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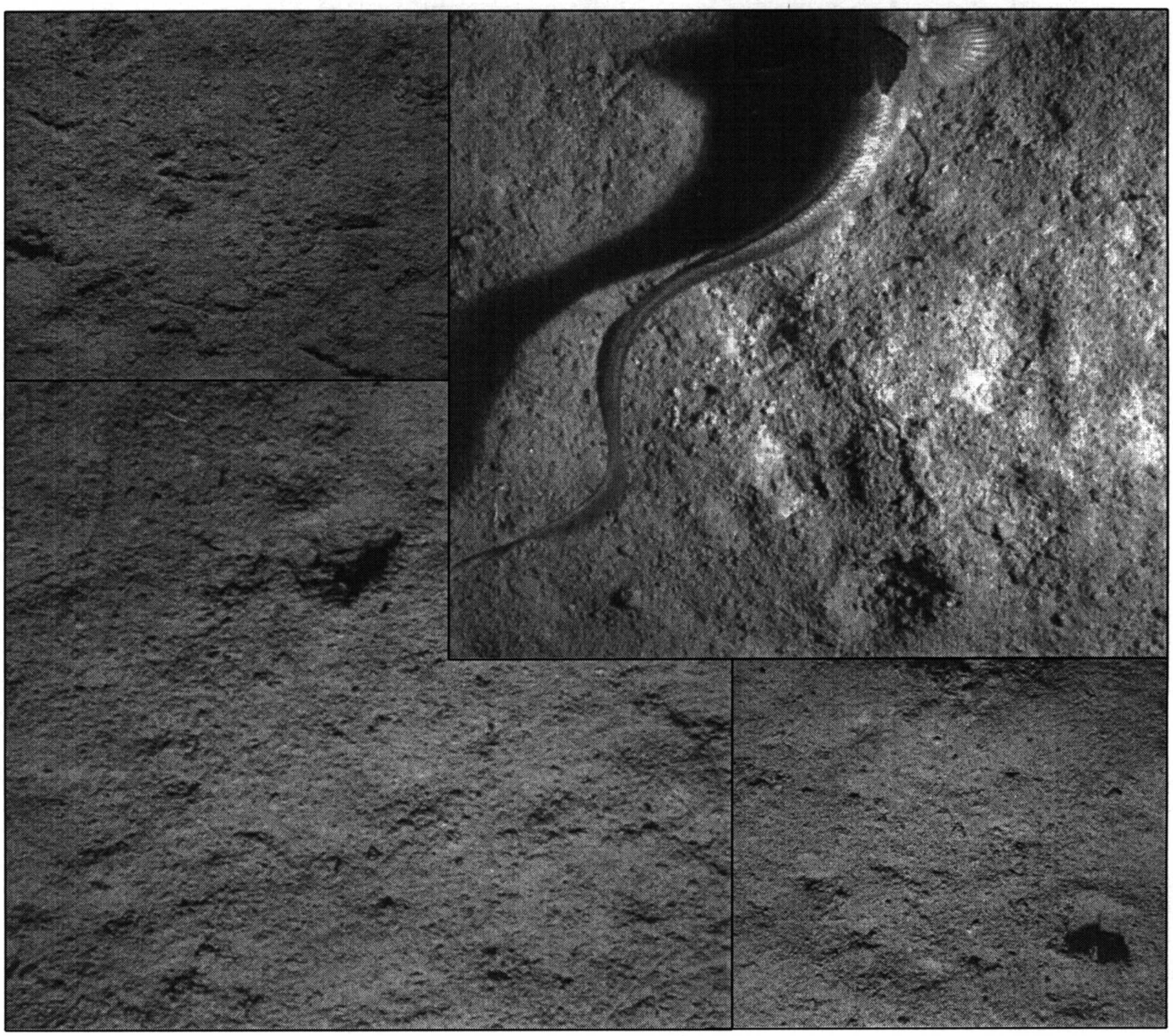
MMS 2001-095

Coastal Marine Institute

Management Applicability of Contemporary Deep-Sea Ecology and Reevaluation of Gulf of Mexico Studies



U.S. Department of the Interior
Minerals Management Service
Gulf of Mexico OCS Region

Cooperative Agreement
Coastal Marine Institute
Louisiana State University

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ABOUT THE COVER

The four photographic images are symbolic of the low level of understanding about the deep ocean ecology that resource managers must contend with. Three images show seemingly homogeneous seafloor with some fine-scale bottom topography of unknown origin. Hidden within that fine structure, however, is one of the highest species diversity on Earth. The upper-right image shows part of a rat-tail fish, but even this well-known animal is poorly understood.

SUMMARY

Scientific knowledge of the deep ocean is meager when compared to that of coastal areas. As a result the Minerals Management Service or any agency charged with environmental management in deepwater is placed at a disadvantage with respect to developing scientifically sound management strategies. Deepwater management requires extensive new data gathering and critical evaluation of the adequacies of existing information. A status review of contemporary deep-sea ecology found four areas of basic research especially relevant to management. First, the sensitivity of deep fauna to impact must be known. Traditional generalities about deep natural histories, however, are being discarded, complicating the task of making predictions about sensitivity. Second, the deep-sea biota is not uniform from the 200 m upper limit of deepwater to the base of the continental slope. The exact nature of faunal gradients must be known to develop depth-appropriate monitoring plans and regulations. Third, the processes that maintain a high species diversity in the deep-sea must be known if impacts are to be avoided. Fourth, if food is truly limited in the deep sea, then interruption of the processes of supply and utilization may be the most sensitive process of the ecosystem.

Past efforts by federal agencies provide relatively little information relevant to regulation of deep oil and gas development. Some of these studies focused on human health rather than ecology, and others addressed very different impacting activities. The studies associated with manganese nodule mining do, however, serve as a useful guide. They focused upon detritus foraging; they linked environmental monitoring to large-scale industry activity, and they included a mix of federal and industry initiated research.

Most information about the Gulf of Mexico typical deep-sea benthos was provided from two studies, the long-term exploratory sampling of Pequegnat and the shorter-term transect sampling of the Northern Gulf of Mexico Continental Slope (NGMCS) study. The former focused upon megafauna and proposed zoogeographic divisions on the basis of biotic and abiotic data. The latter focused upon macrofauna and addressed the validity the zoogeographic patterns through faunal analyses. Lack of balance in statistical testing, however, left the validity or invalidity unresolved. On reanalysis, three important findings emerged. First, the Gulf slope may have higher species richness than found off the US Atlantic coast. The findings however, are technique sensitive. Second, diversity is uniformly high with depth, not showing a lower slope maximum. This suggests different mechanisms of diversity maintenance in the Gulf. Third, the Gulf slope shows a lower biomass than the Atlantic, but the distinction decreases with depth. Again, the results are technique sensitive.

Chemoautotrophic communities represent a distinctive ecosystem of high biomass, low species richness, specialized fauna, and partial isolation from the detritus-based food web of the surrounding deep sea. Between 400 and 1000 m in the northern Gulf of Mexico the chemoautotrophic and associated heterotrophic species composition varies site-to-site. That variation reflects changing combinations of a limited set of species. The factors determining each local fauna combination remain unknown. Species succession, to the extent that it takes place, may be controlled with a geological transition from young, fluid-prone to older mineral-prone seeps. Monitoring of markers found no recovery from sampling disturbances.

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1 Introduction

1.1 Introduction: Environmental Management of the Deep-Sea Floor

The topics of this report are intended to aid ocean managers, especially the Minerals Management Service (MMS), with the task of formulating management strategies appropriate for the deep sea environment. This report supplements the broader consideration of deep oil and gas development contained in Carney (1998). Three topics are considered: (1) general deep-sea ecological knowledge, (2) regionally specific knowledge about the Gulf of Mexico, and (3) hydrocarbon seeps, a special class of deep-sea system. The perspective taken in reviewing each topic is the same, and is based upon a pragmatic view of the task facing MMS. Oil and gas development has been managed by MMS at shelf depths for about 40 years under a strategy based on scientific knowledge of that environment. As industry moves into progressively deeper water, MMS must decide to what extent the shelf strategy can be applied and how to most effectively obtain relevant information about a poorly known environment. In the context of these needs, this review attempts to do three things: (1) determine what is known; (2) determine what is relevant; and (3) critically evaluate the seemingly relevant information.

More detailed information is available in the few excellent books on various aspects of deep-sea ecology that have been published in the past decade. Most notable are the comprehensive review in a textbook format of Gage and Tyler (1996), Deep-Sea Biology: A Natural History of Organisms at the Deep-sea Floor and the consideration of deep fisheries by Merrett and Haedrich (1997) Deep-Sea Demersal Fish and Fisheries. Written coherently by just two authors, both are highly comprehensive and useful books. Van Dover (2000) has produced an excellent compilation and synthesis of information on hydrothermal vents, Ecology of Deep-Sea Hydrothermal Vents. That work provides a brief, but very informative discussion of cold seep systems as well. Multiple author collections have also appeared. A critical evaluation of ideas concerning reproduction in the deep-sea has been compiled by Young and Eckelbarger (1994), Reproduction, Larval Biology, and Recruitment of the Deep-sea Benthos. Trophic structure and carbon influx has been treated in Deep Sea Food Chains and the Global Carbon Cycle edited by Rowe and Pariente (1992). Unfortunately, there are few contemporary books focusing on the major taxa in the deep-sea. A notable exception is the Randall and Farrell (1997) edition of Fish Physiology Vol. XVI devoted to deep-sea fishes.

1.1.1 Origins of the Wasteland View of the Deep-Sea Ecology

In a broad sense, the generic need for deep-ocean management strategies arises from two different development plans for the seafloor. To some developers, the deep-sea floor is valued land offering resources such as food, hard minerals, and hydrocarbons. To others it is inherently valueless, a wasteland providing a socially acceptable repository for highly hazardous materials. Until now, the scientific development of deep-ocean environmental management has been minimal for practical reasons. Little immediate need for management has been seen, since deep-ocean resource plans have been futuristic, and most ocean disposal has been banned. Adding to this lack of pressing need, the deep ocean is comparatively far removed from human habitation, and coastal marine habitats have had a justifiably higher regulatory priority.

While hard mineral mining, waste dumping, and deep-ocean fisheries remain somewhere in the future, oil and gas development is progressing rapidly down the continental slope. Thus, the Minerals Management Service (MMS) of the US Department of Interior now faces the task of wisely managing development of deep US waters. That task is a complex one. MMS must protect a vast poorly known environment from unacceptable impact while avoiding unnecessary restriction of an industry that is accepting great capital risks in pursuing new technologies. Managers at MMS and other regulatory agencies should be prepared to encounter people in industry, the general public, and even ocean science who do not feel there is any need for deep ocean environmental concern. This assumed lack of regulatory need is due to the deep sea's misunderstood status as a wasteland; the last remaining wasteland in some people's view. The classification "wasteland" is a time-honored societal judgement. Society has always produced waste materials and disposed of them in convenient areas of no particular value. Two hundred years ago populations and technology were less waste producing, and wastelands were easy to find. There was much undeveloped land and no understanding of how watersheds, groundwater, and food chains might interconnect. Modern society has virtually run out of terrestrial wastelands, yet, our wastes are more abundant and increasingly hazardous. Unfortunately, the deep-sea is seen by some as an appropriate waste repository.

The origins and persistence of the idea that the deep-sea floor is a wasteland with little ecology to protect has an interesting history in the oceanographic literature that explains the current confusion of some scientists on the matter (Carney 1997). As a result of the Challenger Expedition, Murray (1895) enthusiastically reported a highly diverse but low-density fauna comprised of many species new to science. Oddly, this report had minimal impact on subsequent workers. In a seminal book, Tiergeographie des Meeres, Ekman (1935, 1953) chose to force deep-sea observations to conform to the "biocoenotic principal" and stressed the low abundance rather than high diversity. It was this partial view of deep-sea biology that was incorporated into the first widely used oceanography text (Sverdrup, et al.1942). The Oceans remained in use as a graduate text into the 1970's misinforming many geological, chemical, and physical oceanographers about the deep sea. Even though biological oceanographers are usually taught about the rediscovery of high deep-sea diversity (Sanders et al.1965) during graduate education, the topic is often omitted from marine biology texts and even texts on diversity theory.

1.2 Structure of Report

Chapter two on general deep-sea ecology is organized into eight sections. Where appropriate, the sections are written with conclusions given first and details second. Section one provides a brief sketch of properties that characterize the deep-sea environment and considers which are more likely to be important in environmental impacts. Section two reviews deep-sea fauna by taxa and size category. Section three reviews information about faunal change with depth. Four considers the complex topic of species diversity. Five reviews ecological processes. Six examines past US federal and one English program that attempted to develop science-based management of the deep environment. Seven reviews current methods of deep-sea study. Section eight provides a summary with recommendations.

Chapter three reviews the long-term sampling of Willis Pequegnat and colleagues at Texas A&M and the three year NGMCS study (Northern Gulf of Mexico Continental Slope) conducted by LGL Ecological Research Associates Inc. and Texas A&M. Section one details the procedures used in the review and the limitations of the available data archives. Section two presents an overview of the studies in terms of design, methods, and general results. Section three presents an overview of east-west Gulf differences focusing on oxygen data. Section four provides an introduction to the fauna collected in the Gulf. Since opinions about zonation played a major part in previous Gulf studies, this topic is treated separately in section five. Section six critiques and summarizes the extensive use of analyses of variance in the NGMCS study. The following three sections consider megafauna, macrofauna and meiofauna separately. Section 10 includes conclusions and recommendations.

Chapter four's intent is different from the others in that it seeks to add new information to a growing synthesis about hydrocarbon seep communities. It does this in three ways. First, it adds additional faunal survey sites to the existing MMS-developed geographic inventory. Second, it extends the observation time of recovery experiments and monitoring markers. Third, it summarizes a geological-control model of seep succession, suggesting incorporation of a gradient-competition component to explain natural variation in species composition.

2 A Review of the Management Relevance of Deep-Sea Ecology

The ocean waters and bottom beyond the edge of the continental shelf comprise the largest and least studied ecosystems. As with any poorly studied system, the number of questions about its nature and functions far exceed the number of accepted facts. Even for those facts, the limited amount of sampling and the vastness of the environment call into question exactly how well established they truly are. Thus, the task of developing deep-sea management strategies requires three determinations: (1) what is known; (2) of that, what is relevant; and (3) of that, what is truly valid?

This review is intended as a start to making those determinations. By design, the review is narrowly focuses upon deep-sea benthic ecology. It does, however, begin with a brief consideration of the physical environment since the extreme physical factors are clearly of great biological importance. Serious omissions of the review are the lack of any consideration of the deep pelagic environment and no detailed consideration of the sedimentary environment. The deep pelagic environment is even more poorly known than the benthos. As the habitat of charismatic species such as sounding sperm whales and giant squid, it is a region that can capture the public's imagination. Deep-sea geology is a very active field of research, and certain components are highly relevant to an ecologically relevant characterization of habitat. However, the task of establishing that relevance is substantial and well beyond the scope of the current review.

2.1 Physical Properties Characterizing the Deep-Sea

In asking the thematic question, " is there scientific evidence strongly indicating that shallow-derived management strategies can not be applied to deepwater", it is appropriate to begin by examining the non-biological aspects that set shallow apart from deep. To do this, it is necessary to decide where the deep sea begins. Ocean geomorphology provides the basis for a legal definition of deep sea, beginning at the break of the continental shelf. For the purposes of the Law of the Sea, the United Nations set this at 300 fathoms (Guilcher et al. 1957), an isobath selected to include the deepest breaks. For oil and gas regulation, the depth may be taken as 200 m which coincides with the shelf break in the Gulf of Mexico and is used in the Deepwater Oil and Gas Royalty Relief Act.

When the deep ocean is defined as that zone lying below 200 m, it is obvious that this is not a physically homogenous environment. The uniformity of physical characteristics typically associated with deepwater ecology starts deeper at approximately 1000 m. Thus, management may need to consider the 200 to 1000 m zone (the upper continental slope) a separate zone of environment transitions. It is in this zone where sunlight effectively vanishes, where temperatures and salinity become stable through the seasons, and where oxygen drops to a minimum value. The interaction of physical processes and potentially impacting oil and gas activities may be different in this transition zone than deeper. A summary of concerns appropriate for this transition zone and the rest of the deep environment is presented in tabular form (Table 2.1). Discussions of these points are presented in the following subsections.

2.1.1 Pressure Effects

It is well established that there are major biological effects of hydrostatic pressure. Hydrostatic pressure is a function of depth and the density of seawater. with exact pressure described by the seawater equation of state and depth. For ecological purposes, density variations can be ignored and pressure considered to increase one atmosphere for every ten meters of depth.

Pressure causes some simple physical-chemical changes. First, water is slightly compressible (about 1% decrease in volume at 3500 m depth). Therefore, pressure alters volume concentration of solutes, makes water slightly more acidic, and raises the temperature (adiabatic heating) slightly. These physical effects are treated in any advanced physical oceanography text such as Apel (1987). Second, pressure influences the rates of chemical reactions including dissolution and dissociation. While the theory behind these effects is simple, it has little predictive value, and the actual effects must be measured experimentally. The theoretical basis for pressure effects lies in volume change. If a chemical reaction produces an increase in volume, pressure will oppose that reaction. If there is a volume reduction, pressure will promote that reaction. This model is marginally adequate for inorganic chemical reactions. Organic reactions, which are stereospecific, may be more sensitive to pressure then volume changes predict.

There are three pressure effects that may be most important in deep-sea ecology: enzyme reaction rates, the solubility of calcium carbonate, and the stability of gas hydrates.

- Solubility of Calcium Carbonate - It has long be noted that abyssal sediments below approximately 4000 m lack the abundant calcium carbonate tests of foraminifera that give sand-sized grain structure to bathyal and upper abyssal muds (Biscaye et al. 1976). This depth distribution was formally explained in terms of the calcite compensation depth, CCD, a depth at which the dissolution of sinking tests equals the rate at which the material accumulates. Above the CCD carbonates accumulate in the sediment, while below they do not. The sharp vertical demarcation suggests that the solubility of carbonate must undergo a rapid increase over a relatively narrow depth range, termed the lysocline. The lysocline is primarily the consequence of pressure and pH influencing dissolution (Archer 1991). Since respiration and water mass age influence pH, the lysocline is deeper in the older Pacific water than the Atlantic. The lysocline varies in depth throughout the ocean. In the North Atlantic, it lies at about 4000 m depth. Due to the relative shallowness of the Gulf of Mexico, the phenomenon has been poorly studied there. There are two management-relevant aspects of pressure effects upon calcium carbonate dissolution. First, differences in sediment texture above and below the CCD may cause ecological differences. Second, shallow-water models for fates and effects of carbonate containing discharges can note be applied in or below the lysocline.
- Clathrate Hydrate Stability – Clathrate hydrates are solids consisting of a water molecule cage trapping a low molecular weight hydrocarbon, typically methane. They are associated with chemosynthetic communities, and in some settings may be a prerequisite for their existence (Carney 1994). They

are found in deep-sea sediments where there is an adequate supply of methane, sufficient pressure, and low enough temperature to allow stability. The clathrate stability envelope is defined by the material's liquid-gas-solid phase diagram. At a depth of approximately 500m, the ocean is typically 6.0 C and clathrates can exist. At lower pressures and higher temperatures they are not stable. Due to geothermal heat, clathrates can not exist at depth in sediments. Sloan (1989) has treated clathrates in a comprehensive manner. Although recognized as a geological feature of the deep-sea floor in the 1970's (see summary by Kvenvolden, 1988), they have recently become the source of intense interest due to Japanese plans to exploit them. It is possible that at some point, MMS may be required to regulate clathrate development within the US EEZ. From an ecological perspective, they may constitute a special habitat.

2.1.2 Density, Temperature, and Salinity

The permanent pycnocline (density gradient) is an ecologically relevant physical feature dividing the shallow ocean from the deep. In offshore regions remote from freshwater input, density is primarily determined by water temperature. The permanent pycnocline and the related thermocline are that depth zone where downward flow of solar heat is relatively unaffected by seasonal fluctuations. This region is in contrast with the overlying seasonal thermocline where the density and temperature profiles vary through the year. Since heat input and ocean mixing vary over the Earth, the depth and exact density or temperature range of the respective permanent pycnocline and thermocline also vary.

For many years, the global compilation of deepwater physical data prepared by Mantyla and Reid (1983) has been the basis of descriptions of the permanent thermocline. This sparse and edited data presented oceanographers with a false image of a relatively fixed boundary. During this review, the National Oceanographic Data Center provided access to experimental search engines under development at Scripps Institute of Oceanography. All archived surface to bottom hydrocasts for the Gulf of Mexico were obtained along with comparable data for the coast of California (MMS Pacific Region) and the US east coast south of the Carolinas (MMS Atlantic Region). The scatter plots of these data provide a much more dynamic picture of a fluctuating thermocline (Figures 2.1, 2.2, and 2.3). The main ecological consequence is that fauna between 500 m and 1000 m in the Atlantic and Gulf of Mexico will experience temperature fluctuations associated with vertical pycnocline movement. The same depths in the Pacific will be much more stable.

The water density, temperature and salinity on the deep-sea floor are controlled by the density stratification of the overlying water mass. Temperatures (Figure 2.1) range from about 10°C at the top of the deep zone (200m) to 2°C (>3000m) except in silled basins. The Gulf of Mexico is such a silled basin connecting with the deep circulation of the Atlantic through a 1600 m deep sill in the Straits of Yucatan. This sill blocks the coldest water flow making the Gulf of Mexico isothermal at about 4°C below that depth (ignoring adiabatic heating). The salinity (Figure 2.2) of the deep-sea bottom shows little departure from 35 PSU (Practical Salinity Units).

Table 2.1. Physical and Chemical Factors and Their Relevance in Oil and Gas Industry Impacts to the Deep Environment.

Property	**Natural Condition & Effects**	**Oil & Gas Activity Impact Concern**
Pressure	Increases uniformly with depth as the sum of the weight of overlying water, approx. 1 atmosphere (1atm) for every 10 m. Alters some inorganic and biochemical reaction rates and decreases pH. Alters solubility of carbonates. Increases density, viscosity, and temperature of water.	1. Industry activity can not modify pressure, however: 2. Solution chemistry of discharges may be affected by pressure, making shallow water knowledge inapplicable. 3. Gas hydrates pose a known hazard and an unknown special habitat.
Density (Salinity & Temperature)	Changes non-uniformly with greatest change at permanent pycnocline. Is transitional from 200 to 1000 m then becomes uniform and high in cold deep bottom water (when minimal pressure effects are ignored)	1. Unlikely that industry activity can modify density fields, however: 2. Limited stratification in deep water will allow discharge plumes to easily propagate 3. Stratification in deep Gulf of Mexico is even less understood than in open ocean due to sill depths.
Light	Sunlight decreases exponentially with depth. Is present but low intensity in a transition zone below 200 m and is generally thought of as absent deeper than 1000 m. Bioluminescence important in behavior of deep animals.	1. Industry activity can cause deep plumes of low transmission water. 2. Sunlight is still present in the 200-1000 m range and animals may be especially adapted to low light and be especially subject to increased turbidity. 3. Below sensible sunlight, biological light plays a major role in animal interactions. Increased turbidity may impact such interactions.
Oxygen	Dissolved oxygen distribution reflects upper ocean stratification and has a minimum at 500 m influenced by the balance of local oxygen consumption and horizontal advection of oxygen rich deep water. Below 1000 m oxygen is again high and relatively constant.	1. Through injection (spills) of labile carbon, industry activity may alter local balance of oxygen consumption and replacement. This is most likely to be of concern in smaller silled basins where hypoxia or anoxia may result.
Water Movement	Stratified upper ocean inhibits downward propagation of currents. Deep bottom characterized as low energy low tidal, geostrophic, and thermohaline currents; episodes of high current velocity do occur.	1. Industry activities can not alter major current flows, however: 2. Bottom structures and topographic modification will impact BBL conditions. 3. Prediction of plumes, distal impacts, etc. must consider both prevailing and episodic flows.

Deep-ocean management must view the pycnocline as a very important ecological boundary in the ocean. With respect to plume models and chemical effects of discharges, density stratification limits vertical movement in the ocean of heat, momentum, and solutes. Therefore, processes below the permanent pycnocline are somewhat isolated from the upper ocean. Physiologically, temperature is very important in controlling distributions. The transition from the cold deep ocean to the warmer shallow ocean is considered a major physiological boundary. On the sea floor of the Gulf of Mexico, the thermal gradient between 200 and 1600 m is equal to the continental shelf from Nova Scotia to the Florida Keys.

2.1.3 Darkness and Light as a Defining Features

Since darkness is usually considered a primary characteristic of the deep-sea, it might seem that environmental management of deepwater does not need to be concerned with light. However, this would be incorrect since light is important in the deep sea in two senses. First, ambient sunlight may be sufficient even at 1000 m to be used as a sensory cue by sighted organisms. Second, at depths where the ambient sunlight is of no sensory value, the optical properties of water will determine how well bioluminescent light can be perceived. Therefore, manmade alternation in the optical properties of water, especially increases in turbidity may have profound effects.

The importance of light in the deep sea and the potential for light-associated environmental impact can be shown from a simple treatment of light in the sea. Once light has entered the sea, it is either absorbed or scattered back upward. Scattering and absorption combined are termed attenuation. Attenuation is such that light intensity decreases exponentially with depth. There is color-specific absorption such that in clear oceanic water a wavelength of 462 nm has maximal penetration. Defining the bottom of the euphotic zone as 1% of surface illumination, this may be found at about 100 m. However, below this depth there is ample light for human vision. At 500 m in clear water, the ambient sunlight is about one millionth that of the surface.

Sighted animals on land and in the ocean use ambient light to sense where things are in the environment and to take action based upon such knowledge. These actions include such vitally important activities as locating food, avoiding predators, and finding mates. Due to the great importance of these vision-dependant activities, alteration of the ambient light field in water, usually an increase in turbidity, can be the cause of impact.

The field of sunlight at any depth may be approximated by the equation:

$$I_Z = I_0 e^{-kz}$$

Where $\mathbf{I_0}$ is the intensity just below the ocean surface; $\mathbf{I_z}$ is the intensity at depth **z**, and **k** is the diffuse attenuation coefficient with the unit's m^{-1}. Diffuse attenuation is the sum of absorption and scattering. It is termed an "apparent" property since it is dependent upon the illumination. A related "intrinsic" optical property of water is beam attenuation. In clearest waters the minimum diffuse attenuation (**k**=0.0168) is for blue green light (wavelength 450 nm). We know that **k** varies greatly with wavelength and ocean particulate matter; in coastal waters it can have values higher than 0.25. However in deep oceanic waters, it is relatively low and uniform, around 0.03 to 0.04 (Jerov 1976).

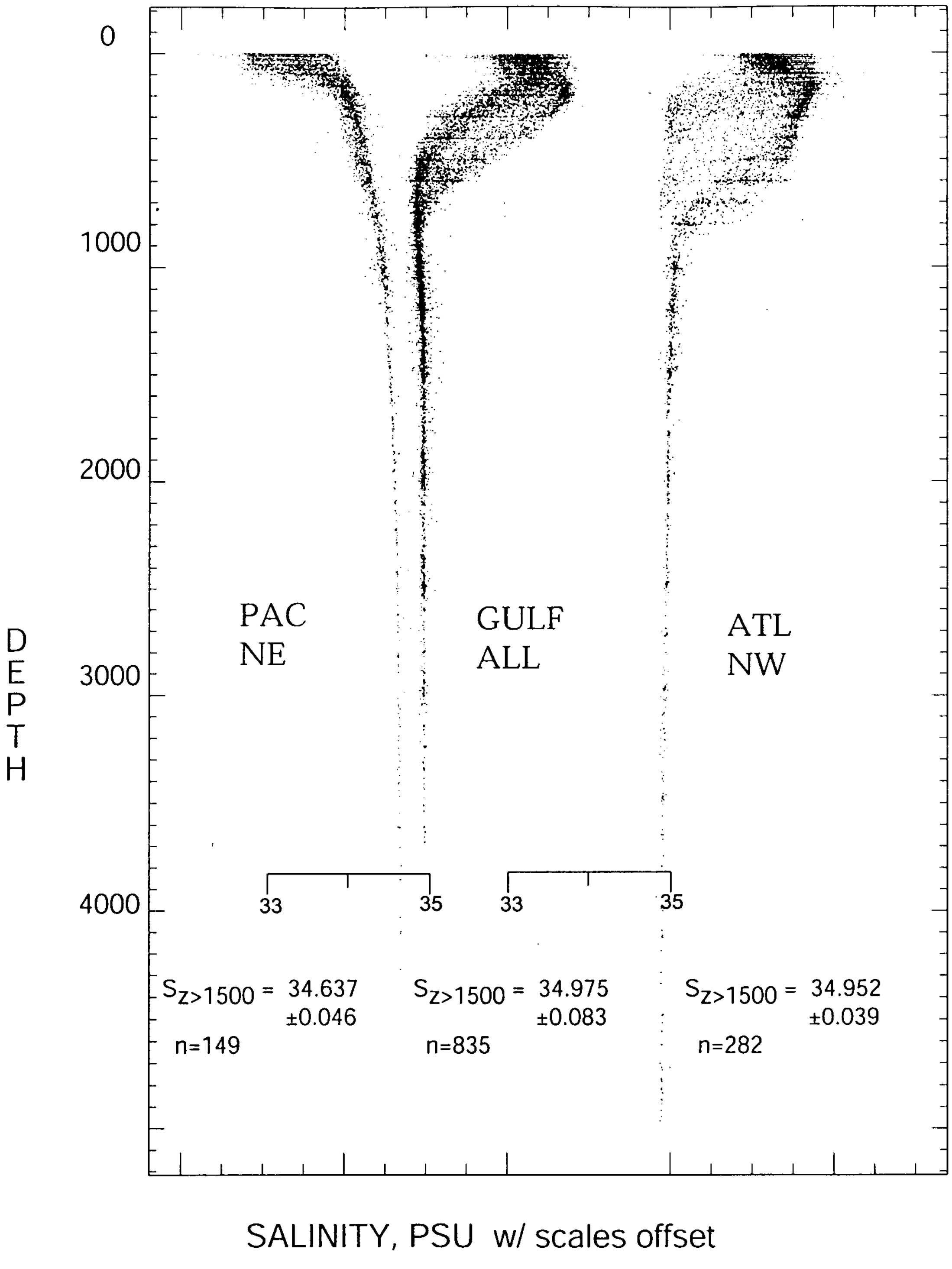


Figure 2.1 Salinity at Comparable Latitudes in the NE Pacific, Gulf of Mexico, and NW Atlantic. Averages based on data below 1500 m.

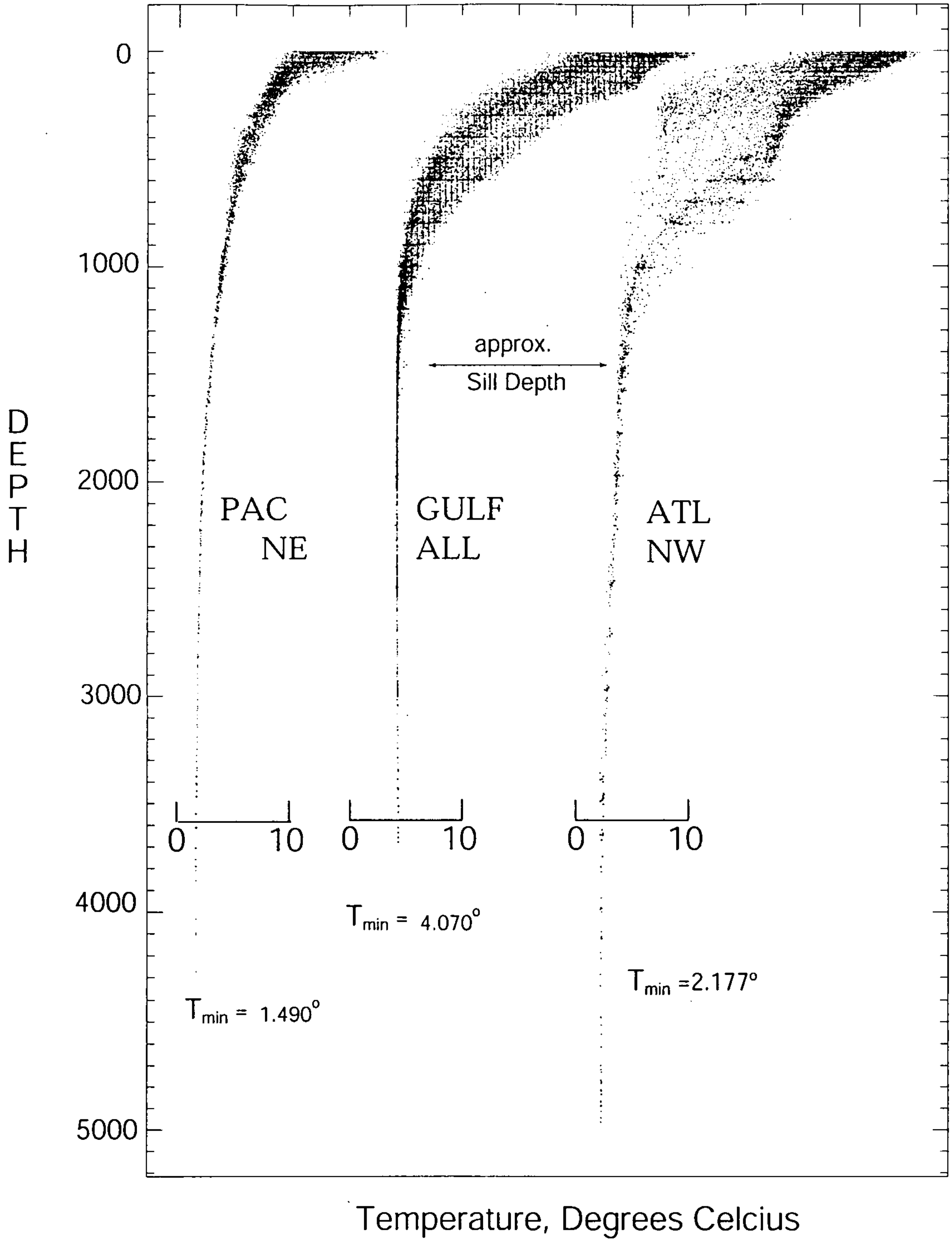


Figure 2.2. Temperature at Comparable Latitudes in the NE Pacific, Gulf of Mexico, and NW Atlantic. Averages based on data below 1500 m.

