CURRENT KNOWLEDGE OF BENTHIC COMMUNITIES IN THE GULF OF MEXICO

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INTRODUCTION

In shallow waters, several species of benthic invertebrate organisms have historically contributed to the economies of the coastal states of the Gulf of Mexico as fishing resources (shrimp, lobster, crab, snails, clams, etc.) and recently, aquacultural production of these species is providing opportunities for development in the three countries that surround the basin. These opportunities include specialized production for the pharmacological extraction of bioactive compounds (from snails, corals, sponges) and other industries based on biopolymers, glues, dyes and other products that are derived from microorganisms and invertebrates. The benthos of deep waters, due to their abundance and the size and structure of their populations, do not offer the same opportunities for sustainable, commercial exploitation. On a global scale, the importance of the benthos is related to species, such as coral, that capture carbon in their centuries old carbonate skeletons and thus participate in the regulation of the climate and carbon cycling of the planet.

DEFINITION OF CONCEPTS

Organisms that inhabit the marine floor are defined as benthos. The benthos in the marine ecosystem are of great importance for the role they play in primary marine processes, and the biogeochemical cycles that are closely related to the recycling of materials in the interface between water and sediment. Benthic components occur all along the bathymetric gradient, from the littoral zone to the abyss. The association of the benthos, whether temporary or permanent, with the substratum is through bioturbation, boring, oxygenation and cementation of the sediment. Interaction with other species permits survival throughout the life cycle. Benthic activity can be on the substratum by those organisms that are termed "epifauna", that are usually large and visible in photographs and can be sessile or motile. Organisms are limited in their mobility; when they are found within the sediment taking advantage of the interstitial spaces they are termed "endofauna" or "infauna". These organisms are characterized by their small size and include macro- and meiofauna. These organisms and the sediments are closely linked, and there are relationships between components that result independent food chains that are affected by spatial relationships that respond in diverse scales in both time and space. At the same time, the benthos includes rooted vegetation, microalgae and biofilms consisting of associations between microalgae and bacteria. The simple presence of humidity means that the bacterial associations and the Archaeas survive in the most extreme chemical gradients of salinity, pH, Eh, and oxygen, both in the sediment-water interface and the inside of the sediment, and also at depths of more than 1 km in the interior of the crust.

BACKGROUND

Benthic communities in the Gulf of Mexico were first recorded during the first half of the 19th century in shallow habitats. Studies of benthos in deeper habitats began with expeditions carried out from large ships during the second half of the 19th century. Studies carried out during the 20th century were descriptive, characterizing coastal ecosystems mainly in the northern part of the basin. Studies in the southern section of the basin started midway through the 20th century. These studies were carried out primarily in shallow coastal habitats and were focused on species richness and systematic documentation of some groups, and have formed the basis of a good characterization of the structure of the benthic community.

Studies of the deep water ecosystems in the southern part of the Gulf were begun by North American colleagues in the 1970s and were continued through the second half of the 1990s by Mexican scientists with Mexican infrastructure. At national level, almost all research institutions have a researcher that specializes in the general study of benthic communities. The majority of researchers study the bays and adjacent littoral waters, and often specialize in a taxonomic group. At the international level, some researchers are highly specialized and each institution has more than one group of researchers that are dedicated to the characteristics of each one of the benthos components in the different ecosystems.

PRINCIPLE HABITATS

Benthos habitats in the coastal zone of the Gulf of Mexico have been widely studied and the best documented habitats include tidal and salt marshes, mangrove roots, and seagrass meadows in the coastal lakes and estuaries, and to a lesser extent, the beaches and rocky coasts. At the same time, information is abundant on the benthos of muddy bottoms and oyster reefs as well as the coral communities on the continental shelf, where resources for research have been concentrated. The benthic communities on the continental shelf that are associated with chemosynthetic activity on the floor, such as methane infiltration, brine, carbonates and clathrates, have been studied recently together with benthic communities in underwater canyons, escarpments, and mountains on the abyssal plain. These studies of the benthos show the wide diversity of ecosystems and habitats in the Gulf of Mexico. At different scales (ecosystem, landscape, and local), this diversity leads to the inference that high potential diversity of the Gulf of Mexico is equivalent to recognized terrestrial tropical and subtropical biodiversity hotspots. Table 7.1 and the text that follows provide a synthesis of the characteristics of the benthic marine habitats in the Gulf of Mexico in waters of Mexico's exclusive economic zone (ZEE) and are based on the results of studies undertaken in past decades by national and foreign researchers in the Gulf of Mexico. Table 7.1 also describes the role of benthic habitats in the ecosystems, their use and the main impacts to which they are exposed.

The coastal zone is a zone of confluence between land and marine ecosystems. Its boundaries are diffuse with marked salinity and temperature gradients as well as other environmental factors.

ESTUARIES

The estuaries or estuarine systems are, in the context of the coastal zone, coastal indentations with a restricted connection with the ocean that remains open at least intermittently (Day *et al.* 1989). Estuaries are considered among the most important ecosystems of the coastal zone because they are transition zones or ecotones between land and marine zones where the drainage of fresh water from the land is mixed with seawater. This interaction creates one of the most productive ecosystems in the world due to the continuous hydrodynamic control, the maximizing of light and the high concentration of nutrients, all of which are closely linked to one another.

Table 7.1. Characteristics of the main habitats and their relationship to anthropocentric values**.**

Habitat	Substrate Types	Extent	Total Area	Depth (m)	Salinity (psu)	Distance from continent (km)	Species Richness	Significant Structures
Coastal lagoons, bays & estuaries	Muddy sediments, seagrasses, mangrove roots	Large	Small	0-15	0-100	0-110	Variable; dependent on gradients of salinity & dissolved O_2	Seagrass beds, mangroves, oyster reefs, marshes, floodplains, tidal streams & rivers, lakes
Beaches & rocky coasts	Sand, gravel, mud, shells & carbonate shelves	Large	Small	30 snm-15	0-80	0-5	Low to moderate depending on substrate	Wetlands, hypersaline flats, *Spartina* marshes, mangrove forests, seagrass beds, polychaete reefs, bivalve reefs, rocky coasts & points
Inner Shelf	Soft sediments, sand, reefs, banks, shell bottoms	Very large	Small	15-60	0-36	0-5	High	Breakwaters, artificial reefs, petroleum platforms, banks, coral reefs, barrier islands, atolones, cenotes, *Halimeda* beds
Outer Shelf	Soft sediments	Large	Large	60-200	15-36	5-200	Moderate to high	Hypoxic zones, spawning areas, artificial reefs, petroleum platforms, atolones, islands
Continental Slope	Soft sediments, carbonate sediments	Large	Moderate	200-2800	34-35	50-300	Moderate to high	Low oxygen zones, infiltrations of methane & hydrocarbon, salt lakes, canyons, mud volcanoes, seamounts, turbid currents; erosion zones
Escarpments	Rocky	Large	Small	5-3800	34-36	5-300	Low to moderate; little studied	Vertical carbonate walls; infiltrations of sulfur, salt & methane; soft sediment deposits
Abyssal Plain	Soft sediments	Large	Very large	2800-3800	34.2	5-300	Low, little studied	Infiltrations of methane, salt & asphalt; salt domes

Table 7.1. Continued.

Ecosystem Function	Complexity	Productivity	Biomass	Anthropogenic Impacts	Anthropogenic Uses
Biogenic carbon production, export, capture & storage; breeding, nesting, nursery & refuge areas; nutrient remineralization	Ecotones; very high	High	Very high	Damming of rivers, urban & industrial waste, dredging, mariculture	Buffer & protection from storms & tidal surges; resources
Biogenic carbon production, export &storage	Very high	Low to moderate	Variable	Extraction of rock & sand, coastal development, mariculture	Buffer & protection from storms & tidal surges; energy, biotechnology & fishery resources
Biogenic carbon production & export; nutrient remineralization	Very high	Very high	Very high	Urban & industrial runoff; port development; mariculture; fishing (dredging & trawling); extraction of energy resources	Resources; biotechnology; genetic diversity
Biogenic carbon production, capture & transformation; nutrient remineralization	High	Very high	Very high	Fishing (trawling & dredging); extraction of energy resources; oceanic waste disposal	Resources
Biogenic carbon production & transformation; remineralization of nutrients	High, depending on fluid infiltration; ecotones	Varies locally	Varies locally	Fishing (trawling & dredging), extraction of energy resources; oceanic waste disposal	Resources; protection against storms & waves; little exploration
Biogenic carbon transformation; remineralization of nutrients	Variable; dependent on gradients of depth & light	Low, little studied	Low, little studied	Unknown	Biotechnology resources
Biogenic carbon storage/sequestration; remineralization of nutrients	Little studied; dependent on allochthonous & autochthonous contributions	Low, little studied; high when associated with asphalt	Low, little studied	Oceanic waste disposal; development of energy extraction facilities expected in the future	Resources; little exploration

In these systems, nutrients are retained and recycled efficiently. They are made up of a fluvial zone, a mixing zone (or the estuary proper), and turbid water in the nearshore zone of the open ocean that is associated with the mixing zone and the tidal plume. Estuaries are complex and vary considerably in geomorphology, hydrography, salinity, tides, sedimentation and energy. As a result of this complexity, biological communities change substantially from one estuary to another as well as within the same estuary. The variability in physical and chemical conditions means that it is difficult to distinguish between their effects on biological communities, natural changes (hurricanes, storms, etc.) and anthropogenic changes.

