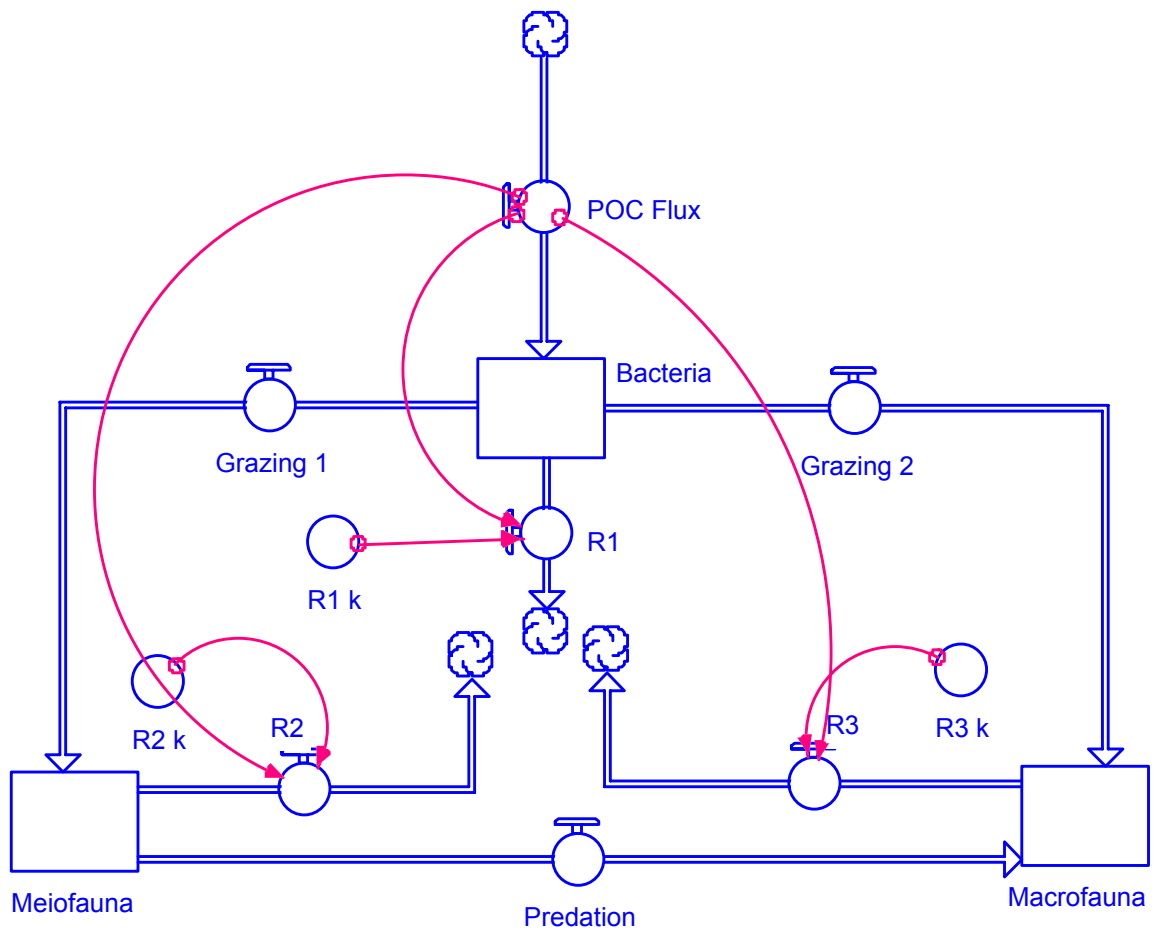
Fig. 7. Non-Seep Sediment Community Model