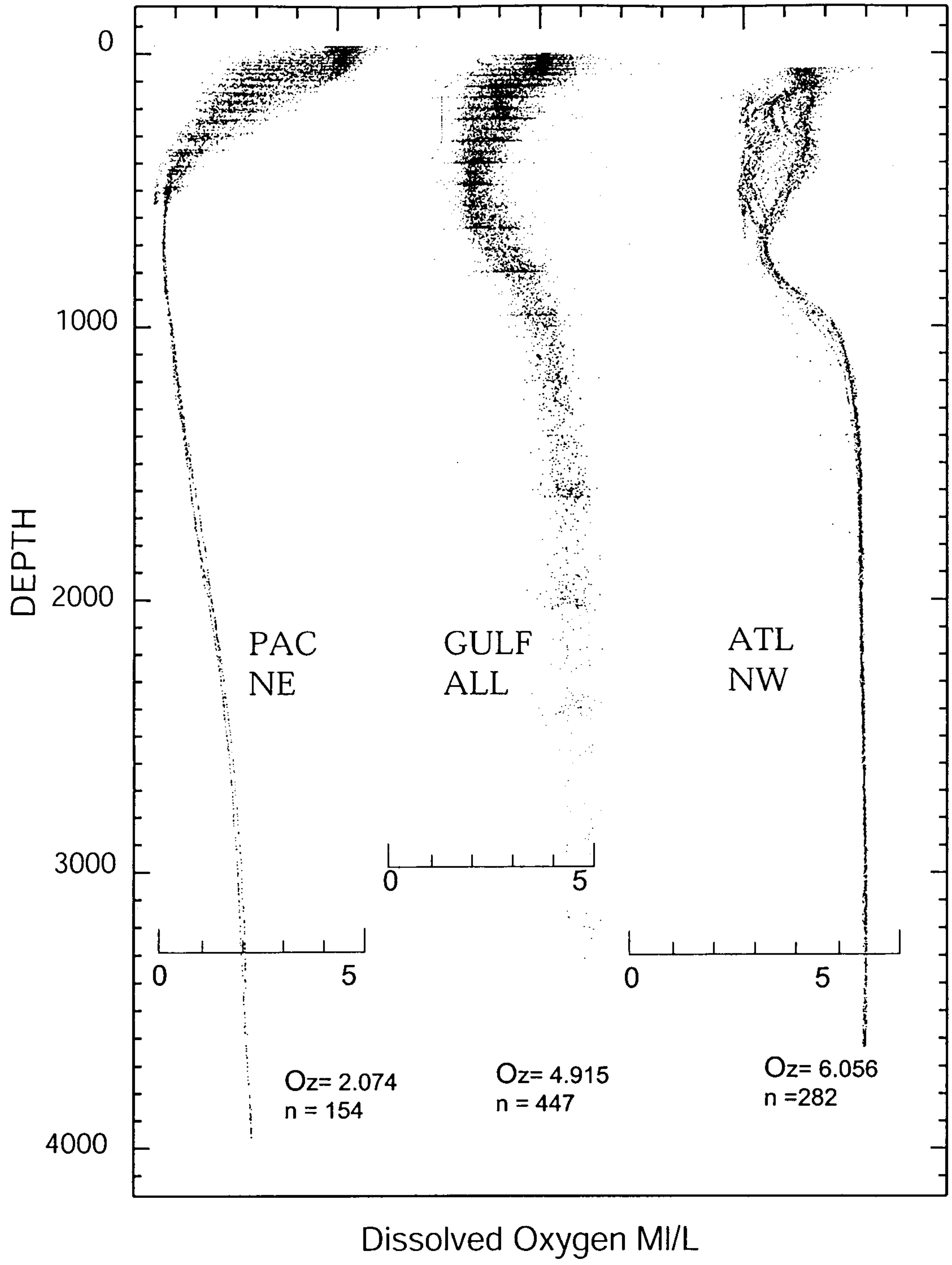


Figure 2.3. Oxygen at Comparable Latitudes in the NE Pacific, Gulf of Mexico, and NW Atlantic. Averages based on data below 1500m.

Theoretically, there is some sunlight thousands of meters deep in the ocean. Darkness is not a physical condition, but a neurosensory one. The degree of darkness is determined by the sensory system of the viewer. At some depth the level of light is so low that falls below the limits of detection or is swamped by neurological noise. On a brightly-lit day in clear ocean water an observer in a deep submersible can perceive dark shapes in the water at depths between 500 and 520 m. The highly dark-adapted eyes of deep-sea fishes may, however, still be sensing ambient sunlight as deep as 1000 m. In spite of very low ambient sunlight levels, many deep-sea animals have very well developed eyes and must make some sensory use of bioluminescence. Unlike ambient sunlight, bioluminescence is a controlled light flash that probably provides some information about the individual transmitting the signal rather than the general environment. If so, the perception and neurological processing of these light signals may be fundamentally different than that association with vision in a lighted field.

Whatever the usage of bioluminescence, changes in the optical properties of water pose a threat to normal ecological functions. Bioluminescent light from an organism can be treated as a point source that spreads out as a sphere and undergoes inverse square decrease in intensity as well as exponential attenuation. This can be shown by the equation

$$I_D = I_0 e^{-kD} D^{-2}$$

Where $\mathbf{I_D}$ is light intensity at some distance **D** and $\mathbf{I_0}$ is the intensity at the source. In clear ocean water (attenuation, **k**=0.04) the decrease in light away from a point source is far more dependent on distance between source and viewer than minor fluctuations in attenuation. However, if turbidity substantially alters **k**, the distance at which bioluminescent signals can be detected drops dramatically.

2.1.4 Oxygen

The restriction on downward movement of solvents imposed by the two-layered ocean has a profound influence upon oxygen distribution in the form of an oxygen minimum. Oxygen enters the ocean from the atmosphere and photosynthesis. In the upper ocean it may be near saturation at the surface with values of about 5 ml/L in the Gulf of Mexico. As dissolved oxygen moves downward, it is biologically consumed by respiration faster than it is replenished, producing a low of about 2.5 ml/L at about 500 m depth. The depth range of low values (< 3 ml/L) lies between 200 m and 750 m in the Gulf of Mexico. The increase in oxygen below 500 m reflects the importance of a second oxygen input, long-distance advection of deepwater. At these depths (1000 - 3500 m) oxygen returns to values similar to those of the surface (about 5.0 ml/L). The picture of the oxygen minimum that emerges from the NODC archives (Figure 2.3) is variable place to place. It is more pronounced (1 ml/L) and fixed with depth in the Pacific. The vertical movement of the thermocline in the Gulf and Atlantic make it more variable at any given depth.

As a result of the oxygen minimum, the benthic environment at that depth is inherently hypoxic (Diaz and Rosenberg 1995). Therefore, management is obligated to treat the low oxygen zone differently than the well-oxygenated regions above (<200-300 m) below (>750 m) maximum depth. Care must be taken that operational and accidental discharges do not result in greatly enhanced biological oxygen demand. Otherwise, bacterial oxidation of spilled hydrocarbons and organic drilling fluids could result in local deep anoxia. It also becomes important to know the actual advection rates of oxygen into the deep environment and natural biological consumption rates in order to predict the impact of discharges.

2.1.5 Water Movement

The buoyancy of warm seawater restricts the propagation of kinetic energy downward. This can be seen for both waves and currents. In the case of waves, buoyancy opposes the oscillating movement of higher and lower density water up and down. This opposition, which can be stated as a stability, buoyancy, or Brunt-Vaisala frequency, is a function of the density-depth gradient and is greatest in the top 200 m of the ocean. It is noteworthy, however, that once the comparatively uniform densities of the bathyal and abyssal depths are reached, there is little buoyant opposition to the transfer of any energy.

When wind drags across the surface of the ocean, it transfers kinetic energy to the ocean surface. The surface layer of moving water then drags over the next deeper layer, and so on with increasing depth. However water is a deformable, viscous fluid, and only a fraction of the velocity at each layer is imparted to the next. Thus, there is an exponential decrease in velocity with depth. The layer over which this velocity transfer takes place is the surface Ekman layer, and it has typical thickness of less than 100 m. Thus, wind driven currents do not typically progress into the deep-sea. The same exponential decrease is seen in wave-induced water velocities. The orbital velocity of water under a wave decreases exponentially with depth as a function of wavelength. Only very long-period waves and tides will have a major effect upon flow in deep water.

Benthic "Storms"

Although most of the deep-sea floor experiences currents of about 1-2 $cm \cdot s^{-1}$, velocities as high as 50 $cm \cdot s^{-1}$ have been encountered. The presence of episodic high velocities was first suspected by geologists who found scour marks and ripples on deep bottoms where the observed currents were not capable of the necessary erosion (Heezen and Hollister 1971). One mechanism for such elevated current velocities was contour currents along an ocean's western margin (Heezen et al. 1966). The term contourite has been given to the characteristic sculpted bottom. A comprehensive study of a deep bottom experiencing high current velocities was supported by the Office of Naval Research (Hollister et al. 1984, Hollister and McCave 1984). The HEBBLE project (High Energy Benthic Boundary Layer Experiment) found that in addition to contour currents, hurricane passage had a marked influence of flow even below 3000 m (Weatherly and Kelley 1985). As might be expected from an area of bottom erosion, the fauna was distinctive (Thistle et al. 1985).

The Benthic Boundary Layer

Biologists are generally aware of the importance of velocity gradients as fluids (air and water) flow over and within organisms. Vogel (1994) treats the subject extensively. Boundary layers (gradients of decreasing velocity approaching a fixed surface), are a flow phenomenon found on many scales, including the very large scale of current flow over the bottom of the deep sea. A major addition to how ecologists view the deep benthic environment was recognition of the importance of the benthic boundary layer (BBL). In the 1970's and 80's geochemists, geologists, and biological oceanographers became increasingly aware that many properties of the benthos are controlled by the physical dynamics of the BBL (Armi and Millard 1976, Wimbush and Munk 1970, Richards 1990, Ludwick and Demura 1982). Here bottom friction between currents and the seafloor produce vertical shear that generates near-bottom turbulence. This turbulent layer is marked by homogenous properties such as salinity, temperature and suspended solids. Simple models (Armi and Millard 1976) have proven inadequate at describing the BBL since it varies in thickness between 5 and 100 m (Weatherly and Martin 1978) rather than the few meters predicted and does not have a simple relationship with current velocity.

The importance of the BBL in both a management and a basic research context is the deep-sea floor is not a completely open or arbitrarily defined system. It has, in effect, a ceiling at which exchange of water column properties are limited. The benthos and the BBL's pelagic fauna form a unit distinct from the ocean above the BBL. The increased suspended material in the BBL may afford improved foraging, such that predators and scavengers are likely to restrict their hunting to the BBL, and chemical plumes released from the deep bottom may be trapped in the BBL and not diluted through the entire water column as some models assume.

Ecologically, the particle rich BBL (sometimes called a benthic nepheloid layer) is not a static suspension. It is an equilibrium feature (Biscaye and Eittreim 1977) of particles moving down under the influence of gravity and up due to turbulence (Ludwick and Demura 1982). This is where recently arrived labile detritus resides before final deposition. Smith and his associates (see Smith 1987) found that fully 10% of benthic carbon consumption actually takes place in the BBL, and Wishner (1980) has established that it is faunally distinct from the larger pelagic environment. The management implication of the physical and ecological aspects of the BBL is that the deep benthos includes more than the surficial sediments. The bottom and the overlying 100 m of water form a unified system and should be studied as such.

2.2 Deep Fauna

This section provides a brief review of deep ocean fauna in terms of generalities and then by the size classes employed in ocean studies. The intent is to aid managers in looking at the fauna from four necessary perspectives. There are no differences between the perspectives needed in shallow or deep management. However, the relative importance to management decisions differ.

- Ecological Importance - In theory, environmental management should be based upon an understanding of the roles that each species plays. Maximum protection can then be allocated to the most important and most sensitive species. In practice, non-fisheries marine management is habitat rather than species directed, because it is far easier to delineate a few habitats than to assess ecological importance of many species. The deep resource manager must consider whether species-level ecological importance can be assessed or whether a habitat approach must be used. It is to be expected that the cost of gaining information on ecological roles will be very high.
- Potential Resource Conflict - In shallow water, many species have a resource value either directly as a fishery or indirectly as an aesthetic component of the habitat. While these issues do apply to the deep ocean, it is to be expected that fewer resource conflicts will exist.
- Public Perception - Decisions concerning resource management are never based only on scientific evidence. While the general public has no direct exposure to the deep sea, it is erroneous to expect a lack of interest. The very high diversity of the deep benthos, the large number of new species which any study will encounter, and the exotic morphologies of a few species appeal to the imagination.
- Indicators - Faunal inventories are the main source of information about natural and impacted conditions. Therefore, management has an obligation to design surveys, monitoring, and experiments so as to be maximally informative and cost effective. The low level of knowledge about the deep fauna and the high number of new species to be encountered will make this difficult. Identifying and focusing on a limited number of indicator species may be the most cost effective strategy.

In development of deep-ocean management strategies, two key aspects of deep fauna are outstanding, uniqueness and ignorance. On analysis, the latter poses more difficulty than the former. Shallow-water resource managers routinely deal with regional uniqueness since marine fauna often changes dramatically from one coastal region to another. The northeast continental shelf has a fauna distinct from the southeast and Gulf of Mexico; the Florida Gulf coast is faunistically different that the Louisiana coast; the fauna off Southern California is distinct from that off the Pacific coast of Alaska; and the fauna of the Alaskan Arctic coast is also distinctive. Region-specific and habitat-specific management strategies can be developed with relative ease since there usually is an extensive pre-existing information base. Typically, such information has accumulated independent of the environmental issues over many decades of basic marine biology and fisheries research. In shallow water, management must seek out, synthesize, and apply this basic information, but it is seldom necessary to undertake information-adding basic research.

The usually implicit and always critical management assumption that adequate basic information exists is definitely invalid in the deep sea. The information about deep-sea fauna is exceedingly limited. For the vast majority of deep-sea species, we do not know such basic information as feeding type, mode of reproduction, life span, predators, and population. Therefore, management must take one of two possible courses. First and most costly, management must undertake information-gaining research at a much more extensive level. Second, the precautionary principal must be applied and regulations based upon unproven worst case scenarios.

2.2.1 Changing Generalities about Deep-Sea Adaptations

Are deep-sea animals different than shallow in being inherently more susceptible to environmental impact? Can it be inferred that uniformity of some physical features has produced species requiring a narrow range of conditions that may be easily upset? Or, does the existence of some environmental variability mean that individuals and populations will be relatively robust when exposed to human perturbations? Presently there are no convincing answers. However, until research directly examines susceptibility, it is reasonable for management to turn to published generalities about deep-sea adaptation when taking a "first cut" at an answer. This section reviews the current status about the most frequently mentioned generalities and considers whether there is obvious management relevance.

In making the critical assessment that a particular generality is valid and relevant, it must be appreciated that scientific generalization is influenced by three important factors, actual evidence, prevailing paradigms, and fashions of science. When evidence is limited, as is the case in the deep sea, paradigm and fashion may be the primary influences. For example, from the 1880's to the 1980's the deep sea has been viewed as a cold and stable environment. Accordingly, the scientists of that era explained their scant evidence of biological and ecological adaptation in terms of the prevailing ideas about such environments. It was also the scientific fashion during this period to selectively reinforce existing ideas rather than challenge them. Today, we know that there are sources of variation in the deep ocean, we have a bit more data about the animals, and the scientific fashion is to replace old ideas with new. New generalizations or old, management must be cautious when accepting and applying general statements about the deep sea.

The era of early deep-sea exploration coincided with a phase in ecological and evolutionary studies where a strong effort was made to explain patterns in nature according to deterministic laws and rules such as Cope's Law on size (Gould 1977) or Thorson's Rule on reproductive mode (Thorson 1950). While the literature contains no such law or rule derived from deep-sea observations, generalities about deep-sea fauna published as late as the 1960's very much reflected this trend of forcing observations into narrow interpretations. This section identifies those generalities that are most likely to bear upon management decisions, then briefly discusses others.

Valid Generalities of Obvious Management Consequence

There are two related generalities about deep species animal-sediment adaptations that seem to be valid for most of the fauna and have immediate management relevance. The consequence of both is that alteration of the soft bottom system (particle input, sediment-water interface dynamics, etc.) should be of higher concern in deep water than in shallow. The shallow-water management strategy of recognizing special habitats on the basis of gross substrate differences (hard versus soft) will be insufficient in the deep environment where important but subtle habitat variation may occur over the vast soft bottom.

Predominance of Soft Bottom Dwelling Organisms - It has been recognized since the Challenger Expedition that the deep-sea floor is overwhelmingly soft bottom. Exposed hard bottom habitat is limited to mid ocean ridges and geochemically unique environments with authigenic substrate precipitation (hydrothermal venting, cold seepage, and mid-ocean nodule fields, etc.). Consequentially, the great majority of deep-sea benthic species are adapted to soft bottoms. The importance in habitat structuring of even small bits of hard substrate, such as a shell fragment, may be greatly increased compared to shallow water.

Predominance of Deposit Feeding - In shallow water, soft bottoms support dense populations of deposit feeders, suspension feeders, and animals capable of switching between the two modes of feeding. However, in the deep-sea the average influx of suspended labile detritus appears to be insufficient to support suspension feeding, resulting in a fauna heavily dominated by deposit feeders. There is some initial evidence to suggest that microphagy (selection and ingestion of small particles) predominates. Suspension feeders are not, however, completely absent. Where suspension feeders are found in deep water, it can be assumed that special habitat conditions prevail that effectively increase the local flux of organic detritus.

Less Well Established Generalities of Possible Management Relevance

Three generalities about the reproduction, morphological and sensory adaptation of deep-sea animals are certainly valid for some species and some deep-sea regions, but the number of exceptions are so many that extent of applicability remains unestablished.

Reproductively Distinct – Larval brooding, as exemplified by pericarid crustaceas, was once thought to predominate in many deep-sea taxa, giving the fauna a unique characteristic. Until recently, few people would have challenged the idea that deep-sea animals are reproductively distinctive (Grassle and Sanders 1973) in terms of non-seasonal breeding, brooding, direct development, and low fecundity. Indeed, the accepted reproductive scenario indicated a fauna highly susceptible to impact. Now, the question is in doubt. The topic of reproductive patterns in the deep-sea fauna has undergone an excellent critical review (Young and Eckelbarger 1994). The lead contribution (Young 1994) and following papers convincingly dispose of the long-held generalizations that deep-sea animals conform to Orton's Rule (continuous reproduction in a non-seasonal environment) and Thorson's Rule (brooding must be the predominant reproductive strategy in an environment lacking a plankton rich pelagic component). Rather than having restricted reproductive patterns, deep fauna (such as molluscs) show as much adaptive variation as encountered in shallow water. This adaptive range is exemplified by measured fecundities ranging from 20 to more than 30,000 eggs per brood (Scheltema 1994). Depending upon the species examined, a full range of periodicity is encountered from continuous to seasonal (Tyler et al.1994). Surveys of size frequency within deep benthic populations also show a range of recruitment patterns rather than a single predominant mode.

Deep Species Differ in Size from Shallow - It has been proposed that deep-sea animals differ in size from those in shallow water. A few deep-sea taxa of pericarid crustaceans (isopods and amphipods) are comparative giants at lengths up to 38 cm. Such gigantism seems to be limited to a few taxa. The case of smaller seems to be better established (Thiel 1975). Especially on the very food poor central seafloors, taxa normally associated with the macrofauna size fraction are in the smaller meiofauna fraction. This size shift is seen as reflecting adaptation to low food levels. The presence of unusually large animals is of peripheral management relevance; although "giants" are of considerable public interest. A general shift to smaller size underscores the need to consider impacts that might alter the food delivery system and argues for the inclusion of meiofauna in any comprehensive survey or monitoring.

Deep Species are Dark Adapted - This generality would seem to be quite self evident, but dark adaptation is a complex topic with unexpected management consequences. There are two apparently conflicting light-related aspects of deep-sea fauna. The first is body color. Deep animals are typically drab (black, gray, white, etc.) and patternless even when colored (bright red organisms are functionally black). However, many deep animals have well developed eyes although some are eyeless. It must be concluded that in the deep-sea, light produced by bioluminescence or as residual low-level solar illumination is still important. Therefore, environmental management must consider those activities that increase turbidity.

Valid Generalities of Uncertain Management Relevance

Pressure Adaptation - Hydrostatic pressure has effects on organisms that are more dramatic than would be expected from simple physical-chemical consideration of reaction product volumes. Aside from gross deformation of gas-filled voids, pressure alters many metabolic processes. Pressure adaptation's direct management implication is that it makes it exceedingly difficult to carryout sensitivity testing of species with a traditional bioassay. Maintaining assay populations under pressure will be very difficult. The most recent review of pressure adaptations is that of Gibbs (1997) focusing on deep fish enzyme systems. Siebenaller (1991) and Somero et al. (1991) have reviewed enzyme-level pressure adaptations and their possible consequences in zoogeography and ecology. Siebenaller (1991) has given a succinct and brief summary. Pressure influences enzyme function via volume change and membrane function by altering the degree of ordering in lipid sheets. Working with congeneric demersal fishes and select enzyme systems, it was found that species occupying broad depth ranges had evolved pressure insensitive enzymes rather than a suite of depth-specific isozymes in genetically distinct sub populations. Working with gills Gibbs and Somero (1990) had suggested that function varied enough with a 200 atmospheres pressure change, that adaptations would be needed in any species spanning a 2000 m depth range. Siebenaller proposes that there is a distinct depth dichotomy of pressure adaptations of cytosolic enzymes. Species commonly occurring deeper than 500-600 meters (50-60 atms) have pressure-adapted (insensitive) enzymes. Species common above 300 m tend to have pressure-sensitive enzymes. This physiological/molecular distinction might serve as on indication of an ecological zonation between shallow and deep.

There has been a change in the focus of pressure studies over the past thirty years. Initially, pressure aquaria (Brauer 1972) were used for species-level research to test whole organisms. Frequently, testing was done on species found in shallow water (Menzies et al.1972), and inability to survive under pressure observed. From our current management perspective with the need for species-level information, it is unfortunate that small pressure cells have replaced pressure aquaria, and whole animals replaced by isolated purified enzymes.

Invalid Generalities of Historical Interest

Evolutionary Antiquity - Any ocean manager faced with funding deep research must be amused by elementary oceanography texts' explanation of the four year voyage of the HMS Challenger. We are usually told that the cruise was an effort to test Forbes' conjecture that the ocean would be azoic below 600 fathoms. What government agency would employ a large ship and scientific party in a long around the world cruise to test a hypothesis that required only a few days at sea off the English coast? There was obviously much more involved. At the time of the Challenger expedition there was widespread curiosity as to what the fauna of the vast, possibly unchanging, and fully connected deep ocean might be in evolutionary and zoogeographic terms. It was an era when the Darwin-Wallace theory of evolution was fully accepted and intellectually fresh. Documentation of geographic species patterns was seen as the primary tool of evolutionary studies, and it was well understood that climatic and geological changes brought about speciation. Would the deep-sea have a fauna that had escaped such influences and remained primitive?

As a general statement, the deep-sea fauna is not primitive in the sense of being populated by living fossils. To a certain extent, however, many deep-sea taxa can be considered primitive. This primitiveness is especially notable for the protobranch mollusc and the pericarid crustaceans. The only management relevance of the partially discredited depth-antiquity relationship lies in public misunderstanding. The statement that the deep sea is a refuge for ancient animals, when taken as an unqualified truth, inappropriately elevates the importance of that environment.

2.2.2 Review of Deep Fauna by Size Group

While terrestrial ecosystems and the very shallow parts of the ocean have a tradition of taxa-specific investigations (i.e. studies of fish, or molluscs, or echinoderms, etc.), studies of the deep sea are usually so restricted by sampling equipment that size classes are the main focus of inquiry. These classes vary a bit in exact definition, but have assumed certain standards in the surveys supported by the MMS. Megafauna are those animals that are retained in trawls and can be seen in videos and photographs; an approximate size limit is one centimeter and larger. Macrofauna are those animals retained on a 300 micrometer sieve and are typically collected with sediment in coring devices. A conflicting 500 micrometer standard has often been applied. Meiofauna is the smallest class defined by sieving. This category passes through a 300 micrometer sieve and is retained on a 63 micrometer. Even smaller classes are not normally studied in routine surveys and require either culturing or staining of microbes.

2.2.3 Megafauna

Deep-sea megafauna are recognizable and give the deep fauna its distinctive nature to non specialists. The deep sea is characterized by an abundance of echinoderms, especially ophiuroids and holothuroids. Sea stars, urchins, and crinoids are also present, but not in equally great abundance or diversity. The ophiuroids (serpent stars) are similar to those found in shallow water, but are more abundant as a general rule. The holothuroids, sea cucumbers, consist of species similar to those in shallow water and the order elasipoda with extremely modified morphology. Deep crustacea are usually not the true crabs of shallow water. Some deep fish have morphologies like their shallow water kin, but, many of relatively unrelated taxa share a common long tapering, "rat tail". Sessile colonial animals are rare, but elegant sea fans are encountered on hard substrate and dense populations of sponges sometimes encountered. These latter examples pose a challenge to the generality that the deep sea is dominated by deposit feeders. General management utility and limitations are presented in table 2.2

Table 2.2. Management Utility of Megafuana in Monitoring and Background Surveying Contracted to Limits of Utility.

MANAGEMENT UTILITY	LIMITS of UTILITY
1. Better Information Base (a) More likely for some natural history to be known. (b) Identification usually easier and (c) More easily studied *in situ* and in lab.	1. Ecological Generality Uncertain Since greatest contribution to diversity is in smaller size classes, knowledge of a few large animals may have little utility.
2. Better Suited for Organism-Level Impact Assessment (a) Large tissue volumes for analysis, and (b) easily assayed organs.	2. Organism-Level Generality Uncertain As with the above, ease of study does not means results will be applicable to other species.
3. Modest Sample Processing Costs Compared to smaller fauna sampling, most sorting and initial identification is done at sea.	3. Trawl Sampling Difficult & Non Quantitative (a) Successful Deep Trawling is time consuming, (b) requires special equipment and (c) experience; (d) photo/video has relatively high taxonomic uncertainty
3. More Likely to Reveal Potential Conflicts in Use (a) Large animals more likely to have a resource value, and (b) large animals more likely to be publicly perceived as requiring protection.	4. More Likely to Trigger Concerns Large crabs and fishes may be seen as potential fisheries even though the populations may be unable to sustain fishing pressure.

Ophiuroids

Ophiuroids, commonly called serpent and brittle stars, are often the most abundant animal collected in trawls. There is no resource utilization and no general public interest in the class. Their abundance makes them an obvious choice as an indicator species. They tend to have wide depth ranges (Gage 1982) making the useful in surveys of large regions. Some species, notably *Ophiomusium lymani*, are thought to be cosmopolitan. If this observation holds up to molecular confirmation, it is another reason to focus upon these animals in monitoring studies. Deep ophiuroids seem to have the same range of natural histories as encountered in shallow water. They include deposit feeding, suspension feeding, scavenging, and predation. The author has even observed ophiuroids suddenly ensnare small fish. Given the range of natural histories and the high population numbers, the species of this class are probably very ecologically important.

Holothuroids

Holothuroids, sea cucumbers, frequently vie with ophiuroids for the distinction of being the most abundant animals in deep trawl samples. There is no resource utilization of deep species, and no deep species is suitable for inclusion in the commercial trepang or beche-de-mer fishery (names applied to holothuroid fishery supplying the Asian market). There is no special public interest in holothuroids, however, some deep species are colorful (purple or orange) and have such unusual morphologies that they can be considered exotic in the sense of attracting public interest in preservation. As in shallow water, infaunal and epifaunal detritus feeding are common although one or two suspension feeders exist. The most unusual groups are the benthopelagic taxa which swim in the BBL between feeding forays on bottom. At least two such families exist. Abundance and size make holothuroids good target species for monitoring and survey. It has been suggested that their extensive sediment feeding may control the habitat complexity required for the high diversity of smaller fauna. As such, they are one of few deep taxa for which a systems-level ecological importance has been proposed.

Fishes

Deep fishes are common in trawl samples, and the almost uniform black color and tapering 'rat tail' bodies are characteristic of the deep sea. There are known resource conflicts. The organ roughy (*Hoplostethus atlanticus*), sable fish (*Anoplopoma fimbra*), and grenadiers (*Coryphaenoides* and related genera) support substantial fisheries; although no such fisheries have been developed in the Gulf of Mexico. It is to be anticipated that as shallow fisheries collapse, there will be continued (possibly ill-conceived) interest in deep fisheries resources. Due to the great scientific and public interest in fish, they are ideal target species for monitoring and survey. In trawl surveys, the grenadiers are the most common group caught. This species/genus complex shares with most other deep fish the habit of feeding on bottom invertebrates and smaller fish. In baited camera and trap studies the predator/scavenger hagfish (Mixinidae) predominate. The predation pressure exerted by the fish population upon the populations of benthic prey species must be great, and predatory population regulation is to be suspected.

Crustacea

The distinctiveness of large deep crustacea lies mainly in a shift of composition rather than special morphologies. The true crabs decline with depth to be replaced by spider crabs, hermit crabs, and more lobster-like crabs such as the galatheidae (squat lobsters). There is actual and possible future resource conflict. The upper continental slope typically has populations of long-lived large crabs that are trapped or trawled. On the US Pacific coast this deep crab fishery targets spider crabs and is largely restricted to Oregon and more northern areas. In the Atlantic and Gulf of Mexico the true crab *Chaceon quinquedens* (long known as *Geryon*) is the target of a limited fishery and is marketed as golden crab. A deep-sea shrimp fishery is also pursued in the Gulf of Mexico and south Atlantic states.

Large crustacea are not as common as ophiuroids and holothuroids but are a fairly consistent part of a deep trawl sample. This lower abundance limits their utility in studies, but the possible resource issue and a well-established taxonomy offset this limitation to a large extent. The penaeid shrimp and hermit crabs are usually the most abundant large forms collected. Due to the great range in morphologies, it is to be suspected that crustacea play many ecological roles. Most are epifaunal, but a few extensively burrow the sediment, contributing to habitat complexity.

Sponges

Sponges are exceptions to the rule that deposit feeders predominate. Most times sponges are rare in trawl samples. However, there are obviously patches of bottom with high population densities. Such a "sponge bank" has been observed adjacent to the Orca Basin in the Gulf of Mexico (T. Bright, personal communication) and possibly encountered in the NGMCS study. There are no resource conflicts and the numbers are usually too few to make a good target species. However, their presence may indicate a special habitat. The Hexactinellidae, approximately 500 species of glass sponges, are abundant in shallow polar seas and the deep ocean. They may be an important structuring element in some deep-sea sediment (Bett and Rice 1992). Where boundary layer conditions provide increased suspended detritus to these microphagous filter feeders, high densities may be achieved ($>1\ m^{-2}$). In these relatively dense stands the sponges and associated fauna may comprise a sponge assemblage that is distinct from the surrounding benthos. Unlike shallow water where sponges encrust hard surfaces, the deep glass sponges are free standing on mud bottoms and provide a substrate for other organisms. Typical colonists are stalked and verrucamorph barnacles, hydroids, tunicates, braciopods, and crinoids. While seldom abundant, deep sponges are conspicuous in bottom photos/videos and comprise one of the major groups that can be studied by that method.

Coelenterates

Coelenterates are a consistent, but usually low abundance, component of deep samples. The numbers are usually too few to make a good target species. However, their presence may indicate a special habitat. Anthozoans are the dominant coelenterate in shallow and deep water. Unlike the shallow environment where there is alternation of generations between dispersive medusan morphologies and sessile forms, deep anthozoan are thought to lack the medusan phase. Species in the order Ceriantharia (burrowing anemones) are ubiquitous in the deep-sea and appear to be opportunist omnivores. These animals bury the posterior end of the body in the sediment and extend the anterior end and feeding tentacles out of the bottom. The more familiar shallow-water sea anemones (order Actinaria), are also found in the deep ocean either attached to hard substrate or resting on the sediment with a broad pedal disk. Order Pennatulacea (sea pens) also anchor in mud and sometimes form relatively dense aggregates in regions of high detritus influx.

Unlike the sediment dwelling coelenterates, Gorgonacea (sea fans), Alcyonacea (soft corals), Antipatharia (black corals), and Scleractinia (stony corals) all require some hard substrate for attachment. This may be massive exposed rock or bits of shell so small that they become indistinguishable as the animal grows. Due to the paucity of suspended food at depth, the presence of such animals is indicative of special environmental conditions.

Corals are of considerable public interest. Therefore resource conflicts with deep oil and gas development are to be expected. Banks of the coral *Lophelia pertusa* in the North Sea (Wilson 1979) have raised public concerns. Similar banks have been located at approximately 800m on the Blake Plateau off Florida (R. Avent per. com.).

2.2.4 Macrofauna

Macrofauna are those animals smaller than megafuana that are retained on a sieve of either 500 μm or 300 μm (the latter preferred). Traditionally, there has not be a sharp division into infauna and epifauna, since the sampling methods do not allow for certain classification. They are usually sieved or picked from a sediment sample. Assessment of ecological roles is speculative. In the deep sea most macrofauna are deposit feeders. They probably comprise the primary forage of many predatory megafauna. There is no current or planned resource usage and little public awareness of this group. However, macrofauna have become the primary focus of surveys and monitoring due to the very high data yield per sample. As a result, the macrofauna are the main component of measured benthic diversity. General management utility and limitations of utility are presented in table 2.3

The pericarid crustacea, polychaete worms, and bivalve molluscs dominate deep-sea macrofauna. There is a substantial, scattered literature on these faunal elements, but no comprehensive treatises. There are relatively few systematic experts. The prevalence of pericarids and protobranch molluscs contributes to the impression that the deep-sea fauna is ancient since both groups are considered primitive within their respective higher taxa. Low fecundity of some bivalves and the brooding mode of pericarids contributes to the impression that reproduction patterns are different in the deep sea.

Polychaete Worms

It is common for polychaete worms to be the most abundant and diverse component of the macrofauna. The families Ampharetidae, Paraonidae and Spionidae tend to predominate with specimens somewhat smaller than found in shallow water (Blake et al.1987). The abundance and diversity of the group make them an excellent target taxon when total species inventory is impractical. The continental slope of the US Atlantic coast has the best studied polychaete fauna in the world. As a result, the taxonomy may be more tractable than is usual for this group. Worms are predominantly deposit feeders, but display a great range of foraging behaviors. Most are infauna, and their burrowing may be the primary determinant of bioturbation rates and depth.

Table 2.3. Management Utility and Limitations of Utility of the Macrofauna Size Class in Background Surveying and Monitoring.

MANAGEMENT UTILITY	LIMITS of UTILITY
1. Captures High Diversity Component (a) This is the faunal class from which deep diversity concepts have been developed and (b) large number of species in sample better suited for statistical analysis.	1. Less Likely to be Well Known (a) limited information on species-level biology available and (b) great difficulty obtaining correct identification due to new species and few specialists.
2. Sampling Standardized and Effectiveness Well Known (a) 0.25 m^2 frame mounted box cores have become the standard for benthic studies, (b) biases due to devices known and controllable, (c) sample processing well standardized.	2. High Per Sample Processing Costs (a) post-cruise sample picking and sorting under microscopes is time intensive and (b) correct and consistent identification of specimens depends upon a limited literature and few experts.
3. Results are Quantitative	3. Results Difficult to Extend to Larger Fauna General public and other ocean users will relate more to larger fauna such as fishes.

Pericardian Crustacean

The Pericarida typically comprise about one third to one half of the species in macrofauna samples (Hessler and Wilson 1983). These small crustaceans include the very abundant orders Amphipoda and Isopoda along with the less abundant Tanaidaceans, Cumaceas, and Mysidacea. The peracarids are predominantly detritus feeders living on or just below the sediment-water interface. Reproductively they share the common feature of having a brood pouch and lacking dispersive larvae. The amphipods are most common on the continental slope and slope base, decreasing in importance in deep oligotrophic basins (Grassle and Maciolek 1992, Wilson and Hessler 1987). Deep-sea species belong to families and genera also found in shallow water. This pattern has been interpreted to indicate multiple and ongoing colonization of the deep (Hessler and Wilson 1983). The Isopods are very successful in the deep-sea. Isopod families span shallow and deep water; there is indication of radiation in the deep environment at the level of genus.

Mollusca

In shallow water it is common to find molluscs in the megafaunal size range. In deepwater they are generally much smaller. They are so common that they are the third most abundant taxon. The deep-sea molluscs are extremely diverse and are dominated by ancient taxa that are poorly represented in shallow water. Deposit feeders predominate. Allen (1983) and Knudsen (1979) have reviewed the general biology of deep bivalves.

Similar general reviews have not been produced for the deep gastropods, however, the geographically and taxa specific works of Bouchet and Warén (1986) provide some general information.

Deep bivalve molluscs are dominated by the more primitive subclass Protobranchia. The shallow ocean is dominated by the subclass Lamellibranchia. In addition to small size, the deep species are notable for the lack of both color and shell ornamentation. Allen (1983) has posed the interesting speculation that deep protobranchs have diversified according to digestive strategies in a food-poor environment. Not all deep bivalves are deposit feeders. The Septibranchia are well represented predators (Allen and Morgan 1981). Unlike the deep bivalves that are dominated by a single taxon, deep-sea gastropods are in all three major groups of the class, Archaeogasatropoda, Mesogastropoda, and Neogastropoda; the names implying evolutionary age. Feeding types are not strictly associated with any one order, although deposit feeders tend to be Archaeogastropods and predators tend to be Neogastropoda.