Estuaries support high biotic density and biomass. Biological diversity is notably low, but almost all animal phyla are found in high densities and these are represented by organisms in a wide range of sizes; the largest are demersal fish, crustaceans and mollusks. The habitats of the Gulf of Mexico have perhaps been the most studied by Mexican institutions. The habitats associated with wetlands and flood plains adjacent to the estuary include supratidal mudflats, beaches and salt marshes. The margins of tropical estuaries are often characterized by mangrove swamps. With respect to the smallest components, heterotrophic bacterial associations and bacterial associations that degrade oil respond to seasonal changes and have a combined metabolism that is determined by the species composition of the association. These groups inhabit sediments with different gradients of salinity and levels of organic material (Lizarraga Partida *et al.* 1987). The studies of Rogers and Garcia Cubas (1981) showed that oysters, a typical benthic fishery resource that forms banks and grows on mangroves, go through different maturation phases with low percentages of hermaphrodites (2%) and sex ratios of 1:2. Results of this type of study are useful to the management of biotic resources under variable conditions and in the context of the introduction of exotic species such as *Crassostrea gigas*. The development of faunal inventories of estuarine systems is considerably advanced. Reguero and Garcia-Cubas (1993) cataloged the malacofauna for 12 lagoons of the Gulf of Mexico documenting 25 molluscan species. The species richness of this group is highly variable. Thirty-two species documented in the Larga-Redonda-Mandinga lagoon system on the Veracruz coast, with 20 gastropods and 12 bivalves that feed from organic material that is deposited in the sediment (Reguero and Garcia-Cubas 1993). Similarly, 60 species of mollusks, dominated by two species of *Neritina* and a species of *Mulinia*, have been described in the Sontecomapan system in Veracruz in a simple system composed of sand and clay (Garcia Cubas and Reguero 1995). Gastropods dominate the 40 molluscan species in Laguna de la Mancha and they inhabit a great diversity of habitats (Flores-Andolais *et al.* 1988). It is estimated that there are 1,000 and 1,500 species of mollusks in the whole basin (Reguero and García-Cubas 1993).

At the subtidal level are found the seagrass beds, oyster reefs and sandy and muddy bottoms. These habitats are places for feeding, reproduction and refuge for benthic larval and juvenile stages. Two types of food chains characterize estuaries. In the first, primary production moves through a detrital food chain in which dead organic material (primarily vegetation) is decomposed by bacteria and fungi. In the second, the food chain in the water column is supported by phytoplankton primary production, that enters the benthos via filter feeding organisms and the next trophic level contains a high number of omnivores. Trophic efficiency is low, with losses of up to 90% between primary production and consumption. Detrital food webs are more conspicuously developed in shallow coastal bays and lagoons that support extensive salt marshes, mangrove swamps and seagrass beds.

WETLANDS, SALT MARSHES AND FLOOD PLAINS

The wetlands, salt marshes and flood plains of the Gulf of Mexico associated with the coastal zone on the boundary between the land and the sea are subject to flooding by rain and or other causes of excessive fluvial contributions. They form dikes and canals that carry out important functions in the coastal landscape and contribute to the high productivity of the coastal zone. Soils in flood plains are very fertile and valuable for agriculture, shrimp production and aquaculture in general. The coastal zone associated with rivers is interconnected by an extensive network of wetlands and temporary and perennial flood plains that act as filters, permit water retention, are sources and sinks of various substances, and are habitat for diverse submerged and emergent plants that are specifically adapted to this type of environment and associated fauna.

The main external factor is hydrology, which in the Gulf of Mexico is subject to considerable fluctuations in water levels depending on the season. Permanent wetlands are characterized by high diversity. Both flora and fauna require water level fluctuations and take part in the recycling and transference of nutrients between land and water. The recent re-damming and construction of canals or drainage systems has had a dramatic impact on populations in these systems due to loss of connectivity between flood plains and permanent bodies of water. In these conditions, only organisms with short life cycles survive.

The quantity and quality of solids and dissolved and suspended materials determine primary and secondary production in the wetlands, while the sediments and associated benthic fauna collaborate to trap nutrients, organic carbon, contaminants and toxic substances. There is a tendency toward eutrophication and salinization in wetlands of the northeastern Gulf and they are highly vulnerable to additions of nutrients originating in urban and agricultural areas. Many inhabitants of these environments have physiological adaptations that allow them to tolerate nutrients. Study of these adaptations at the molecular level is fundamental for aquaculture using high productivity hybrid lines. The studies that have been undertaken have focused on mollusks (Rodriguez *et al.* 1983) and fish in lagoon systems, and mostly on species that have potential for future aquacultural development and production (Maldonado-Monroy *et al.* 1985; Garcia Molina and Uribe Alcocer 1989; Uribe-Alcocer and Ramirez-Escamilla 1989; Uribe Alcocer *et al.* 1994) or use as biomonitors of environmental changes in the Gulf of Mexico (Uribe-Alcocer and Diaz-Jaimes 2000).

MANGROVE SWAMPS

The mangrove swamps are the only forest located at the convergence between land and sea in the Gulf of Mexico. They have unique ecosystem characteristics because they are ecotonal and develop best in protected areas with low energy. Their presence promotes deposition of fine particles that allow recolonization of the bottom with roots and propagules. Mangrove swamps represent a continuous gradient of geomorphologic types in a coastal zone that is dominated by fluvial contributions, modified by the tidal fluctuations, and determined hydrographically by waves, coastal currents and configuration of the flooded valley. The biomass generated is generally larger than in any other aquatic ecosystem in the Gulf of Mexico. The biomass of the roots under the substratum is the same as that above it. The benthic food web is simple and consists of interacting land and marine species. The architectural complexity of the roots provides the substratum for development of larvae, and accumulation of sediment, contaminants, nutrients and carbon. In addition, the roots are a refuge for invertebrate juveniles and larvae of commercial importance. The richness of the habitats is reflected in the diversity of species that inhabit and colonize the mangrove swamps and is determined by tidal amplitude, salinity and water quality.

As an example of the wide biological diversity associated with red mangrove (*Rhizophora mangle*), in Laguna de Terminos, 43 species of benthic polychaetes have been documented (Table 7.2). The polychaete assemblage is dominated by species from the genera *Capitella*, *Mediomastus*, *Laeonereis*, *Streblospio*, *Melinna*, *Parandalia*, *Marphysa* and *Eteone* (Hernandez-Alcantara and Solis Weiss 1991). In addition to the polychaetes, 17 species of mollusks and 27 species of macrobenthic crustaceans are also associated with the red mangrove. These communities vary seasonally in their composition and the abundance of species (Hernandez-Alcantara and Solis-Weiss 1995).

Biological diversity is correlated with the area represented by mangroves. Connectivity between mangrove swamps and adjacent ecosystems (e.g. coral reefs, seagrasses, etc.) is very close and influences the species composition. The relationship and characteristics of open waters of the continental shelf are relevant to species diversity and, in particular, to migration of larvae into the mangrove swamps and their return to the continental shelf.