A model of the sediment community at a non-seep site. Known values of POC flux and macrofauna standing stock were used. Basic trophodynamic principles and rules were used to complete the food web. At standing state the values of R1, R2, and R3 should equal the POC flux.
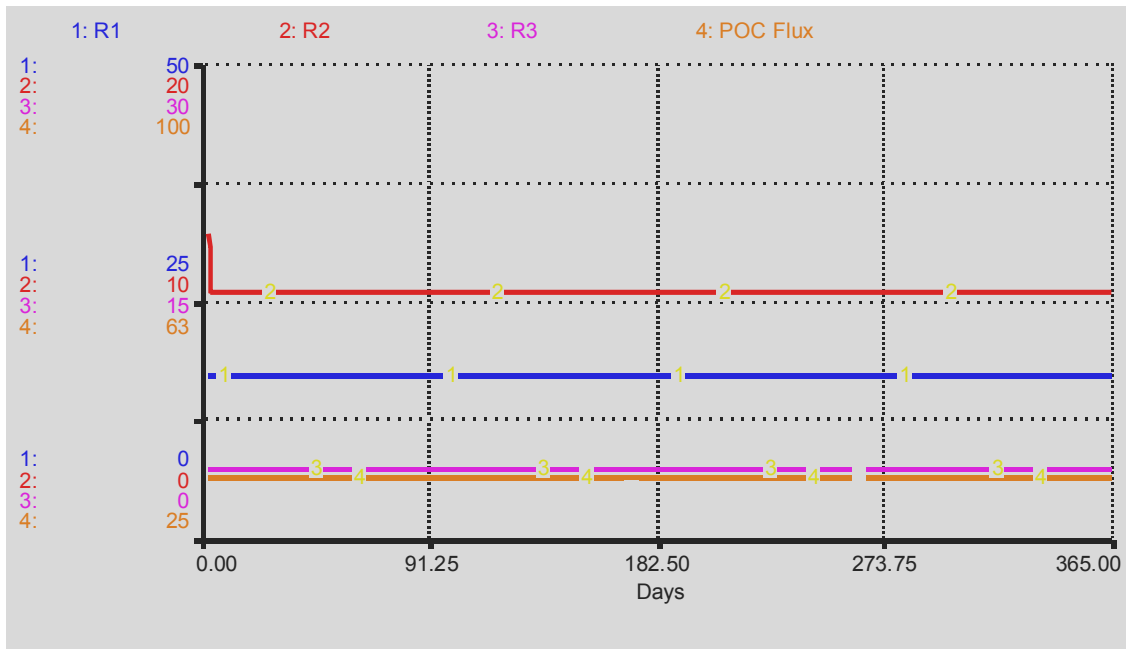
Fig. 8. Graph of Non-Seep Model Results

Graphical display of non-seep model community attributes. R1 = 17 mg-C m^{-2} d^{-1} (bacterial respiration). R2 = 10 mg-C m^{-2} d^{-1} (meiofaunal respiration). R3 = 4 mg-C m^{-2} d^{-1} (macrofaunal respiration). POC Flux = 34 mg-C m^{-2} d^{-1} (particulate organic carbon flux).

Figure 9. Non-Seep Model Parameters

Steady state equations and constants used in the model run for non-seep communities.

NON-SEEP

Bacteria(t) = Bacteria(t - dt) + (POC_Flux - Grazing_1 - Grazing_2 - R1) * dt
INIT Bacteria = 10
INFLOWS:
POC_Flux = 34.4
OUTFLOWS:
Grazing_1 = 12.9
Grazing_2 = 4.3
R1 = R1_k*POC_Flux

Macrofauna(t) = Macrofauna(t - dt) + (Predation + Grazing_2 - R3) * dt
INIT Macrofauna = .91
INFLOWS:
Predation = 2.58
Grazing_2 = 4.3
OUTFLOWS:
R3 = (POC_Flux/2) * R3_k

Meiofauna(t) = Meiofauna(t - dt) + (Grazing_1 - Predation - R2) * dt
INIT Meiofauna = 1.8
INFLOWS:
Grazing_1 = 12.9
OUTFLOWS:
Predation = 2.58
R2 = (POC_Flux/2) * R2_k