2.2.5 Meiofauna

Meiofauna is that faunal component smaller than 500-300 μm and retained on a 63 μm sieve. As with macrofauna, they are usually sieved and picked from sediment, and division into infauna and epifauna is not practicle. However, various accepted methods of facilitating sample processing have been developed. An excellent comprehensive guide to study of the meiofauna has been compiled by Higgins and Thiel (1988) that includes sampling methods (Fleeger et al.1988). That volume has been updated in a single author publication (Gieve 1993), that is less comprehensive but includes a better review of habitats. Neither reference gives detailed review of deep-sea fauna. The ecological role of the meiofauna is problematic; deposit feeders predominate. The group probably serves as forage for macrofauna. There is no current or planned resource use of the meiofauna. There is little public awareness. The use of meiofauna in applied ecology is greater in Europe than the US. Since meiofauna and macrofauna can be extracted from the same sample, there should be no additional field cost associated with including both groups. However, the taxonomy of the smaller group is so poorly known that lower taxonomic resolution and various faunal indices are usually used to keep the sample sorting work within reasonable bounds. Utility and limitations are summarized in table 2.4.

Nematoda

Our knowledge of deep-sea nematodes is very restricted by the poorly developed taxonomy of the group. They are probably the most abundant component of the meiofauna and may exceed the macrofauna in both number and diversity. As a practical matter in surveys that can not support a long taxonomic effort, the group must be treated as a whole and not sorted to species.

Harpacticoid Copepods

These small benthic copepods are less abundant than nematodes, but a better developed taxonomy makes them a useful tool in deep-sea studies. Three functional groups have been identified in deep sediments (Thistle 1983). One group has prominent dorsal spines that anchor a mucus/sediment mix that probably serves as camouflage for these sediment-water interface dwellers. A second group consists of burrowers that use modifies appendages and setae in excavation. A third group has developed a vermiform body to assist in interstitial existence. Thistle found a taxonomic and morphological analysis to be very informative in comparing environments of different energy level.

2.2.6 MMS Management Needs

When management focuses at the species level, data costs quickly become excessive. As a practical matter, it is necessary to select target species for detailed sensitivity studies and devise ways of gaining optimal information from collections sorted to less-than-species-level. Ideally, target species might be selected from the dominant organisms in each size category. Of special interest would be studies of the sensitivity of these species to turbidity, chemical discharge, and alteration of the habitat. Sensitivity studies should examine population-relevant parameters such as fecundity. In all the faunal groups the lack of taxonomic expertise is a critical factor. While it is not the obligation of MMS to revitalize the field of systematics, MMS should take steps to assure that deep-sea samples are studied in a timely manner by competent experts.

Table 2.4. Utility and Limits of Utility of the Meiofauna.

MANAGEMENT UTILITY	**LIMITS of UTILITY**
1. <u>Captures High Diversity Component</u> (a) This faunal class probably has a high species richness and (b) large number of specimens in small samples are well suited for statistical analysis.	1. <u>Least Likely to be Well Known</u> (a) limited information on species-level biology available and (b) most difficulty obtaining correct identification due to new species and few specialists.
2. <u>Sampling Standardized and Effectiveness Well Known</u> (a) subsamples from 0.25 m^2 frame mounted box cores have become the standard for benthic studies, (b) biases due to devices known and controllable, (c) sample processing well standardized.	2. <u>Very High Per Sample Processing Costs</u> (a) post-cruise sample picking and sorting under microscopes is time intensive and (b) correct and consistent identification of specimens depends upon a limited literature and few experts.
3. <u>Results are Quantitative</u>	3. <u>Results Difficult to Extend to Larger Fauna</u> General public and other ocean users will relate more to larger fauna such as fishes.

2.3 Zonation - The Depth Gradient As Multiple Habitats

2.3.1 Summary Statement

It is reasonably well established that benthic fauna changes progressively with depth with the pattern of change showing some regional specificity. The simplicity of this change with depth has lead to often confused debates about rates of change, where to draw imaginary lines, and appropriate nomenclatures (Table 2.5). Fortunately, this debate has subsided and simple schemes adopted until more productive research can be carried out. In general, three faunal groups can be identified in most regions. There is a well-defined upper-slope (200-1000 m) group which drops out with depth, an abyssal plain fauna (greater than 3000m) which increases with depth, and a lower slope fauna (1000-3000 m) which overlaps the other two. Dividing these three into sub zones is highly arbitrary since the ranges of the component species overlap extensively. Gage and Tyler (1996) advocate a even simpler view that there are only two major faunal groups contributing to the apparent zonation. Avoiding the confusing terminology of predecessors, they recognize a bathyal zone corresponding to the continental slope and an abyssal zone. Compared to the actively researched and debated deep-sea topic of diversity, the study of faunal zonation is now a relatively inactive area. The identification and naming of zones, homogenous bands, summarized by Menzies et al. (1973), has largely ceased and been replaced by analysis of adaptations in taxonomically restricted groups. From the management perspective, this shift in research emphasis is unfortunate since knowledge of species change across the vast areas of the deep-sea is needed to determine what management strategies are needed in different areas. Clearly, it would be simpler for management if one faunal zone existed and extended over large areas of the continental slope and abyss. If, on the other hand, each region of the continental margin had a locally unique bathymetric pattern of species change, the management task will be greatly complicated.

2.3.2 State of the Art

The description of deep-sea faunal zonation is a less active area of ocean research now than ecological study of specific habitats, the biological study of specific organisms, and consideration of diversity-maintaining processes. There is little discussion of zone placement, names, and validity. Some resumption of species-level distribution studies should be anticipated by management as deep studies follow the lead of shallow biodiversity studies where description of distributions is being replaced by two lines of research (Butman and Carlton 1995). The first of these, characterized by the review of Palumbi (1995a) examines populations and larval transport using genetic markers (Palumbi 1995b). The second is a critical reexamination using molecular genetics of the broad distribution of apparent cosmopolitan species (Knowlton 1993, Knowlton and Weight 1997).

Dispersion studies and reexamination of cosmopolitan distributions are both of appreciable management impact since they challenge the current views available to management that: (1) the sea floor becomes faunally homogenous with depth due to an increase in species depth range, that (2) deep megafauna tends to be increasingly cosmopolitan with depth, and that (3) deep macrofauna shows an increasing degree of regional endemism with depth. The need to challenge these widely accepted ideas lies in the subjectivity of traditional taxonomy. Most deep-sea families and genera were established in the era of national ocean exploration (1880' s-1950). At that time, diagnosis of new species by taxonomists was strongly influenced by developing, often conflicting, concepts about ocean zoogeography. Physiological-based concepts of distribution held that the monotonous and stable deep environment below 1000 m should be dominated by cosmopolitan species. Evolution-based concepts, stressing isolation, held that each ocean basin should be populated by narrowly distributed endemic species.

The expert's decision to split or lump was, in large part, controlled by one or the other of these ideas. The unfortunate consequence is that present day deep-sea zoogeography may be greatly distorted by concept-biased taxonomy. Etter and Rex (1990) have begun reexamination of the North Atlantic deep molluscs using DNA techniques and found, so far, that the prevailing idea of widening vertical ranges with increasing depth is correct.

For management purposes it may not be necessary to know that widespread morphological species are actually genetically differentiated species and sibling species complexes. Genetic screening of the deep-sea fauna would add great expense to any survey or monitoring effort. However, to ignore the possibility runs the risk of miscalculating the size of a potentially impacted population. One possible and cost effective means of solving this problem would be to continue emphasis upon morphological species study. New quality assurance and quality control portions of any study could include the requirement that a selection of dominant species tissue samples be cryogenically stored and archived in a repository that maintains such a collection. These samples could then be genetically screened during the course of subsequent museum-based research.

2.3.3 History of Zonation Concepts

A full discussion of the history of deep ocean zonation studies is of no particular management relevance and can be found elsewhere (Carney et al.1983, Gage and Tyler 1996). However, it should be understood that zonation is a descriptive fact for which the actual causes remain unknown. Therefore, management decisions should not presuppose any particular mechanism.

The fact that deep-sea species are restricted to vertical ranges of varying width was implicit but relatively speculative in early faunal studies. The first detailed discussion of this zonation and careful analysis of species data were given by LeDanois (1948), who favored temperature and sediment type as the causative factors. Until the advent of competition theory (reviewed by Paine 1977), zonation continued to be seen as being the result of physical factors. The great popularity of competition theory coincided with the rediscovery of high diversity in the deep-sea (Sanders et al.1965) and called into question the importance of community structure in that environment (Mills 1969). Could deep zones represent biotically controlled shifts in communities rather than physical control?

It was reasoned that if integrated and biotically controlled communities existed in the deep sea, then the transition from one community to another might be sharp and unrelated to any obvious suite of physical parameters. Alternatively, physical control and an absence of interacting communities should produce gradual species change with any sharp changes coinciding with distinctive physical conditions. The relative importance of biotic or physical factors remains unresolved. However, a strong hint that biotic factors are important can be found in the work of Rex (1977) who found that the rate of species replacement with depth changes with the taxa and feeding type examined. To better interpret observed distribution patterns, Pineda (1993) and Pineda and Caswell (1998) have taken a neutral model approach to zones, finding that some patterns are simple artifacts of the upper and lower boundaries.

2.3.4 The Analysis and Criteria Problem

The finding that ocean fauna changes with depth is one of the oldest and uncontested facts established in earliest ocean exploration. The issue becomes clouded, however, when attempts are made to describe this change and give explanations for it. Directly or indirectly, much of the problem lies in the choice of criteria used to recognize and describe compositional change. When drawing a map line showing a faunal change, there is an implicit assumption that a sharp fauna break actually exists. In many instances, however, the student of zonation may be employing criteria that impose a break upon the data that would not be found upon other analyses. A very brief historical review can illustrate this.

Prior to the 1980's, deep-sea faunal zones were proposed and named without hesitation. Since the seafloor morphology and water column properties of the world ocean were far better known than the ocean biota, physical parameters were actually the primary criteria employed (Ekman 1953, Hedgepeth 1957). Starting with LeDanois (1948) faunal distribution became the primary criteria for recognizing zones. However, employing physical criteria for dividing biological distributions was still used as in the zonation scheme proposed by Pequegnat (1983a) for the Gulf of Mexico.

The history of zonation studies reflects an increasing sophistication of analyses. All such analyses are based upon the examination of a matrix of inter-site similarity coefficients. In the past, the relatively simple Percent Similarity Coefficient (Whittaker and Fairbanks 1958) and Bray-Curtis Coefficient received the greatest use. More recently, Normalized Expected Species Shared, NESS, (Grassle and Smith 1976) has gained popularity. NESS is conceptually appealing since it is based upon expected probabilities (Hurlbert 1971), but is computationally complex and only recently been incorporated into statistical computer programs. The actual analysis of the similarity matrix can either be clustering or multivariate ordination. The conceptual simplicity of the former has resulted in its more frequent usage. As with the choice of coefficient, there has been a progression in the techniques used. The Flexible Linkage clustering strategy gained popularity in the oceanographic community for what must now be considered an undesirable property. Flexible Linkage clustering is highly subjective; by changing a single parameter, the clusters can be "tuned" until a preconceived result is obtained.

Analysis of similarity using ordination techniques is often viewed as the preferred method of zonation analysis since they eliminate the subjectivity and forcing inherent in cluster analysis (Carney et al.1983, Gage and Tyler 1996). However, these methods can be so conceptually complex that the final results are extremely abstract and of meaning only to the expert. Selection of a technique is difficult. Currently, Detrended Correspondence Analysis (Hill and Gauch 1980) is popular in benthic studies. Correspondence analysis is a technique intended to remove some distortions among relationships that principal component analysis and factor analysis impose.

Table 2.5. Depth Zone Names and Applicable Regions Proposed by Various Workers.

Approximate Starting Depth	**Hedgepeth (1957) Global**	**Carney et al. (1983) NW Atlantic**	**Pequegnat (1983a) Gulf of Mexico**	**Gage & Tyler (1996) Global**
< 200 m	Littoral	Shelf Province	Shelf	Shelf
200 m	Bathyal		Shelf/Slope Transition	
250 m		Transition Zone		
500 m		Upper Bathyal	Archibenthal Zone Horizon A	Bathyal
1000 m		Lower Bathyal	Horizon B	
1500 m		Abyssal	Upper Abyssal	
2000 m		Upper Abyssal		
2500 m		Meso Abyssal	Mesoabyssal Horizon C	
3000 m			Horizon D	
3500 m			Lower Abyssal	
4000 m+	Abyssal	Lower Abyssal	na.	Abyssal
6000 m+	Hadal	Na.	na.	

2.3.5 MMS Information Needs Concerning Zonation

MMS' primary need relative to deep-sea fauna zonation is to determine the degree to which species composition changes across the region of sea floor subject to development. There are two purposes for this information.

- Depth-Specific Management - If a region proves to be faunally homogenous then a uniform management strategy may by be employed. If a region contains distinct faunal zones then a suite of depth-targeted strategies may be needed.
- Confounding Factors - In subsequent effects studies, sample stratification must take into account any depth related natural fauna changes to prevent them from being confounded with possible impacts.

The above information can be derived from a conscientious faunal survey employing high taxonomic resolution. It is very important that samples be spaced at close regular intervals along depth transects to avoid zonation artifacts arising from spatial gaps in sampling. Emphasis should be placed upon generation of a high quality data base first and data summaries second. Useful descriptive analyses should employ the NESS similarity coefficient, cluster analysis, and ordination by a detrending method such as multidimensional scaling. Criteria need to be developed for the degree of faunal change needed before a change in management strategy is considered.

2.4 Deep Diversity - The Most Confusing Management Concern

The deep-sea benthos is very species rich, usually with a diversity maximum near the base of the continental slope (approx. 2000-3000 m), and this richness is quite hard to explain. The fact of this high and enigmatic diversity sets the deep sea aside from shallow water and poses something of a dilemma to management. How do you protect something that is so poorly understood? Unfortunately, as discussed below, our understanding of deep-sea diversity is really quite speculative and in a state of development. Thus, if the resource manager is going to make use of the developing concepts, they must understand the overall progress of concept development. Fortunately as a practical matter, a resource manager does not need to be a student of the subtleties of diversity theory. It is sufficient to know what the major processes are that maintain diversity and to adopt conservation measures which protect those processes. However, the burden on the manager increases when the underlying theory provides few practical guides and has not been rigorously developed through testing and criticism. Then, good management requires an understanding of the strengths and weaknesses of the developing theory so that preliminary management can lead to a fuller and more useful development of that theory. Unfortunately, deep-sea diversity theory as it now exists is of minimal immediate utility.

The following sections are intended to do four things. First, definitions of diversity will be considered. Second, a brief explanation of diversity theory will be presented. Third, deep-sea diversity concepts will be presented in historical sequence. Fourth, management information needs about diversity will be developed.

2.4.1 Definitions and Measures of Diversity

Diversity can be a very troublesome concept to both researchers and managers. It is easy enough to define intuitively, but mathematical expression of it that permits the necessary analyses and rigorous testing tends to get much more complicated. Interpreting it relative to basic or applied ecology has proven to be exceedingly difficult. The difficulty of interpretation is compounded by the fact that many proponents of diversity's management utility have been uncritical of speculation of how diversity relates to overall ecosystem condition. While it is always hoped that some index of diversity might be a precise indicator of ecosystem health, this simply has never been established.

Diversity is defined according to its intended use. Basic ecologists use definitions that derive from the resource utilization approach to ecology. Applied ecologists and managers usually want a simple descriptive definition.

- Theoretical: Diversity is the variety of organisms in a given environment, habitat, or ecosystem. In a yet unknown way, it reflects the history of emigration and immigration along with the competitive utilization of resources by different species. Evolutionary splitting of species may also be a factor in isolated systems. The exact mathematical form of its expression is not of major import so long as it supports investigation of the underlying processes.
- Utilitarian: Diversity is the variety of organisms in a given environment, habitat, or ecosystem. It represents the state of the system and no inference needs be drawn about the underlying processes. The exact mathematical form of its expression must be uniform across many studies and support comparisons from place to place and time to time.

The management need for simple indices has two origins. First, it facilitates comparison and analyses across varied studies. Second, it spares the manager the burden of having to deal with large and complex data sets. With the development over the past few years of computers that easily handle very large data sets, the need for standardized summary indices in ecology and many fields has greatly changed. If high-quality data are correctly stored, it is a simple and very fast task to calculate and compare every imaginable index. However, for comparison with past studies that may not have a good data archive, standard indices still have a place.

A useful review of the dozen or more indices used in benthic ecology can be found in Washington (1984) and Margurran (1988). Estimation of species diversity from deep-sea samples is usually hampered by sample sizes that are low compared to shallow water and very variable across a large region of study. Therefore, the very close relationship between sample size and species richness has received considerable attention in deep studies and is of considerable management interest. A very well written text on rarefaction (estimating species richness in a reduced sample size) and abundifaction can be found in Hayek and Buzas (1997) Surveying Natural Populations. Sanders (1968) initially devised rarefaction as a graphical means of comparing species richness between unequal samples. His method is simple and effective, but mathematically flawed. Hurlbert (1971) developed Sander's method in the mathematically correct form based upon the hypergeometric distribution. The most important thing to remember about diversity indices is that none of them convey any special information about the underlying processes behind diversity. Thus, there is no universal "best" index. The choice of index is dictated by the questions being asked. There are basically three approaches to diversity.

The Inventory and Simple Species Richness

Due to the utility and popularity of diversity indices, it is often overlooked that an inventory of species is not just raw data, it is an excellent expression of diversity. This is the simplest and most easily understood of all approaches and directly links the abstract notion of diversity with the actual species. When a mathematical expression is needed, the number of species in an inventory is the simplest diversity statistic and is typically called Species Richness. There are two criticisms of Species Richness that greatly limit its management utility. First, it does not consider abundance, leaving management with no tools for allocating study effort. Second, it is exceedingly sensitive to sample size.

Species richness is frequently used in theoretical work where sampling is not a problem. There are ad hoc methods of judging whether most of the species have been taken in a survey. These are based upon the rate at which new species are collected as sampling progresses. At some point, fewer and fewer new things are found, and sampling is judged to be adequate

Simple Probability-Based Diversity Index

When a species inventory contains data on proportional abundance, probability theory affords parsimonious ways of summarizing population patterns. Ideally, diversity indices allow for comparison of diversity among samples without having to standardize the sample size. The first index based on proportions was Simpson's Λ, but it is seldom used. Shannon's H' based on information theory (Shannon 1948) is widely used in applied ecology and is contractually required by MMS. Normalized Expected Species Shared NESS (Smith and Grassle 1977) has been extensively used, but is seldom included in statistical packages.

Simpson's Λ is the oldest probability-based diversity index. Simpson reasoned that a simple measure of the diversity of a particular habitat would be the probability of an observer encountering the same species twice in a row. The great appeal of this approach is that it may have some ecological reality to it. Probability must play a role in predator-prey encounters, breeding encounters, competition encounters, etc. The perceived problems of probability-based indices are all associated with the nature of proportions. High proportions produce high probabilities, and low proportion species are much less important. Simpson's Λ is based upon the square of proportion, making the relative importance of rare versus common things all the worse.

The most useful modification of the probability approach is the development of Normalized Expected Species (Smith and Grassle 1977). This index directly addresses the problem of sample size by calculating the expected number of species in a hypothetical sample of a specified size. This size, however, must be equal or lower than the actual sample. In other words, it can not be used to estimate species number in a hypothetical sample larger than any sample actually taken. Expected Species is an extension of Sander's rarefaction method. It is unfortunate that Expected Species is not widely used since it has very nice properties. It is a simple extension of species richness. It employs relative abundance in its estimation, and a wide range of abundance makes equal contribution to the index. Furthermore, it has the practical benefit of defining acceptable sample size. If 500 individuals is the level to be used, sampling can be optimized to produce that 500, and samples judged as adequate or not on the basis of having at least 500 specimens.

Information Theory Diversity Index

Information theory deals with the successful transmission of information through media that are inherently noisy. It can be considered a branch of probability theory. Margalef (1958), receives credit for the use of common information, H', as a diversity index. He argued that in an evolutionary or succession sense communities were analogous to information channels. Pielou quickly discounted this analogy, and it is rarely mentioned now. However, even if you strip common information of its proposed ecological relevance, it remains a mathematically useful formula. Whereas probability is based upon multiplying proportions, information is based upon logs of proportions. H' is a poor choice of indices for deep benthic studies. The index is best used when the dominant species exceed 50% of a sample. In the typical deep-sea study the most abundant animals are less than 20%. These mid-to-low percentages completely dominate the analysis, and the many rare species make no contribution.

Multispecies Competition Models

The following material is intended to establish the intellectual framework within which deep-sea diversity theory has been developed. The problem may be quite simply summarized. Simple and credible mathematics models indicate that when two or more species compete for a common resource, one will eventually displace the other(s) by competition. Why then are environments so full of many different species? The answers range from simple to complex and from plausible to dubious. The simplest is that there really are many resources and little or no competition is taking place. A bit more complicated is claim that there are numerous resources but not enough to prevent competition, and that various other processes intervene to prevent competitive exclusion. Intervention models can get quite complex and ultimately take the form of a mutualism argument.

The basic mathematics model of competing species was developed by Gause (1934) as an extension of the Lotka-Volterra population growth model. Levins (1968) extended them to multi-species form. Prior to May's (1973) exploration of stability and complexity in model ecosystems, a common explanation for high levels of species diversity was that competitive interaction between two species was in some way mediated by addition of a third, fourth, and so on. Ultimately, the more complex the community, it was argued, the more stable. May showed quite convincingly that neither stability nor complexity produces the other. Furthermore, competitive exclusion is to be expected except for special community matrices. If you are faced with a species rich community and you do not want to invoke increasingly complex intervention models, your principal explanation must be that there really are many resources available and competition is minimal.

2.4.2 Ideas About Deep-Sea Diversity

Historical Development, Stability-Time to Cropper Hypotheses

While proponents of various explanations for high biological diversity can argue the merits of their ideas, proof of any particular hypothesis is lacking and supportive evidence equivocal. To a large degree, the progression of ideas has not been driven by tests, falsification, and alternative hypotheses. Rather, growing information about the environment's physical heterogeneity and temporal pulsing (Smith, 1994) has been factored into diversity explanations which initially struggled with explaining high diversity in what was then viewed as a monotonous environment. Of course, this lack of a history marked by rigorous debate, extensive field observation, and hypothesis testing is not a just criticism of deep-sea diversity research. There have been too few people, too few facilities, and too few opportunities for the history to be otherwise. However, this history poses a dilemma in seeking a scientific basis for deep-sea diversity conservation; none of the ideas can be ruled out and none may be right.

An understanding of the extent to which deep-sea diversity concepts are untried is best developed through a brief historical review. More detailed reviews of the content and development of ideas can be found in Grassle (1989), Rex (1983), Gage and Tyler (1996) and, Rex et al.(1997). Unlike the fall into obscurity of the Challenger discovery of high deep diversity, the findings of Sanders et al.(1965) were immediately recognized to be a paradox of the plankton question (Hutchinson 1961), asking how so many species can arise and coexist in such a seemingly monotonous, homogenous and undivided environment? In the context of competitive exclusion thinking at that time, the answer put forward was quite bold, the Stability-Time hypothesis (Slobodkin and Sanders 1969). This hypothesis, or explanation, essentially said that competition in an environment that is stable over very long periods of time leads to coexistence through a type of resource partitioning termed accommodation, not exclusion as might be predicted for such a system. This explanation for high diversity fully accepted and built upon the monotony and homogeneity of the deep sea.

The Stability-Time hypothesis gained some acceptance in shallow marine studies of apparently stable systems but was largely ignored by terrestrial workers who were rapidly abandoning similar temporal-stability explanations for tropical diversities in favor of herbivore/predator effects (Janzen 1970) and long-term habitat change (Prance 1982). Biological control in the deep-sea was first introduced as the Cropper Hypothesis (Dayton and Hessler 1972) borrowing directly from intertidal ecology. Grassle and Sanders (1973) corrected an omission in the Cropper Hypothesis, but rejected it as being inconsistent with the few known life histories of deep species, interpreted by those authors as K rather than r selected. No testing of the Cropper Hypothesis per se was conducted. Except for an attack upon epistemological limitation of the Stability-Time hypotheses that concluded that deep-sea diversity is just another diversity-area relationship (Able and Walters 1979), all subsequent explanations for the diversity have explicitly invoked environmental heterogeneity as a diversity maintaining factor. Thistle (1983) used diversity predictions based on the Stability-Time hypothesis to compare a less physically stable abyssal area in the northwest Atlantic with a more stable bathyal site in the eastern Pacific and found no support for the hypothesis.

The adoption of hypotheses that stress heterogeneity of the deep-sea environment is due in large part to two factors. First, seminal ideas about population dynamics and evolution in patchy environments such as Levins (1968) were influencing deep-sea workers. Second, increased deep reconnaissance and monitoring of the deep-sea floor showed that it was reasonable to think of that environment as patchy. In reviewing these sources of variation over small (1 m^2) to large areas (100 - 1,000's km^2), Smith (1994) has stressed the pulsed nature of bioturbation, benthic storms (Thistle et al. 1985) and detrital influx (Lampitt 1985). Since habitat change occurs in pulses, processes ultimately controlling diversity might also be sporadic, intense, and localized. According to models of species in patchy space, high diversity may be maintained if the outcome of competition differs among patches. Such high diversity may exist within a patch or summed across many lower diversity patches, depending upon exactly how dispersion and local-regional interactions are modeled (McLaughlin and Roughgarden 1994). Efforts to explain deep-sea diversity in terms of habitat patchiness have focused on using faunal samples to determine the scale of patches and sampled or experimentally simulated bottom structure to identify the agents of such heterogeneity.

The infusion of patch-related thinking into the deep-sea took place largely in the 1970's during innovative studies in the laboratory of Robert Hesseler of Scripps Institution of Oceanography. The focus of these studies was the role in diversity maintenance of the biogenic structures created by the interaction of flow and biological activity. Central to the development of these ideas was sampling at controlled scales and in-situ experimentation. Important faunal scales were examined by clustering samples at different scales, partitioning box cores into sub samples, and employing remote devices to collect multiple samples from known positions over an area of approximately 500 m^2. The studies were summarized and reconsidered by Jumars and Gallagher (1979) and Jumars and Ekman (1983). These ideas, which can be called the Grain-Matching hypothesis, did much to refine ideas about spatial scale and cause testing of patchy-environment hypotheses. Four points remain especially important. First, faunal distribution patterns can be found on many scales, but the scale on which intra-species interactions occur in a succession mode are probably quite small, approximately the same size as the organisms themselves. Second, biogenic structure should be more persistent in the deep sea and is likely to be a very important agent of habitat heterogeneity. Third, the statistical power associated with analyses of faunal dispersion is very low, introducing considerable uncertainty into the analysis of surveys. Forth, significant progress in understanding how competition regulates diversity will require an understanding of what resources are being utilized by the fauna.

Patchy Environment Grain Matching

The points drawn from controlled sampling by Jumars and his associates had a strong influence upon in-situ experimental studies of the role of heterogeneity, especially the studies on the interaction of macrofaunal structure upon meiofauna diversity and the effect of simulated megafaunal mounds upon macrofauna. Eckman and Thistle (1991) demonstrated that water flow around the ball-like mud tube of the polychaete *Tharyx luticastellus* influenced some meiofaunal distributions. This effect was attributed to alteration of the sediment-water interface in the area around the mud ball by hydrodynamic flow. Smith et al.(1986) simulated the sediment mounds of large infaunal deposit feeders and found rapid colonization of this biogenic structure. The experiment was repeated with refinements (Kukert and Smith 1992) and the results produced evidence of immediate effects, longer-term succession effects, and an eventual return to near background conditions.

Since the artificial mound studies were so well designed and executed it is important to look at the results closely. Did the artificial mound constitute a patch that might contribute to the overall high diversity of the bottom? The dominant species in the background fauna, *Levinsenia oculata* was also dominant in all samples of the experiment. Few of the rarer species with enough specimens to be included in analysis showed any effects through time. The mound showed no evidence of being a haven for rarer forms in the sense that none of the rarer forms were elevated to dominance during the sampling period. The results of Schaff and Levin (1994) are particularly noteworthy in this regard. At a depth of approximately 800 m in the Atlantic off North Carolina, they targeted submersible sampling at conspicuous biogenic structures. They found no significant difference in the fauna between the background and the biogenic structure. In conclusion, these manipulations have shown that populations respond to alterations. However, it is not yet clear that such responses reflect the processes that maintain high diversity. Far more comparative study needs to be done.

Patchy Environment Contemporaneous Disequilibrium

An alternate hypothesis, termed the Contemporaneous Disequilibrium hypothesis has been developed by Grassle and his associates based upon the slowly accumulating information on the natural history of deep-sea fauna (Grassle and Sanders 1973), observation of detrital input periodicity, and extensive surveying on the continental slope (Grassle and Maciolek 1992). The central idea is that not all biogenic structure is important. Some structure and bottom hydrodynamics interact to create patchy deposition of labile organic detritus. Changing biological structure and extended post-depositional diagenesis in these special patches then provides the resource diversity to support a diverse fauna in a mosaic of succession stages. As a food-driven heterogeneity, these different patches can support higher-than-background source populations. Adult larval exported from these source patches maintain diversity over the much larger food poor areas. The Contemporaneous Disequilibrium idea has also gained some support from experimental studies. Colonization of defaunated sediment boxes showed very slow recruitment rates (Grassle and Morse-Porteus 1987), while colonization of food enriched sediment showed treatment faunal densities an order of magnitude greater than controls and ambient in just 23 days (Snelgrove et al. 1992).

2.4.3 Larger Scale Views of Diversity

While the dynamics of inter-species competition in small-scale patches on the sea floor are important in local diversity maintenance, other processes and historical events on regional scales control the available species pool (Ricklefs 1987). Rex et al.(1997) in press) provide an extensive review of large-scale diversity patterns in the deep-sea. The first and most fully considered of deep-sea diversity patterns was that western Atlantic benthic samples showed a distinct diversity maxima between 2000 m and 3000 m, which has been termed a parabolic pattern (Rex 1983). Application of the word parabolic invites explanations in which there are two interacting processes.

Huston's (1979, 1994) dynamic equilibrium model seemed applicable to the deep-sea diversity maximum and had the great benefit of leading to testable hypotheses about competition and predation gradients with depth (Rex 1983). According to this model, diversity is suppressed by competitive exclusion as an area reaches equilibrium, while diversity is promoted or permitted by predator and abiotic disturbance. The difficulty with this and other models employing competition is poor linkage to known gradients in the deep-sea. Pressure has the most simple and ever increasing gradient. It does impose physiological limitations of the fauna, but it would seem to have no link to competition. It is now well established that the influx of organic detritus is a negative exponential function of depth (Rowe and Pariente 1992), and population size should be linked to food input. It is less clear, however, if increasing food should be limiting diversity via competitive exclusion by larger populations, or promoting diversity through an overall increase of resources. Indeed, the diversity maxima may simply reflect the depth mode of an environmental factor such as sediment texture as suggested by Gray (1974) or sediment diversity as found by Etter and Grassle (1992).

In the context of competing processes that vary in opposite directions with depth it may be worthwhile to modify the argument of Able and Walters (1979) that high deep-sea diversity is simply another manifestation of the ubiquitous species-area curve. Taken alone, the hypsometry (distribution of depth) of the ocean leads to the prediction that diversity will be greatest at abyssal plain depths below 4000 m, not shallower as it has been found to be. However, if the exponential decrease in food with depth is combined with hypsometry, then a maximum on the lower continental slope may be expected. If species are to some degree bathymetrically restricted by low detritus influx, then historical increases in influx may have spread species across the vast area of the abyssal plain, and decreases caused restriction to the slope.

A less well-established diversity gradient in the deep sea is that of latitude in which diversity is higher at tropical latitudes than boreal and Arctic (Rex et al. 1993). Since this finding has been based on scattered and dissimilar studies, it has been attacked as an artifact of regional glaciation effects (Gray 1994), and as conflicting with other results (Brandt, 1995). These criticisms should not be taken too seriously as yet. Indeed, glaciation may be one of the important causal mechanisms behind latitudinal gradients even in deep water. There was a distinct change in benthic foraminifera dominance in the north Atlantic at the Pleistocene-Holocene transition (Schnitker 1979). It appears that it took place progressively over the continental slope beginning about 15,000 years ago at 1000 m and only reaching completion at 5,000 m 5,000 years ago. Similarly, criticism based on conflicts with regional-scale patterns is misguided. Even over distances of several hundreds of kilometers, intra-region variation in diversity may be expected to mask latitudinal trends. A novel example of this is approach of Voight and Walker (1995) comparing epibionts on the gastropod Gaza sp. from the continental slope of the northern Gulf of Mexico with Caribbean specimens; higher diversity in north was attributed to differing sediment regimes rather than a refutation of latitudinal patterns.

2.4.4 MMS Information Needs

Identifying MMS' need is simple; obtaining it is the hard part. Management needs to know exactly what the diversity maintaining processes are and then regulate industry activities so as to minimize disruptions. Current deep-sea ecology does not identify those processes conclusively. Of the two views, a homogenous environment with complex competition or a heterogeneous environment with normal competition, the second is more tractable. If the deep benthos is a habitat rich system on the very small scale, then the physical and biological processes causing this variety must be known and protected. Presently, these appear to be creation of biogenic structure, flow interactions at the sediment water interface, and redistribution of detritus.

There are practical needs concerning surveying fauna and producing diversity analyses. The need for a diversity index as a descriptive summary statistic in species inventories has been greatly reduced due the ease of use of interactive data base analysis.

However, retention of the index facilitates comparison to older studies and assures the data continuity that MMS requires in its contracted surveys and monitoring.

2.5 Ecosystem Processes

2.5.1 Biomass and Trophic Structure

Environmental managers have often faced the criticism that they did not follow the lead of academic ecologists in switching from species inventories to process-oriented studies. Such criticism however, is seldom accompanied by convincing arguments that knowledge of particular processes is management relevant. Upon review of current concepts of deep-sea ecology, it does appear that the influx of organic detritus and the biogenic structuring of the benthos are processes of considerable management relevance. This apparent relevance stems from the ideas that both processes are far more important in the deep sea than on the continental shelf. The influence of detritus influx is most readily seen in biomass or population density data. The vertical pattern of biomass in the ocean is the simplest bathymetric trend, the most easily measured, and the readily interpretable of all biological depth gradients. Excluding the relatively rare chemosynthetic systems, productivity is limited to the upper photic zone. The consumer community of the upper mixed ocean is relatively efficient at retaining much (90 to 95%) of this productivity. Thus deeper bottoms are dependent upon a meager detritus influx. The longer this detritus is in transient to the bottom, the more degraded it becomes with the results that biomass decreases progressively with depth. Biogenic structuring is much less understood, but bioturbation studies are the starting point for future research.

There are four primary management consequences of the pattern of organic detritus influx.

- Biomass harvesting (i.e. fishing) is unlikely to be a serious conflicting use of the deep-sea floor.
- Dramatic biomass differences between the slope-shelf break at 200 m and the slope bottom at 3000 m suggest that these environments are different and may require depth specific management strategies.
- In areas of low biomass, food may be so rare and limiting that disruption of natural patterns of detritus input may be the primary agent of environmental impact.
- The response of bottom populations to natural variation in detritus influx may be a major source of confounding variation when seeking environmental impacts.

Identifying the Flux

Prior to the 1970's ideas about deep-sea biomass were greatly influenced by Danish and Russian sampling in the hadal trenches adjacent to continents. Since these 6 - 11 km deep special environments at the continental margin had relatively high levels of standing stock biomass (Bruun 1957, Belyaev 1966), depth per se was considered less important than distance from land in regulating biomass. The weight of evidence now indicates that for most regions of the ocean, depth is the more important factor. Examination of biomass versus depth for benthic fauna and for deep-ocean plankton

(Vinogradov 1961) shows an exponential decline in biomass with depth. Place to place variation in this curve has been attributed to surface productivity (Rowe 1974), width of the continental shelf (Rowe and Haedrich 1979), and latitude (Belyaev 1966). However, the actual controls are poorly known.