SEAGRASS MEADOWS

Seagrass ecosystems have been recognized as crucial for the coastal zone of the Gulf of Mexico and their growth is restricted to marine and brackish environments (values higher than 5 PSU, sub-aquatic irradiance with values greater than 11%) that define their extent (approx. 30 m) and distribution inside coastal lagoons, bays, estuaries and on the continental shelf. In the Gulf of Mexico, seagrass meadows are distributed in soft sediments where organic material content is <6%, sulfur concentrations are <300 µM, and potential redox is >100 mV. Seagrass meadows are the most productive ecosystems on the planet although only 50% of this productivity is available to benthic herbivores that only consume emergent vegetation. The exportation rate of seagrasses to neighboring marine ecosystems is approximately 20% providing important trophic connections between coastal areas and the continental shelf/slope and abyssal plain.

Among the main functions of seagrass meadows is provision of dissolved oxygen to estuarine bottoms, lagoons, bays and the nearshore shelf. At the same time, marine grasses stabilize sediments, preventin re-suspension and improving water clarity. In addition, these plants diminish the impact of storm waves and protect the coastline, facilitate nutrient capture, and because of their architectural complexity, provide habitat and refuge for diverse organisms, including a highly diverse benthic invertebrate community.

ROCKY COASTS

Rocky coasts in the Gulf of Mexico are limited to the margins of Campeche, the Tuxtlas in Veracruz and increasingly, by vertical breakwaters and wharves in the states of Yucatán, Tabasco, Veracruz and Tamaulipas, where zonation of invertebrates, marine algae and land plants is in its early development. The vertical gradient is unidirectional with stress that increases from the emergent zone to more exposed portions where wave action has greater impact. Rocky coasts are extensions of terrestrial environments and as open systems they have the capacity to disperse larvae, propagules and adults of different species. Development of benthic communities on rocky coasts depends on the capacity of species to colonize locations and tolerate diverse gradients of conditions, and on their interaction with other organisms that respond quickly to change because of their physiological adaptations. Benthic communities on rocky coasts show great natural variation in both space and time. Diversity of these communities is generally lower than other coastal ecosystems in the Gulf of Mexico and they are composed of species that are predominantly filter-feeders that maintain water quality and may help reduce the spread of toxic algae. Because of their accessibility and position in the land-sea interface, benthic communities of this ecosystem are more vulnerable to impacts that originate on land and those that result from spills.

BEACHES

Sandy beaches are the most common ecosystems throughout the littoral zone of the Gulf of Mexico and are found in protected areas of bays, coastal lagoons and estuaries in addition to the open ocean coastlines. Beaches are dynamic coastal environments with unstable substrates and variable physical conditions that determine the type of community associated with the sediments. Particles of continental and marine origin that have been deposited by waves have diameters of 0.05-2 mm. In the Gulf of Mexico, the beach ecosystem is composed of dunes, beachface and surf zones, and there is constant interchange of materials between the three subsystems. The beaches on the southern Gulf of Mexico are largely characterized by the absence of rooted vascular plants in the intertidal zone and the apparent absence of large benthic organisms. Beach fauna are mobile and adapt to the changeable conditions caused by tides and exposure to air. The number of resident benthic species is low. They are cryptic species that emerge from the sand only at night or when the tide is in. When the tide is out, terrestrial species will come to the beach in search of food. The biological diversity of the benthic community, with all existing phyla represented, is mainly composed of fauna that inhabit interstitial spaces. Species richness and abundance are determined by the speed of tidal retreat, which is rapid in the Gulf of Mexico. The asteroid and echinoid fauna is relatively poor in littoral species (17) when compared to the Pacific Ocean or other tropical seas, although the faunas in the Gulf of Mexico have received less study than similar faunas on Mexican Pacific coast (Solis Marín *et al.* 1993). *Astropecten* and *Linckia* are characteristic asteroid genera, and *Diadema*, *Arbacia*, *Eucidaris* and *Encope* are characteristic echinoid genera (Solis Marín *et al.* 1993).

The transport of sand along the coast is a critical factor in the budget of sand deposition on beaches. The transported sand is accompanied by other materials that provide essential nutrients to intertidal benthic communities, given that primary producers are not abundant. The remains of wood and algae as well as the bodies of organisms are mainly consumed by larger epibenthic carrion eaters such as crustaceans and gastropods and also attract terrestrial predators and insects. The smaller suspended particles sustain filter feeders such as bivalves that live in the sand. The remineralization of uneaten material occurs within subtidal sediments to a depth of several centimeters. The scattered, gently sloping beaches that characterize the Gulf of Mexico are less hostile to fauna, which are both abundant and diverse, with more complex food chains.

SOFT BOTTOMS ON THE CONTINENTAL SHELF

In the Gulf of Mexico, the coastline continues subtidally on the continental shelf, defined as a relatively shallow platform that reaches from below the low tide mark to the continental edge, where the continental shelf abruptly drops off. The extent of the continental platform in the

Gulf of Mexico varies. The shelf is wide on Campeche Bank and narrow in the states of Veracruz and Tamaulipas. Similar to other ecological boundaries in the coastal zone, it is diffuse and not clearly delimited with respect to depth or characteristics of its sediment and associated fauna. The extent to which water from the continent influences the shelf varies in relation to fluvial discharges, with contributions from the rivers Champotón at the extreme southwest and Bravo at the extreme north of the ZEE. In addition, the influence of continentally derived waters is also affected by circulation, topography and the climate. A wide-ranging review of benthic communities on the continental shelf of the Gulf of Mexico is found in Rabalais *et al.* (1999).

Up to 50% of the floors of the continental shelf are muddy, and more than 40% of them are sandy with some gravel and fragments of shell and coral. In this sediment, called soft bottoms because of the dominance of mud, the dominant components of the benthic community are the invertebrates as well as economically important demersal fish.

The species richness is low in comparison to the shallow environments; however, the number of molluscan species is apparently higher than in the coastal lagoons of the Gulf of Mexico. In the north and northeast regions of the Yucatan Peninsula, 110 species of benthic gastropods have been reported between 28-617 m (Garcia Cubas *et al.* 1999) and 17 species of lumbrinerid (Family: Lumbrineridae) polychaetes have been found on soft bottoms between 15-200 m from Tampico to Yucatán (Solis-Weiss *et al.* 1995). These figures on diversity contrast with those recorded in systems where anthropogenic modifications seem to promote biological diversity. On the oil platforms located on edge of the continental shelf in the Bay of Campeche, 14 species of annelids have documented from the families Phyllodocidae, Glyceridae, Goniadidae, Hesionidae and Pilargidae (Granados-Barba and Solis Weiss 1997a), 14 from the family Spionidae (Granados-Barba and Solis Weiss 1998) and six more from the families Orbiniidae and Cossuridae (Granados-Barba and Solis Weiss 1997b). These types of descriptive, exploratory studies have led to the recognition of new species (Granados-Barba and Solis Weiss 1997a; Tovar-Hernandez *et al.* 2002), and new records in the Gulf of Mexico (Granados-Barba and Solis-Weiss 1994). Table 7.2 presents a comparative synthesis of the species richness of polychaetes by habitat. In the case of the echinoderms, 48 species of asteroids and echinoids have been recorded, mainly in Tamaulipas, Campeche and Yucatán (Caso 1971; Solis Marin *et al.* 1993; Barbosa-Ledesma *et al.* 2000). There are still a large number of species in the little studied taxonomic groups that await description, as in the case of many of the lesser phyla and very small and/or cryptic organisms. Some recent studies have revealed some of this fauna. One example of this is the new species of bopyrid isopod that infests the bronchial chamber of galatheoid crab *Munidopsis* from the continental slope in the southeastern Gulf of Mexico (Roman-Contreras and Soto 2002).

Hydrographic processes play a key role in structuring the continental shelf system through distribution of sediments and organic material from the water column to the bottom. Organic material on the bottom is then transported and redistributed by tidal currents and lateral transport, and its distribution largely explains patterns of species richness and faunal abundance. The distribution pattern that is commonly seen is that the quantity of organic contribution from the water column is related to the density of fauna in the sediment. This is an equilibrium relationship. At the same time, this correlation is linked to the rate of nutrient remineralization through bioturbation; trawling in the Gulf of Mexico also contributes significantly to the rate because it also moves bottom sediments. The nutrient contribution on the shelf is directly related to biomass and fishing productivity, however, the present equilibrium could be broken when the contribution is excessive and a large part of primary production in the water column is not ingested by herbivores and is exported to the floor consuming dissolved oxygen in the sediment-water interface. When this happens, hypoxia and even anoxia occur, preventing the presence of fishes, crustaceans and other organisms that compose the benthic community on the bottom. Hypoxia and anoxia simplify the benthos communities to such an extent that they promote change from metazoan communities to bacterial associations and anoxic environment microorganisms. This process is well documented in the northern Gulf, but is only just beginning to be studied in the southern Gulf of Mexico and requires stricter monitoring to determine its causes.