Constants
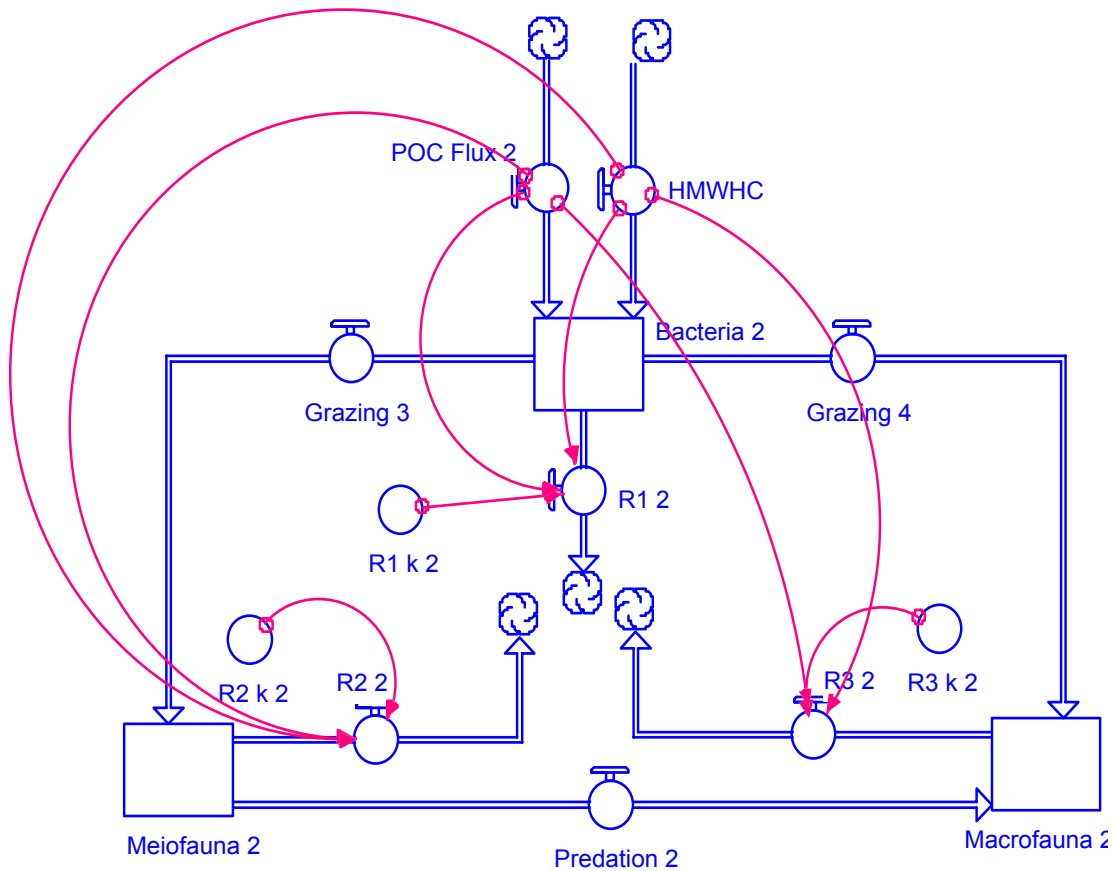R1_k = .5
R2_k = .75
R3_k = .25

Fig. 10. Seep Sediment Community Model

A model of the sediment community at a cold seep which shows the input of POC from overhead production and the input of High Molecular Weight Hydrocarbons (HMWHC) from seeping methane and oil. At steady state the sum of R1, R2 and R3 should equal the total flux into the system from POC flux and HMWHC input.