The primary source of food for the benthos is organic material sinking down from the photic zone (Fowler and Kanuer 1986). This material which leaks into the deep-sea from the euphotic zone is approximately 10% of the productivity (Walsh 1992). Large food falls are apparently rare in the larger scheme of things (Stockton and Delaca 1982), but may be locally important (Smith 1994). There is clearly a scavenging component of the fauna adapted to exploit both recent carcass falls (Isaacs and Schwartzlose 1975) and the longer-term chemical environment they produce (Smith, et. al 1989). Even the relatively rare sinking of wood into deep water is exploited by a specialized community (Turner 1973, Maddocks and Steineck 1987). It is thought that adaptation to very low food levels is the main evolutionary theme in the deep-sea fauna (Jumars et al. 1990).

A full determination of which component of the detritus flux carries the most food to the benthos has not actually been made. Fine particles (< 10 μm) are unlikely to carry much nutritional value since they are in transit too long. Much larger particles (> 1 cm) sink much faster and carry more material, but seem to be relatively uncommon. Thus, mid-range material (10-500 μm) is the most likely candidate (Fowler and Knauer 1986). One of the most seminal observations in deep-sea ecology was the episodic and rapid sinking of phytoplankton blooms to abyssal depths (Billett et al.1983, Lampitt 1985). All at once this suggested many things. First, it laid to rest any residual ideas that the deep sea is a stable environment. Second, it showed that while the deep-sea may be food poor much of the time, there are period of relative plenty. Lastly, the observation that BBL conditions redistributed the detritus pulse into a complex patchwork on the bottom suggested a mechanism for environmental heterogeneity .

A six year time series of detritus flux measurements at 3200 m in the north Atlantic (Deuser, 1986) revealed a range of inputs varying by a factor of 2.3x between minimum and maximum. Smith and Baldwin (1984) demonstrated that benthic metabolic consumption varied in response to such influx variation. Tyler (1988) and Tyler et al.(1994) suggest that breeding in some species may be keyed to high levels of influx. Thus, it may be assumed that population levels will vary in response to year to year differences.

Missing Pieces of the Puzzle

Four major discrepancies have been noted in our understanding of how detrital flux fuels the deep benthos (Carney 1989). These are:

- Biogeochemisty indicates that detritus becomes highly refractive in transit to bottom, but its rapid consumption on the bottom indicates that it must be biologically labile.
- Biological estimates of detritus utilization indicate rapid consumption in 10 to a few 10's of days. Geochemical estimates suggest slower utilization of 15 to 150 days!
- Calculated biological demand may exceed apparent supply (Smith 1987).

- The isotopic content of deep fauna is not always freshly input carbon (Pearcy and Stuiver 1983).

There are still pieces of the puzzle missing, but these may simply reflect the current crude state of measurement. Benthic ecologists determining the energy needs of the benthos find that most, if not all of the influx must be labile material to support the measured need. By contrast, studies of the sinking material indicate that the influx should be highly refractory due to bacterial attack during sinking. While it is tempting to invoke bacterial infallibility (bacteria can eat anything) and the resulting biomass as food for the benthos, this is trophically unlikely. To support bacterial metabolic needs, as little as 15% of the influx might be converted to labile bacterial biomass. Thus, there would be far too little material to support the metazoan benthos. The most likely explanation is that the benthos is feeding off a labile detritus which is not the same fraction being collected in traps and studied by the organic geochemists.

The Suess and Rowe Relationships

Benthic ecologists have a good general understanding of the gross patterns of detritus influx and the biomass that it supports. This understanding is based upon compilations which have been confirmed in many studies. Suess (1980) compiled data comparing euphotic zone primary productivity with apparent carbon flux at progressive ocean depths and used regression to generated equation 1.

1. $$C_{flux} = C_{prod} / (0.0238*Z + 0.212).$$

Where C_{flux} is the flux of organic carbon at any given depth and C_{prod} is the primary production. Z is depth in meters such that Z must be greater than 50 m. Suess chose this formulation by analogy with a chemical reaction so that a process rate could be calculated. Inspection of the equation shows that only about 10% of the euphotic zone productivity makes it below 1000 m. Thus, based on Suess, little productivity is expected from mid-slope and deeper.

Macrofauna biomass in the world ocean was compiled by Rowe (1983) based upon 709 quantitative samples reported in 36 publications. This remains the definitive compilation, and in spite of many possible biases associated with different sampling and processing methods, it affords the deep-sea manager a simple picture of how typical biota changes with depth. Describing biomass decrease with depth as an exponential decrease is more than an algebraic convenience. It reflects a biologically realistic process. The basic form of the relationship is given in equation 2 after Rowe (1974, 1983).

2 $$M = Ae^{-bz}$$ where M = biomass in g/m^2 wet weight

e = the base of the natural log

A = Biomass at 0 depth

z = Depth in meters

b = exponent

Determination of A and b from field data is usually based upon regression of the log transformation, equation 3. LogA is simply the intercept and b the slope of the line.

3 $$\text{LogM} = \text{LogA} - bz$$

Negative exponentials are found whenever some process decreases an initial amount of material by a fixed fraction over and over again during a fixed unit of time. For example, let primary productivity inject 1 kilogram of sinking biomass into the upper ocean. It is immediately colonized by bacteria and attacked by consumers as it sinks. In one hour, 50% may be consumed, and the next hour another 50%, and so on. If this scenario is plotted against time, a negative exponential is seen. When sinking rate is constant, time and depth are readily interchangeable.

Treating b, the rate of consumption of sinking biomass, as a constant over all depths is a biologically unrealistic simplification, but it is justifiable at this time due to a lack of more detailed information. It probably decreases in the water column with depth. Low temperatures may inhibit bacterial activity, and the declining zooplankton will be less likely to consume the material that passes by. If management of the deep-sea ever requires a detailed understanding of natural biomass fluctuations, then the processes of degradation will have to be more fully explored.

Using logarithms to the base 10, Rowe found the following relationship: equation 4. When this equation is considered two important patterns are found. First, biomass can drop by half over as little as 500 m or as much as 2000 m. Second, most biomass decline can be expected on the upper slope above 2000 m.

4 $$\text{Log}_{10}\text{M} = 1.25 - 0.00039z$$

The primary management value of the Suess detritus relationship and the Rowe biomass relationship is that they provide standards for comparison. If a particular region's measured influx fits the Seuss relationship well, then it is not an unusual deep environment. Similarly, if the biomass agrees with the Rowe relationship, it is a typical system. Departures above or below either relationship should be examined very carefully to determine exactly why the system is unique. It might be exceptionally productive, or especially stressed by natural conditions.

Management Consequences of Biomass Decrease: Deep Productivity and Fisheries

This report does not focus upon the issue of deep-sea fisheries. In theory such fisheries are possible if very carefully managed. However, the dramatic failure of presumably well managed fisheries targeting well known shallow-water species should cast serious doubts on any deep ocean plans. As traditional nearshore fisheries targeting top predators have collapsed, fishermen have switched to different target species. This shift has resulted in the exploitation of lower trophic level fishes in the upper ocean and deep demersal populations. The pressure to expand deep fisheries will persist, and ocean managers must anticipate resource conflicts. These mineral-versus-fish conflicts will be different from those which have taken place in shallow water because deep fisheries are new rather than traditional. In effect, the fisheries proponents know as little about the environment as the mineral developer. An excellent and comprehensive account of deep fisheries has been written by Merrett and Haedrich (1997).

There is a small deep-sea fishery for crabs, shrimp, and rattail fish in the US. However, the best documented fisheries are in the Northeast Atlantic and the Indian Ocean. The orange roughy fishery is the best studied. Orange roughy (*Hoplostethus atlanticus*) is a slope-dwelling species found over a variable depth range between 500 and 2000 m. It grows to more than 50 cm in length and has desirable market properties. Prior to the discovery of spawning schools over topographic highs between Australia and New Zealand (Robertson 1991) it was considered a relatively rare species. Fishing with trawls began in the 1980's, peaked in about 1988, and declined subsequently. Orange roughy does occur in the northern Gulf of Mexico, but is not fished as yet.

Merrett and Haedrich make three strong cases against large scale deep ocean fisheries, both which relate to the biomass decline and trophic structure of the deep sea. First, fish populations show the Rowe biomass decline. Unusually high biomass species are rare and of considerable age. Second, in shallow water commercial fish species are seldom the terminal predator. Therefore, fishery is just the addition of one more predator to species adapted to predation. This is not true in the deep. In that environment fish are the top predator and the populations are not adapted to being prey. Thus, populations may be unable to sustain exploitation. The third argument, related to the first, concerns age structure. Due to the low food input to the deep, many large animal species have spent many years growing to reproductive size. Therefore, harvesting targets a biomass that turns over very slowly. It may require decades for populations to recover from even minimal fishing pressure.

2.5.2 Bioturbation Tracks and Trails

Biogenic structuring of sediments has been proposed as a very important diversity maintaining process, but not well studied in that context. Conceptually, a simple experimental means of estimating the kinds and rates of such modification could be devised. However, such development has not taken place as yet. The specific study of animal-sediment interaction has been incorporated in some deep-sea programs as an ancillary activity in faunal surveying. In this section, the topic is briefly reviewed, inherent limitations identified, and future uses suggested. Two main types of animal-sediment interaction studies have been attempted in deep-sea applied ecology programs: the study of lebenspurren and the study of bioturbation. The first is related to the paleontology field of ichnography and studies tracks, trails, and other marks made by animals on the seafloor. The second derives from the study of chemical tracers in marine sediments and considers the effects of biological stirring upon gradients.

Tracks and Trails

Oceanographers have treated lebenspurren in three ways. First, it has been simply a description of an obvious and pervasive small scale topography (Ewin and Davis 1967, Heezen and Hollister 1971). Second, the various marks have been treated as surrogates for observations of animals. The hope was that surveys of tracks and trails might provide estimates of population density. Third, the actual trace morphology has been examined in an effort to learn something about foraging behavior of deep-sea animals. This behavioral aspect grew out of the paleontology work of Adolf Seilacher (1967) who interpreted some fossil traces as reflecting a depth related increase in foraging efficiency. The simple descriptive use of lebenspurren will not be considered here since it is somewhat devoid of ecological relevance.

Unfortunately, benthic surveys of lebenspurren have proven of little value for either population estimation or behavior studies. As will be discussed shortly under the topic of bioturbation, the deep-sea floor is exposed to animal disturbance far longer than the shallow bottom due to very low sedimentation rates. This exposure is so long, in fact, that the animals can completely homogenize the sediment layer they occupy. As a consequence, animals both make marks and erase marks by their activities. Wheatcroft et al. (1988) have treated this make/erase relationship with mathematic formality.

The limited utility of lebenspurren studies was well demonstrated in a MMS-funded deep baseline survey (Gallaway et al.1988). The failure of this effort is easily understood. The count of lebenspurren in a photograph is a snapshot in time as well as space reflecting the contributions of both trace making and trace erasing at that place and time. Logically, trace making increases in some simple manner, possibly a linear relationship, with the extent of animal activity on the sediment surface. The persistence of these traces, however, must decrease as more and more new traces obliterate the old. As a result, the number of observed traces by itself provides ambiguous information about the extent of animal activity. A few traces may indicate either low populations or very high populations. Indeed, traces only become informative if the population of trace makers and erasers is known. Obviously, if you know that, the study of traces is unnecessary.

The behavioral utility of lebenspurren in the deep sea has been extensively considered by Kitchell (1979) and Kitchell et al.(1978a, 1978b). Predictions from the Seliacher model of foraging efficiency were not supported in either bathymetric surveys or trophic surveys under polar ice cover. It was concluded that feeding is a multi-factored process, the efficiency of which can not be judged from tracks and trails.

Bioturbation

While lebenspurren studies look at discrete structures made by animals, bioturbation studies consider biological activity in sediments as an homogenizing process. Early in the use of microfossils in deep-sea sediment, it was recognized that animal mixing blurred the fossil record, and some crude models of mixing developed. Guinasso and Shink (1975) formalized these models as analogous to Fickian diffusion and started the practice of describing bioturbation as a dimensionless mixing coefficient operating through a sediment mixed layer of a specific thickness. Ecologists have always been somewhat dissatisfied with the lack of biological reality of these models (Wheatcroft et al.1988), but they have proven suitable in chemical tracer studies and have been extensively developed (Boudreau 1986a, 1986b).

So far, the importance of bioturbation studies in the deep sea and shallow environment has been in the context of pollutant fates rather than ecology. In the simplest models of pollutant incorporation into bottom sediments, the pollutant moves down into the sediment at a rate determined by diffusion and sedimentation. Both of these processes are very slow, especially in the deep-sea. If these models were correct, then most pollutants would be limited to the top few millimeters of mud. Bioturbation models show that mixing by animals far exceeds sedimentation or diffusive influx and can spread pollutants through a mixed layer of sediment typically 10 cm thick. Therefore, to predict the distribution of a pollutant in a biologically active bottom, it is necessary to determine both the mixing coefficient and mixed layer depth. These are estimated from chemical gradients in the sediment with supportive sediment structure data.

2.5.3 MMS Management Needs

For the most part MMS has been correct to remained focused on species-level survey while being criticized for not taking a process-oriented approach. This is because in shallow water it is not clear how impacting activities and natural processes interact. In deepwater, however, a process approach may be much more useful. The fact that most deep-sea animals are deposit feeders depending on detritus influx for food suggests a simpler trophic structure. In addition, the simplicity of this system suggests that interference with them may be a major impacting activity. With respect to influx, a full description of a deep habitat should include time series sediment trap studies.

The study of tracks and trails is too detailed and too information poor to have great management utility as a measure of benthic processes or fauna. On the other hand, bioturbation studies that usually focus upon gradients of chemical tracers are on the wrong time scale to be of much use. Management simply needs a means of determining the extent to which the sedimentary environment is biologically structured. This might be most easily done in an experimental setting. Such a measurement might gently smooth the surface of the sediment and then employ image technologies to provide a times series description of the reestablishment of microtopography.

2.6 Case Studies

2.6.1 Introductory Summary

Development of management strategies appropriate for deep oil and gas development can only benefit to a limited degree by the examination of prior work undertaken for regulatory purposes. The limitation of previous work must be stressed, since the planned activities were very different than oil and gas development, and projects were usually terminated prematurely when the regulatory need vanished. Deep regulatory studies have been undertaken in the US in conjunction with dredge spoil disposal, hazardous waste (nuclear and chemical) disposal, manganese nodule mining, polymetallic sulfide mining, and oil and gas development. In the following sections mining and hazardous waste dumping are reviewed and the overall relevance to oil and gas management considered. In addition, the case of the proposed scuttling of the oil storage facility Brent Spar is considered as an example of a poorly executed oil industry deep activity.

Of the mining studies, nodule mining provides some excellent guidance for future oil and gas relevant environmental work.

- Massive impact was to be accepted in some areas balanced by total protection from impact in large-area preserves.

- The studies carefully considered the unique aspects of deep-sea ecology and focused upon fauna and plume effects on detritus influx.
- Industry and regulators undertook cooperative environmental research during large-scale trial mining programs.
- Industry undertook some environmental research on its own initiative.

The dumping studies are somewhat less value in the context of planning oil and gas development.

- High hazard studies, typified by radioactive waste disposal, focussed on human health issues rather than environmental impact.
- Low hazard studies, typified by sewage sludge dumping, initially structured tasks around inappropriate models. Thus, little relevant information was gathered prior to cessation of dumping.

In each case considered the studies of deep-sea environmental impact were terminated prematurely due to a shift in government priorities. Deep ocean mining is non economic and dumping has been effectively banned. While it may seem appropriate that regulatory agencies have ceased extensive deep-sea work, this cessation places the oil and gas manager in a sensitive situation. There is a growing need to dispose of hazardous wastes, and there remains an interest in renewed ocean disposal. Any industrial use of the deep-sea may be seized upon by the advocates of ocean disposal as justification for renewal. The oil and gas industry and its managers should carry out the needed ecological research fully aware that other industries will use the results for unintended purposes.

2.6.2 Deep Ocean Mining

Of all proposed deep-ocean uses, mining is most similar to oil and gas development since it is involves a similar industry and lies under a related regulatory umbrella. It is quite different, however, in that mining severely impacts and permanently alters large areas of seafloor habitat. By comparison, the impact footprint of oil and gas is small and temporary under existing decommissioning regulations. Two deep mining activities have received varying degrees of interest. Nodule mining of the central Pacific is the most familiar topic. However, MMS' deep activity has already included the less known subject of polymetallic sulfides. The US studies undertaken to look at environmental impact of nodule mining are especially noteworthy. Even though international sea floor was involved, the US Congress issued restrictive regulations. With the National Oceanic and Atmospheric Agency (NOAA) as lead, scientific consensus as to the most important studies was developed and then selected studies carried out. Studies took advantage of industry proof-of-method projects and involved international cooperation.

Ocean Mining of Manganese Nodules and Polymetallic Sulfides

Manganese nodules were discovered during the voyage of the HMS Challenger. The dense nodule aggregations of the central north Pacific first received economic interest when cold-war economics dictated that the US move toward self-sufficiency in strategic metals. Mero (1952) is first credited with proposing manganese nodules as a viable oar for manganese, cobalt, nickel, and copper. By the 1970's six international consortia had been formed to prospect and develop mining and refining technologies (United Nations 1985). Several patents were subsequently issued for different mining methods, all of which depended upon gouging the seafloor down to 45 cm in the sediments, separating nodules from sediments, and returning just the nodules to a surface ship.

Three consortia, Ocean Mining Association (OMA), Ocean Management Inc. (OMI), and Ocean Minerals Corporation (OMC) pursued development to the point of trial mining at 1/4 to 1/5th commercial scale during the 1977-79 period. OMA tested their system in 1977-78 aboard the Ocean Miner II producing 25-70 tons of nodules/hr with an overall haul on the best trial of about 500 tons. During a November 1978 trial, NOAA monitored the environment as part of the DOMES (Deep Ocean Mining Environmental Studies) program. OMI used a converted drill ship, the SEDCO 445, for hydraulic mining trials in 1978, producing about 800 tons of nodules. OMC successfully tested their system in that same year, employing the heavy lift ship GLOMAR EXPLORER, the Central Intelligence Agency (CIA) vessel which used nodule mining as a cover activity for recovery of a sunken Russian submarine.

Since widespread public concern over environmental degradation was a product of the 1960's and 70's, plans to exploit the seafloor were closely paralleled by concerns about environmental impact (Gerard 1976). Barkenbus (1979) has characterized the prevailing environmental views about deep-sea mining at the time as ranging from confidence that there would be no impact up to fear of catastrophic damage. This review, however, found no literature taking this latter extreme view. Indeed, environmental concern, as evidenced by the literature was quite moderate. The National Research Council (NRC 1975) called for assessment of impact and monitoring during the development of technology by industry. There were no moves to block development prior to better environmental understanding.

International and Federal Policy Advocacy for Stable Reference Areas

In the 1970's the US participated in the United Nations with respect to (LOS) Conference, expressing fundamental reservations about the provisions for seabed mining contained in Part XI. So as to provide site security for US companies without the LOS, the US Congress passed in 1980 the Deep Seabed Hard Minerals Act as an interim measure. It assigned both licensing and environmental regulation to NOAA. Internationally, the Preparatory Commission of the Law of the Sea registered claims for Russia, Japan, China, France, India and Interocean Metals. Conflicting overlaps were settled through negotiations. The major US concerns about the LOS provisions were how seafloor activities would be administered and how the resources of participating companies might be directed toward non participating countries and corporations.

With respect to seafloor mining, both LOS and the US Deep Seabed Hard Minerals Act called for the setting aside of preserves which would not be mined. Termed Stable Reference Areas (SRA's) (Post 1983). These areas were to be large and fully representative of the habitats to be destroyed by mining. A key difference between LOS and US implementation of SRA's was that LOS gave designation and study responsibility to industry, while US law gave the responsibility to NOAA. In 1982 NOAA received the first applications for nodule exploration from four US consortia: Ocean Minerals

Company, Ocean Management, Inc., Ocean Mining Associates, and the Kennecott Consortium. All four licenses were granted in 1984 permitting 10 years of exploratory activity. Pursuant to Section 109(d) of the Deep Seabed Hard Minerals Resources Act (P.L. 96-283) and 102(2)(c) of the National Environmental Protection Act, the administrator of NOAA submitted an Environmental Impact Statements limited to the potential effects of exploration. The EIS process was greatly complicated by the issue of international waters and the evolving law of the Sea treaty. The sites of the four licensees were originally kept confidential. Following international resolution of overlapping license areas claimed by foreign programs, and US the revised coordinates were made public. NOAA argued that the changes in coordinates did not alter the conclusion of no significant impact, and supplemental EIS's were not prepared.

Establishment of SRA's is a prudent management strategy that trades assured protection of a bit of seafloor for permitted impact upon similar habitats elsewhere. The concept of settling aside areas of the seafloor as preserves was an effective means of dealing with the limited level of understanding about the deep environment while not calling for a cessation of industry development. It was envisioned (Anonymous 1981) that research comparing impacted and preserved bottoms could be carried out in parallel with industrial development in permitted tracts. As ecological understanding increased, industry procedures could be modified so as to minimize environmental impact.

Environmental studies of the effects of deep-sea nodule mining fall into three broad categories: NOAA's initial Deep Ocean Mining Experiments (DOMES), NOAA's final studies supporting the Stable Reference Area (SRA) concept, and industry studies supporting license application and EIS submission. Due to severe technical and logistical restraints, these three components tended to build upon and cooperate amongst one another. There are no currently active studies. NOAA concurs with the assessment that nodules have no economic value in the foreseeable future (Hoagland 1993, NOAA 1989, 1994).

The Project

DOMES, the Deep Ocean Mining Environmental Study (NOAA 1982, Amos et al. 1982) was the initial project which considered the full range of possible mining impacts from the benthos up to the ocean surface. By itself, this is not an especially noteworthy project. However, it led to subsequent work on deep-sea stable reference areas. Contributing to the weakness of the DOMES project is a peculiar focus. Oddly, it expended considerable effort on the upper ocean where it was thought that sediment plumes might impact primary productivity. However, box core surveying was conducted (Hecker and Paul 1979). The conclusion that mining would destroy fauna in and near the path of the mining device, was arrived at more from the examination of bottom photos (Oztergut et al.1981) taken before and after trial mining (technologies reviewed by Smale-Adams and Jackson 1978) than from faunal samples. A small-scale follow up study was inconclusive. Although lacking a preliminary baseline and having no means of assessing the extent of plume effects, a descriptive post mining study, the ECHO I Expedition, was supported by NOAA in June 1983 (Spiess et al.1984).

The SRA Concept Studies

The requirement that SRA's duplicate the environment to be subject to mining dictated that SRA's be located in close proximity to mined areas. The initial criterion for citing thus became determination of how far from a mining operation the near-bottom sediment plume has an effect (NRC 1984). The design of a controlled dose sediment exposure experiment underwent considerable discussion, with initial specifications for a mining simulator being developed by The Glosten Associates of Seattle (1987).

The most concisely stated and conceptually well founded environmental concern about deep-sea mining was that the downward flux of even small amounts of resuspended material in a mining plume could greatly upset faunal foraging. This idea was first articulated in correspondence by Drs. Peter Jumars and Robert Hessler and later elaborated in the open literature (Jumars, 1981). The essential parts of the argument are as follows. Most biodiversity in the deep nodule province is represented by small polychaetes and crustaceans which feed directly upon a very thin dusting of labile carbon in settling detritus, or upon bacterial biomass exploiting more refractive carbon buried in the sediment. Net inorganic sedimentation in this region may is very low. Given such a low natural sedimentation rate, even miniscule amounts of old sediment dropping out of a mining plume may be experienced as a dramatic dilution of the labile carbon supply. If the fauna has developed foraging strategies adapted to natural rates of influx, then this artificially high sedimentation regime may prove deleterious.

The initial concerns that mining impact beyond actual mining vehicle track tract would be due to acute and chronic burial were developed in detail by Craig Smith and his colleagues (Smith et al. 1988). Employing a clever model that determined the amount of burial needed to cut off observed levels of oxygen consumption, it was estimated that approximately 4 cm of acute burial would cause asphyxiation of the fauna. Effects of acute burial were experimentally examined at bathyal depths off San Diego using cores dosed with a 1 and 4 cm sediment cover. Cores were emplaced, dosed, and harvested after six days by a remote vehicle. Unfortunately, logistical problems limited both the number of replicates and the duration of the study. Statistical test of abundance changes associated with degree of burial could find no impact. However, the investigators strongly suspected that the short incubation prevented actual effects from being detected. In support of this contention, it was noted that fauna in cores with 4 cm added sediment showed no sign of repositioning upward, while such upward migration had occurred in cores with only 1 cm of added material.

Industry Studies

In any potentially impacting activity there is an inherent conflict between developers and regulators. While there may be regulatory mandate that industry carry out pre-development impact assessment, such studies often suffer from the understandable fact that industry seldom invites regulation. As a result, the studies are seldom more than a cursory look at the fauna. Such a mandated study is reflected in the license application filed by the Ocean Minerals Company (OMC 1982) in compliance with Public Law 96-283 and NOAA rules pertaining to such applications as published in 46 Federal Register 45985-919, provides insight into environmental concerns. It was proposed to strip nodules from the seafloor with a self-propelled vehicle connected by flexible link to a relatively rigid pipe running to the surface vessel. A miner as large as 10 m wide and sweeping over 1m of bottom a second would be used (Welling 1981). The license gave minimal attention to collector and plume effects. While it was acknowledged that NOAA identified these as concerns, impact prediction was not attempted. It was commented that impact could not be assessed until actual mining and environmental monitoring had begun.

Supportive studies included box core samples for macrofauna and photo/video for megafauna. Recolonization experiments were anticipated in conjunction with mining trials. Reports on megafauna both photographed and recovered during nodule collecting makes the point that there appeared to be no fauna characteristic of the nodule field, just representatives of a ubiquitous regional fauna. No infauna results have ever been reported. Megafaunal results have been published (Foell and Pawson 1986). There was no use made of survey data in the license application.

Polymetallic Sulfide Mining

Polymetallic sulfides are ore bodies created when metal-rich hydrothermal fluids are emitted at the seafloor (Francheteau et al. 1979). In 1983 MMS issued a draft environmental impact statement (DEIS) preparatory to a planned federal mining lease sale for US EEZ sea bottom on the Gorda Ridge off Oregon and Washington. This DEIS was issued in an environment of unclear regulatory authority between the departments of Commerce and Interior and an environment of no serious industry interest. Adding to a poor public acceptance was the fact that the DEIS was produced quickly and depended too heavily on inapplicable ecological studies of nearby seafloor but very dissimilar environments. A multi-participant group, the Gorda Ridge Technical Task Force, was established to address these problems (McMurray 1986).

Following an initial assessment of knowledge (Boudrais and Tagon 1986), a cursory benthic survey of the actual planned lease site was supported by the Task Force using DSV ALVIN to make bottom photographs and videos (Carey et al.1986). The quality and spatial control of the images did not support detailed analysis. However, an interesting discovery was made. Contrary to the generalization that deposit feeders predominate, sessile suspension feeders were common. Due to a lack of industry interest, there was no subsequent study.

2.6.3 Ocean Dumping of Hazardous Wastes

The deep-sea has been used as a dumping ground for many decades due to its remoteness and presumed lack of resource conflicts (Palmer 1988, Simpson et al 1981). Dumping has included dredge spoils (Pequegnat 1983b), industrial wastes (Pearce et al.1979, Vaccaro et al.1981), sewage sludge (Walker and Paul 1989), and munitions. Of these, munitions' dumping is shrouded in mystery. A glance at any navigational chart shows numerous sites on the continental slope and deeper marked "Explosives Dumping Area". In the case of the Gulf of Mexico, these sites are located on seafloor subject to leasing by MMS. Information of designated munitions sites is scant. The Oceanographer of the Navy (1972) released a summary of oceanographic conditions at "number sites", where munitions-laden ships were scuttled. The data behind these studies seldom consisted of more than a photographic survey (Carey et al.1973).

Deep Water Dumpsite 106

The most extensively studied and published environmental studies are those of the multi-use deepwater dumpsite DWD 106 off the coast of New Jersey. While this site has received municipal waste, military radionuclide waste, and industrial waste, the work dealing with sewage sludge is of greatest general management interest (Walker and Paul 1989). Prior to the effective imposition of the ban on such dumping, coastal residents of the New York Bight area perceived that near-shore sewage and waste dumping were producing unacceptable impacts on human health, environmental aesthetics, and ocean ecology. Political action arising from this public concern produced the Ocean Dumping Ban Act (ODBA) that was to have stopped sewage sludge and industrial waste dumping. However, the affected sewage programs had the conditions of the ODBA set aside by a New York District Court in 1981. With the ban in suspension, the US EPA did close the nearshore dump site on the basis of environmental degradation and designated the DWD 106 as the permitted site for sewage disposal in 1984.

The shifting of the sludge to a deep water site did nothing to placate public concerns. Although never well substantiated, there were reports of increased fish diseases. Adding to public distrust in the wisdom of dumping deeper was the adoption of a NOAA monitoring program structured around an obviously inadequate plume dispersion model which predicted that no dumped material would reach bottom. In effect, NOAA studied the wrong part of the environment. Ultimately, the terms of the ODBA were applied to DWD 106 and sewage dumping halted entirely. The banning of sewage sludge and industrial wastes into the oceans by the Ocean Dumping Ban Act (ODBA) passed in 1977 and amended in 1988 stands out as the most dramatic case of the U.S. government regulating deep ocean environmental impact. Rather than just prohibiting an anticipated activity, this ban actually stopped ongoing sewage sludge dumping at Deep Water Dump Site 106 in the North Atlantic. This action forced adoption of far more expensive sewage disposal options for New York City and surrounding communities. While there was a substantial research effort associated with this ban and concern about deep ocean environmental impacts at DWD 106, review of testimony and questioning at Congressional Hearings suggest that concerns over deep-sea ecology played a minor role (U.S. House of Representatives 1992).

Long-term monitoring of DWD 106 is a major programmatic focus of the NOAA Undersea Research Program at Rutgers University (F. Grassle per. com). This work involves international scientific cooperation and participation by the United State Geological. Survey. Much of this monitoring focuses on chemical tracers (Bothner et al.1992, Takada et al.1992, Van Dover et al.1992) along with a high resolution description of the physical environment (Butman et al.1992, Robb and Grassle 1992). Several recent projects were published in 1996 and show the mixed result that all effects studies tend to show. A review of earlier work and a summary of results been presented by Hunt et al. (1996). Fish populations did not show conspicuous impact (Musick et al.1996), and disease in commercial species could not be attributed to site effects due to confounding effects (Ziskowski et al.1996). However, contaminants did seem to enter the pelagic nekton (Zdanowicz et al. 1996), but were species specific in benthic megafuana. Some species showed no contamination concentrations (Steimle et al.1996), while others did (Sennefelder et al.1996).

Nuclear Waste Disposal

The proliferation of the nuclear industry following World War II for electrical power and weapons took place with full government awareness that technologies did not then exist for safe long-term disposal of radioactive waste. Protected by secrecy, weapons wastes were disposed of in the ocean as a simple extension of ocean dumping. More exposed to scrutiny, nuclear power facilities were built with on-site storage capacity awaiting better options. By the mid 1960's ocean dumping was being viewed as unacceptable, and progress towards better disposal options were not appearing. Thus, the problem was growing.

The concept developed in the Sandia Labs Subseabed Disposal Program was a multi-barrier containment program. Wastes would be chemically and structurally processed to solidify and stabilize them, then encased in a vessel capable of containment for many 1000's of years. These vessels would then be buried in about 20 m of seafloor clay in central regions of the ocean at depths greater than 4km of water. Five technical and one policy arguments were initially put forward in favor of the subseabed disposal option.

- The deep-sea floor in the middle of continental plates is a geologically stable area.
- The clay layers in these regions affords a good barrier against seepage of nay materials that might leak from containers.
- These areas are low in other resources and the biota is small and rare.
- Sediment geochemistry in these areas is predictable.
- Even if something does leak and escape containment, dilution still affords a high degree of protection.
- Being in international waters it could be a disposal option open to all nuclear countries.

Subseabed Disposal Program

The SDP was divided into six task areas: site assessment, barrier assessment, environmental studies, engineering, systems, and regulatory issues. The ecological studies of the SDP are distinct from other environmental studies in two ways. Firstly, they had not progressed to a baseline study since the disposal method was in its earliest developmental stages. Secondly, most of the research could be considered as process-oriented. Rather than carry out traditional research aimed at determining population and distribution parameters, the research was driven by ecological models. Ecological activities of the SBD study revolved around two models of ecological function, a multi-compartment food web model (MFM) and a Deep-Sea Carbon Model (DSCM). The former sought to prediction movement of released radionuclides from the buried repository through 16 model compartments. The latter was restricted to the cycling of organic carbon in the bottom and near-bottom environment. Both models lumped fauna into fairly coarse groups either by position (epibenthic, infauna, pelagic, etc) or size (meiofauna, macrofauna, etc). Therefore adequate research had only to determine the biomass in these model compartments and the types and degree of exchange between compartments. Species inventories, diversity, etc. were superfluous in this context.

Seabed Disposal of Contained Low-Level Wastes

Unlike programs seeking to develop disposal schemes like the SDP discussed above, and nuclear submarine disposal discussed below, EPA programs were undertaken to establish regulations that would control permitting for disposal. The starting point for such studies was International Atomic Energy Agency (IAEA) site criteria suggested to the London Dumping Convention (Table 2.6). Stated quite simply, small sites could be established on the seafloor greater than 4000 m depth in regions of oceanographic stability, no possible use conflict, limited biological activity, and at locations where operations were practical. Stabilization, containment, and emplacement were not specified.

Federal Policy History

The SDP is an especially interesting case since the program was initiated after the ban on ocean dumping. Thus, SDP faced three stiff policy challenges. First, the program would have to show the ocean option to be superior to other options. Second, the superiority of the ocean option would have to be so great as to justify reversal of a ban. Or, as a last-resort, the technology of the vastly superior ocean option would somehow be exempt from the ban. None of these proved to be the case.

While the Nuclear Waste Policy Act (NWPA) authorized study of the subseabed disposal option, no program could have been put in place due to restrictions contained in MPRSA (the Marine Protection, Research, and Sanctuaries Act of 1972 (Public Law 92-532)). In Title I, Ocean Dumping Prohibited Acts, Section 102, the issuance of permits by EPA for radioactive dumping is specifically prohibited. Thus, had the studies lead to the recommendation by DOE that subseabed disposal begin, Congress would have to have amended the act, probably giving EPA specific approval to permit such activity and NOAA authority to monitor the sites. Internationally, a similar exemption from the prohibitions of the London Dumping Convention would have had to be arranged, and international accords adopted as to permitting and monitoring.

In 1986 the study of the subseabed disposal option was halted for policy reasons. In effect, it was decided by DOE and congressional committees that the US should vigorously pursue only the land-based disposal options. Thus, an operational program with its regulatory structure was never implemented. Prior to this premature cessation, DOE began funding in 1974. This task was then reaffirmed and expanded under authority of the NWPA, Nuclear Waste Policy Act of 1982 (Public Law 97-425), Sec. 222 Reassert on alternatives for the permanent disposal of high-level radioactive waste act. The initial timetable called for a preliminary assessment in 1976, progressing though four stages to a demonstration project in the year 2010. By 1985 the U.S. program was well into phase two of research associated with concept feasibility at its maximum. Annual funding had reached approximately $13M/year, and about $116M had been spent on the life of the project.