In comparison to the temperate and cold marine systems, secondary production and fishing in the Gulf of Mexico, as in other tropical seas, is low. However the production/biomass ratio in the Gulf of Mexico is high, due to the high metabolic rate of the organisms. In the Gulf of Mexico benthic abundance, biomass and community composition vary with distance from the coast and the proximity of rivers, estuaries, bays and coastal lagoons. These three components of soft bottom community structure on the continental shelf can also vary due to the presence of fossil hydrocarbons. The effects of hydrocarbons on distribution, abundance and biomass has been observed in penaeid shrimp in the Bay of Campeche, where the greatest density of larger individuals with concomitant higher biomass is found where oil is being produced (Soto and Gracia 1987). These observations can be related to the protection that the oil platforms give to the populations, by providing a refuge with high concentrations of labile organic material that has been degraded by clastic hydrocarbon bacteria.

HYPOXIC BOTTOMS

The term "hypoxia" is used to characterize water masses with dissolved oxygen concentrations lower than 2 mg/L (1.4 ml/L or 63 µmol/L). Hypoxia on the continental shelf of the Gulf of Mexico has been widely documented west of the Mississippi delta in late spring and during summer. The area affected each year varies but has increased from 8000-9000 km^2 between 1985-1992 to 15,000-19,000 km^2 between 1993-1997 (Ferber 2001; Battaglia and Goolsby 2001). Since 2000 this area has exceeded 20,000 km^2. Previous studies have identified some of the factors controlling the annual extent and variability of the hypoxic zone. It has been proposed that the concentration of nitrates originating form fluvial sources promotes local production, and at the same time, high biological activity under the pycnocline consumes dissolved oxygen (Rabalais *et al.* 2002). On the other hand, pycnocline stability is an important factor that prevents renewal of dissolved oxygen (Wiseman *et al.* 1992). The hypothesis that hypoxia is under biological control is based on the fact that the concentration of nutrients from rivers is significantly greater than to that normally found in ocean waters. The Mississippi River alone contributes 120 µmol/L of nitrates and up to 200 µmol/L of silicates to the waters of the Gulf of Mexico (Turner and Rabalais 1991). These concentrations of nutrients promote growth of phytoplankton, which as been widely recognized in Gulf waters off the Mississippi Delta and other saltwater areas adjacent to large rivers (Lohrenz *et al.* 1990, 1997; Sklar and Turner 1981; Biggs and Sanchez 1997).

The blooming algae that are not consumed by herbivores eventually sink to the bottom as detritus, are consumed and excreted degrading both sediment and water on the bottom through the consumption of dissolved oxygen and generation of hypoxia during summer when the pycnocline is stable. The flow of biogenic carbon that is exported to the floor varies between 500-600 mg C/m/d at a depth of 20 m (Redalje *et al.* 1994; Qureshi 1995). The hypothesis that hypoxia is controlled by physical factors depends on changes in local currents throughout the year (Li *et al.* 1997). Added to this is the lack of gas interchange waters on the bottom and above the pycnocline, due to slow advection and stratification which contributes to hypoxia. In years of excessive fluvial contribution, presence of fresh water in coastal surface waters strengthens the pycnocline. Both biological and physical mechanisms are important (Rabalais *et al.* 2002) and have lead to alteration of agricultural practices focused on controlling nitrate contributions in the northern Gulf of Mexico (Mississippi River/Gulf of Mexico Watershed Nutrient Task Force 2001; Ferber 2001) with the goal of mitigating the effects of hypoxia by reducing the affected area to just 5,000 km^2 by 2015.

The results obtained from research carried out during the LATEX and NECOP cruises have led to the recognition that, although a large part of the Texas and Louisiana shelf is affected by low concentrations of oxygen, the hypoxic region is well delimited and the water that does not come from the minimum oxygen zone of the slope. The lowest values that have been detected on the continental shelf are located below the seasonal pycnocline at salinities greater than 33 PSU in zones that present secondary thermoclines (Wiseman *et al.* 1992). The surface water (salinity less than 10 PSU or 25 PSU) comes from the Mississippi and Atchafalaya rivers. The salinity of marine water beneath the pycnocline is 34-36 PSU, and is the contrast between the density of both water masses, the surface and the floor, that determines the stability of the water column (Murray *et al.* 1998) and the capacity for the interchange of gases. The relation between fluvial contribution, light and currents that generate the physical control of the system is non-linear (Justic *et al.* 1993; Chen *et al.* 1997; Lohrenz *et al.* 1999; Chen *et al.* 2000). The frequency of hypoxia over time varies and depends on fluvial contributions to the coastal zone during the previous season. Information about this is scarce but it has been documented that local concentrations of dissolved oxygen in the 50 m isobaths are 6.0-6.5 mg/L at 25ºC in winter, and this is a consequence of the mixing that occurs as a result of wind action (Jochens *et al.* 1998). In some locations, conditions are maintained below the oxygen saturation point only in winter (Rabalais *et al.* 1999).

Primary production east of the Mississippi Delta is moderately high (300 g $C/m^2/y$; Lohrenz *et al.* 1990; Sklar and Turner 1981; Biggs and Sanchez 1997), but its origin has generated controversy. Some studies demonstrate regeneration of nutrients in the water column (Bode and Dortch 1996; Nelson and Dortch 1996), whereas others downplay the role of regeneration (Wilson-Finelli and Powell 2001) and identify its origin from nutrients generated in the sediment (Morse and Rowe 1999), and surging at the continental edge (Lopez Veneroni 1998). This controversy has increased with the recognition that nutrients limit production on the continental shelf in the Gulf of Mexico. The contribution of nutrients has been indicted as the main cause of hypoxia (Rabalais *et al.* 2002); however, the sediment N:Si ratio has increased since 1975 (Turner and Rabalais 1991), reflecting recent increased contributions of diatom tests to the bottom (Rabalais *et al.* 1999). Another factor that determines hypoxia in marine bottoms is the physical control exerted by bottom current velocity and stability of the thermocline.

Hypoxia acts on the benthic community of the continental shelf by reducing the number of vertebrate and invertebrate species to those that can tolerate low dissolved oxygen concentrations. The persistence of hypoxia over long periods replaces the metazoan community for anaerobic bacteria. Sulfuric acid is usually absent on these bottoms but is sometimes found in the water column suggesting that nitrates are the oxidizing agent in the water-sediment interface. The average rate of oxygen consumption by plankton in the deepest water mass is 2.2 mg $O_2/m^3/h$ with a continuous demand of almost 1 mg $O_2/m^3/h$ (Turner and Allen 1982). Maximum activity has been documented in summer and areas near the rivers. Oxygen consumption values of 318 mg O_2/m^3/d or 13.25 mg O_2/m^3/h are found with benthic respiration rates of 161-799 mg O_2/m^3/d or 6.6-33.0 mg O_2/m^3/h (Dortch *et al.* 1994). Average sediment community oxygen consumption is 32.13±14.02 mmol O_2/m^2/d and the respiration rate equivalent in carbon is 327.67±142.99 mg C/ m^2/d at an average depth of 22 m and temperatures on the bottom of 25ºC. There is wide variation between locations within the region (Morse and Rowe 1999) and is controlled by chemical, biological and physical factors. Chemical factors include increased turbidity, sandy particle flocculation rates, sediment accumulation, organic carbon and anaerobic metabolic activity in the sediment that produces ammonia, sulfur compounds and reduced iron and manganese species. High primary production is the main biological factor that controls hypoxia, and is related to the high light penetration, with high concentrations of nitrates and silicates and exportation of diatomic and other waste products that initially decompose under aerobic conditions and continue under anaerobic conditions. These factors lead to hypoxia and the loss of nitrates. An example of physical factors is density stratification prior to interchange of gases and reoxygenation of the water mass on the bottom. In this example, production is controlled by regenerated nitrogen (nitrites and ammonia) rather than nitrates. Sediment community respiration is aerobic with low organic carbon content and limited denitrification. Analysis of the sensitivity of current deterministic models of dissolved oxygen in the water on the bottom indicate the contribution of fluvial water and its effect on stratification better explains hypoxia than contribution of nitrates (Rowe 2000).