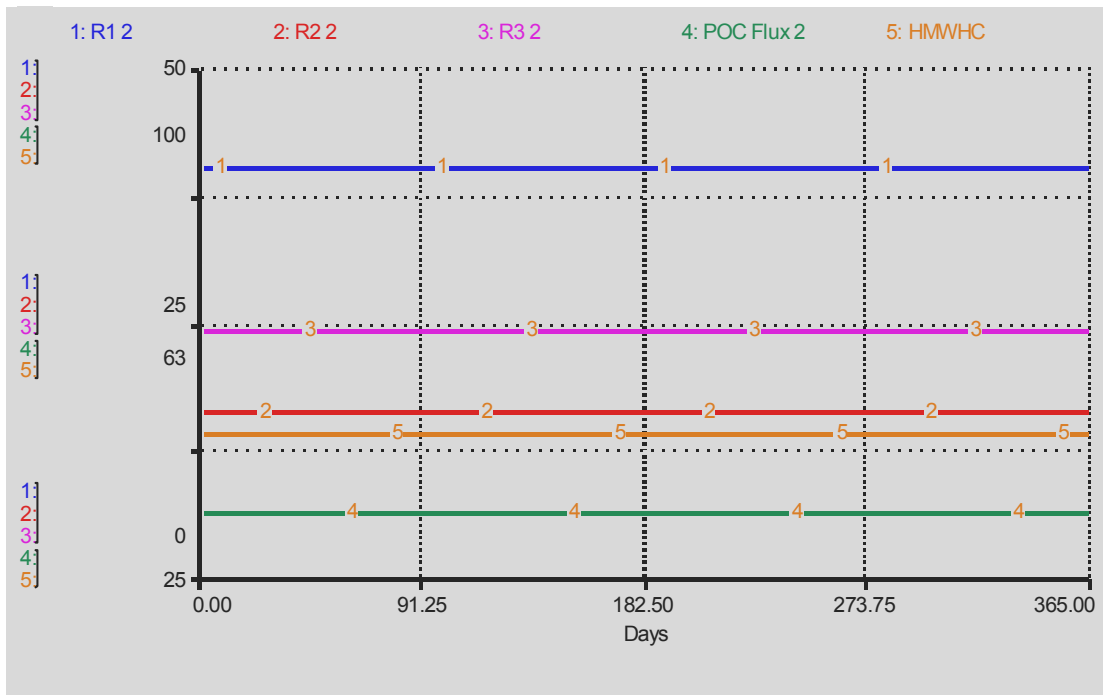**Fig. 11. Graph of Seep Model Results**

Graphical display of seep model community attributes. R1 = 40 mg-C m^{-2} d^{-1} (bacterial respiration). R2 = 16 mg-C m^{-2} d^{-1} (meiofaunal respiration). R3 = 24 mg-C m^{-2} d^{-1} (macrofaunal respiration). POC Flux = 34 mg-C m^{-2} d^{-1} (particulate organic carbon flux). HMWHC = 46 mg-C m^{-2} d^{-1} (high molecular weight hydrocarbons).

Figure 12. Seep Model Parameters

Steady state equations and constants used in the model run for seep communities.

SEEP

Bacteria_2(t) = Bacteria_2(t - dt) + (POC_Flux_2 + HMWHC - Grazing_3 - Grazing_4 - R1_2) * dt
INIT Bacteria_2 = 25
INFLOWS:
POC_Flux_2 = 34.4
HMWHC = 45.9
OUTFLOWS:
Grazing_3 = 24.09
Grazing_4 = 16.06
R1_2 = (HMWHC+POC_Flux_2)*R1_k_2

Macrofauna_2(t) = Macrofauna_2(t - dt) + (Predation_2 + Grazing_4 - R3_2) * dt
INIT Macrofauna_2 = .071
INFLOWS:
Predation_2 = 8.03
Grazing_4 = 16.06
OUTFLOWS:
R3_2 = ((HMWHC+POC_Flux_2)/2) * R3_k_2

Meiofauna_2(t) = Meiofauna_2(t - dt) + (Grazing_3 - Predation_2 - R2_2) * dt
INIT Meiofauna_2 = 1.8
INFLOWS:
Grazing_3 = 24.09
OUTFLOWS:
Predation_2 = 8.03
R2_2 = ((HMWHC+POC_Flux_2)/2) * R2_k_2

Constants
R1_k_2 = 0.5
R2_k_2 = 0.4
R3_k_2 = 0.6

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7.   SUMMARY

The community structure of macrofauna at cold seeps was compared to the food-limited benthos on the northern continental slope of the northern Gulf of Mexico. The macrofauna communities studied at cold hydrocarbon seeps were are structurally distinct from the food-limited slope communities. This structural difference between the macrofauna indicated that the total sediment community composition is different between the two habitats. The overall changes in the structure of the sediment communities at cold seeps have also changed the total sediment community function.

Cold seeps in this study are found to have a greater density of macrofauna than the food-limited slope communities, but the macrofauna at seeps is smaller in individual size. The total biomass of macrofauna at cold seeps was also less than in the food-limited benthos. A shift in community structure towards smaller animal sizes is a common faunal trend in high-food environments. The competition for food in food rich setting is intense and the time of population turnover becomes less, thus animals have a shorter growth period until death. The diversity of macrofauna at cold seeps was also diminished due to the competitive removal of entire taxonomic groups from the habitat. Reduced diversity was also seen in the Tanaidaceans, the dominant seep taxa. Morphological changes in the Tanaidacean fauna, like the diminished size of mouthparts gave them a competitive advantage in harvesting resources from the sediments.

The change of the macrofauna community structure is indicative of changes within the entire sediment community. The shift in community composition was evident in the increase of the total sediment community oxygen consumption. This linkage between structure and function is mostly due to increased bacterial biomass, which in turn causes a greater use of oxygen in metabolic processes. The decreased size of the macrofauna causes them to respire at a faster rate, also increasing the sediment oxygen demand.

The high food environment created by the cold seeps biologically enhanced the sediment community. The bioenhancement of the fauna precipitated an increase in the total respiration of the sediment community. The use of a steady state model accurately showed how these changes in the fauna impacted the community function of a cold seep sediment community.

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