Bettis Project

The Bettis Project was undertaken to determine the feasibility of deep ocean disposal of defueled, decommissioned nuclear submarines as they passed their effective operational life. Activated metals in the submarines' nuclear systems would be the primary radioactive material and are classed as low-level wastes. The Navy envisioned two disposal options. The deep-sea option consisted of removing high-level material, placing miscellaneous low level materials in the steel pressure vessel for containment, then sinking the sub in a deep-water site within the US EEZ. Alternately, the land option consisted of cutting up the sub, placing nuclear waste material in a sealed section, and burying that section at a land-based site near Handford Washington.

The Navy's desire to dispose of material in US controlled water added complexity to the International Atomic Energy Agency (IAEA) submission to the London Dumping Convention on acceptable site criteria (Table 2.6). These criteria tended to favor sites in international waters far from land. Thus, part of the project was finding EEZ sites that otherwise met the criteria. Compromising the Navy's desire to be in the US EEZ with IAEA criteria resulted in identification of two Atlantic and two Pacific. In the Atlantic were the Antillies Study area off Puerto Rico and the U.S. Virgin Islands and the Hatteras Study area off the Carolinas. In the Pacific, a Western-Northern site lay off Cape Mendocino in Northern California and a Western-Southern site seaward of San Diego.

Table 2.6. IAEA Categorized Criteria for Deep-Sea Nuclear Waste Disposal Sites

I. Criteria Based on Ecological Concerns

1. Sites should be between 50 North and 50 South. Thus avoiding the highly productive polar regions along with associated operational problems.
2. Depth at the site should be more than 4000 m. Thus being in the least productive and most homogenous part of the marine ecosystem.
3. Sites should be remote from the continental margins. Thus avoiding the biological activity and biological resources closer to land.

II. Criteria Based on Abiotic Aspects of the Environment.

1. Sites should be away from areas containing active geological phenomena such as volcanoes, which would be unsuitable. Thus avoiding geologically unstable regions.
2. Sites should be away from areas, such as marine canyons, which have a high rate of exchange of the deep waters with surface layers of an adjacent continental shelf. Thus avoiding rapid transport of spilled wastes to man.
3. Bottom current shear stress should not exceed critical erosional shear stress. Thus avoiding resuspension.
4. Sites should be away from areas of intense mesoscale eddy activity. Thus avoiding rapid transport to man.

III. Criteria Based on Conflicting Usage.

1. Sites should be away from areas of potential seafloor resources.
2. Sites should be away from cables in use.

Table 2.6 Continued.

IV. Criteria Based on Practicality of Operations.

1. The area of a site should be defined by precise coordinates, with an area as small as practicable, but no larger than 104 km^2.
2. Sites should preferably be in areas covered by navigational aids.
3. Sites should be chosen for convenient conduct of operations and to avoid, so far as possible, the risk of collision with other traffic and undue navigational difficulties.

General oceanographic survey programs were initiated at the study areas with a strong emphasis upon geological and physical oceanography. The possibility of deep nekton as a connection to human food chains was considered. No effective study of biota or of possible biological effects was ever undertaken. A draft EIS was filed by the Navy for the ocean option. That document contained no serious discussion of ecological impact. It did however, attempt to develop a worst-case model for human exposure via the foodweb. While, the model may have been conceptually sound, the lack of data supporting its assumptions and parameters rendered it useless.

2.6.4 A Flawed Proposal to Scuttle an Oil Storage Facility

The Brent Spar, a floating storage and offloading structure in the North Sea, was destined by its owner in 1991 to be scuttled in deepwater. The plan lead to heated public debate and strong opposition by Greenpeace (Rice and Owen 1999). The Brent Spar controversy in the United Kingdom is particularly relevant to deep ocean oil and gas development in the United States for four reasons.

- Although not directly related to deep development, the proposed disposal in deepwater was an activity of the offshore oil and gas industry.
- The superficiality of the environmental studies and the failure of both government and industry to insist on an adequate program utilizing the best available scientific talent are a case of exceptionally poor management.
- When the general public's attention is directed by advocacy groups and the press, very strong negative sentiment can arise despite the deep environment' s remoteness and unfamiliarity.
- The Brent Spar debate persists in the European scientific community and will greatly influence developing standards of completeness and quality for deep management studies.

Since Rice and Owen (1999) have provided a detailed account of the Brent Spar decommissioning, only a brief sketch will be provided here. In 1991 Shell UK decided that the Brent Spar should be decommissioned. Over the next two years, feasibility studies were conducted by university-based contractors with a history of industry and government work but no deep-sea experience. Most were engineering studies. Two could be considered oceanographic, the Aberdeen University Research and Industrial Services (AURIS) Report (AURIS 1994) and the Metocean Report (1993). In late 1994 a field program was undertaken, and a final request for disposal in deepwater was submitted just three months later in Dec. 1994. The advocacy group Greenpeace seized upon negative sentiment for major oil companies, exaggerated the contaminants issue, and mobilized public sentiment against ocean disposal. In the course of subsequent debate and review, the factuality of claims declined in importance and the poor implementation of the permitting process became the focus of argument.

The debate about deepwater decommissioning became so heated and political that a review was initiated by the House of Lords Science & Technology Committee. The primary non-government reviewing body was the Natural Environment Research Council (NERC). The report of the Scientific Group report on Decommissioning Offshore Structures (NERC 1996) concluding that the procedure for arriving at a Best Practicable Environmental Option (BPEO) for the Brent Spar was poorly executed and that fore drawn conclusions had been advocated without sufficient inquiry and participation by interested parties. The report did not, however, condemn deepwater disposal in general or specific disposal of the Brent Spar.

The BPOE

The BPEO Assessment concluded that deepwater disposal was preferable on grounds of: (1) reduced technical risk; (2) reduced safety risk to the workforce; (3) insignificant environmental impact, (4) and total cost. Preparatory to disposal the Spar would be made safe and cleaned of accessible hazardous materials for disposal onshore. Three potential sites in U.K. waters deeper than 2000 m were identified by the Scottish Office Agriculture and Fisheries Department (SOAFD) as potentially suitable for the disposal of redundant offshore structures: North Feni Ridge, Rockall Trough, and Maury Channel. Consistent with 1991 Oslo Commission Guidelines for the Disposal of Offshore Installations at Sea an 'impact hypothesis' was prepared for the Brent Spar. Three sinking scenarios were ranked by likelihood and a dilution argument but forward to support the conclusion that impacts would be minimal and acceptable under all three scenarios. A field study was conducted by Shell Exploration and SOAFD in August - September 1994, to determine site suitability and provide a baseline for monitoring. The published results of this study (Rudall Blanchard Associates Ltd. 1994) were generic and developed from the literature rather than data analysis.

Scenario 1. Most Likely - the spar would sink intact to the sea floor and remain intact after impact. Contaminants would be slowly released.

Scenario 2. Less Likely - storage tanks would be damaged during sinking or impact with an initial rapid release of contaminants at the seafloor followed by chronic discharge associated with corrosion.

Scenario 3. Least Likely - storage tanks would be damaged and discharged near the surface followed by chronic discharge associated with corrosion at the seafloor

Official Post Hoc Criticism of the BPOE

From the US management perspective, the most notable aspect of the BPOE review is that it occurred at high levels in response to great public pressure rather than as part of a routine process. The greater public participation in the US EIS process makes such an extraordinary review less likely. The report (NERC 1996) contained twenty nine conclusions. Five are of special interest in the context of deep oil and gas management in the US.

- Scientific assessment of ecological impact is only one factor is accessing the suitability of a disposal plan. Allowing or banning any waste dumping involves social, economic, ethical, and aesthetic considerations.
- Cumulative rather than acute impacts of the disposal of offshore oil installations must be assessed.
- Public acceptability must be considered in evaluating future marine environmental impact assessments. Relevant documentation about disposal of the Brent Spar was confidential too long.
- Onshore versus offshore options should consider general considerations such re-using and re-cycling.
- The deep sea is biologically rich, and impacts are not yet predictable in that environment. Study of natural and man-made analogues might prove beneficial.

Criticism from the Scientific Community

As part of the review of the Brent Spar controversy the British Scientific community issued two important comments that stressed the inadequacy of the studies undertaken. The first was in the form of an official statement by the Institute of Biology, British Ecological Society, and the Linnean Society of London. The second was an open letter expressing the opinions of the scientists working on the ecology of the Rockall Trough. The Rockall Trough studies have been one of the most scientifically productive studies of the deep sea ever undertaken.

The 15,000 member Institute of Biology submitted comments along with its affiliated societies, the British Ecological Society and the Linnean Society of London. It was concluded that deep-sea disposal should be included amongst the Best Practicable Environmental Options (BPEOs) considered for the disposal of North Sea oil and gas installations, but only after a cradle-to-grave resource analysis has been conducted for each option. Where costs and benefits between deep-sea disposal and on-shore dismantling are comparable, the precautionary principle should prevail in favor of dismantling. In the event of deep-sea disposal long term monitoring of the site is required. Specific rephrased recommendations included:

- Deep-sea disposal should be considered as an option when facilities are first constructed so as to minimize impacts and costs.
- The BPEO process should seriously consider more than a single option and make the details public during the process.
- While there is no evidence that deepwater disposal of something like the Brent Spar will have unacceptable environmental impacts, there is no evidence that it will not. The question remains open.
- There are moral and ethical dimensions to 'environmental options' that cannot be defined in absolute terms. It is to be anticipated that moral and ethical opposition can arise regardless to the extent of scientific knowledge. To minimize such opposition, the disposal process must be considered very early; disposal of oil and gas installations must be considered in the design stage and approved by the appropriate authorities.
- The basic BPOE process is adequate to address future disposal problems. The Brent Spar controversy arose from poor and secretive implementation.

- In the deep sea, where uncertainties are many and data limited, it is not prudent to allow the operator to develop the BPEO. The best science needs to be applied.

One of the single most damaging aspects of the studies undertaken as part of the Brent Spar decommissioning planning is that they made no use of the very considerable deepwater expertise of the Scottish Association for Marine Science. In effect, the British government paid for a study which specifically identified the Rockall Trough as a potential disposal site, yet totally ignored excellent and ongoing research in that area! Thus, once the controversy arose, the true experts convincingly identified the failings of the study. Indeed, it was the advocacy groups and the press that included the appropriate experts in the debate, not industry and government.

Due to the comprehensiveness of an open letter to Greenpeace, it is excerpted here. The letter addresses three serious failings of the disposal plan. First, the plan is based upon ignorance of actual deep-sea species diversity. Second, the plan fails to consider deepwater fisheries. Third, the plan is based upon ignorance of deep-sea high energy events (benthic storms).

THE SCOTTISH ASSOCIATION FOR MARINE SCIENCE (SAMS)
P.O. Box 3, Oban, Argyll, PA34 4AD

Dr Helen Wallace,
Greenpeace,
Canonbury Villas,
London N1 2PN
28th July 1995

Dear Dr Wallace,

We should like to express broad agreement with the "facts" ... justifying Greenpeace's actions. We might add that scientists at SAMS with by far the greatest experience of deep-sea ecosystems in the Rockall Trough area ... were never consulted for information.

We would also like to point out additional deficiencies in both the Brent Spar Abandonment BPEO report that you copied to us, and the Brent Spar Abandonment Impact Hypothesis report (both dated December 1994) as known to us:

(a) The assertion in BPEO under 8.3.3 that "the deep ocean environment supports ... a small range of species".

This is inconsistent with now widely reported data indicating very high diversity associated with the benthic fauna of the deep sea sediment. Indeed it is now becoming recognised that the biodiversity of the smaller invertebrates inhabiting the deep ocean sediments may rival that of the tropical rain forest (see Gage & Tyler 1996, Deep-Sea Biology, Cambridge University Press; Grassle, Maciolek & Blake 1991 in Woodwell (ed.) The Earth in Transition: Patterns and Processes of Biotic Impoverishment. Cambridge University Press, New York pp 384-359)

In addition to this, knowledge emerging since the last major consideration of deep-sea dumping - that of high and medium-level radioactive waste in the late 1970's/early 1980's has indicated clearly that a whole range of biological rate processes ranging from the respiration of microbial communities and individual animals from fish to larger invertebrate 'megafauna', or the measured or inferred growth rates of small deep-sea invertebrates, may be much faster than previously supposed (see Gage 1991: Biological rate processes in the deep sea. Reviews in Aquatic Sciences 5: 49-100). Although not stated explicitly in either of the Reports prepared for Shell Expro, any disposal option based implicitly on characterization of the deep-sea as a "low-activity ecosystem" clearly now is highly inappropriate.

(b) The statement under 8.3.4 that exploitation of the resources of the deep ocean (>1,500 m) is limited to laying of submarine cables and military activities fails to recognize the growth in deep-water fishing in recent years.

While it is true to say that most of these fisheries take place at depths down to about 1,200 m there are some targeted fisheries which go deeper. There is little doubt that orange roughy has been fished to at least 1,800 m to the west of the British Isles. ... There is also a need to question the rather simplistic views on deep-water fishes embodied in Section 5.3 of the Brent Spar Abandonment Impact Hypothesis (December 1994). There is ample evidence that the continental slope west of the British Isles supports a high biomass and diversity of fish down to about 1,500 m. This biomass could never be supported by the benthic fauna and studies by SAMS, over the years, have shown the importance of benthopelagic and pelagic organisms in the diet of these fishes. This implies a much more efficient transport of food from the surface than that obtained from 'the downward flow of material derived from the surface water above (e.g. corpses, faecal pellets etc)'. The impingement of both the mesopelagic fauna on the slope is a rich source of food replenished from the surface by overlapping food-chains and diel vertical migration.

We finally also question the justification for the three potential sites. The "North Feni Ridge" site is actually a deep hole, probably caused by current scouring, at the base of a seamount, the Rosemary Bank. Seamounts are where some of the targeted fisheries for species such as orange roughy occur. The "Rockall Trough" site located south of the Anton Dohrn Seamount, is very close to one of the main deep-water fishing areas. It is also an area which has been the subject of investigation by SAMS for many years. The Maury Channel site is the deepest of the three, but still close to developing deep-water fisheries in international waters. The arguments put forward in favour of the dumping option in the Scotsman (Dr M.V. Angel) and in the recent Nature editorial (vol. 375, p. 708) referred to abyssal sites. Slope sites have different characteristics and should be treated differently.

(c) The apparent uninformed consideration in the Brent Spar Abandonment - Impact Hypothesis report of the effect of likely mesoscale high-energy events ("benthic storms") at the benthic boundary on the dispersal and transport of material into the water column mesoscale processes.

Clearly such processes now need to be taken into consideration in modelling the dispersal of toxic compounds in deep water. The claim ... that mean (presumably near-bed) current velocities were only 1 - 2 cm*sec^{-1} is not particularly useful in the present context where maximal velocities may be largely determining potential dispersal. We do not have available to us the Metocean (1993) report cited under 5.2.5. so we are not able to assess the quality and appropriateness of the data on which that report was based. But we would comment that any general interpretation of relatively quiescent regime is at odds with the results from numerous long-term current meter time series undertaken by SAMS (then SMBA), the Institute for Oceanographic Sciences (IOS) and by MAFF (Lowestoft) at various sites in the Rockall Trough area. The picture of eddy kinetic energy (KE), the low-frequency peaks derived from mesoscale eddies in theupper water column, spun off strong surface flow or by storms, that emerges from the analysis indicate a very dynamic regime... It is also curious in view of what we have heard informally of the results from the SOAFD work for Shell Expro from their near-bed current meter time series data covering the period from the field work in 1994 to April 1995. Apparently preliminary analysis of the data show sustained current peaks at the site where Brent Spar was to be dumped well over 50 cm sec^{-1} - indicative of severe benthic storms.

Yours sincerely,

John D. Gage,

John D.M. Gordon

2.6.5 Summary of Lessons Learned

In many of the cases presented above, deep-ocean field studies were terminated prior to completion due to changes in priorities or regulations during the extended life of the programs. Therefore, the scientific utility of each is very limited. However, there are five very important policy points to be made.

- Public Interest - There is a broad public sentiment for preservation of the ocean environment in some idealized un-impacted state. This public interest applies to all parts of the ocean, even the deep sea. Public opposition to deep-sea environmental impact must not be underestimated.
- Government Regulation - As clearly evidenced both by the Law of the Sea and the US Seabed Hard Minerals Act. Environmental regulation will follow resource development no matter how deep or far offshore. The most easily decreed regulation in the face of limited ecological knowledge is protection through prohibition.
- Ignorance in Unexpected Places - A historically dated and inaccurate wasteland view of the deep-sea floor persists even in the non-biological sub disciplines of oceanography. It is to be expected that deep-sea exploitation plans can progress to highly advanced levels in total ignorance of potential environmental consequences.
- Narrow Focus – Rather than attack all topics about the deep sea, models or first principles have been used to narrow the focus of inquiry. In the case of the initial NOAA studies of DWDS 106, an inappropriate plume model wasted much effort. However, in the SRA studies for nodule mining, emphasis upon detritus influx served as a very good central theme.
- Industry Participation - Deep-sea research is logistically expensive and its difficulty is compounded by the novelty of the technologies which may cause impacts. Therefore, environmental studies by managers and technological trial programs should be combined.

2.7 Deep Survey Design and Methodology

2.7.1 Introduction

It is the purpose of this chapter to review the design and execution of deep-sea data collecting methods, indicating which can be considered relatively standard and discussing the merits of each. A more general account of benthic sampling can be found in Holme and MacIntyre (1984). A manager charged with getting information pertinent to the regulation of any marine habitat is faced with competing choices in the adoption of sampling methods and designs. First, there is need for standardization in order to make data collected through time, at different places, and by different investigators truly comparable. Second there is the need for innovation when it is known or strongly suspected that standard methods are inadequate. As a general statement, it is easier to adopt standard methods in shallow water than in deep. This is because far more equipment development, use, and maturation has taken place shallow. In contrast, deep-sea studies are still relatively innovative in terms of equipment and design.

2.7.2 Sampling Design

The most common and damaging series of errors in ocean impact studies has been the failure to concisely define the question being asked, the failure of adopting a sampling design which allows the question to be answered, and the failure to analyze the data in a way that produces unambiguous statements (Carney 1987). In part, these errors have stemmed from a preoccupation with the logistical problems of working at sea, such that "design" comes to mean cruise schedules and gear deployment rather than an orderly collecting of data suitable to the testing of prior hypotheses. Given the special logistical problems of the deep sea, these errors will be very easy to repeat. Therefore, this discussion of methodology begins with a consideration of design.

Developing Trends In Data Analysis

Since deep-sea resource management is a relatively new field, program planners are somewhat more free to take advantage of new ways of conducting studies. It is important that trends in data analysis be recognized. Data analysis in oceanography and ecology has undergone a dramatic change in the past ten years. As studies of the deep environment are undertaken, these changes afford both new opportunities and new challenges. The most easily implemented opportunities are associated with the relative ease with which the massive data typical of ocean monitoring can been manipulated and subjected to simple visual inspection. There are few uncertainties associated with this technology. Much more complex is the changing conceptual issue of how data are used and the link between analytical result and conclusions.

2.7.3 Increased Data Access and Ease of Visualization

We are presently experiencing a revolution in the manner in which data can be accessed and examined which should profoundly effect all environmental studies that produce large volumes of data. In the past, the difficulty of managing data forced managers to depend upon statistical abstractions such as means, variances, diversity indices, etc. to arrive at conclusions about patterns in data. Presently, it is now possible for anyone with a fast and memory-loaded personal computer or a relatively modest workstation to easily accesses many gigabytes of data from a standard archive, such as those being developed by the National Oceanographic Data Center (NODC). These data can then be examined "by eye" using visualization techniques ranging from simple plotting to image-based data representation.

There are two very important management consequences of this ready access to data.

- Better Sequencing of Study Tasks - Traditionally, fiscal restraints and the long lead time between data collection and final analysis forced managers to combine tasks which should logically be completed step by step. Rather than determine the physical aspects of an environment first, and then undertake an appropriately partitioned sampling of fauna, physical and biotic aspects would be determined simultaneously using designs that were poorly suited to either task alone. Fiscal restrictions are now the only cause for such ineffective studies. The collection-analysis gap has been so greatly shortened that it is possible to do complete analysis of preliminary physical surveys in a shorter period of time and then undertake optimally designed ecological work.

- Decreased Emphasis upon Summary Statistics - Now that it is possible to calculate every known diversity index for a given data set in a matter of seconds, management need to depend upon a standard value such as H' is greatly decreased. This advancement places a much greater burden on the quality and timeliness of original data. As computer developments have brought the end user closer to the massive raw data, the quality of that data must be improved. Summary statistics often hide poor data quality which are glaring during simple eye examination. Therefore, management must stipulate that data be submitted in a clean and usable form early in a project, rather than as the final act.

2.7.4 Changing Approaches to Statistical Analysis

Ecologists have a long tradition of being dissatisfied with statistics. In some instances such dissatisfaction has been intended to mask insufficient understanding of techniques and sloppy design. However, beyond the masking of inadequacies, there has been a real and very legitimate feeling that traditional statistics are too demanding upon design and not especially informative if all demands have been tediously met. Often it seems that only trivial hypotheses can be correctly tested. Especially in applied ecology, we encounter the greatest interest in development of more informative statistical methods. As a result, every decade there is a resurgence in Bayesian methods, and such a resurgence is now underway.

Most oceanographers or ecologists taking a graduate course series in statistics might have encountered the term "Bayesian statistics" but gained no other insight of this approach. Typically, we are instructed in traditional statistics derived from a synthesis of the concepts of hypothesis testing and estimation developed by Fisher, Neuman and Pearson. This highly standardized approach is sometimes called sampling-theory statistics, frequentist statistics, etc. Bayesian statistics takes a different view of hypotheses which specific causality. Rather than testing them *per se*, Bayesian methods seek to improve upon prior knowledge about the probability that an event has occurred and been caused by one particular factor out of two or more possibilities. The applicability of Bayesian methods in ecology has been discussed for at least thirty years but is now enjoying a resurgence of interest due to the linking of statistics and decision making. Bayesian-oriented centers, such as the Duke University Institute for Statistics and Decision Theory, are emerging and actively pursuing ecological application.

The most often cited basic reference to Bayesian methods is Box and Tioa (1973). A non-dogmatic text is that of Press (1989), and new texts focusing on applied ecology will surely appear soon. The origin of Bayesian statistics are attributed to the theorem concerning conditional probabilities of an event being due to one of many possible causes developed by the English cleric Thomas Bayes in the 1700's. The Bayesian central idea is that prior information often exists and should be expressed as an informative prior probability distribution. The primary task of sampling and analysis thus becomes gathering data to revise this prior information and arriving at a posterior distribution.

Bayesian statistics are conceptually appealing since they appear to deal with the needs and information level of ecological managers. Rather than rigidly test alternative hypotheses, Bayesian methods seek to improve our understanding of the likelihood of a hypothesis, and they employ prior knowledge. Unfortunately, while the application of Bayesian methods to applied ecology is increasingly advocated (Anderson 1998), managers must keep in mind that the overall validity of some Bayesian concepts is not agreed upon (Moore 1997).

2.7.5 Times Series and Intervention Analysis

While the term "baseline" is still useful for describing initial conditions in an environment, we now know that environments are not static, and the "baseline" data collected at a particular point in time are unlikely to have much long-term value. Certainly, deep-sea population data collected in the 1980's are not the best data to use as the before case in drilling associated impact in the year 2000. These older baselines are still valuable, however, in letting us anticipate the fauna present, anticipate the need to partition sampling in a non-homogenous region, and estimate the degree of replication needed for certain levels of statistical power.

Ideals of appropriate "before and after" data have been evolving (Stewart-Oaten 1996a) and now can be viewed in the context of time-series analysis, especially the topic of Intervention Analysis. Intervention Analysis is a development in time-series analysis attributable to the same two statisticians who popularized the Bayesian approach, Box and Tiao; in this instance the basic reference is Box and Taio (1975). It is understandable, that the advocates of Bayesian methods and of Intervention Analysis are often the same people. The approach is very attractive to management because it focuses upon a factor that is very often known, the moment in time that a potentially disturbing event starts. Underlying the approach is a hypothesis about when a change in time series data is expected. The hypothesis may be simple or complex in terms of what type of response takes place. The task of the analysis is to determine from data prior to the impact the normal patterns present and then predict the conditions which should be present at the onset of impact (intervention). Impact is assessed as departures from the expected behavior.

Among the major problems of time-series analysis is the need to understand the underlying model (Stewart-Oaten 1996b). Obviously, in the deep sea many different factors may be controlling benthic populations, and these factors may come and go in various combinations through time. Therefore a simple time-series model, while it might fit past data well, will be of limited predictive capability.

2.7.6 The Role of Replication

There has been a tendency in ocean monitoring to be too rigid about replication when specifying performance requirements (e.g. there should 3 or 5 replicates), matched by a casual disregard for the purposes of replication in the final data analysis (analyses are often based upon pooled replicates). In undertaking deepwater studies these two errors need to be avoided. The level of replication should be appropriate to the question at hand. It is common for statisticians to see replication as serving one primary purpose. However, in species-level ecology it often serves two. In the statistical context it allows for the estimation of inherent variation within a site so that statements about variation among many sites can be made with a known level of confidence. In sampling theory replicates are the sole source of information about variation, and under certain conditions of homogeneity variance decreases as replication increases. Therefore, extensive replication is seen as desirable if not necessary, and replicates are never pooled. In Bayesian statistics prior information is used to determine prior distributions which are an initial model of variation. In such an approach, replicates are not the sole source of information , and the need for extensive replication may be relaxed. In the biodiversity sense (species inventory), replicates produce the cumulative list of species within a site.

The deep sea is always under sampled and there are many rare species. Therefore extensive replication is considered necessary, and replicates are always pooled when estimating species richness. Letting the degree of replication be driven by the need to maximize the estimate of species diversity is very difficult in deepwater where diversity can be very high. Jumars (1981) has discussed this problem in conjunction with nodule mining in the mid Pacific. The problem is basically this: the deep sea is diverse and has many rare species which may be represented by a single specimen in a sample of thousands of individuals. Presumably, there are many other rare species which have gone uncollected. If, replication is extended until some high portion of these very rare forms have been collected, they will be so rare in the data that they can not serve as a basis for statistical comparison. Therefore, the great effort and cost of considerable replication contributes little of practical use.

Deep-sea studies should be undertaken with the primary purpose of replication being statistical in the sampling theory sense, and pooling only done analytically, not physically. The degree of replication will depend upon the purpose of the study and the variances found in preliminary data, Baseline studies should take a mapping form. Since the deep-sea is poorly known and many sampling programs carried out back when the environment was assumed to be homogenous on the scale of kilometers, it can be argued that a mapping of fauna on finer scales is needed. For example, rather than restrict samples to a narrow transect of stations, scatter numerous samples across a swath of ocean bottom. Replication at each station would be traded for greater spatial coverage. Specific impact studies should continue in the tradition of within site replication. However, by placing fewer sites wisely and carrying out only adequate pre-impact time series, overall effort can still be kept to reasonable limits.

2.7.7 Ships, Submersibles, and Other Sampling Platforms

Access to the deep ocean environment has traditionally been by means of ship and submersible. While these will play an important role in deep environmental studies, the ocean manager needs to consider the incorporation of advanced technologies. We find ourselves in a peculiar situation. The offshore oil and gas industry is exploiting deep resources through the development and application of pioneering technologies. However, as leasors these developers lack incentive to study the deep environment with the same level of sophistication. The primary burden of gaining knowledge of the environment resides in the "property manager", MMS, which has neither mandate nor funds necessary to undertake the necessary development. There would seem to be fertile grounds for cooperation.

Ships

A comprehensive deep-sea bottom survey requires the use of a general-purpose oceanographic vessel. The principal vessel requirements for deep-water surveys are related to the need for long lengths of cable and over-the-side gear handling capability. Trawling and use of a large box core require a wire rope at least 0.5 inches in diameter and at least twice the depth to be sampled. For example, in the Gulf of Mexico about 8,000 m of line is needed. Adequate winches with more than 10,000 m of suitable line are found on University National Oceanographic Laboratory (UNOLS) vessels in the 180' class and larger. The A or U frame of the vessel must be large enough to accommodate the box core frame. In addition, a conducting hydrowire slightly greater than maximum bottom depth is needed for CTD sampling of the water column.

Submersibles

Submersibles are specialized sampling platforms that have carried out a wide range of basic science sampling missions in the deep-sea. However, there use in applied deep-sea ecology has been much more limited to work on unique habitats such as seep communities and sampling around waste containers. The actual need for submersible in any particular study must be carefully weighed against the cost. It can be expected that the combined cost of a submersible with its support ship will be triple the cost of a similar size research vessel alone. The operators of the two readily available submersibles, Johnson Sea-Link and Alvin, do try to offer full oceanographic capabilities on their support vessels. In practice, however, deck space and gear limitations combine with inexperience and time conflicts to make submersible support ships of limited utility in general deep sampling. This reality requires that either a survey be almost entirely submersible based or employ two vessels at great expense.

Deep submersibles are the sampling platform of preference when three conditions prevail.

1. When a high degree of spatial control in sampling is needed.
2. When samples must be taken with the absolute minimum of disturbance.
3. When deployments of experiments or monitoring devices require precise control and at-the-site operator discretion.

However, these advantages are obtained at a great dollar cost and a great reduction in sample yield when compared to ship deployed equipment. Therefore, from a management perspective, submersible operations must be justified on a relative cost of information basis. In many cases submersible sampling may be more appropriate for basic research into deep ecosystem function than for routine monitoring. In the following sections, the types of data that submersibles are ideally suited to gather will be briefly outlined and discussed from a management perspective.

Submersibles are virtually mandatory in the study of deep special environments. When the region of seafloor under management is known to contain special habitats, such as chemosynthetic communities, then manned submersibles are the sampling platform of choice. These habitats are very spatially homogenous, and sample site location requires on-the-site discretion. Use of submersibles for deep soft bottom sampling is probably justified in a research, rather than survey context. A central theme in current thinking about deep-sea diversity if that geological and biogenic structure of the bottom is extremely important as agents of habitat heterogeneity. If this is true, then the knowledgeable placement of samples in the bottom becomes critical. A core taken next to a burrow may not be biologically equal to one taken far from a burrow. Similarly, but on a somewhat larger scale, a core taken on the up current send of a low relief rise may not be equal to one taken on the down current side. To some degree, simply adding video or photography to a corer can provide this information, but in a very low efficiency manner. From a submersible, an investigator can seek out the particular bottom fabric of interest and execute a highly efficient sampling program.

Submersibles have a host of limitations; the first is availability. In the US only two submersibles capable of high spatial control sampling are routinely available to the oceanographic community. These are the DSV ALVIN and the Johnson Sea-Link. The ALVIN is housed at Woods Hole Oceanographic Institutions and operated by the National Science Foundation (NSF), the Office of Naval Research (ONR), and the National Oceanic and Atmospheric Administration (NOAA) under a three party agreement. Research projects supported by these agencies receive prepaid dive time and are given priority in long-term scheduling. It is not unusual to wait three years to get on the ALVIN schedule once a project is completed. The Johnson Sea-Link is operated by the Harbor Branch Oceanographic Institution (HBOI). Initially the sole focus of HBOI oceanographic activity, the submersible is now managed as an operational capability add on to the HBOI vessels in the University National Oceanographic Lab System (UNOLS). HBOI maintains two Sea-Link submersibles, but only one is presently operated.

Remotely Operated Vehicles and Autonomous Vehicles

Deep submersibles are an available, time-tested technology of known limitation. However, they are expensive and suffer from limitations. As industrial activity increases in deep water, it can be assumed that better means of working at depth will become available. Remotely operated vehicles (ROV) and autonomous vehicles (AV) will be able to meet the same sampling needs as submersibles. A manager's primary concerns about both these systems should revolve around cost and reliability.

Sampling Devices and Sample Processing

Macrofauna, meiofauna, interstitial water, sediment components, contaminants, and tracers are all sampled simultaneously by a coring device. Due to the very high data yield of this activity, it requires highest priority in planning and execution. Megafauna is sampled by trawling, and image-based systems provide a survey of some megafauna along with some appreciation of bottom conditions. Comprehensive surveys need to employ these techniques well, but the lower data yield suggests a reduced allocation of resources.

Changing Deep-Access Technologies

Table 2.7 presents a summary of five technologies based on cables. When large cores and trawls are needed, there is still no replacement for a wire rope of at least 0.5

inches diameter on a heavy duty winch. Pingers and clever design of the on-bottom device can greatly reduce uncertainties about sampler performance, but data telemetry via the cable is not possible. Conducting cables are now routine on all oceanographic ships, but with few exceptions are limited to smaller diameters and lower load application. The most common application is in CTD casts. Since the conducting coaxials are quite sensitive to strain these cables are ill suited for heavy loads. The bandwidth of these coaxial cables is limited.

The newest application of conducting cable technology is in the area of fixed bottom stations. The telecommunications industry is replacing its conducting cable submarine networks with fiber optical systems. The latter can transmit much greater data rates, are immune to electrical ground fluctuations, are immune to electromagnetic fluxes, are more resistant to corrosion, and much more resistant to ease dropping. There have been discussions between the telecommunications industry and the oceanographic community for approximately 10 years as to how abandoned lines might be used in research. Hilo-I was brought on line in 1998 as a deep seafloor seismic station operated by Scripps Institution of Oceanography, and future development of that system can include biological experimentation. Use of seafloor cables in applied studies will be limited by the distribution of such lines. There are none in the northern Gulf of Mexico.

Fiber optic cable has an extremely wide bandwidth for data transmission. Fiber optic tethers to deployed gear have been employed in oceanography to a limited degree since the 1980s. However, the special cables capable of large weight loads and compact coiled storage are extremely expensive and still developmental. Permanent deployment of communication lines to fixed ocean stations is now being developed at Rutgers University and Woods Hole Oceanographic as part of the LEO-15 program. Currently, this is a nearshore program only 9 kilometers off New Jersey, but the concept can be extended to deep water. This seems to be a technology well suited to fixed-site monitoring in other deep areas such as the Gulf of Mexico, where extensive fiber-optic communication system development is anticipated. Support of fixed stations could be from vessels or fixed facilities. Vessels include ships, submarines, drilling platforms, storage spars, floating production facilities, and any other ship-like platform capable of deploying and recovering instruments and samplers. Fixed facilities include shore-based terminals, immobile seafloor structures, fixed buoys and other platforms which may connect to a transmission cable but do not deploy, recover, and redeploy instruments and samplers in a traditional mode.

Box Cores

Box Cores

As with all of deep research, coring methods continually evolve, and managers need to weigh the benefits of new methods against the comparability of data. The desired sampling goal is to recover a section of the seafloor retaining all epifauna and infauna while preserving the geological structure and chemical gradients. Such an ideal sampler would work identically at all depths and on all soft substrates. For approximately 25 years, the 0.25 m^2 U.S. Naval Electronics Lab (USNEL) boxcorer (Hessler and Jumars 1974) has been the most widely used sampling device for deep studies conducted in the US and Europe (Gage and Tyler 1991). Now there is a shift in interest away from box samplers that yield a single large volume of sediment to multi-core devices that produce multiple small samples.

The USNEL boxcorer has a frame mounted, 0.25 m^2 spade closed box. The frame is lowered to bottom on a heavy cable, where weight and cable tension insert the box and close the spade. The frame assures a constant angle and rate of sediment penetration, independent of wire angle and descent rate. It was recognized by biologists and geochemists that the bow-wave of the device caused some disturbance of the sediment water interface. To minimize that bias and examine within-core spatial patterns, the box was partitioned five-by-five and only the inner nine partitions used in faunal analysis (Jumars et al.1977). The outer series of partitions could be used for chemical and geological analyses that were not dependent upon sampling the interface. This device and methodology have become the standard of reference for shipboard sampling of deep sediment and the associated chemistry, macro, and meiofauna. The fact that all these parameters could be determined from the same sample has been a strong feature of box core sampling.