Other instances of hypoxia in the southern Gulf of Mexico are found in Laguna Madre de Tamaulipas, Laguna Tamiahua and outside the Río Coatzacoalcos delta. The first two areas experience hypoxia diurnally due to high concentrations of organic material and extensive cover of submerged vegetation. In the case of Río Coatzacoalcos, hypoxia is caused by a combination of high primary production on top of fluvial contributions and eutrophication caused by urban and industrial development in the adjoining coastal zone. Among the factors that can cause hypoxic areas in the littoral zone of the Mexican Gulf of Mexico are isolation of bays and ports, incorporation of untreated wastewaters, agricultural contributions of nutrients and sediments, agriculture, and deposition of airborne nitrogen compounds that result from hydrocarbon combustion for electricity generation and transportation.

CORAL REEFS

Coral reefs are shallow, subtidal ecosystems characteristic of the Gulf of Mexico continental shelf and edge that provide innumerable resources. They are characterized by the biological deposition of calcium carbonate by corals, mollusks, foraminiferans and algae on marine bottoms where water temperatures exceed 18ºC, with high illumination and excellent water quality, high aragonite saturation, stable, marine salinity and low concentrations of dissolved nutrients. Tolerance of the physicochemical factors that influence formation of coral reefs determines distribution patterns of characteristic reef organisms. When conditions differ from those described previously, the capacity to develop massive structures, such as those found on barrier reefs and atolls, is reduced and only small, poorly developed and low diversity patches are found.

Although physicochemical factors determine distribution, growth and success of organisms that form coral reefs, it is biological interactions within the reef that determines species abundance and organic and inorganic carbon production. The reefs in the Gulf of

Mexico are characterized by intermediate species richness with 28 scleractinian coral species out of 68 species documented in the Gulf of Mexico and Caribbean Sea (Castanares and Soto 1982). Dominance by algae or corals on a reef is determined by interactions between herbivores (e.g., fish, sea urchins) and algae. Balance between reef building and reef eroding processes is critical for optimum reef growth. Species composition and abundance are the result of the balance between organism activities and environmental factors. Differences between reefs are explained by three growth variables, which are density, rate of expansion and rate of calcification. These variables change with turbidity and sediment load. When the environment is more extreme, corals densities decline and although their skeletons continue to grow, they contain less calcium carbonate, as has been observed with *Montrastraea annularis* in the southern Gulf of Mexico (Carricart-Ganivet and Merino 2001).

The organic production of a reef is determined by herbivores and benthic algae. Increase nutrient concentrations and organic material in marine waters and reduction calcareous and coralline algae, corals, and predatory fish favors reefs with a high number of eroding organisms. On the other hand, increased sand production and low herbivory favors displacement of reefs by seagrass beds and microalgae. Despite the importance of seagrass beds in tropical ecosystems, when compared with coral reefs, they support fewer species and inhibit reef formation. Nine percent of the reefs found in the world's oceans are found in the Gulf of Mexico and Caribbean Sea. Chavez and Hidalgo (1989) documented platform-type reefs in the waters offshore from Tuxpan (e.g., Isla Lobos), Veracruz (e.g. Isla Verde) and Antón Lizardo (e.g., Isla Enmedio) and on Campeche Bank (e.g. Alacrán Reef). A comparative analysis of their structure shows that the reefs in the southern Gulf of Mexico are at different stages of development. In 1989, the main sources of disturbance to these reefs were urban effluent and oil spills, whether temporary of chronic, and with different degrees of intensity. These reefs are subject to great pressure from coastal development that brings, among other things, changes in reef community structure, due to overfishing, the mass mortality of the sea urchin *Diadema antillarum*, increased dissolved nutrients due to growth and urban development in the coastal zone, loss of the coral *Acropora cervicornis* due to the white band disease, and bleaching and infection by microorganisms conveyed by dust (atmospheric sources) and sediment (fluvial sources).

Both physicochemical and biological factors affect the patterns of species richness and abundance and the processes that determine biological production. Physicochemical factors include increased nutrients, changes in water transparency, dissolved oxygen, resuspension of sediment, heavy metals, other contaminants and potential redox change, and the disruption of the re-mineralizing process. Biological factors include loss of habitat, reduced species richness and key functions, disruption of connectivity, invasive species, and disruption of the capacity to decompose organic material. Reef recovery after perturbation is slow, because many reef components (e.g., corals, sponges) are slow growing (Haase-Schram *et al.* 2003). Species diversity is high, for example for the sponges, 13 species of the class Demospongiae were recorded in 1977 (Green 1977a) but almost a decade later 20 species were found between 2-15 m (Green *et al.* 1986). The interactions that exist among about 75% of reef species, particularly in the tropics, has resulted in acquisition of metabolic strategies that allow colonization of open spaces, predator avoidance, and resistance to bacterial infection, through production of highly toxic bioactive and antimicrobial substances (Green 1977b; Green *et al.* 1986).

DEEP SEA COMMUNITIES

The benthic communities in the Gulf of Mexico represent fauna of peripheral abyssal zones; basins where evaporation exceeds freshwater inflow and where waters from the Atlantic Ocean have an indirect effect via the Caribbean Sea. This connection is important because of the associations between the abyssal benthic faunas of the Atlantic Ocean, Caribbean Sea and Gulf of Mexico. This last connection is through the Yucatán Canal that separates the two basins: the eastern Caribbean (3,500 m) and eastern Gulf of Mexico (3,000 m) with a crest of 1,500 m. The counterpart of this relationship in the Gulf of Mexico and the Atlantic Ocean is through the Gulf Stream. The deep circulation has been little studied, however its residence time has been calculated at about 350±100 years (Broecker *et al.* 1961). Depth of this water mass varies between 2,000-3,000 m and has a potential temperature of (θ)=4.05ºC at (θ)=4.016ºC and salinity of 34.971-34.973 PSU (McLellan and Nowlin 1963) where the dissolved oxygen concentration varies from west to east between 4.2 ml/L and 4.4-5.0 ml/L.

Davie and Moore (1970) recognized five sediment provinces in the Gulf of Mexico. The deep sea sediments primarily originate from the Mississippi River(97%) and to a lesser extent, the Rio Grande River. This scheme was recently revised by the work of Balsam and Beeson (2003). Research into the export of biogenic carbon on the marine floor is in its infancy but it is estimated that because the Gulf of Mexico is an oligotrophic basin with a well-defined stratification, carbon fixation (expressed chlorophyll values) will be low between May and August (>0.06 g C/m^2/d) and high during the mixing period between October and March (>0.18 g C/m^2/d (Muller-Karger *et al.* 1991), thus export is limited to additions of greater size (7mm) that will sink at rates of at least 80 m/d (Diercks and Asper 1997).

The abyssal benthic communities that depend on the export of biogenic carbon in the Gulf of Mexico, inhabit soft floors characterized by sediments of biogenic origin and compounds of sand and mud. These communities have received greater study in the northern Gulf than in the southern section, but in general, megafauna (larger animals) are scarce and more widely dispersed when compared to the smaller components (e.g., macrofauna). Abyssal macrofaunal density and biomass are related to primary production at the surface. Densities in the southern Gulf (794-1,669 individual/m^2; Escobar *et al.* 1999) notably exceed densities in northern Gulf (19-31 individuals/m^2; Rowe *et al.* 1974). Higher values of macrofaunal density and biomass are found just below the minimum oxygen zone on the continental shelf. The main macrofaunal components of these benthic infaunal communities are polychaetes and pericaridean crustaceans; the primary meiofaunal components are nematodes and harpacticoid copepods. At the same time, there is great variability at depths >3,000 m, and suggesting that organisms inhabiting soft abyssal floors are patchily distributed. These communities represent the extreme opposite to those sustained by autochthonous sources and present a superposition in some cases, particularly in fauna with greater mobility such as crustaceans and some fish. Another important group associated with the benthos that has been studied in the Gulf of Mexico are scavenging crustaceans, including the amphipod genera *Orchomene* and *Eurythenes*, and isopod in the genus *Bathynomus* (Barradas *et al.* 2003). Because *Bathynomus giganteus* is abundant on the continental shelf, it has been possible to study variations in its diet and reproductive strategies throughout the year.