A desire to obtain better meiofaunal samples lead to development of new sampling devices in the 1980's. Traditionally, when boxcorers were used, subsamples for meiofauna analysis were taken on deck with small diameter push cores. Since large bow waves are not generated by such narrow tube, it seemed reasonable to replace the large frame-mounted box with a frame-mounted cluster of narrow core tubes. Named the Scottish Marine Biological Association (SMBA) multiple corer (Barnett et al. 1984). The device, gained wide endorsement by meiofauna biologists, and its superiority over subsampling of box corers definitively demonstrated (Bett et al. 1994). Although a better means of sampling meiofauna, the multicorer produces too small of sample volume to meet all the needs of macrofauna, chemical, and geological sampling. Thus, its adoption in large-scale surveys requires substantial additional sampling, and the all-from-one-box benefit of boxcore sampling is lost.

Trawling

While macrofaunal and meiofaunal ecologists have adopted a frame-mounted 0.25 m^2 as a standard to employ and a system to improve upon, the selection of towed nets for megafaunal sampling remains largely subjective. However, an atlas of North Atlantic deep demersal fish was produced by Haedrich and Merrett (1988, 1992) using a Gulf of Mexico semiballoon otter trawl, making that net a standard of comparison. The maximum possible gape of the trawl is 14.7 m, but actual width while towing is unknown. The main net is 1.5 inch stretch mesh, and the cod end is lined with 0.75 stretch mesh. The Marinovich Brothers net company of Pascagoula Mississippi custom makes these nets for scientific use. Smaller and easier to deploy are beam trawls. The fixed geometry of the trawl mouth allows for an attempt at quantification, and the rigid beam provides a mounting point for cameras and other gear (Rice et al.1982). Odometers can be added as part of the effort to quantify samples, but they tend to be unreliable (Carney and Carey 1980).

Table 2.7. Cable Technologies Suitable to Deep Ocean Environmental Studies.

Technology	Status and Era	Applications	Limitations
Wire Rope From Vessel	Mature Technology 1880 - present	Heavy load box coring, trawling, etc.	Imprecise sampling location and geometry.
Conducting Cable From Vessel	Mature Technology 1950's - present	CTD casts, slow scan video & telemetering	Limited weight load, limited data bandwidth
Conducting Cable From Fixed Facility	Trial Application 1998 Based on abandonment of conductive telecommunication cables.	Multiple instrument telemetering.	No sample returned, limited access to serviceable telecommunication cables. Deep vehicle maintenance required.
Fiber Optic Tether From Vessel	Second generation development. 1980's - present	CTD cast, video rate scanning, multiple instrument telemetering	Very limited weight load, no electrical power transmission, very sensitive to damage during deployment and recovery.
Fiber Optic Tether From Fixed Facility	Trial Application Proposed Based on Developments in submarine telecommunications industry	Very broad band multiple instrument telemetering.	No sample returned, limited access to serviceable telecommunication cables. Deep vehicle maintenance required

Deep-sea trawling is not an especially sophisticated activity, but it is very easily done wrong if operators assume it is similar to shallow trawling. The basic physics were developed by Kullenberg (1951) during the Danish Deep-Sea Expedition aboard the Galathea. Large trawls are high drag devices of low mass which tend to "kite" as line is payed out. This causes line to go out horizontally much more than vertically, so much so that at shelf depths seven times the depth must be payed out to reach bottom. With that much wire out, for example 1400 m of wire in 200 m of water, the weight of the wire overcomes the combined drag of wire and net and carries the net to the bottom. In deepwater less scope is needed, not more. Below 1000 m twice depth is usually adequate. The reason for less scope is that the weight of 2000 m+ of wire rope is heavy enough to overcome the drag of the net. However, a common error is to pay out large amounts of line from a vessel moving at more than 1 or 2 kn. In such cases, the drag of the net is greatly increased and the weight of even a lot of wire can not sink the net.

Decreasing scope and going slower is the successful method. If an otter trawl is used and speed through water becomes too low, the trawl boards will cross and tangle. Assuring successful trawling requires use of beam trawls, which can not collapse, and acoustic pingers mounted on the trawl wire. Frequently the directionality of a ship's hydrophone is too narrow to receive the direct sound and ping from a pinger trailed behind the ship. In such cases a trailing hydrophone must be used.

Image-Based Sampling

The term Image-Based Sampling is applied to those methods which produce an image of the seafloor rather than return an actual sample of fauna and substrate. Today this includes still film photography, film cine, still digital images, and digital or analog video employing electronic storage media (i.e. magnetic tape, CDROM video, etc.). Digital systems may depend upon either a matrix or line scanning device. Presently, there is very rapid development of high-level and consumer-level digital imaging that is already spilling over into deep-sea equipment development. Therefore, it is not prudent to make a flat statement as to the best system to be used. Rather, it is better to consider film photography the standard by which other methods may be judged.

Image-Based Sampling is extremely appealing, but must be considered critically in designing studies. What is the purpose of the images to be obtained? Hecker's camera sledge work is noteworthy both in terms of relating animals to structure (Hecker 1982) and sampling in deep-sea canyons where coring is inapplicable and trawling impossible (Hecker 1990). Excellent quantification and aggregation analysis for dominant megafauna have been obtained from submersible (Grassle et al.1975) and cameras mounted to beam trawls (Wakefield and Genin 1987). However, the literature presenting successful studies gives no hint of the vast majority of photo and video surveys that are never analyzed. Bulk-load survey cameras can take approximately 800 frames per deployment, while video takes 10,000's. Extracting useful final data from such massive raw data usually proves to be overwhelming. Imaging technology is appealing, but the actual benefits are not often evident. Unless specimens are required for other analysis, image-based sampling generally gives a better measure of items on the seafloor, but not those buried (Kidd and Huggett. 1981).

When it is decided that image-based sampling is needed, a decision must be made among competing technologies. Film photography is a mature technology that achieved a very high level of sophistication in the early 1960's. As such, methods of deep-sea photography developed during that era (see Hersey 1967) are still applicable. Resolution is the primary criteria by which technologies are compared.

Resolution is the ability to record fine spatial details. In film photography it is expressed as resolving power measured in lines per mm. In video it is expressed as scan lines per image frame, and in digital imaging it is expressed as pixels per unit length or area. Very high resolution film can record about 200 lines per mm. This equates to about 400 pixels/mm in digital terms. For a 35 mm by 25 mm photographic slide, that is 14,000 by 10,000 pixels. If they are color pixels stored at 12 bits per primary color, that is 0.63 gigabytes per image! Film is still an impressive medium.

In typical deep survey applications, resolution of video and digital systems is most often limited by the display system, then by the storage system, and least by the camera. There is little value in using cameras with a resolution more than twice that of the display device. The most common resolution in consumer electronics is that of computer monitors for MAC and Windows operating systems. These systems are designed to employ 72 pixels/inch. Even if the monitor is capable of higher resolution, the operating system use of better resolution is limited. There are an increasing number of color printers that print at very high resolution. However, with printers there is a complicating factor. In color monitors a dot equals a pixel. This is not always the case in printers, since most printers create color by clustering dots. Thus, a 1440 dpi (dots per inch) laser printer that dithers 2x2 produces a resolution of about 720 pixels/inch. Digital systems are still far behind film.

Moored and Free Deployments

Moorings are the traditional means of obtaining time-series physical data and can be used in that capacity in the deep sea. In studies of the deep benthos the vertical placement of meters should focus upon monitoring of the benthic boundary layer. Particle flux traps must be suspended within and above the boundary layer so that reflux can be partitioned from flux.

At-Sea Cost Factors in Deep-Sea Studies

In spite of the host of new and potentially useful technologies, it can be assumed that deep-sea applied ecology will primarily employ traditional sample collecting from ships. Some of the costs can be relatively well anticipated and are summarized in table 2.8. Equipment must either be purchased at full costs or leased, if available, at 10 to 20% of cost per cruise. A trawl is the least expensive equipment item, with a set of boards and a custom made net estimated at about $3000. Due to the low costs and likelihood of damage, trawls are not leased. Due to a lack of available 0.25 m^2 box cores, existing ones must be leased or fabricated. The design is not protected by patent and could be duplicated by a qualified machine shop for a cost of approximately $15,000 per unit. Most oceanography programs have some corer sitting around rusting, but these should not be used in place of the standard device. Image systems using film can be purchased off the shelf for about $100,000. Digital systems usually have to have some degree of custom fabrication due to the rapidly advancing technology. Camera, lights, and data systems should be equal in costs to those of film photography or several times more expensive. Proprietary systems, such as laser line scanners, are protected by patent and must be leased or manufactured under license. Mooring costs will be determined by the equipment attached. Current, salinity, and temperature meters with the necessary pressure housing will cost approximately $25K per unit. Particle traps can be fabricated for about $2000 per unit.

Processing costs are determined by the parameters measured. Megafauna sampling is low cost due to size and relatively low diversity. Full sample sorting is often completed at sea. Box core samples are labor intensive. Sorting the fauna from a single sample will take an experienced technician about one month. Chemical and geological parameters carry various per analysis costs but lack an extensive manpower loading.

Table 2.8. At-Sea Cost Basis for Major Activities of Trawling, Box Coring, Bottom Surveying, and Moored Instruments.

Activity	**Samples Produced**	**Cost Scaling**
Trawl Sampling	Megafuana for: Species Inventory, body analyses, and tissue analyses.	Initial Equipment costs ($3k per trawl system) plus vessel time. Low processing costs since samples can be fully sorted at sea.
Box Core Sampling	Macrofauna for: Species Inventory, body analyses, and tissue analyses. Meiofauna for: Species Inventory, body analyses, and tissue analyses. Sediments for: Grain and bulk property description, and chemical analysis	Initial Equipment costs plus vessel time ($15K per corer system): High processing costs of at least 1 month per .25 m^2 sample for fauna. Processing low for abiotic measurements, but variable on exact parameter measurements.
Survey Photo/ video	Megafuana for: LTR spatial patterns. Bottom Images: textural description.	Initial Equipment Costs ($100K & up) Field costs as with trawling. Processing variable with method; about 10 images/hour for photography to 0.1 images/hour for advanced digital.
Mooring Deployments Meters, Traps, etc.	Current profiles and time series. Particle flux Light and transmission	Initial Equipment Costs ($100K per mooring). Concurrent deployment for synoptic data requires multiple units with number set by number of moorings and depth strata. Field costs similar to box core case. Processing costs based on analysis of data and will be variable.

Image data are highly variable in cost. Photographs processed by an experienced worker can produce faunal data at about ten frames per hour. If the images are digital the processing time actually increases. The more computer manipulation, the greater the processing time. Moorings produce digital records and particle trap samples. Current, salinity, and other digital records can be processed in less than one man month per sampling interval. Particle trap samples can be processed at about the same cost rate as chemical measurements from box cores and will vary with parameters required.

2.8 Conclusions and Recommendations

2.8.1 Introduction

At the beginning of this review a central question facing MMS was identified. Is there strong scientific evidence indicating that shallow-water management strategies are inappropriate for deepwater? After various topics have been considered, this single question can be rephrased as two related queries.

1. Is there strong evidence that the deep environment is so physically different than the shallow that impact concerns must also be different?
2. Is there strong evidence that the ecology of the deep fauna is such that impacts are more or less likely?

It is the tenant of this conclusion that the answer to the physical question is yes. An answer to the ecological question is more tenuous, however, there does seem to be some valid concern that impact is more likely. In this concluding chapter the arguments for the answers will be reviewed and recommendations made.

2.8.2 The Physical Deep Environment

Conclusions as to the Unique Nature of the Physical Environment

When deepwater is defined as starting at 200 m depth the environment demarcated by that line is both highly variable and different from the shelf environment. It is not, as assumed by some, a physically uniform system.

1. Density, Salinity and Temperature - In avoiding impacts and planning studies, management should divide deepwater into two physical zones, a transition zone of rapid temperature change from 200 m to the bottom of the permanent thermocline (pycnocline) and a deeper zone of minimal temperature change. The demarcation will vary from place to place, but can easily determined from the literature and physical data archives for the region in question. In studying the upper zone designs must anticipate both seasonal fluctuations and short term transitions caused by mesoscale physical processes such as storm and eddy passage.
2. Light – Sunlight is present in the upper physical zone, although near the threshold of human vision. The importance of residual sunlight and

bioluminescent signaling means that increase in turbidity may have negative impacts.

3. Oxygen - While the oxygen minimum is usually thought of as having little ecological consequence, its presence requires special attention to discharges. Any material that has a biological oxygen debt may produce local hypoxia.
4. Water Movement – Bottom currents in deep water are typically low energy, but episodes of high flow are sometimes encountered. A full understanding is needed to understand the biological environment and model plumes dispersing on or near bottom.

Recommendations Based on Physical Results

1. Pressure - Fate and effect models used in shallow water should be reviewed. Employing reasonable physical chemistry models the effect of pressure upon critical reactions and solubility's should be considered. Based upon the results of this review, targeted physical chemistry investigations should test reactions for pressure effects. If significant effects are found, then new deep fate and effects models must be developed.
2. Density, Salinity and Temperature – Due to the paucity of data, management is obligate to either develop the needed time-series data sets or work jointly with industry to make the necessary measurements. Due to its more dynamic nature, the upper physical zone should be sampled with greater temporal and spatial resolution. In general, sample density should increase towards bottom and not follow the oceanographic tradition of fewer samples near bottom.
3. Light - Light field measurement is needed for a full description of the deep environment. When turbidity is measured, large volume measurements (such as back scattering) may be more ecologically informative then beam transmission.
4. Oxygen - The oxygen minimum will fluctuate with the water density structure. Oxygen can be measured concurrent to temperature and salinity. The biological oxygen debt at appropriate temperatures and pressure of any discharged material should be determined and evaluated in terms of producing local hypoxia.
5. Water Movement – Traditional physical oceanography is best suited for studying the surface movement of the ocean. Management should avoid this orientation and require that the dynamics of the larger benthic boundary layer (BBL) and the dynamics of the sediment-water interface be the major focus of study. Deployments should most heavily sample the 100 m nearest bottom, with "at bottom" conditions being directly measured.

2.8.3 Deep Biology

Biological Conclusions

As stated above, it is hard to provide definitive answers about deep-sea ecology and impacts. The few studies which set out to detect such impacts were either done poorly or were terminated prematurely. Basic studies can only suggest possibilities. After some consideration it seems probable that deep ecology may be more sensitive to impacts. This point is developed in the following conclusions and recommendations.

1. Habitat – Deep ocean management can not accept the shallow-water strategy of recognizing special habitats on the basis of gross substrate differences (rock versus mud). The degree of habitat change which causes one area to be more important than another is not known for the deep environment.
2. Natural History – Up until ten years ago generalities about deep-sea adaptations were seldom challenged. The slowly reproducing and slow growing animals envisioned would certainly be highly subject to alterations of their stable environment. Now it seems that the natural histories are as varied as the environment is variable. However, one pattern seems true and relevant. Detritus feeding is dominant and variation in food input is a major source of heterogeneity in time and space. Activities that alter such input and redistribution of food should be of primary concern.
3. Zonation – If the fauna in one part of the ocean differs from that in another, then possible impacts and management concerns might also be different. This is the fundamental issue, not where to draw lines and apply names. Deep-sea fauna does change with depth either gradually or rapidly on a species by species basis. Therefore, uniformity of impacts is unlikely. It is an easy undertaking to sample fauna at many places and quantify differences. Pre-defined zones are not especially useful.
4. Diversity - The unexpected very high diversity of the deep sea remains one of the primary distinguishing factors separating the shallow form the deep. In a management context, this high diversity is difficult to deal with since it is unexplained. Current proposed explanations for deep high diversity suffer from the absence of comprehensive geographic data. However, diversity does not increase the stability of systems, it affords more species which might be impacted.
5. Trophic Structure – In the shallow ocean productivity and consumption have a rapid feedback loop through the nutrient cycles. This is not true for deep animals. They must depend upon a supply of detritus which decreases with depth. Since food decreases exponentially with depth, abyssal populations will be more food stressed then upper slope. Therefore, activities which alter detritus influx may produce major impacts which worsen with depth.
6. Biogenically Structured Environment – Central to some explanations of high diversity in the deep sea is the possibility that soft sediment biogenic structures (burrows, mounds, etc.) are vastly more important structuring elements than in shallow water. This suggests that activities altering such structuring may have major impacts.

Biological Recommendations

When considering physical aspects of the deep sea it was easy to give definitive recommendations since the results were straightforward. The uncertainty of the biological conclusions calls for a different approach. Management needs to first test the conclusions borrowed from basic studies before applying them fully. The recommendations below attempt to provide such tests.

1. Habitat – Management needs to test the hypothesis that all deep soft bottom habitats are similar within the overall changes imposed by faunal zonation. This test requires that the physical environment be known first and then sampling carried out with appropriate stratification across different physical regimes. A high level of spatial control would be needed for any such sampling. Box corers and imaging systems would be the major devices used once the physical environment had been described.
2. Natural History – Since previously useful generalities are being challenged, management must discover the necessary facts. Reproduction studies are most immediately relevant since they bear upon the ability of a species population to recover from impact. Such studies could be initiated on the dominant species in each size class.
3. Zonation - The pattern of species change with depth should be determined across any deep area subject to development. Samples should be evenly spaced with depth rather than placed according to a proposed scheme of zonation. Analyses should be limited to degree of species sharing after adjustment for different abundance's in samples. If high degree of faunal overlap is found, the a uniform management strategy may be used. If a high degree of faunal difference is found, then depth-specific strategies must be used.
4. Diversity - Surveys should continue to be carried out at the species level. When possible industry activities should be incorporated into experimental studies which monitor diversity changes.
5. Trophic Studies - The influx and utilization of organic detritus to the deep benthos should be included in future studies. The preponderance of deposit feeding and the low food levels indicate that this process may be easily impacted.
7. Biological Structuring. - A means needs to be devised to effectively describe and quantify the extent of biogenic structuring of soft sediments. Such a "structuring parameter", would allow testing of the hypotheses that the deep bottom is habitat rich and allow monitoring of possible impacts.

3 Reanalysis and Synthesis of Gulf of Mexico Deep-Sea Benthic Studies

3.1 Introduction

This review is based upon published reports and data archives provided by the original contractors and the National Oceanographic Data Center (NODC). Material appearing in the original reports is repeated only to the extent needed. Early in the review it was found that the NODC files for the Northern Gulf of Mexico Continental Slope Study (NGMCS) were unusable. Dr. Benny Gallaway of LGL Ecological Associates, the original contractor, provided printed data files contained in the 3rd annual report of the project (Gallaway et al.1988). The fact that macrofauna counts were provided at the replicate level in those reports made reevaluation feasible. The Pequegnat data do not yet exist in a computer archive form, and the main report Pequegnat 1983(a) does not provide full information. In order to compare the Gulf of Mexico with another well-studied region, the NODC archive for the Atlantic Continental Slope and Rise study (ACSAR) was obtained. Since that archive did not reflect final sorting at the species level, the original contractor, Battelle Inc., provided an updated data archive.

The studies of Willis Pequegnat and his students (the author being one) were largely exploratory investigations of a type no longer supported by funding agencies. They were a prolonged zoogeographic survey with great emphasis upon species-level taxonomy rather than processes and concepts such as diversity maintenance, trophic structure, etc. Such exploration really never has a definitive conclusion, but in Pequegnat's case it can be concluded that they were prematurely terminated due to shifts in funding. Pequegnat's studies were the initial invaluable observations upon which hypotheses were to be drawn and tested. In this content of hypothesis generation, Pequegnat (1983a) should be seen as a compilation of ideas rather than conclusions. Subsequently, the Northern Gulf of Mexico Continental Slope (NGMCS) study adopted many of Pequegnat's ideas as hypotheses to be tested.

3.1.1 Data Sources for the Gulf and Comparison Studies

The main publication of the Pequegnat studies is Pequegnat (1983a). Much of the work based on those samples appears only in theses and dissertations. The most comprehensive of these is Bright (1968), Firth (1971), James (1972), Kennedy (1976), Lipka (1975), Pequegnat (1970), and Roberts (1977). The specimens from this study were extensively circulated in the international community of systematists, and it is assumed that there is a substantial systematic literature not easily linked to the Pequegnat studies. Since the deep sea was so poorly known when Willis Pequegnat of Texas A&M undertook his sampling in the 1960's every sample yielded important additions to understanding. Dr. Pequegnat died prior to the preparation of this report. His notes, samples, and other program related documents are archived at Texas A&M under the direction of Dr. Gilbert Rowe. Vouchers of most of his species are catalogued in the collection of the U.S.National Museum of Natural History.

The sampling results of Pequegnat are compiled into a single volume (Pequegnat 1983a). The NGMCS study produced a series of reports; most useful are the third and fourth year annual reports (Gallaway et al. 1988; Gallaway 1989). An open literature publication (Pequegnat et al. 1990) provides a very brief summary of results. The appendix volume of the year III report is an exceptionally valuable document since it contains sample-level data for the macrofauna and megafauna samples. Dr. Gallaway was extremely helpful during the course of the review. Some specimens are still archived at LGL in Bryan, Texas. Fish samples are archived at Teax A&M. Voucher specimens were filed by taxonomic specialists at the U.S. National Museum of Natural History. Most of these vouchers have only been accessioned, the first step in the cataloguing process, and are less accessible than the Pequegnat material.

The primary studies upon which to base comparisons of the Pequegnat and NGMCS results are the parallel studies supported on the US Atlantic coast by MMS. The most extensive summary of results are given by Maciolek et al. (1987).

A Caution About Data Archives

Working with reconstructed data is always problematic because the archival source may introduce errors and be easily misinterpreted. In terms of all faunal components, the reconstructed data had 2157 taxon, and the NGMCS 2198 (Gallaway et al. 1988 Appendix A4). Greater differences were found between the reconstructed archives and summary statements (Gallaway et al. 1988) when subgroups were compared. The reconstructed macrofauna archives list 69,161 specimens in 1613 taxa from 326 samples. The final report of the NGMCS study cites 324 samples, but only about 50,000 specimens, and 1121 species. The reconstructed megafauna invertebrates contained 41,827 specimens in 544 taxa from 56 samples. The NGMCS study reports a similar "more than 40,600 invertebrates", but only 432 taxa.

The method of reconstruction was as follows. Appendix C2 (Gallaway et al. 1988) contains ten fauna count tables, two for each of five cruises (1 for polychaetes and 1 for all other invertebrates). The counts for each taxa in each replicate sample are given in 405 pages. Appendix C3 (61 pages) gives megafaunal in a similar manor, treating fish and invertebrates separately. Appendix C1 lists meiofauna with replicates pooled. All data were read, reentered into a text file, and verified. As a check for errors, all unique taxonomic names and all unique stations were extracted. Obvious errors were corrected. The data were then structured as an ordered triple (name, sample, count) for additional analysis.

The greatest source of difference between the reconstructed and original data may be due to the manner in which mixed taxonomic resolution was handled. The NGMCS study excluded nematodes and harpacticoid found in macrofauna samples. This review does not, accounting for some of the difference in specimen numbers. It is assumed that between the third year report and the final analysis an unspecified number of taxa not identified to species were dropped before analysis. This review retained all taxonomic categories. Additional errors may be due to hand reentry of hand-typed tables. As a result, faunal counts and species richness reported in this review can be expected to be higher than those of the original NGMCS study.

The NODC files for the ACSAR study contained less-than-species data and incorrectly formatted and positioned header records. Dr. Blake, one of the original investigators provided a more detailed file from the original contractor, Battelle. The Battelle archives employed a consistent, but non-standard, species code rather than the NODC code. Position and depth data were not recorded for each sample as per NODC requirements, but only for stations. Therefore, none of the scatter in location and depth associated with these surveys was preserved. Metadata, (information about the data) was not included, but could be gleaned from the various reports.

3.2 History of Major Gulf of Mexico Deep Ecological Studies

3.2.1 Pequegnat Studies

Between 1964 and 1973 Willis Pequegnat at Texas A&M undertook extensive sampling of the deep fauna in the Gulf of Mexico. Although occupying only nine years of his diverse professional life, this research produced a lasting association between the name Pequegnat and deep-sea ecology, especially in the Gulf of Mexico. In reviewing the utility of Pequegnat's work in the context of contemporary deep oil and gas development, it is important to understand the unique nature of those studies. Most importantly, the work was a long-term commitment strongly focused upon taxonomy and zoogeography of the larger organisms. While the study of deep-sea animals collected through extensive collecting does lead to ecological insight and conjecture, it does not meet the criteria of design and statistical strong inference that have been required in sampling programs for the last fifteen years. Due to Law of the Sea restrictions, vessel costs, and decline in the systematics' expert base, these contributions could not be repeated now. However, ecological conclusions beyond this outstanding species-level biology were acknowledged by Pequegnat to be highly conjectural and intended as a starting place for continued inquiry.

The primary contributions from the Pequegnat deep trawling remain in seven doctoral dissertations that were not subsequently published in the peer reviewed literature. Some of this information was provided in the open literature in the form of taxonomic papers in Pequegnat and Chace (1970) and a folio series (Pequegnat et al.1971). Fortunately, as deep-water oil and gas exploration became a more likely undertaking, the Gulf of Mexico Region Office of the Minerals Management Service (MMS) had the foresight in the early 1980's to support compilation and synthesis of this important information.

Pequegnat Objectives and Design

The Pequegnat studies spanned the entire Gulf (Figure 3.1) over 9 years of sampling very much in the zoogeographic spirit of the European national programs of the 1890's to 1950's. As such, its primary goal was discovery and it lacked the formalization of sampling according to a design specifically for the purpose of statistically testing a hypothesis. It was, the observation which comes before hypothesis. However, in providing a summary of this extensive work for management, four objectives were stated in retrospection.

1. Describe and discuss the megafauna in the northern Gulf of Mexico.
2. Provide photo-documentation of that environment.
3. Identify Information gaps.
4. Provide reasonable assessments of potential for impacts

Pequegnat Methods

The Pequegnat sampling program was evolutionary with respect to equipment. Samples were taken with six primary devices. Larger epifauna were originally collected with a Menzies dredge/trawl (Menzies 1964). Due to the fine mesh and overall small size of this device, it was replaced after only seven samples by a much larger rigid dredge, the epibenthic skimmer. A three meter wide skimmer was used for 87 samples and a 2 m version for an additional seven. In the later years of the sampling, the skimmer was replaced by a 20 m head line otter trawl that produced larger samples but with an increase in specimen damaged. A total of 25 trawl samples were taken.

The epibenthic skimmer is described in detail in Pequegnat and Chace (1970). It was intended to sample large epifauna. It was a rigid welded frame with a gape of 3.06 m x 0.92 m covered on the sides with 1/2inch mesh and in the cod end with 1/4 inch mesh hardware cloth. Its rigid construction made it a rugged device which did not mangle specimens. Quantification was attempted using a odometer wheel device. However, as with similar systems (Carney and Carey 1980) this proved unreliable.

When high species diversity was reported in the deep sea by Sanders et al.(1965), Pequegnat added to his equipment pool a macrofauna sampling device. Here again, sampling methods were evolutionary. A Campbell grab with a 0.62 m^2 bite was used 14 times between 1964 and 1966. It proved to be unreliable at depths below 200 m. A novel plow dredge was used 11 times in 1965 and 1966. It employed cultivator disks borrowed from farming equipment to turn sediment into a bag of 1/4 to 1 inch mesh. This device was subsequently replaced by a quantitative dredge, scoop dredge equivalent to Sanders' epibenthic sledge. It was intended to fill a 360 liter canvas bag with a 1m wide slice of sediment sliced 5 or 10 cm deep. Depending on the cutting depth, a full bag would represent 0.36 m^2 to 0.72 m^2. Today, such small dredges have been replaced by box corers. Twenty nine samples were taken with this device.

Two camera systems were used for bottom surveys. An Edgerton-design 35mm pressure-housed shutterless camera made by Alpine Geophysical Associates was initially used. It was replaced by a medium format (70 mm film) Shipek-design pressure housed camera made by Hydroproducts. An Edgerton-type shuttered camera is still available from Benthos Inc. of Falmouth Massachusets. The Shipek camera is no longer made. In typical application, the camera as triggered by a bottom contact switch. Bottom contact was controlled with some precision through use of a camera mounted pinger and a trigger-sweep oscilloscope connected to a hydrophone.

Pequegnat General Findings

Pequegnat's exploratory sampling gave rise to two major conclusions concerning the zoogeography of the deep Gulf. The most pronounced pattern was that of bathymetric species change, that Pequegnat chose to describe in the terms of zoogeographic zones. It should be noted that the study of species gradients of macrofauna rather than zones of megafuana did not become popular until the 1980's, a time by which Pequegnat had completed most of the Gulf sampling.

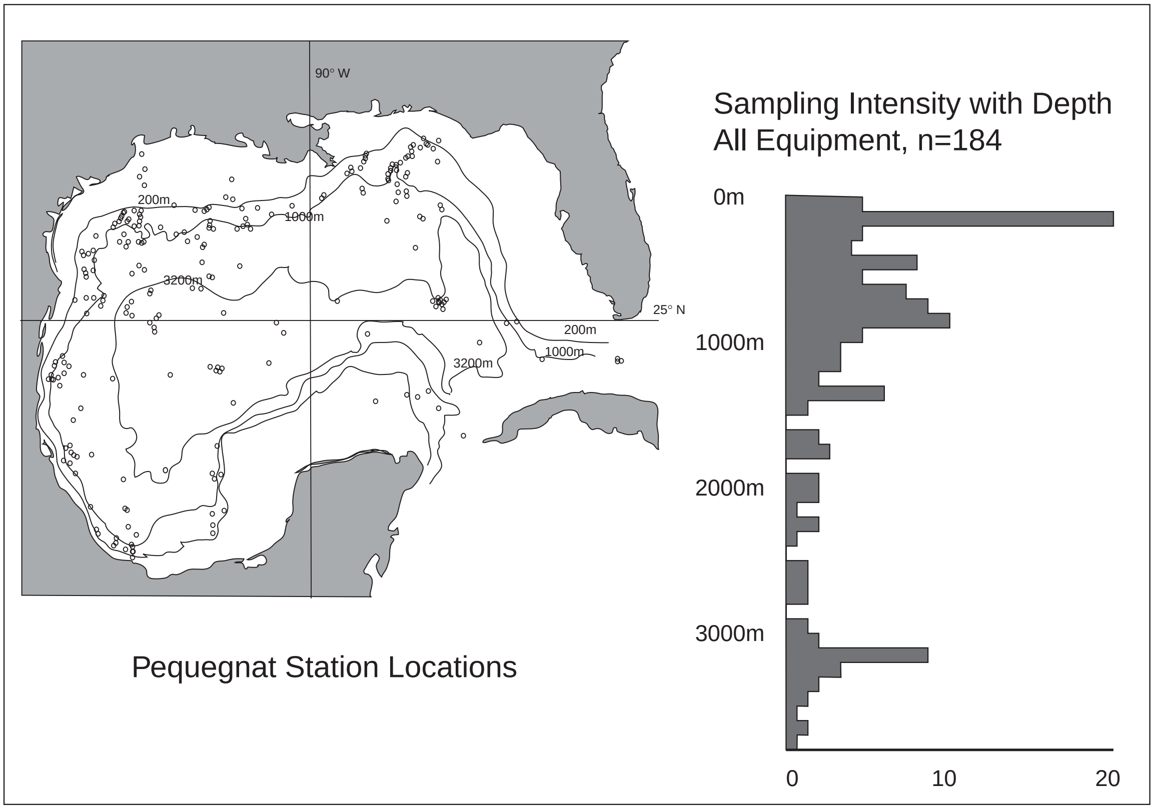


Figure 3.1. Locations of Pequegnat Samples Across Gulf of Mexico and Depth Sampling Effort.

In establishing zonal boundaries, Pequegnat employed a "polythetic" (many types of evidence) approach (Sneath and Sokal1973). He used geomorphology, the position of the permanent thermocline, the position of the oxygen minimum layer, the depth of the Straits of Yucatan sill, and the distribution of fauna. With the advent of computer methods and gradient analysis, it has become more usual to describe depth changes monothetically, using only faunal data. The polythetic approach of Pequegnat versus the monothetic approach of others is important to bear in mind when contrasting various proposed depth patterns.

Pequegnat set the beginning of the deep sea by two criteria. The first was physical and consisted of the depth of the 18° C. isotherm. Typically found between 125 and 150 m this was the depth at which physical oceanographers thought seasonal variation became minimal (± 3°). The second criteria was faunal and consisted of that depth at which the fauna had no estuary-dependent species. On the basis of shrimp, this end of the shallow ocean could be set at about 250 m.

Table 3.1. Faunal Criteria for Establishment of Pequegnat Depth Zones.

ZONE	FAUNAL CRITERIA
Shelf/Slope Transition **150 - 450 m**	Abundant and species rich fish fauna, paucity of holothuroids, and abundance of burrowing urchins
Archibenthal **475 - 950 m**	Horizon A - Fish still abundant, holothuroids increasing, replacement of burrowing urchins by regular urchins, and replacement of shelf galatheid species by slope species. Horizon B - Fish still numerous but past the center of abundance, marked reduction of bracyuran crabs.
Upper Abyssal **975 - 2250 m**	Encounter fewer fish with deeper centered populations, holothuroids increasing, upper species fewer but still present.
Mesoabyssal **2275 - 3200 m**	Horizon C - Marked reduction in species for all taxa. Horizon D - Additional reduction of species with a few deeper species reaching their population maximum here.
Lower Abyssal **3225 - 3850 m**	Reduced fauna, but distinctive species of holothuroids and fish.

Overlapping this upper boundary and extending to the maximum depth of the Gulf, Pequegnat envisioned five progressively wider major zones, the Shelf-Slope Transition (150-450 m), the Archibenthal (475-950), Upper Abyssal (975-2250 m), Mesoabyssal (2275-3200 m), and Lower Abyssal (3225-3850 m). Within these zones, the Archibental is divided into two horizons, A (475-750 m) and B (775-950 m), and the Mesoabyssal divided into a Horizon C (2275-2700 m) and D (2725-3200 m). These subdivisions were not uniformly obvious in the entire Gulf of Mexico.

A review of the faunal criteria used by Pequegnat for the recognition of these zones (Table 3.1) shows that taxa were given very selective weights. Fish, holothuroids, urchins, bracyuran crabs, and galathaid crabs were the primary determinants. Recognizing the subjective choice of criteria, Pequegnat's zones can serve as a useful nomenclature. Overlying the basic pattern of depth zonation Pequegnat detected two larger-scale geographic divisions. Drawing a line somewhat arbitrarily at 90° W, the eastern region was considered a physically active (dominated by deep currents), and the western was tranquil. These physical differences were viewed as giving rise to habitat and faunal distinctions. There was no attempt to explain the differences in terms of trophic relationships, since no studies of surface productivity or detritus influx were attempted.

Beyond these major distribution patterns, Pequegnat offered some interesting speculation about trophic relationships. It was suspected that organic detritus influx through the water column might be insufficient to meet the demands of the benthic population. Dissolved organic carbon was dismissed as a possible food source, and large plant and animal falls considered minor factors. Food input via mass sediment transport was considered highly probable. The question can now be resolved through application of carbon influx studies and metabolic demand of the fauna.

3.2.2 NGMCS Study

The Northern Gulf of Mexico Continental Slope study was carried out by LGL Ecological Research Associates Inc. of Bryan, Texas. The principle investigators included Dr. Pequegnat, then an emeritus professor of oceanography at Texas A&M. LGL had prior experience in benthic studies on the Gulf continental slope, and sought to add deepwater expertise through an advisory panel which included Dr. Robert Hessler of Scripps Institute of Oceanography (SIO), Dr. Fred Grassle of Woods Hole Oceanographic Institution(WHOI) (now Rutgers), Dr. Richard Rosenblatt of SIO, and Dr. Robert Ballard of WHOI (now the Jason Foundation). In the last year of the project Dr. Ballard was replaced by the author, Robert Carney then at Moss Landing Marine Lab (now Louisiana State University).

NGMCS Objectives

The NGMCS study in its approved form was quite ambitious and had a list of eleven objectives.