Together with the Mediterranean Sea, the Gulf of Mexico is one of the few peripheral seas that are not sustained exclusively by exported biogenic carbon. Autochthonous benthic communities sustained by methane or sulfuric acid were discovered at the beginning of the

1980's. These communities are located on the continental shelf in the northern Gulf of Mexico at depths of 500-2,000 m associated with areas of oil and methane hydrate production (Kennicutt *et al.* 1985, 1988). Paull *et al.* (1984) described chemoautotrophic benthic communities associated with infiltration of sulfur-rich hypersaline waters in the Florida Escarpment at 3,000 m. The benthic components of these communities are tubeworms in the genera *Lamellibrachia* and *Seepiophilia* that, unlike the hydrothermal vent worms, are sustained by sulfuric acid that flows from the sediment, through the rhizosphere and into the coelom. The tubeworm genus on the slope, *Escarpia*, depends on sulfur oxidation, in spite of existing methane infiltration and microbial and geothermal sources of sulfuric acid. Benthic components als include a diverse assemblage of molluscs including bivalves in the genera *Acesta*, *Bathymodiolus*, *Callyptogena*, *Solemya*, *Vesicomya* and *Idas*, and the gastropod *Bathynerita*. This type of environment is similar to an oasis with regard to the abundance of food and abyssal benthos associated with chemoautotrophic communities, such as sponges, hydroids, limpets, echinoderms, crustaceans, polychaetes and fish, are abundant.

The studies described above have been undertaken in the northern Gulf of Mexico. In the south, similar studies were not carried out until 2003. The information generated by oil exploration has been confidential until now and the oil industry's refusal to collaborate with research institutions has significantly delayed basic research. However, during the research carried out in Campeche Bay in 2003, abyssal benthic communities associated with newly discovered and described geological formations, asphalt volcanoes, have been documented. These volcanoes are generated by the eruption of asphalt (Figs. 7.1, 7.2 and 7.3), that is sufficiently ductile to flow freely for hundreds of meters down the slope of salt domes. The solidified structures of asphalt are similar to lava of the pa'hoe hoe and aá types. The asphalt flows are colonized by chemoautotrophic fauna whose biogeochemical dependency is significant different from that occurs in cold infiltrations that have been described in the world's oceans to date. These findings from 2003 permit the recognition of a new geological process, a new location of methane hydrate deposits and have significantly widened the zoogeography of deep sea chemoautotrophic fauna. These formations of asphalt were documented by Pequegnat (1971) in a unique photograph of a salt dome at a depth of 3,325 m, 12 years before the first tubeworms were discovered in Rose Garden in the Galapagos, leading us to speculated that this type of asphalt volcano could be widely distributed in the Gulf of Mexico and the Caribbean Sea.

The preliminary description of these communities includes, in contrast to the other chemoautotrophic communities, increased species richness and abundance of echinoderms and fish, crustaceans and bivalves that appear to feed on bacterial mats that grow in the cavities in the asphalt flows of volcanoes with differing activity periods.

ASSOCIATIONS OF DEMERSAL FISH

There are few studies of deep-water fish in the Gulf of Mexico and due to their low commercial importance. Currently, 119 species of demersal fish have been documented (Pequegnat *et al.* 1990) that are distributed at different the depth zones that correspond to the outer continental shelf and edge, upper, mid and lower continental slope, and the continental elevation.

The most abundant species on the outer continental shelf is *Antigonia capros* (McEachran and Fechhelm 1998). At greater depths, the ichthyofauna is dominated members of the Macrouridae: *Bathygadus macrops* and *Caelorinchus caribbaeus* in the upper slope, and

Figure 7.1. Hillock of added asphalt on the soft abyssal floor on which a crinoid, a colony of hydroids and coral branches are growing. Photograph from the joint campaign Mexico-Germany-U.S.A. on board the B/O *Sonne.*

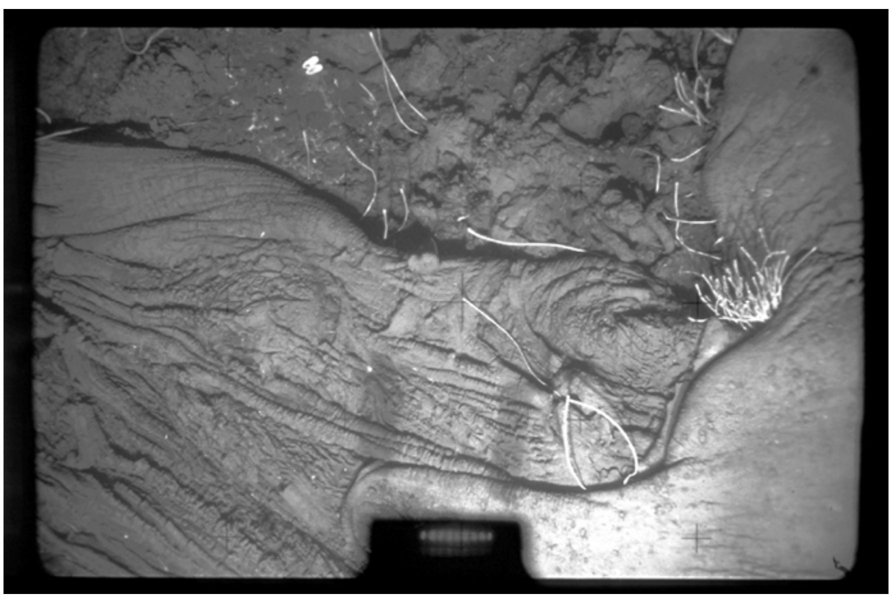

Figure 7.2. Margin of the asphalt volcano in the abyssal zone of the south of the Gulf of Mexico. The image shows folding activity and the most recent flow and is covered with still living specimens of associations of Phylum Vestimentifera tube worms of the genus *Escarpia*; groups of bacteria and open valves of a *Bathymodiolus* sp. can be seen on the bottom. Source: photograph from the joint campaign Mexico-Germany-U.S.A. on board the B/O Sonne.

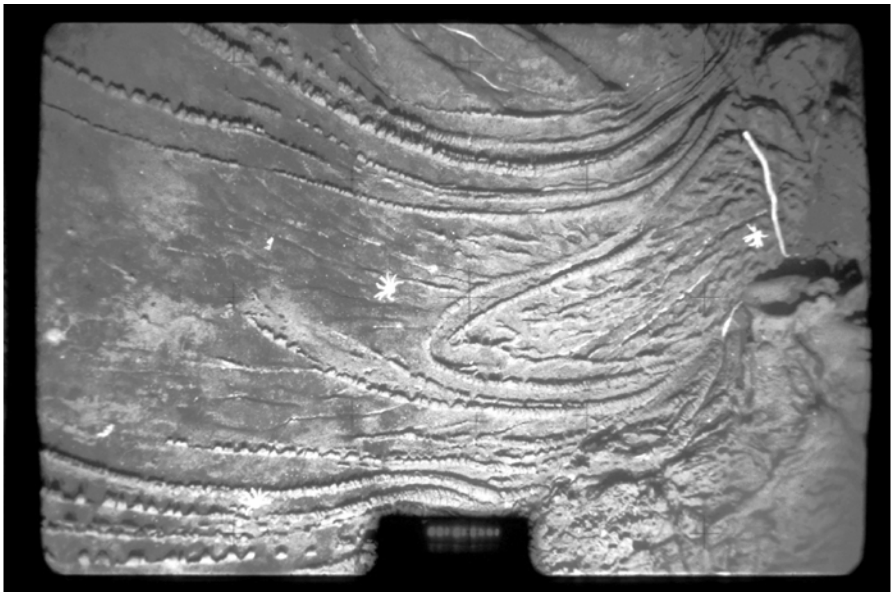

Figure 7.3. Surface of the asphalt volcano in the abyssal zone in the south of the Gulf of Mexico. The image shows three galatheid crabs of the genus *Munidopsis* and a Phylum Vestimenifera tube worm of genus *Escarpia*; the white marks that are in the cavities of the flows are bacteria and near the tube worm and the galatheid are two holothurians. Source: Photograph from the joint campaign Mexico-Germany-U.S.A. on board the B/O *Sonne*.

Nezumia cyrano and *N. aequalis* in the mid slope. The lower slope and the continental elevation are characterized by species in the family Ophidiidae, *Dicrolene kanazawai* and *Acanthonus armatus*, respectively(Powell 2001).

Species richness is greater on the upper slope, with 53 species, and decreases with depth; on the continental elevation only 17 species have been documented. Abundance shows the same pattern. The abundance of oil on the continental shelf and the present and future exploitation of energy resources will have a negative impact on communities and ecology of habitats that are found at these depths.