- To determine the hydrographic structure of the water column and bottom conditions at selected sites within the study area.
- To determine and compare sedimentary characteristics at selected sites within the study area.
- To determine the abundance, structure and distribution of animal communities in the deep-sea in the Gulf of Mexico
- To relate differences in biological communities to hydrographic, sedimentary, and geographic variables.`
- To assess seasonal changes in deep-sea biological communities in terms of abundance, structure, animal size, and reproductive state.
- To measure present levels of hydrocarbon contamination in the deep-sea sediments and selected animals prior to, and in anticipation of, petroleum resource development beyond the shelf break.
- To assemble together and synthesize appropriate published and unpublished data with the results of this study, summarizing on a seasonal and spatial basis all biological, habitat, and environmental observations and parameters.
- To compare the biological and non-biological characteristics of the deep Gulf of Mexico with that of other temperate and subtropical deep-sea regions.
- To assess the need for, and determine the type of studies to be conducted in future program efforts.

- To conduct an effective quality assurance and quality control program which insures that all data acquired are accurate and repeatable within standards normally required for each type of observation, measurement, or determination.
- To critically review, interpret, and analyze all observations and data acquired to redefine, as necessary, the research program in such a way as to avoid or minimize redundancy and to optimize the efficiency of all field, laboratory, and data management operations for future deep-sea studies sponsored by MMS in the Gulf of Mexico

NGMCS Design

Superficially, the NGMCS study looks much like a typical benthic survey with 3 transects containing 5 stations each. If consistently sampled over a series, of cruises a factorial analysis of variance could be used to test the importance of differences among transects (geographic position), differences among depths (bathymetric position), and differences among times. In execution, the NGMCS study executed a very different design that sought to ask a series of independent questions with a changing strategy of sample placements. Sampling effort within the 3 by 5 design was varied cruise to cruise, and auxiliary samples were added as new questions arose. In order to understand the intention of the final design, it is useful to first consider the original proposal.

Originally Proposed Design

In 1983, well in advance of the current industrial interest in deepwater development, MMS issued Request for Proposal (RFP) 3046 calling for investigations of the Gulf of Mexico beyond the shelf edge. Ultimately, the winning proposal was that of LGL Ecological Associates of Bryan Texas. LGL pulled together a research team with elements from Texas A&M in a research capacity and consultants from WHOI and SIO. Willis Pequegnat served in a senior advisory capacity.

As initially proposed by LGL, the study would not be the repeated sampling of fixed transects through time that typified previous shelf-depth studies supported by MMS in the Gulf of Mexico (Carney 1993). Rather, it would be a three phase effort beginning with two descriptive survey cruises followed by an "experimental survey", "natural experiments", and "short-term field experiments". Since these departures from traditional surveying would be developed from the initial descriptive efforts, they were not specified in advance. Somewhat prophetically (chemosynthetic communities were not discovered until 1984) it was anticipated that oil seeps might be studied in a "natural experiment" mode.

When the somewhat vague proposal was modified to a more traditional transect sampling, a western, central, and eastern transect were selected to coincide with MMS planning regions. The five stations of each transect were centered in the middle of a Pequegnat bathymetric zone. The descriptive value of the stations sought to take advantage of previous studies and topographic features of interest. There would be a core of three transects, Eastern, Central, and Western. The Eastern would stretch from 27° 40'N 85° 15'W to 27° 30'N 85.40'W across the Florida Escarpment in a region of moderate to strong bottom currents (scour obvious) and limited terrigenous input. The

Central would stretch from 28° 20'N 89° 40'W to 26° 40'N 89° 20'W near the Mississippi Trough in a region of high sediment and terrigenous input. The Western transect would lie from 27° 25'N 93° 40'W to 25° 50'N 93° 30'W. and be a seaward extension of the well studied Flower Garden Banks area. This Western transect would cross a topographically complex region.

In addition to the three core transects, five other possibilities were proposed but never sampled. Pequegnat (1983a) had viewed the Desoto Canyon as being both a distinct ecosystem and a zoogeographic boundary. Therefore, it would be sampled by two transects, one each on its eastern and western flanks. Oil seep effects and brine habitats would be studied by an additional western transect crossing both an active seeping area and the Orca Basin brine lake. As a final transect, two alternatives were proposed. There could be a westward-most transect forming a seaward extension of the South Texas Baseline Study or a southeastward most transect off the Southwest Florida coast. The western-most transect might also allow detection of IXTOC spill effects, while the Florida transect would be considered pristine.

NGMCS Actual Design

Whenever a sampling design is modified during execution of a project, some elements of the original design inevitably remain, sometimes at cross purposes with the final design. This effect can be seen in the NGMCS study. A conditional sampling mode, basing each subsequent step on each previous result was carried out. The great advantage of this approach is a high degree of flexibility that allows changes if the initial design proves pointless early in a study. Its great weakness, however, is that changes of purpose usually limit the strength of the conclusions that can be drawn during final analysis. In the NGMCS study, geographic and bathymetric range was improved, but the validity of hypothesis testing weakened by the changes that took place.

The NGMCS study had to accommodate two major changes during its course. The most obvious change, discovery of chemosynthetic communities, was not the major cause of design problems, as might be thought. Rather, design modification to accommodate basic questions about deep-sea ecology not anticipated in the proposal were most detrimental. At the time the NGMCS study was proposed, the academic deep-sea community was actively questioning the nature of faunal depth change, high species diversity, and detritus-based trophic structures. The ideas arising from this debate were collected in review papers that same year (Rowe 1983) and were not incorporated into the NGMCS design. As the project progressed, the scientific advisors saw this as a serious deficiency in the project, and major shifts in design were made in an effort to address the omissions. Most of the changes were made concerning the depth placement of samples and, the need to test the validity of the Pequegnat zonation schemes upon which the design was based. Unsuccessful pursuit of such a test drove sampling in the three final cruises at the cost of useful time series and consistency across transects. Cruise III was devoted to filling in depth gaps and completing a time series only at the Central Transect, while Cruises IV and V undertook sampling along isobaths at the Eastern and Western Transects.

Failure to successfully test the zonation scheme was due primarily to a misunderstanding. This misunderstanding can be found throughout the documentation of the NGMCS study where the debate about zones is incorrectly characterized as a matter of scale, Pequegnat's (1983a) fine scale versus Carney et al. (1983) coarse scale. While Carney et al.(1983) does suggest use of some simple terms for faunal zones that can be used when zone naming is convenient, the main point of that review was to call into question whether such zones were anymore than a subjective and technique-biased cutting of continuous gradients. Appropriate testing required higher sampling density across isobaths and sample placement independent of any prior zonation scheme.

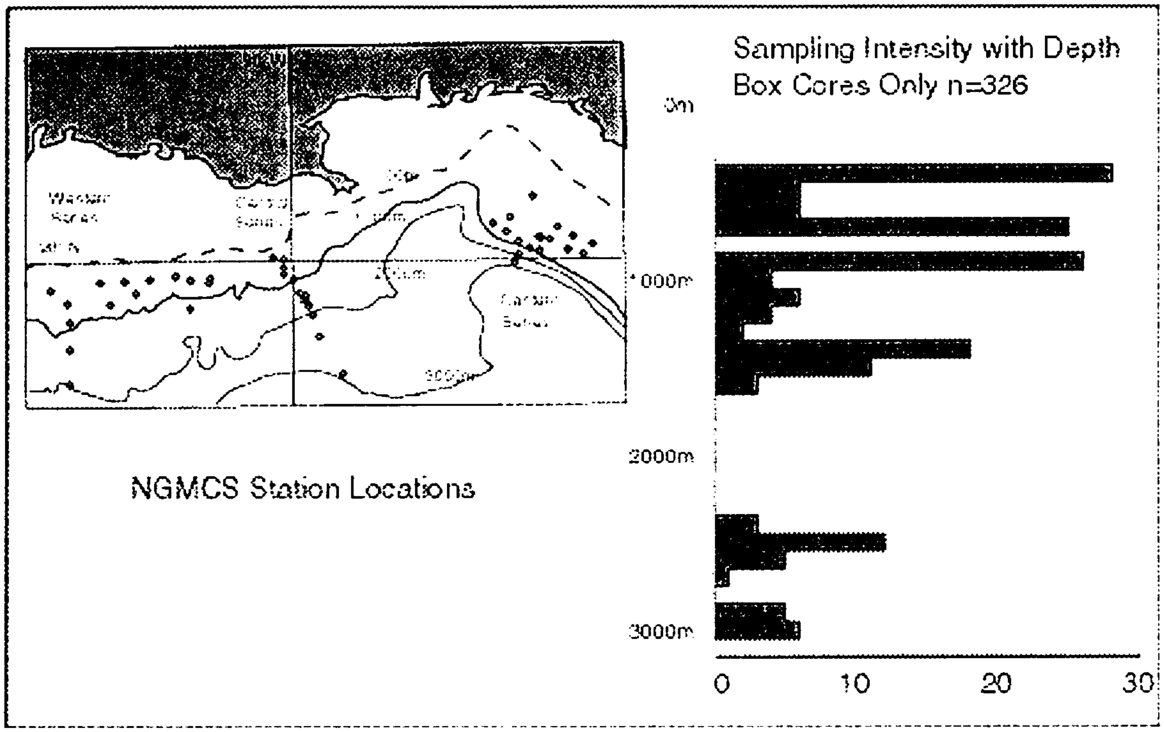


Figure 3.2. Locations of the NGMCS Study Transects and Supplemental Stations with Depth Effort of Boxcoring.

Regional Transects and Ancillary Stations

The three main transects are shown in figure 2.2. The Western Transect extended from near the Flower Gardens at 27° 25'N 93° 40'W to 25° 50'N 93° 30'W. This was viewed as a region of low currents and high topographic complexity. The Central Transect lay near the Mississippi Trough, beginning at 28° 20'N 89° 40'W and ending at 26° 40'N 89° 20'W. It was seen as a region occasionally impacted by the Loop Current, typified by high sediment movement and minimal topographic variation. The Eastern Transect crosses the Florida escarpment, beginning at 27° 40'N 85° 15'W and ending at 27° 30'N 85° 40'W. This region was seen as under the influence of strong currents and having limited terrigenous input. Since there was no replication of transects within each region, inter-transect differences could be confidently ascribed to the regional factors noted.

Consistent sampling of the fifteen primary stations (3 transects x 5 depths) was dropped after the second cruise. Ancillary stations were added for mixed purposes. On the third cruise, 11 stations (356, 492, 633, 881, 1017, 1191, 1428, 1465, 2100, 2518 and, 2945m) were occupied on the Central transect to increase depth resolutions and sampling within isobaths increased. Rather than repeat this increased depth resolution on the other transects, cruise IV added 12 stations at the same depths as the primary stations,, effectively replicating within three depth zones (625, 850, and 2900m). Again changing design, on the fifth cruise, a series of 12 stations lying between the Western and Central Transect were added. These W-C stations started at 150 m and ended at 2250 m. In effect, they were a diagonal depth transect. In the end, none of the transects or depths had been sampled with sufficient consistency to allow for strong statistical testing of the intended three factors, transect, depth, and time.

Primary Depth Series

Prior to alteration of sample design, the NGMCS study sought to compare transects in the Eastern, Central and Western Planning regions. Sampling would span three years, 1983-85, allowing a minimal time-series study. Fiscal constraints limited sampling to only two seasons, spring and fall, for a minimal seasonal study. Pequegnat's (1983a) depth zones were used to partition the transects by depth. The depths of stations is shown in table 3.2. Pequegnat's Lower Abyssal Zone did not exist in the study area. Since there was no replication of stations within depth zones, inter-zone differences could not be confidently ascribed to scheme of zonation.

Table 3.2. Main Depth Series Stations Based on Pequegnat Zones.

Depth Series	**Pequegnat Zone**	**Station Depth**
1 Series Stations	Shelf-Slope Transition 150-450 m	Approx. 300 m
2 Series Stations	Archibental Horizon A 475-750 m	Approx. 600 m
3 Series Stations	Archibental Horizon B 775-950 m	Approx. 800 m
4 Series Stations	Upper Abyssal 975-2250 m	Approx. 1250 m
5 Series Stations	Mesoabyssal Horizon C 2275-2700 m	Approx. 2500 m

Time Series

It is common for offshore surveys to encounter difficulties in maintaining a consistent time series of samples due to vessel and weather related problems. This problem is obvious in the NGMCS Study (Table 3.3). Only the Central Transect was repeatedly sampled on three occasions, fall 83 (Cruise I), fall 84 (Cruise II), and spring

84 (III). Subsequently in the final analysis only these fall 83 and 84 samples were compared to test inter-annual variation and the spring contrasted to the fall as seasonal variation. Both must be considered extremely weak tests which grossly under replicate season and years.

The Eastern and Western Transects were sampled twice to a certain extent, but the objectives and station placement were different on the separate cruises. When initially sampled in the spring of 84 during Cruise II, the Eastern and Western Transects consisted of the same 5 Pequegnat depth zone stations used at the Central transect during Cruise I and Cruise II. However, following the second cruise, the program objective began to drift. Western and Eastern transects were not re-sampled until the spring of 85 (Cruise IV Eastern only) and one month later (Cruise V Western-Central only). By that time, additional design-biased reexamination of the Pequegnat depth zones was no longer viewed as appropriate and along isobath sampling was preferred.

Table 3.3. Timing of Sampling of Primary and Auxiliary Stations

	Western	**Central**	**Eastern**
Primary Stations		Cruise I Fall 83	
	Cruise II Spring 84	Cruise II Spring 84	Cruise II Spring 84
		Cruise III Fall 84	
			Cruise IV Spring 85
	Cruise V		
Ancillary Stations		Cruise III Fall 84	
			Cruise IV Spring 85
	Cruise V Spring 85	Cruise V	

NGMCS Methodology

The basic field methods are presented here. Sample processing methods are discussed in conjunction with each if the faunal size groups. The NGMCS study employed a Neil-Brown Mark II CTD with a 12 bottle rosette sampler for water and a 25 cm beam path Sea Tech transmissometer. A pair of yoked box corers were used. These were described as Gray-O'Hara modification J&O box corers with a 24.5 cm x 24.5 cm bite in the NGMCS report (Gallaway 1989). Subsequently (Boland and Rowe 1991) applied the name Gulf of Mexico (GOMEX) corer, giving the dimensions as 25 cm x 25 cm The core samples were partitioned by the use of cylindrical core tubes (Figure 3.3). During Cruise I only six 3.5 cm diameter tubes were fixed in the central portion of the box. On subsequent cruises the tubes were moved to an edge. Four of tubes were allocated to meiofauna analysis with a 63 µm sieve. The contents of the box cores, exclusive of the core tubes, was sieved at 300 µm for macrofauna. After counting, biomass was estimated from counts using conversion factors in Faubel (1982) and Rowe et al.(1974). Megafauna were collected with a 9-m semiballoon otter trawl equipped with 60 cm doors and a 3.8 cm stretch mesh net and 1.3 cm mesh cod end liner. Photography was carried out with a Edgerton-design 35 mm camera drifted above bottom.

General NGMCS Results

The specific results of the NGMCS study will be considered in the following sections as the results of reexaminations are presented. As a very brief review, the primary conclusions were.

- Macrofauna diversity is high but lower than in the Atlantic. This conclusion was not supported by reanalysis.
- Macrofauna diversity lacks a deep maximum. This conclusion was supported by reanalysis.
- Macrofauna biomass is lower than the Atlantic and is supportive of the Rowe and Menzel (1971) designation of the Gulf as an oligotrophic region. This conclusion was not supported by reanalysis.
- Meiofauna biomass is very high. This conclusion could not be reanalyzed.
- ANOVA at the species level reveal few differences transect to transect and even depth to depth. Reanalysis confirmed this conclusion.
- The Pequegnat zonation scheme was considered valid. This conclusion was inconsistent with ANOVA results and to be subjective on reanalysis.
- Unique systems exist in the form of chemosynthetic communities. This discovery can be considered the major contribution of the project.

3.2.3 Atlantic Continental Slope and Rise: a Comparative Study.

The primary studies upon which to base comparisons of the Pequegnat and NGMCS results are the parallel studies supported on the US Atlantic coast by MMS, ACSAR). The most extensive summary of results are given by Maciolek et al. (1987). The Atlantic Studies considered for comparison consist of three separate efforts carried out by the same organizations and people. These consist of a Northern, Middle, and Southern cross coast series. The Northern and Southern were traditional descriptive surveys. The Middle Series were carried out in this same mode, but specifically anticipated deepwater development at a specific site on the 2000 m isobath. Therefore, the Middle series sampled bracketed a specific location.

Inter-study comparisons are always problematic, and there are four primary differences between the NGMCS study and the Atlantic series which will cast doubt upon results.

- Different Sampling Device - The Atlantic Studies employed a partitioned 0.25 m^2 box core similar to the NELS Hessler design and devoted 0.09 m^2 of sample to macrofauna. The NGMCS Study used 0.06 m^2 GOM cores with two replicates taken in tandem. From that, 0.0569 m^2 (Cruise I) and 0.0475 m^2 (Cruises II-IV) were devoted to macrofauna from each replicate.
- Different Experience/Expertise - The Atlantic studies benefited from long history of macrofauna studies centered at Woods Hole, especially experience in sorting and identification. The primary deep experience in the NGMCS Study resided w/ Willis Pequegnat whose experience lay in megafuana.

- <u>Different Depths of Sampling</u> - The Atlantic design did not draw upon prior zonation schemes, and samples were generally collected at 500 m depth intervals (500, 1000, 1500, 2000 , 2500, 3000, and 3500 m). The NGMCS study based sample placement upon a prior zonation scheme and sampled in the center of these zones (350, 600, 850, 1400, and 2500 m).
- <u>Longer-term Context</u>. The Atlantic studies have been well reported in the peer reviewed literature while the comparable data from the NGMCS Study results have not. As a result, the data base for the Atlantic studies has been progressively refined during the production of publications, while the NGMCS data base remained little used.

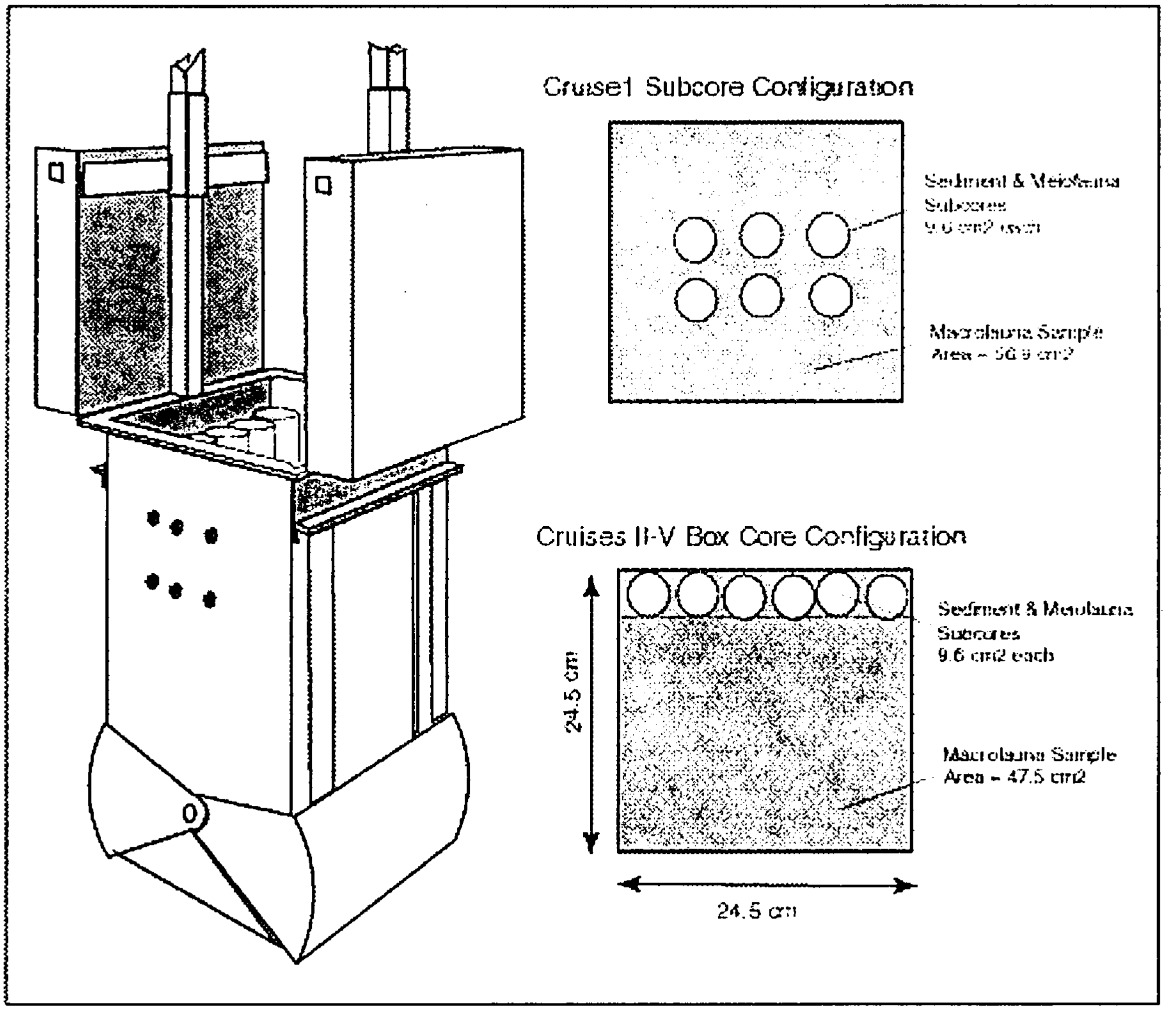


Figure 3.3. Box Corer and Arrangement of Subcores Employed in NGMCS Study.

3.2.4 Problems of Sampling Effort

Patterns of diversity and distribution seen in samples from the deep sea are extremely subject to distortions imposed by sampling. Such distortions are especially prevalent when there are faunal gradients and sampling effort along those gradients is unequal. Sampling gaps and unevenness can produce false indications of boundaries. Therefore, it is important to review the actual bathymetric sampling effort.

Neither Pequegnat or the NGMCS Study sampled equally along the depth gradient. Pequegnat's sampling (Figure 3.1) was most concentrated above 1500 m. Below that, most depths (in 100 m intervals) were sampled once, twice, or not at all. The 3000 m to 3100 m interval was sampled with the same intensity as the upper zones. Initially, the NGMCS study (Figure 3.2) accepted a pattern of zonation proposed by Pequegnat and selected sample depth accordingly. During the course of that study an effort was made to modify the sampling design so that Pequegnat's zones could be tested. In spite of these changes, in the end sampling was focused above 1500 m with unequal sampling within zones, and the region between 1500 and 1800 m left un-sampled.

Several artifacts can be expected from the decrease in sampling with depth and the gap in intensity between 1500-2000 m First, species richness below 1000 m will be underestimated relative to the upper region when depth patterns are observed. Second, faunal dissimilarity between the upper and lower slope will be exaggerated since more rare species will be collected in the upper region. Third, the homogeneity of fauna in the deeper region will be exaggerated. Fourth, gradients will appear to be split with one set of values above 1000 m and another below 2500 m.

3.3 Physical Environment of Northern Gulf of Mexico

The purpose of this chapter is to present a general picture of thermohaline density and dissolved oxygen in the Gulf I of Mexico. Both of these are important in division of the legally defined deep sea (200 m and deeper) into an upper zone which experiences fluctuations (200 to 1000 m) and a deeper more consistent zone. The Pequegnat studies included only cursory physical sampling, depending on the physical oceanography program at Texas A&M to provide a general oceanographic context. Consistent with MMS research stipulations, the NGMCS study included hydrocasts, but those data provide only a narrow time frame. Therefore, the profile database of the National Oceanographic Data Center was accessed using the trial data search system GOODBASE under development at Scripps Oceanographic Institution.

When hydrocasts were taken by the Pequegnat program they employed the methods recommended by the Naval Hydrographic Office at that time. Water was collected in reversing nisken bottles set at fixed sampling intervals most appropriate for upper ocean studies. Temperature and depth were determined from protected and unprotected reversing thermometers. Salinity and oxygen were determined by appropriate wet chemistry titration. Consistent with the techniques of that time, the NGMCS took hydrocasts with a Neil-Brown Mark III CTD equipped with a twelve bottle rosette sampler and a twenty five centimeter beam Sea Tech transmissometer. Oxygen was measured by wet chemistry titration. The data reported in the GOODBASE searches are limited to bottle samples.

Thermohaline Density

The density structure of the ocean is of fundamental importance in separating the deep sea from the shallower environment. The division into a low density upper and high density lower environment is due to solar heating and downward momentum transfer. As the result of these physical causes of the two layers, the deep environment contrasts with the upper in several important ways. Its is extremely low light, almost uniformly cold, almost uniformly of high salinity, relatively isolated from wind driven water movement, and dependent upon long-distance slow transport for oxygen. Many oceanographers would probably put the start of this deep zone, marked by isolation from the upper ocean, at about 1000 m. This is the approximate depth at which the permanent pycnocline (or the associated thermocline and halocline) become relatively constant. Since the legally defined deep sea begins at 200 m, it seems physically appropriate to treat the 200-1000 m range as a separate region.

The important point arising from examination of the temperature and salinity plots of the Gulf of Mexico (Figures 2.1 and 2.2) is that the depth of the permanent thermocline and halocline are quite variable through time. The "text book" notion that the permanent thermocline is a fixed feature is a product of limited sampling and too much simplification. It is now understood that mesoscale events such as eddies and storms cause temporary fluctuations of a few hundred meters. These displacements are of such a magnitude that the bottom at 500 m may experience a temperature change of more than 5°C. independent of seasonal heating and cooling. It is not known if such a shift has direct biological consequences, but it must alter the stability of gas hydrates and thereby place some role in the distribution of hydrate-based systems.

A characteristic feature of the thermohaline profile of the Gulf of Mexico is the stability below 1600 m. The deep Gulf is filled through the straits of Yucatan. The sill depth effectively isolates the Gulf from the colder bottom waters of the Atlantic and Caribbean. This homogeneity may have major effects on water movement. In the open ocean water density usually decreases all the way to the deepest part of the bottom. This vertical stratification, although slight, is sufficient to oppose vertical transport of water, solutes, and momentum. Without such deep stratification in the Gulf, vertical transport is not opposed. One basic consequence is that the deep Gulf water is well mixed with an estimated residency time of only about 100 years (Chan and Welsh, per. comm.). From the perspective of management, plumes and bottom water movement may be different in the Gulf than in more typical deep regions.

Pequegnat (1983a) felt that the Gulf Loop and associated eddies must play some role in regional deep ecology, even though this physical system was poorly understood at that time. Accordingly, he proposed that a gradient of physical energy existed with a low energy "Tranquil" bottom in the west and a high energy "Active" bottom in the east. The primary cause was the presence of deep currents underlying the more easterly Gulf Loop.

Oxygen

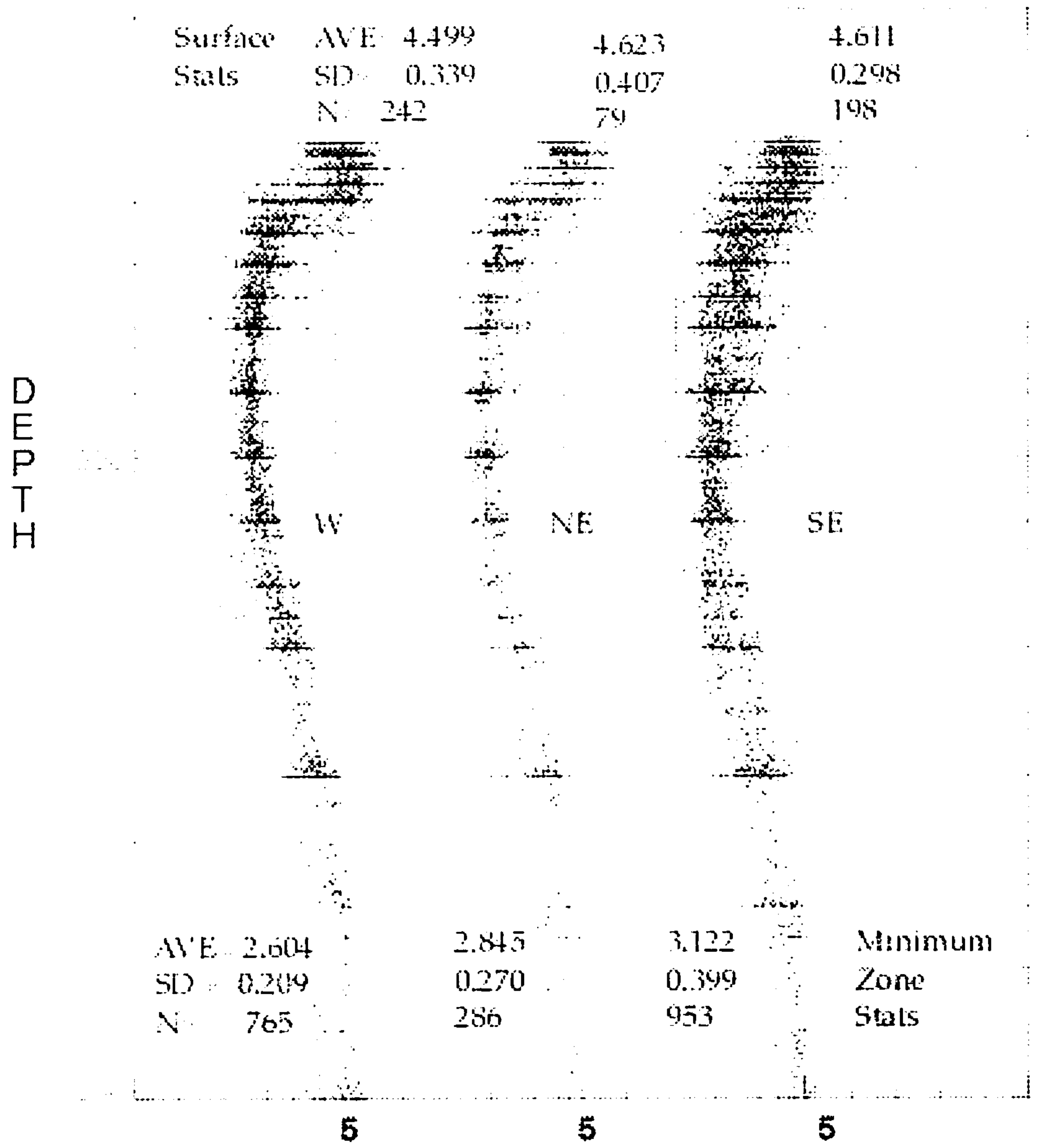
Although the juncture of the upper ocean and lower ocean is usually marked by an oxygen minimum, more pronounced in the Pacific than the Atlantic (Figure 2.3), it is usually not considered a physiologically important feature. It should, however, be important in a management context where discharges are an operational or accidental possibility. Any discharge released into the oxygen minimum might contribute to local hypoxia or anoxia. As a partial product of the physics that create the permanent thermocline, the oxygen minimum shows some of the same features as the thermohaline profile (Figure 3.4). From the scatter of archived data it is seen that the Gulf has an oxygen minimum lying between 300 and 520 m. Below this minimum oxygen concentrations are high with some statistical suggestions of an east to west decrease.

A detailed examination of oxygen in the top 1500 m shows indication of regional differences within the minimum zone. This can be seen in simple averages ignoring the structure of the curve (Figure 3.4) and in polynomial fits to the scatter (Figure 3.5). For averages, data above 100 m was compared with data between 100-600 m. The near-surface values ranged from an average of 4.623 to 4.499 ml/L with no significant differences. The lowest values were in the west and may be due to warmer temperature. The averages within the minimum zone ranged from 3.122 to 2.604 ml/L with a consistent trend away from the SE quadrant. The use of a polynomial fit helped illustrate depth differences as well as confirm the concentration patterns seen in the averages. On average, the SE quadrant lying under the Gulf Loop has a deeper (508 m) minimum with a low concentration of 2.970 ml/L. In the NE, where the Gulf Loop is only an intermittent feature, oxygen is slightly less well mixed downward resulting in a shallower minimum (417m) and a lower concentration (2.767 ml/L). Possibly due to a slightly longer residence time, the water in the western Gulf has an almost identical depth of the minimum (405 m), but an even lower concentration (2.517 ml/L).

3.4 General Observations About Fauna

By far the most important result of previous studies of the deep Gulf of Mexico is the compilation of a faunal inventory and the slow gaining of natural history information at the species-level. This review has made no effort to add new information, and repeating of the excellent descriptions in Pequegnat (1983a) or the detailed size-frequency data of NGMCS (Gallaway1989, Gallaway et al.1988) is beyond the projects' scope. As an introduction to that work, this section briefly reports the species-level information in the third annual report of NGMCS, then addresses through a reanalysis how many megafauna species there may be. This question arises from the observation that the NGMCS study produced different results than reported by Pequegnat.

A list of Pequegnat megafauna ordered by abundance is given in appendix A. It was derived from tables in Pequegnat (1983a). Appendix B gives a similar list of macrofauna found in the NGMCS study archives. Appendix C gives the macrofauna taxa lists of NGMCS. These lists are intended as a quick reference for persons designing species-level studies in the future.



Oxygen ml/l with Statistics at Surface (0-10m) and Minimum zone (300-500m)

Figure 3.4. Upper Gulf Oxygen Values Obtained from NODC.

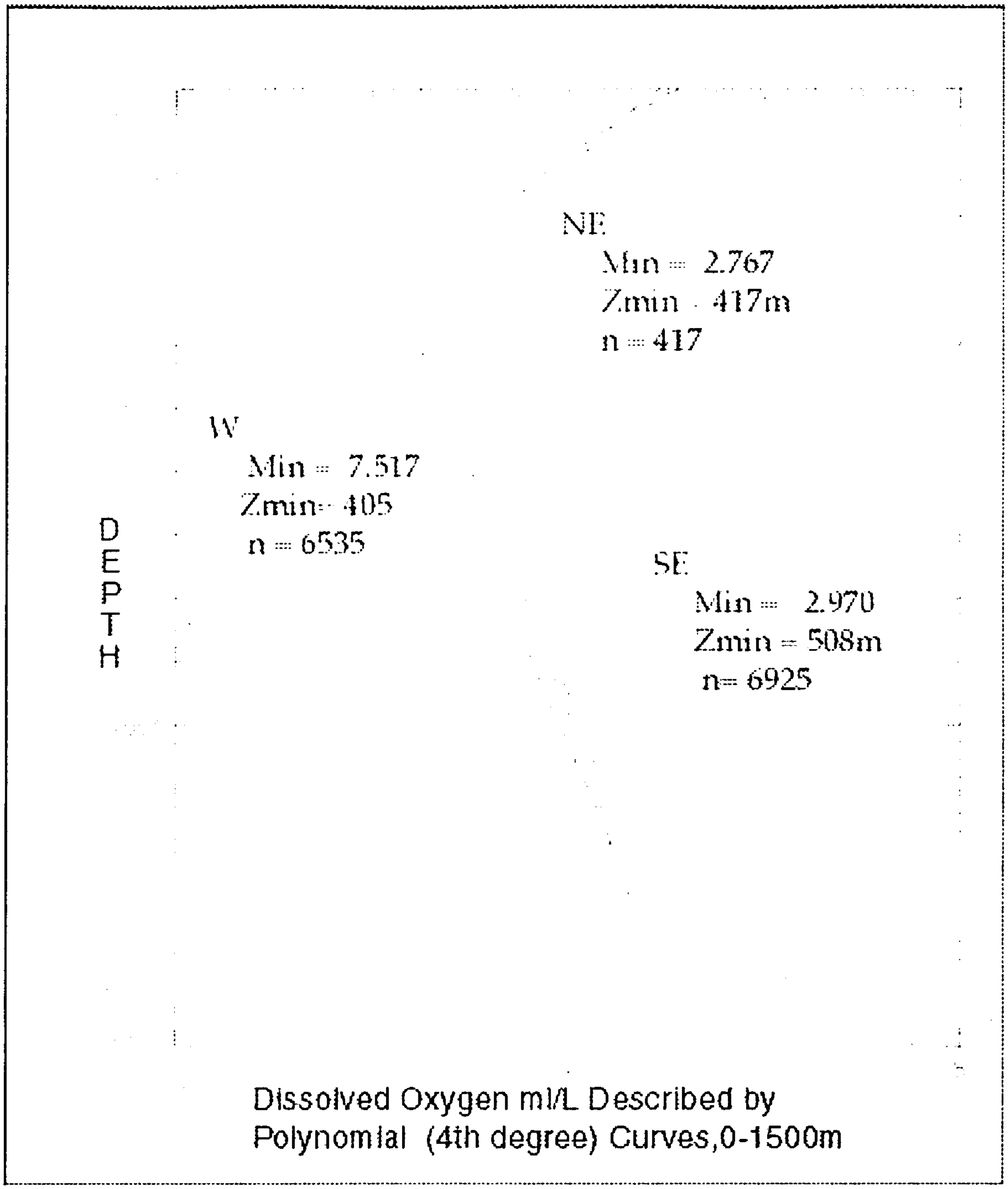


Figure 3.5. Upper Gulf Oxygen Polynomial Curves Based on Fourth Degree Fits

3.4.1 NGMCS Natural History Studies

Gallaway et al.(1988) provides excellent information on the size frequency of trawled fauna and the stomach contents of selected fish. Eleven crustaceans and eight fish were analyzed for size frequency: the crabs *Bathyplax typhla*, *Benthochascon* *schmitti, Rochina crassa;* the shrimp *Benthesicymys bartletti, Glyphocrangon aculeata, Nematocarcinus rotundus, Penaeopsis serrata, Plesionika holtuisi, Stereomastis sculpta;* the squat lobsters *Munida valida, Mundopsis robusta ;* The fish *Dibranchus atlanticus, Nezumia aequa, Bembrops gobiodies, Coelorinchus caribbaeus, Coelorinchus coelorhyncus, Poecilopsetta beani, Gadomus lomgifilis, Chaunax pictus, Chloroptalmus agassizi, Synaphobranchus oregoni, Uropphysis cirratus,*and *Peristedon grayae.* It was concluded and confirmed in reanalysis that no age cohorts could be definitely identified. This was originally attributed to a lack a adequate sampling frequency. Examination of compiled size data, however, showed that most species had size truncation below 1 or 2 cm in length. It seems more likely that that newly recruited sizes were not retained by the mesh of the trawls. A shift in sampling gear is needed to extend these studies. It was also concluded that a tight correlation between size and weight was evidence against variation between seasons, years, depths, etc. This conclusion should be viewed as tentative, since size at a given age is the appropriate parameter .