DEEP SEA CORALS

In the Gulf of Mexico more than 110 species of deep sea corals have been recognized, 51 of which were collected on the continental shelf and the continental elevation. The presence of extensive banks of *Lophelia pertusa* was first recognized in the study undertaken by Moore and Bullis (1960). In 1983, Pequegnat published a survey of the megafauna in the northern Gulf of Mexico between 300-3,000 m that included species of octocorals and hexacorals. More recent studies describe the geology and distribution of the species in the northeastern part of the Gulf (Schroeder 2001, 2002). Deep sea corals are common in canyons and on escarpments. The species *Funiculina quadrangularis*, *Stephanocyathus diadema*, *Chrysogorgia*, *Acanalla* sp., and another species of *Keratiosidinia* are characteristic of canyons in the northern Gulf of Mexico.

Examples of the octocoral *Ombellula* have been collected in the central Gulf between 1,800-3,700 m and are the most abundant organisms that have been collected at these depths. Many coral species are only known from photographs and have not been collected. At the same time, a large number of bigger fish (43 species) are associated with corals. Among the fish commonly associated with corals on the slope are species of *Sebastes*, *Urophycis*, and members of the Macrouridae and *Pollachius*. Occasionally, flatfishes (Pleuronectidae) in the genera *Hippoglossoides* and *Limanda*, have been reported, as well as sculpins (Cottidae), various rays and cods (Gadidae).

Because of their importance to fish, many deep sea coral systems have been destroyed by fishing nets. The diversity of invertebrates associated with deep sea coral banks includes sponges, polychaetes, crustaceans, echiurans, mollusks, bryozoans, brachiopods, echinoderms and cnidarians, many of which have been affected by complete destruction of the structural complexity of the system. Approximately 35% of the species that live in the Gulf of Mexico are common to higher latitudes and the only differences are found in the Octocorallia and the Hexacorallia (Cunningham 2002). The majority of species of deep sea scleractinian corals in the Gulf of Mexico exhibit tropical or temperate amphiatlantic or western Atlantic distributions and this contrasts with high latitude species with cosmopolitan or cold temperate amphiatlantic distribution pattern. The similarity between western tropical Atlantic and Gulf of Mexico corals is 75%.

Due to their extraordinary biological diversity, shallow water corals have been likened to forests and are potentially the most diverse ecosystems on the planet. However, deep water reefs have only recently been discovered, and even without the provision of light, are equally complex and diverse as shallow water reefs and also important to fisheries. These reefs are dominated by corals in the genus *Lophelia* with up to 1,300 species of associated invertebrates. More than 850 species of macro and megafauna have been recognized on deep reefs associated with oceanic mountains in the tropical eastern Pacific. The longevity of deep sea corals, and the diversity of demosponges such as *Ceratoporella nicholsoni* (Haase-Schram *et al.* 2003), provides a climatic archive that permits climatic change to be traced. These communities are equivalent in importance and diversity to shallow coral reef communities but human perturbation is more recent.

Development of these deepwater associations has only been feasible because of the slow growth of the corals and sponges and low disturbance during previous decades and centuries. Recent technological developments that allow exploitation of exploit deep sea resources, such as extraction of petroleum, natural gas, methane hydrates and minerals, and deep sea fishing, as well as the still unknown effects of global climate change, are just beginning to impact these little-known communities. Human activities, particularly trawling, have led to unprecedented damage to coral and sponge communities on submarine mountains, and on the continental shelf, edge and slope.

CANYONS

The deep canyons and channel that cut through the continental slope are habitats where deep sea corals are common. Studies of the canyons in the western Atlantic have shown that corals and other sessile fauna are more abundant there than on the continental shelf where bottom sediments are soft. Canyons are unique habitats because they contain heterogeneous substrates including rocks of various sizes and shapes, rocky aggregates, and carbonate blocks that differentiate them from the rest of the continental slope. Canyons provide suitable substrates for settlement by deep sea corals and play an important role in their ecology and distribution. At the same time, currents are more intense and distribute organic material from the continental shelf. These currents provide a steady source of food particles that can be filtered by deep sea corals.

Corals in the genus *Lophelia*, among others, are common where current velocities are higher and are sometimes found precisely where internal waves are generated. These currents also contribute to dispersal of corals and associated fauna in the systems where *Lophelia* dominates (Mortensen *et al.* 1995). In the Gulf of Mexico there are at least 20 canyons, five in the northern Gulf have been explored (Mississippi, Keathle and, Bryant, Alaminos, De Soto; Rowe and Kennicutt 2001), but only in the Campeche canyon in the southern Gulf has begun to be explored. In canyons, the ichthyofauna is as abundant as the corals (Powell 2001), and this is attributed to greater availability of food resources and productivity associated with the hydrodynamics of the habitat.

ESCARPMENTS

The walls of the escarpments differ significantly from soft slope areas of on the continental shelf or in some canyons. Escarpments are hydrodynamically active areas of the ocean floor where moderate currents are present, and octocorals and scleractinians are associated with these environments (Marshall 1979). The presence of gorgonians and alcyonarians is an excellent indicator of high energy. The study of these habitats is just beginning in the Gulf of Mexico due to the complexity of taking samples which advanced technology such as submersibles with robotic arms that are operated by remote control.

COMMUNITY STRUCTURE

Community structure of benthic communities in the Gulf of Mexico includes a wide variety of species of each of the different kingdoms. Large numbers of new species of archaea (bacteria-like organisms in extreme environments) and bacteria associated with chemosynthetic environments have been described in recent decades. These species of archaea and bacteria form microbial mats, are found in the water column and are symbiotically associated with benthic invertebrates.

In past decades, the processes of fermentation, reduction and oxidation were only detected by presence of diverse chemical compounds in the sediment, but have led to recognition of the yeasts and bacteria that carry out the reactions. New cryptic species of invertebrates and vertebrates associated with extreme habitats and are difficult to collect using traditional methods (nets and dredging nets), have been documented with photographs and retrieved with the aid of submerged apparatus.

The list of species of vertebrates and invertebrates is extensive encompassing 27 of the 28 phyla that are recognized in marine environments and including 13 endemic marine species. Of these phyla, six are frequent and abundant in benthic communities in the Gulf of Mexico: polychaete worms, pericaridean and decapod crustaceans, echinoderms, mollusks, nematodes and hydroids. Among the most complex benthic communities in the Gulf of Mexico are those associated with sessile benthic components such as seagrass beds, calcareous microalgae, pogonophoran worms and coral reefs. Species richness on the abyssal plain is similar to that on the continental shelf, but species composition is different as is the size of the organisms, which tend to get smaller with increasing depth. Among the determining factors for the biodiversity in the basin is sediment type, quality and concentration of organic material in the sediment, concentration of dissolved oxygen on the bottom and lateral transport and resuspension of sediments due to bottom currents.

COMMUNITY FUNCTION

Benthic communities are intimately related to neighboring systems allowing continuous multi-directional flow of energy and materials. Recruitment of benthic invertebrate species that spend a part of their life cycle in the neighboring ecosystems, both in the water column and on the bottom, is one of the closest links for the flow of energy. Length of food chains, changes in the biomass over time, metabolic rate, and remineralization rates describe community function at the interface of water and sediment.

Food chains in coastal ecosystems of the Gulf of Mexico are long and complex and link the herbivores and detritivores. Detrital food webs are the most common in the deep sea where light is absent. Each habitat also contains commensal and parasitic species (Román-Contreras and Soto 2002) and other biotic interactions that lead to complex food chains. Omnivores are abundant in the food chains and obtain energy plant fragments, fish remains, polychaetes, crustaceans, micromollusks and detritus, as in the case of *Callinectes similis* on the continental shelf of Veracruz (Chazaro-Olvera *et al.* 2000). In addition, there is a wide diversity of scavengers that respond to chemical stimuli from corpses that are deposited on the sediment. These chains consist of invertebrates and arthropods that are primary and secondary consumers, are efficient and extend to several trophic levels. The rate of biomass production by the benthos is high in the first trophic levels and responds to seasonality in the basin.

The benthic communities in mangroves, seagrass beds and coral reefs contain an abundance of resources that sustain high densities of organisms. Oxygen consumption varies in sediments; bacteria are the main consumer of oxygen in the shallow coastal zone and the lagoon and river systems adjacent to the shelf. Oxygen consumption is low in the abyssal zone and reflect metabolic adaptations to low temperatures and high pressure, rather than low abundance and species richness.

SEASONALITY AND THE ORIGIN OF FOOD CHAINS

Coastal and deep water benthos respond to two well defined seasons in the Gulf of Mexico; that correspond to the periods of winter storms and summer rains. The largest inflows of material and energy begins in winter and is associated with winter cold fronts or “nortes” that provide particulate material generated from mixing in the water column and riverine contributions. In summer, the coastal zone benefits from materials that arrive with rains; in contrast, the deep sea benthos receives few inputs during this season because thermohaline stratification of the water column impedes their export from above the thermocline. Excessive contribution of materials to the coastal zone, added to the production from the continental shelf, generates hypoxic zones. An example of this is the Mississippi River delta benthic recruitment is limited, creating depauperate zones that in turn affects fishing activities.

The hydrodynamics of mesoscale structures is one of the most important factors defining export of materials to the benthos in oceanic waters. Another mechanism is lateral transport of sediments that come from rivers on the edges of continents that is displaced to depth by turbid currents. The shelf adjacent to Río Coatzacoalcos receives materials exported through the anticyclone gyre and with the addition of nutrients from the river and hypoxic zones form in summer.

Other allochthonous contributions that sustain benthic communities come from shallow bottoms where seagrasses, the leaves, flowers, and roots of mangrove, and sediment are exported during storms or by turbid currents. This material is commonly found over the continental shelf and abyssal plains and is slowly degraded by bacterial associations. Scavenging organisms such as the amphipod *Eurythenes gryllus* lives off corpses of pelagic and demersal fish that inhabit some fishing grounds or, in their absence, they live on infaunal components found in the sediment. There are several studies with the support of stable isotopes that use a carbon isotopic composition ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), and that include the determination of the sources of organic carbon and the trophic position of the benthic faunal components in the food chains of estuaries, lagoon systems and the continental shelf, and more recently in the deep sea.

BIOGEOGRAPHY

The connectivity between benthic species in the basin depends on the presence of pelagic larval stages that allow transport across great distances by surface currents. Studies on connectivity have centered on species with commercial importance (lobster, mollusks, demersal fish), or of those whose habitat is at risk such as coral reefs, seagrass meadows, mangrove swamps, etc.). Larval retention largely depends on seasonal and local current patterns that guarantee the conditions for larval development until they recruit into the ecosystem in question. In biogeographic terms, many components of the benthic communities in the Gulf of Mexico are associated with the Caribbean Sea and the western Tropical Atlantic Ocean. A few of the oldest components have are linked to Carolinian and Virginian provinces. Many of these species area smaller in size in the Gulf of Mexico where the food availability is lower.

Endemism of benthic components is high in bays in the coastal zone with unique hydraulic conditions. Species without pelagic larval phases, i.e. those with direct development such as the tanaids and amphipods, are often endemic in basins of the continental slope. Similarly, detailed mapping has revealed the existence of sub-basins on the continental shelf that are separated from one another by walls up to 100 m high and delimited by currents with speeds greater than 1m/s. These sub-basins which isolates species that are not dispersed pelagically, often meiofauna, promoting endemism that remains to be studied.

The west and east winds in low latitude north Atlantic wind field, transports warm surface water to the Lesser Antilles. These currents move into the Caribbean Sea where they eventually converge with the Caribbean Current and are displaced to form the Loop Current when they move into the Gulf of Mexico through the Yucatán Channel. These currents eventually return to the Atlantic Ocean through the Florida Straits. A large number of benthic larvae in the Gulf of Mexico are linked with the Caribbean Sea and the western tropical Atlantic Ocean through this mechanism.

The Caribbean Sea is the basin that is richest in shallow coral reefs in the tropical Atlantic and is connected to the Gulf of Mexico and transports and disperses pelagic larvae of benthic organisms (e.g. lobsters, corals, shrimps, mollusks). This has been shown with buoys that were dropped at several points in the western Atlantic Ocean, the Caribbean Sea and the Gulf of Mexico. A number of contaminants that remain in the water mass for prolonged periods are also dispersed in this manner. The experiment with YOTO buoys (Wilson and Leaman 2000) has been fundamental in the region and has led to the identification of several current connectivity patterns, with some tending to retain the buoys for months within cyclonic gyres, whereas others flow directly in a few weeks. At the same time, the patterns depend on where the buoys were originally dropped and this is of great importance for the connectivity of populations of benthics fauna, their genetic interchange and how management and restoration programs should be applied in coastal systems.

Seventeen Palace type buoys were registered between 1998 and 2002 at water mass depths of 900 m in the Gulf of Mexico. The trajectories and water temperatures recorded by almost 1,300 buoys reveals a cyclonic flow pattern throughout the continental shelf in the western Gulf of Mexico that intensifies in Campeche Bay. These results suggest limited communication in the flows between the eastern and western Gulf of Mexico at the depth of the slope as well as persistence of a cyclonic gyre in the southeastern Gulf of Mexico where there is continuous contribution of coastal water. The relevance of these results in the framework of the deep sea benthic fauna is related to the possible genetic isolation of populations in the Gulf.

FACTORS THAT DETERMINE DIVERSITY

With the exception of communities subject to extreme conditions, benthic communities in the majority of habitats are diverse and with high species richness and low abundance. The extreme habitats that are exposed to salinity extremes, high temperatures, low dissolved oxygen concentrations, or are subject to high velocity currents, or the bottoms are exposed to chronic disturbance, are characterized by communities with low species richness and high abundance.

The benthic communities of the Gulf of Mexico are exposed to a number of natural or anthropogenic activities that modify habitat. The extreme effects generated by natural processes are seen in tropical cyclones that fragment coastal ecosystems and disturb spatial heterogeneity. The recuperation time for the loss of diversity as a result of this type of phenomena is about a decade. Other variations due to natural phenomena such as winter cold fronts, El Niño, La Niña and the North Atlantic Oscillation have just begun to be explored.

The anthropogenic activities in the basin are diverse and include excessive flow of nutrients from rivers that promotes hypoxia and anoxia in the coastal zone. The damming of water on the land affects habitats in the coastal zone, with reduction of mangroves and seagrass meadows due to retention of sediments and dominance of marine water. Agricultural activities on the land have an influence through the contribution of fertilizers, herbicides and insecticides to the coastal zone that are incorporated into the food chain or accumulate in sediment influencing structure and functioning of communities as they affect benthic components. Dredging sediments in the coastal zone for navigation, marinas and construction of port structures expose the environment to contaminants. Dredging is a common activity that results while fishing for benthic resources. The greatest perturbation occurs during the first dredging when the three-dimensional structure of the habitat is destroyed, analogous to cutting down a forest. Successive dredging has chronic consequences because it simplifies community structure. The basin is characterized by great reserves of non-renewable resources such as caltrates, gas and oil, and their extraction requires construction and/or suspension of structures on or over the bottom. A large number of studies of shallow waters, estuaries and coastal lagoons have evaluated the concentrations of demersal invertebrate and vertebrate fauna and the effect of oil on the benthic organisms in the Gulf of Mexico. Botello *et al.* (1997) revised this subject that deserves attention. The concentrations of PAH in the tissue of 685 benthic organisms varied from 8-2,340 µg/g (dw), and this indicated incorporation of oil from spills, accidental discharges, exploitation and natural infiltration.

FINAL CONSIDERATIONS

With regard to the benthos, almost all habitats and ecosystems can be considered vulnerable. Only in those subject to environmental instability and those susceptible to chronic perturbations has reduced diversity been recognized. However, diversity in other habitats that are disturbed has not been affected. In the future, actions and efforts for conservation of benthic communities include investments in basic scientific studies that will provide a better understanding of connectivity between/among benthic communities. Life cycles and physiology of the species with potential for use in marine biotechnology need study. In addition, long-term studies of communities in habitats and ecosystems that are not currently considered vulnerable should be undertaken with the objective of discovering natural community variations in the context of global changes and the effects of connectivity.

Until now, predicting change is one of the least documented aspects and requires databases on environmental factors and community related factors to make predictions and support decision-making over long time scales. In Mexico it is important to increase the number of benthic community specialists so that each of the communities is widely understood. Specialization among researchers has contributed considerably to the understanding of the northern basin and has led to the development of adequate proposals for its management. A possible starting strategy would be to make an intensive effort to study priority regions of the Gulf of Mexico where little is known, or those regions with high species richness.

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