3.4.2 Megafauna: How Well Known ?

Since the Pequegnat samples were taken through out the entire Gulf of Mexico over an extended period, that species inventory for megafuana should be the most complete. If the NGMCS megafauna inventory is a subset of the Pequegnat inventory, then it can be concluded that the megafauna is relatively well known. A comparison of the two inventories suggest that many more species may remain to be discovered.

The comparison was based upon simple matching of the species names in one study against the other. The reconstructed Pequegnat database contained 713 invertebrate megafauna taxa and the NGMCS database 544. Fish were excluded due to greater concern over sampling artifacts. Wherever possible changes in genus and species nomenclature were corrected for. When the taxonomic resolution of the studies differed, an informed decision was made as to whether there was an actual match. Generally, if a species-level identification and a genus-level identification had the same genus, similar ranges and somewhat similar abundance, they were considered a match. Identifications to species in both lists were considered valid. All in all, species-level identification predominated, and the subjective judgements had only a minor effect upon the results.

3.4.3 Different Lists of Rare Species

The matching of the two inventories is most informatively considered by rank of abundance. Since the NGMCS study was most consistent in reporting abundance, it was used as the primary study. The results are shown in table 3.4. Abundance was split into five ranges on a somewhat logarithmic basis, species taken in NGMCS more than 1000 times, 100-999 times, 10-99 times, 2 - 9 times, and once. Treating singletons separately placed special emphasis upon the rarest species.

The megafauna inventories of the NGMCS study and Pequegnat overlap to some degree, but NGMCS is not simply a subset of the larger inventory. Of the 544 NGMCS taxa, only 208 were previously reported by Pequegnat. This suggests that the species richness for deep Gulf of Mexico megafauna invertebrates exceeds 1049 species, the sum of the species unique to Pequegnat (505 species), plus the species unique to NGMCS (336 species), plus the species in common (208). The contention that the species inventory is under sampled is reinforced by the abundance-level comparison. For very abundant (1000+ count) species the studies agree closely (89%). Even at abundance down to a count of 100, overlap is still pretty high (73%). However, when rarer species are considered (9 and fewer), the studies report very different inventories.

Table 3.4. Taxa Overlap by Abundance Level in NGMCS and Pequegnat Studies.

ABUNDANCE GROUP Specimen Count	NGMCS TAXA	ALSO IN Pequegnat
1000+	9	8 (89%)
100-999	48	35 (73%)
10-99	116	56 (48%)
2-9	206	67 (33%)
1	165	42 (33%)

While it is easy to explain the low percent of inventory overlap for rarer species as arising from sampling differences, the limited overlap at mid-level (10-99) warrants more attention. It could be caused by a combination of five causes.

- Temporal Variability – There were major changes in faunal composition.
- Regional-Scale Zoogeography - While the most abundant animals are widespread through the whole Gulf, there may be regional subdominant taxa.
- Local-Scale Zoogeography - The two studies may have unknowingly sampled different unique deep habitats.
- Sample Gear Biases - Pequegnat employed a variety of gear, using the epibenthic skimmer the most. The NGMCS study made consistent use of an otter trawl.
- Taxonomic Inconsistency - Identification of species spanned more than twenty years and utilized different experts.

Long-term (decadal) trends in deep-sea faunal composition have not been studied in the western Atlantic or Gulf of Mexico, and changes in methodology would make any attempt to identify such changes from archival data highly dubious. However, major changes in megafauna dominance have been found using similar methods over a period of 10 years (Billet et al. in press). The possible causes of a dramatic shift in holothuroid dominance are now under investigation.

Unfortunately, large-scale zoogeography can not be examined with the data at hand. Pequegnat (1983a) does not report station-level quantitative data, and quantitative summaries do not include geographic data. Given the marked change in bottom geomorphology around the Gulf, some degree of regionalism is to be expected. Similarly, local-scale zoogeography is not easily addressed with the data. There are, however, suggestions that unique habitats were sampled. The NGMCS study seems to have encountered chemosynthetic and sponge-bank communities that Pequegnat did not. The high incidence of sponges (*Polymastia (Radiella) sol*, *Thenea* spp., and *Desmacella* sp.) in only the former study represents evidence of sponge banks. Pequegnat seems to have sampled more often in urchin aggregations that the NGMCS study missed. This is evidenced by the unequal abundance of the epifaunal regular urchins *Plesiodiadema antillarum and Phormasoma placenta*, and the usually infaunal irregular urchin *Brissopsis atlanticus*.

The third possible cause of inventory differences, sampling biases, is hard to evaluate without direct gear comparison. The two studies did produce very different ranks of abundance (Table 3.5). When the twenty most abundant species in each study are compared only four have roughly equal rank in both. Three of these are relatively mobile crustaceans, *Penaeopsis serrata*, *Nematocarcinus rotundus*, *Stereomastis sculpta*, and the fourth a relatively seditary ophiuroid, *Ophiernus adspersus*. If the gear used were grossly dissimilar in collecting bias, the agreement for these species would not be expected. As noted above, the mismatch for sponges and urchins suggests that differences reflect habitats sampled more than gear usage.

Taxonomic inconsistency is a very difficult issue to address. While taxonomists go to great lengths to publish revisions as they are made, this is an arcane literature to the ecologist. Even more complex than application of the correct name, is changing expertise. Not only are different experts used, but the same expert has changes in opinion over many years of experience. In general, the megafauna of the NGMCS study should have been fairly consistently identified by the same experts or criteria used in the Pequegnat studies. This is especially the case for the crustaceans, molluscs, and some echinoderms. In other taxa there is certainly reason to expect taxonomic inconsistency. The ophiuroids are a prime example. During the Pequegnat studies the abundant ophiuroids were identified ad hoc by various people and never made the focused study of one expert. In the NGMCS study, Dr. Gordon Hendler of the Los Angeles County Museum examined voucher specimens. Pequegnat reported a dominant species *Ophiomusium planum*, but NGMCS did not report such a species at all among its many ophiuroids.

Table 3.5. Rank Comparison of Dominant Megafauna in NGMCS and Pequegnat. Bold face indicates roughly similar ranks; ? indicates unresolved taxonomic confusion, and > indicates only a possible genus-level match.

DOMINANT SPECIES	RANK Pequegnat Study	RANK in NGMCS Study
Aega sp.	?	1
Desmacella sp.	?	15
Plesiodiadema antillarum	1	67
Brissopsis atlanticus	2	332
Penaeopsis serrata	**3**	**3**
Phormasoma placenta	4	139
Parapagurus sp.	5	>55
Nematocarcinus rotundus	**6**	**2**
Sytellaspsis pellucida	7	122

Stereomastis sculpta	**8**	**12**
Gemmula periscelida	9	349
Ophiomusium planum	10	>91
Benthodytes typica	12	55
Glyphocrangon nobilis	**15**	**18**
Ophiernus adspersus	**16**	**9**
Benthesicymus bartletti	17	39
Pasipaea merriami	18	?
Mesothuria lactea	20	34
Bathyplex typha	21	4
Glyphocrangon aculeata	31	21
Plesionika holthuisi	44	44
Benthochascon schmitti	61	7
Munida valida	63	6
Polymastia sol	124	13
Uroptychus nitidus	146	19
Ophiocamax fasciculata	172	11
Chrysogorgia agassizii	287	8
Thenea sp.	290	14
Trilasmis kaemferi inaequilaterale	306	17
Amphilepis ingolfi	>316	10

3.4.4 Specific Taxa Considered

The Enigmatic Holothuroid *Peniagone*

In the photosurveys of the NGMCS study, the holothuroid genus *Peniagone* was the most abundant animal encountered. Oddly, no specimens at all were collected by trawling. In order to explain this dramatic difference in results, the literature on the genus and museum records were consulted. *Peniagone* (the name meaning spawn of poverty) is frequently dominant in trawl samples and photosurveys at the base of the continental slope (below 2500 m) in the Atlantic and Pacific. Pequegnat (1983a) did sample a few badly damaged specimens of this genus during his earlier sampling, and they were variously identified as *P. islanticus*, *P. azorica,* and *Scotoanassa* sp. (a closely related genus).

Peniagone is the most species rich genus in the deep-sea holothuroid order Elasipoda. Like other elasipods, it can be considered an indicator of deep-sea conditions. The Gulf of Mexico specimens are best identified as *P. islandica* on the basis of body morphology and spicules. However, species identification in this group is problematic, at best. Whatever the exact species, the Gulf *Peniagone* fits into the Vitrea Group. This group includes at least ten species from all over the ocean that are intermediate in morphology between animals that are known to be primarily pelagic (such as *P. diaphana*) or benthic (such as *P. azorica*). Whether swimming near bottom with highly modified podia or crawling on bottom with more traditional tube feet

Linked with the interesting range of foraging behaviors for this sediment feeding genus is the peculiar habit of forming dense aggregates, mounds of several hundred specimens per square meter (Menzies et al.1973). Such extreme aggregation was not noted from NGMCS sampling, rather there appeared to be larger patches. Actual tests of aggregation were not presented, but at Central Transect station 4 aggregates persisting for a distance of over 200 m. Some *Peniagone* appear to be highly mobile and capable of finding and exploiting regions of high detritus influx. Such influx may reflect localized redeposition of material suspended by bottom currents. This adds to the suggestion that special topographic habitats may be common at mid depths in the northern Gulf of Mexico.

3.5 Zonation

This reanalysis seeks to make a point about the management utility of zones and then determine the nature of change most appropriate to management. A substantial amount of discussion in the reports of the NGMCS study addresses the issue of the validity of the "zone concept". Actually, delineating faunal zones is not a concept, it is a convenient means of summarizing complex distribution data. Its very real management value lies in that convenience, not an unproven list of causes.

3.5.1 The Zonation Controversy

The basic points are straight forward. Many deep benthic species do show distinct depth ranges, and it was popular during the early years of oceanography to define particular depth zones based on subjective use of scant biological data and better-known physical patterns. As more biological data were obtained and multivariate analysis became popular questions of the validity, homogeneity, and cause of apparent zones arose. Unfortunately, the added objectivity of the analyses was often outweighed by unrecognized biases, making some of the debate unproductive.

In the 1970's the discussion about depth zones, which was largely unpublished, had centered on three different opinions. The most traditional view was that faunistically homogenous zones were present with sharp breaks (much like the tree line on mountains) associated with certain oceanographic conditions. Pequegnat held this view. A much more complex view was that homogenous and sharply delineated zones were the geographic manifestation of integrated ecological communities. Boundaries did not have to coincide with oceanographic features in this scheme. The third view, as represented by the review of Carney et al.(1983), was that homogenous zones and distinct boundaries may exist in places, but that subjectivity and analytical biases play too great a role in the recognition of such zones. Many analyses, especially cluster analysis, break continuous gradients into artificial zones. Rather than constantly seeking refinement of sampling and analysis, the more productive course of research would be to study and understand distributions at the species level.

The NGMCS study was designed to test the repeatability of Pequegnat's zones rather than the possibility that they were sampling artifacts. This criticism was voiced by the scientific advisor board of the project and efforts made to remedy the situation. Sampling density was increased on the central transect, but not in a zonation neutral manner. The sampling repeated the Pequegnat zonation scheme at a finer depth resolution. Then stations were added along isobaths. However, the finding of faunal homogeneity along isobaths was not a definitive proof of the validity of the zonation scheme.

3.5.2 NGMCS Analyses of Zones

The NGMCS study examined faunal zones by a variety of methods: cluster analysis of similarity, coincidence of range limits, and by analyses of variance. All results were interpreted to be supportive of the Pequegnat zonation scheme. However, as stressed throughout this report, that conclusion was built into the design. In actuality, the only thing proven was that fauna was not homogeneous with depth.

3.5.3 Consideration of a Null Model for Restricted Depth Zones

If fauna is distributed within homogenous zones that subdivide the continental slope, then species should show restricted depth ranges. A standard part of the education of ecologists is development of an appreciation for non-random patterns of distribution. Implicitly, we test all observed patterns against randomness, which is now often called a null model. Pineda (1993) is now exploring the null models of depth zonation. When his work is complete, there will be a much better basis by which to judge the natural of faunal change with dept.

3.6 Geographic Differences Tested by NGMCS ANOVA

The most extensive analysis of pattern undertaken in the NGMCS study was a series of four analyses of variance, ANOVA. Species-by-species, using 61 most abundant animals, 244 analyses (61 spp. X 4 ANOVA) were conducted. Together, these ANOVA tested 60 contrasts for a total of 3660 tests. (61spp. X 60 tests). A careful consideration of these analyses is appropriate since they were the primary basis for five out of seven primary conclusions of the NGMCS study (see Section 11).

1. There were significant east to west variations.
2. There were no significant inter year variations.
3. There were significant seasonal variations.
4. There were significant depth variations.
5. There were no significant differences within depth zones (note conflict with 1 above).

On reevaluation it was found that the inconsistency of sampling caused many of these tests to have uneven samples and a resulting low power. In this section these multiple tests are briefly reviewed. In reviewing and discussing the very extensive use of analyses of variance in the NGMCS study it is most informative to consider something of an ideal usage

3.6.1 Consideration of an Ideal Case of ANOVA Use

Analyses of Variance (ANOVA) have a special high standing as a means of designing studies, carrying out sampling, and testing hypothesis. While they may not be the best way in which to study the natural environment and are often misused in ecology. Green (1979) strongly endorsed their use for reasons amplified by Carney (1987). The formality of ANOVA forces the user to be specific about intent and consistency in sampling.

The failure to maintain a consistent sampling program through time resulted in an inability to carry out a simple balanced analysis using all samples to assess the apparent influence of transect (3 levels), depth (5 level), season(2 levels), year (3 levels), replication (3 to 6 levels) and the interaction terms. The four ANOVA actually carried out were piecemeal unbalanced comparisons. The approach used was that of examining all possible linear independent effects (orthogonal contrasts).

Transect studies of ocean fauna typically have hypotheses testing the apparent importance of three factors: transect location, depth along transect, and time. It is recognized that many factors may be at play in creating location , depth, and time effects. However, these are usually too poorly known to be used a priori to select sample sites suitable to specifically test them. When sampling is undertaken, a series of transect locations is selected, then stations marked at fixed depths. These stations are then sampled with some fixed level of replication at seasonal intervals to create a time series. This fixed station approach may not offer the statistical advantages of randomization within quadrats employed terrestrially. However, its logistic simplicity has made it a traditional offshore approach.

The appropriate null hypotheses would be:

H_1 Faunal parameters are homogenous across transects at different locations.

H_2 Faunal parameters are homogenous across different depths.

H_3 Faunal parameters are homogenous across the time of sampling.

H_4 There are no interactions of transect, depth, and time (actually multiple hypotheses).

3.6.2 ANOVA of Macrofauna in the NGMCS Study

Macrofauna data were culled of nematodes, harpaticoids, and species-level groups with fewer than 90 specimens. This produced 60 taxa to which *Vesicomya* sp. was added as a sixty first due to an interest in the distribution of this apparent chemosynthetic form. Four main ANOVA were run separately for each species for a total of 244 main analyses. Within these main analyses a total of 60 contrasts were tested on each species for a total of 3660 tests. Each test had an explicit null hypotheses. In effect, there were approximately ten times more hypotheses than there were grab samples. There may be nothing wrong with this extreme degree of "data fishing", and it could have lead to unexpected insight. However, in the case of the NGMCS Study it did not produce such insight, and the design used did not allow simple and powerful testing of the simple hypotheses about location, depth, and time.

ANOVA # 1 Location and Time Differences

Only the Central Transect had a time series of samples and was suitable for seeking seasonal or cruise effects. The primary regional hypothesis (H1) was a null statement of no difference in faunal abundance between all three transects. Logically, this primary regional hypothesis gives rise to three pair-wise comparisons, W vs C, C vs E, and W vs E, but only one can be independent. The contrast of C and W was taken as the second regional hypothesis.

The list of ANOVA # 1 hypotheses is quite complex (Table 3.6). Within the five depth stations of each transect, the primary regional hypothesis can logically be divided into a series of depth and depth group versus depth and depth group comparisons. Regional differences were tested twice, seasonal differences once, and depth differences twenty times. Again, only four comparisons among the 5 depths meet the requirement of independence. These are the shallowest versus all the deeper in each transect (H2,H7, and H12); the two shallowest versus the three deeper (H3,H8, and H13); the second compared to the third (H4,H9, and H14), and finally, the deepest compared to the next shallower (H5,H10,H15).

The results of ANOVA#1 showed only a modest number of significant differences. Of the sixty one species analyzed separately only twelve species showed significant regional variation among transects. Therefore, within the limitations of this analysis, there were few strong regional differences demonstrated. The conclusion that regional differences exist may be correct, but it is only weakly supported by this series of tests. The time-series design for yearly and seasonal sampling was extremely weak and limited only to the Central transect. Of the sixty one species sampled, only five showed significant spring-fall variation. The conclusion that seasonality exists may be correct, but it is ill-supported by this testing. Two showed significant inter-annual variation The weakness of the design makes any statement of dubious value. Even though two species did show significant effects, the study concluded that inter-annual variation was not significant.

It is difficult to see the utility of the depth contrasts undertaken in the first ANOVA due to the confusion of the orthogonal contrasts method and the very inconsistent level of replication. In the Western transect which had only 3 replicates per station in Cruise I, the results of 61 separate species ANOVA could not reject a hypothesis of faunal homogeneity (no depth restriction) except for the two polychaetes *Litocorsa antenna* and *Phole sp.* C. It is to be suspected that the results are due to limited sampling. At the better sampled Eastern and Central transects, there were more definitive results, but again, the meaning is obscure. When the shallowest stations (series 1) were compared to all the deeper (series 2,3,4 and 5 combined) only 10 of 61 species show significant differences across these dramatic depth boundaries. Are the boundaries not distinct or was the comparison too unbalanced to be informative? The latter is suspected. The largest number of species showing significance differences were found when the most samples and most balance number of contrasts are compared.

Table 3.6. Hypotheses and Applicable Samples for ANOVA #1.

Hypothesis	**Applicable Transects**	**Type of Question**	**Statement of Hypothesis**
H_1:	E & W	Regional	Abundance Eastern = Western+Central
H_6:	C & W	Regional	Abundance Central = Western
H_{11}	C	Seasonal	Abundance fall 83 = fall 84.
H_2:	E	Depth	Abundance E1 = E2 through E5 combined
H_3:	E	Depth	Abundance E1 & E2 = E3 through E5
H_4	E	Depth	Abundance E2 = E3
H_5	E	Depth	Abundance E4 = E5
H_7	W	Depth	Abundance W1 = W2 throughW5 combined
H_8	W	Depth	Abundance W1 & W2 = W3 throughW5
H_9	W	Depth	Abundance W2 = W3
H_{10}	W	Depth	Abundance W4 = W5
H_{12}	Cruise II C	Depth	Abundance C1 = C2 through C5 combined
H_{13}	Cruise II C	Depth	Abundance C1 & C2 = C3 through C5
H_{14}	Cruise II C	Depth	Abundance C2 = C3
H_{15}	Cruise II C	Depth	Abundance C4 = C5
H_{16}	Cruise III C	Depth	Abundance C1 = C2 through C5 combined
H_{17}	Cruise III C	Depth	Abundance C1 & C2 = C3 through C5
H_{18}	Cruise III C	Depth	Abundance C2 = C3
H_{19}	Cruise III C	Depth	Abundance C4 = C5
H_{20}	Cruise IV C	Depth	Abundance C1 = C2 through C5 combined
H_{21}	Cruise IV C	Depth	Abundance C1 & C2 = C3 through C5
H_{22}	Cruise IV C	Depth	Abundance C2 = C3
H_{23}	Cruise IV C	Depth	Abundance C4 = C5

Of the 12 out of 61 species that showed significant inter-transect differences, the species in each of the two regional contrasts were different (Table 3.7), making it unclear what it means. There may be a hint of higher populations on the Eastern Transect, When East is contrasted to the West, only 5 of 61 species show significant differences, with four more abundant in the East. However, an East to West gradient is less obvious when

C is contrasted to W. The 7 of 61 significantly different species are split four more abundant Central and three more abundant Western.

Table 3.7. Twelve Species Showing Regional Differences and Direction of Abundance Differences Within Transects of ANOVA#1 (ns= not significant).

Species	**Western**	**Central**	**Eastern**
Phole sp C	ns	Less	More
Ceratocephalis oculata	ns	Less	More
Malletia sp. B	ns	Less	More
Angulorostrum sp. A	ns	Less	More
Apseudidae	ns	More	Less
Tachtrypanes sp.A	Less	More	ns
Maladne sp. A	Less	More	ns
Prionospio ehlersi	Less	More	ns
Prochelator sp.202	Less	More	ns
Litocorsa antennata	More	Less	ns
Lumbrinerides dayi	More	Less	ns
Ischnomesus sp.208	More	Less	ns

ANOVA#2 Depth Again

ANOVA two was intended as a statistically rigorous examination of the Pequegnat (1983a) scheme of five faunal zones which determined the depth placement of the primary stations. In fall of 1984, 11 stations were sampled on the Central Transect, the original five plus an additional six to fill in the gaps. Unfortunately, the resulting gap filling did not correct for the progressively wider intervals of the original five stations. The stations still had greatly varying intervals, 200 m or less above 1200 m and about 500 m below that depth.

The hypotheses of ANOVA #2 dealt only with abundance on the Central Transect where finer scale sampling took place on Cruise III. There were ten variations of the same hypothesis of no difference in abundance. The variants of the hypothesis treated different depth comparisons. First, a shallower group of stations were contrasted to a deeper, and then those two groups teased apart in various combinations of ones, twos, and fours. These versions of the same hypotheses are presented along with the results and the stations combined in the contrasts are shown in table 3.8.

Only 10 out of 61 species were significant across the major faunal transition, shallower versus deeper contrast As with the other ANOVA, interpretation is difficult and the final report avoided conclusions drawn on the results. However, the intent of testing the original zonation scheme was not carried out, and it is unclear what the finer scale sampling accomplished. The one suggestive finding was that there may be a greater change in species between 1021 and 1192m than elsewhere. This might mean that Pequegnat's Archibenthal to Abyssal boundary does mark a depth of greater fauna change.

The possibility of greater faunal change between 1021 and 1192m can be seen in pair-wise contrasts. When the five pair-wise contrasts are sorted out and ordered by depth and interesting pattern is exposed. Most notably, few of the 61 species show any significant difference, from none to six, depending on the particular contrast. The maximum number of six is found at two contrasts , the comparatively narrow depth range between C7 and C8 (1021, 1192m) and the wider range between C2 and C3 (633, 881m). This can be cautiously taken as evidence that the species replacement rate is highest in this 1000 to 1200 m range. The results seem to point to rather uniform change otherwise. This is especially noted for contrasts between four shallower and four deeper, where each had 8 of 61 species being significantly different.

Table 3.8. Ten ANOVA#2 Depth Contrast Hypotheses Tested on Central Transect and Results

Hypothesis	Taxa of 61 with Significant Differences	Stations Compared In Depth Order Parentheses Indicate Groupings for Testing
H_1	10/61	(1, 6, 2, 3) vs (7 ,8 ,9 ,4 ,11 ,5 ,12)
H_2	8/61	(1,6) vs (2,3)
H_3	2/61	(1) vs (6)
H_4	6/61	(2) vs (3)
H_5	4/61	(7,8,9,4,11) vs (5,12)
H_6	0/61	(5) vs (12)
H_7	4/61	(7,8,9,4) vs (11)
H_8	7/61	(7, 8) vs (9,4)
H_9	6/61	(7) vs (8)
H_{10}	1/61	(9) vs (4)

ANOVA#3 Variation Across Isobaths in Eastern Gulf

The third set of analyses was similar to the second in that there was a single hypothesis repeated in fifteen variants. The hypothesis tested on each of the sixty one species was of no significant difference in abundance between various parings of stations taken on the Eastern Transect. The hypotheses, the pairings, and the results are presented in Table 3.9. The NGMCS study attempted to phrase some of the fifteen hypotheses as addressing differences in substrate. Since these post hoc hypotheses were not anticipated in the original design, their results were ambiguous.

The results of the third set of ANOVA are as expected. When large numbers of stations at different depths were compared, relatively large numbers of significantly different species (19,15, and 11) were found. The fewer the stations contrasted and the more within isobath the contrast, the fewer significant species. Unfortunately, within isobath is confounded with fewer stations. It should be noted, however, that if the Pequegnat zones were very pronounced, many more of the dominant 61 species should have been significantly different. It appears on the basis of the limited design that few species reflect the zonation scheme.

Table 3.9. Hypotheses, Number of Significant Results, and Stations Contrasted in ANOVA # 3.

Hypothesis	Taxa of 61 with Significant Differences	Eastern Transect Stations Ordered by Depth Parentheses Indicate Groupings for Testing
H_1	19	(1a, 1, 1b, 1c) vs (2, 2b, 2c, 2a, 2d, 2e, 3,3a,3b,3c,3d, 5)
H_2	3	(1a) vs (1,1b,1c)
H_3	1	(1) vs (1b,1c)
H_4	2	(1b) vs (1c)
H_5	11	(2,2b,2c,2a,2d,2e, 3,3a,3b,3c,3d) vs (5)
H_6	15	(2,2b,2c,2a,2d,2e) vs (3,3a,3b,3c,3d)
H_7	2	(2,2b,2c) vs (2a,2d,2e)
H_8	3	(2, 2b) vs (2c)
H_9	1	(2) vs (2b)
H_{10}	6	(2a) vs (2d,2e)
H_{11}	5	(2d) vs (2e)
H_{12}	0	(3,3b) vs (3a,3c,3d)
H_{13}	0	(3) vs (3b)
H_{14}	1	(3a) vs (3c,3d)
H_{15}	1	(3c) vs (3d)

ANOVA#4 Variation Along Isobaths Between the Central and Western Transects

Directed at the ancillary sampling between the Western and Central Transect, these analyses tested 11 orthogonal contrasts and the associated hypotheses. Here again the factors considered in the sampling design, depth and position in isobath were used. However, post hoc factors were also tested. These were sediment type, topography, and presence of seeps. As with ANOVA #3, these post hoc factors had not be sampled for in the design, and the results are ambiguous. An additional problem lay in the fact that the W-C series crosses both depth and position diagonally. The deepest stations lie near the

Central transect, while the shallowest lie near the Western. Depth and position are, thus, confounded. Hypotheses, station contrasts and results are shown in table 3.10.

The results were as expected for depth contrasts. The farther apart stations are, the more the abundance of fauna differs. This would be true for Pequegnat zonation or gradual change. That so few dominant species show this effect suggests that dramatic zonation does not exist. The other contrasts are hard to interpret. Within isobath comparisons and contrasts assumed to test topography, sediments, and seeps, there were from 1 to 8 significantly different taxa. Without proper replication the cause can not be identified.

Table 3.10. Hypotheses, Type of Question Asked, Number of Significant Species, and Samples Contrasted for ANOVA #4.

Hyp.	Nature of Question	Significant Taxa of 61	W-C Stations Ordered by W-E Position & Depth
H_1	Depth	16	(5,1,7,6,8,2,4) vs (9,10,3,11,12)
H_3	Depth	14	(5,1,7,6) vs (8,2, 4)
H_5	Depth	11	(5,1) vs (7,6)
H_6	Isobath~750 m	3	(9,10) vs (3)
H_7	Isobath~750 m	1	(9) vs (10)
H_{10}	Isobath~550 m	8	(8) vs (2,4)
H_{11}	Isobath~550 m	5	(2) vs (4)
H_2	Sediments	6	(5) vs (1)
H_4	Topography	2	(11) vs (12)
H_8	Seep	7	(7, 6) vs (5,1,4,8,2,3,9,11,12)
H_9	Within Seep	6	(7) vs (6)

3.7 Meiofauna

3.7.1 Introduction

The meiofauna results of the NGMCS study are quite interesting and have management relevance if substantiated. Unfortunately, the archived data are reported only on a per station per cruise basis, and not at the sample level. The study reported more than 230,000 specimens in 43 major taxa with 98% consisting of nematodes, harpacticoid copepods, polychaetes, ostracods, kinoryncha, and naupliar crustacean larvae. Mean density was 700 org/10 cm^2 ranging from a low of 200 to a high of 1,100. These values are among the highest reported (Thiel 1983). Initially proposed by Dr. R.

Titgen, the meiofuana component did not address specific hypothesis. Dr. Titgen left the project prior to completion.

3.7.2 Methods

Meiofauna samples were the top 5 cm of sediment in 4 core tubes mounted inside a GOMEX box corer. The tubes were 43.5 cm long and 3.5 cm (also reported as 2 cm) in internal diameter. During the II through IV cruise, these cores were mounted against the wall of the core box, a location subject to washing. During Cruise I they were mounted centrally. The samples were narcotized in isotonic manganese sulfate for 30 min. then fixed with buffered formalin and stained with rose bengal. Sampling effort is shown in table 3.11.

The stations were as for the overall box coring programs. Western, Central, and Eastern regions each had main stations that consisted of a 5 station down-slope transect. Supplemental stations consisted of isobathyal transects of 12 stations each in the Western and Eastern Region. The supplemental stations at the Central region consisted of 7 stations added to the cross slope transect. Biomass was not actually measured, but was based upon published values for similar taxonomic groups. This dependency upon published values was not tested and will not be considered in this reexamination.

Table 3.11. Meiofauna Sampling Effort.

Cruise	WESTERN		CENTRAL		EASTERN	
	Main Stations	Suppl. Stations	Main Stations	Suppl. Stations	Main Stations	Suppl. Stations
I			12 at 5			
II	6 at 5		12 at 5		6 at 5	
III			12 at 5	12 at 7	12 at 4	12 at 12
IV						
V		12 at12				
Stations	**5**	**12**	**5**	**7**	**5**	**12**
Pooled Tubes	**30**	**144**	**180**	**84**	**78**	**144**

3.8 Megafauna Trawl and Photo

3.8.1 Introduction

Megafauna have already been discussed with respect to an estimation of how species rich the group might be (section 6), and how some species contribute to the scheme of bathymetric zonation proposed by Pequegnat (1983a). This section focuses on the remaining topic of density estimates based upon trawling versus those based on photography.

The megafauna data summarized by Pequegnat (1983a) are probably the most extensive study of that size class for any deep ocean region. The Gulf samples are unique with respect to the ninety four skimmer samples that preserved fragile specimens in excellent condition. The taxonomic detail devoted to the material was also excellent. This same care was expended upon the megafauna of the NGMCS. Sampling of megafauna by trawl in the NGMCS study followed essentially the same design as box core sampling, but did not replicate within stations. As a result there was a total of 58 samples (Table 3.12).

Table 3.12. Executed Trawl Sampling Design

Cruise	WESTERN		CENTRAL		EASTERN	
	Main Stations	Suppl. Stations	Main Stations	Suppl. Stations	Main Stations	Suppl. Stations
I			1 at 5			
II	1 at 5		1 at 5		1 at 5	
III			1 at 5	1 at 6		
IV					1 at 3	1 at 12
V		1 at12				
Stations	5	12	5	6	5	12
Trawls	5	12	15	6	8	12

3.8.2 Photosurvey

During the first cruise of the NGMCS Study, bottom photography was conducted by the Deep Submergence Engineering Group at WHOI under direction of C.M. Young. These initial and subsequent bottom surveys were conducted with a 800 frame Edgerton-type pressure housed 35mm camera and strobe system purchased from Benthos Inc. Initially configured as a "mini Angus System", the camera package was suspended on a hydrowire and kept near a depth 2m above bottom. During Cruise I depth above bottom was determined acoustically on the surface. The pinger on the camera package produced a double ping with the time lag between pings being controlled by an acoustic altimeter on the frame. The "mini Angus" had not previously been used for quantitative biological sampling, and the lack of reference between height and actual photo image proved to be inadequate for the task. For cruises II-V, LGL obtained its own Benthos system modified such that the height information was both telemetered and recorded on the film data recorder. Analysis of the images was conducted by G. Boland with data processing and management by J. Baker.

Sixty surveys were conducted producing a total of 48,000 images. The length of survey was determined by drift rate, ranging from 1500 to 5000 m long. Excluding Cruise I results due to poor altitude control, Each 800 exposure film roll was subsampled employing the method of Cochran(1977). For Cruise II, 100 subsamples were used. This was increased to 200 on subsequent cruises. Images were then projected onto a Houston Instruments DT-11VA digitizer. In addition to general information about the image, six data categories were considered: (1) invertebrates, (2) fishes, (3) man-made items, (4) terrigenous and nearshore material, (5) consolidated material, and (6) lebenspurren. The examination of lebenspurren (tracks, trails, etc.) was conducted only on cruise II and III images. This special analysis employed 2321 images representing about 6569 m^2 of bottom Of the 44,000 images (45 stations) taken after Cruise I, 9,147 (24,590 m^2 of bottom) were analyzed for fauna. Data has been derived for about 20% of the images. The films are archived at LGL Ecological Associates Inc.

3.8.3 Megafaunal Biomass: Two Estimates and Possible Special Habitats

Two means of estimating megafauna biomass exist from the NGMCS Study, bottom photography and trawling. A simple comparison of the two (figure 3.6) produces different results. Trawl sampling reveals a wide range in faunal density estimates. With only eight samples taken below 1000 m, there is not a good basis for establishing depth trends, however there is some indication of a decrease with depth. Distinctly different are the photograph-based data. Total fauna density estimated from photographs tends to be a full order of magnitude greater than trawl estimates. There is also an indication of a very wide biomass range at mid depths (1000-2000 m).

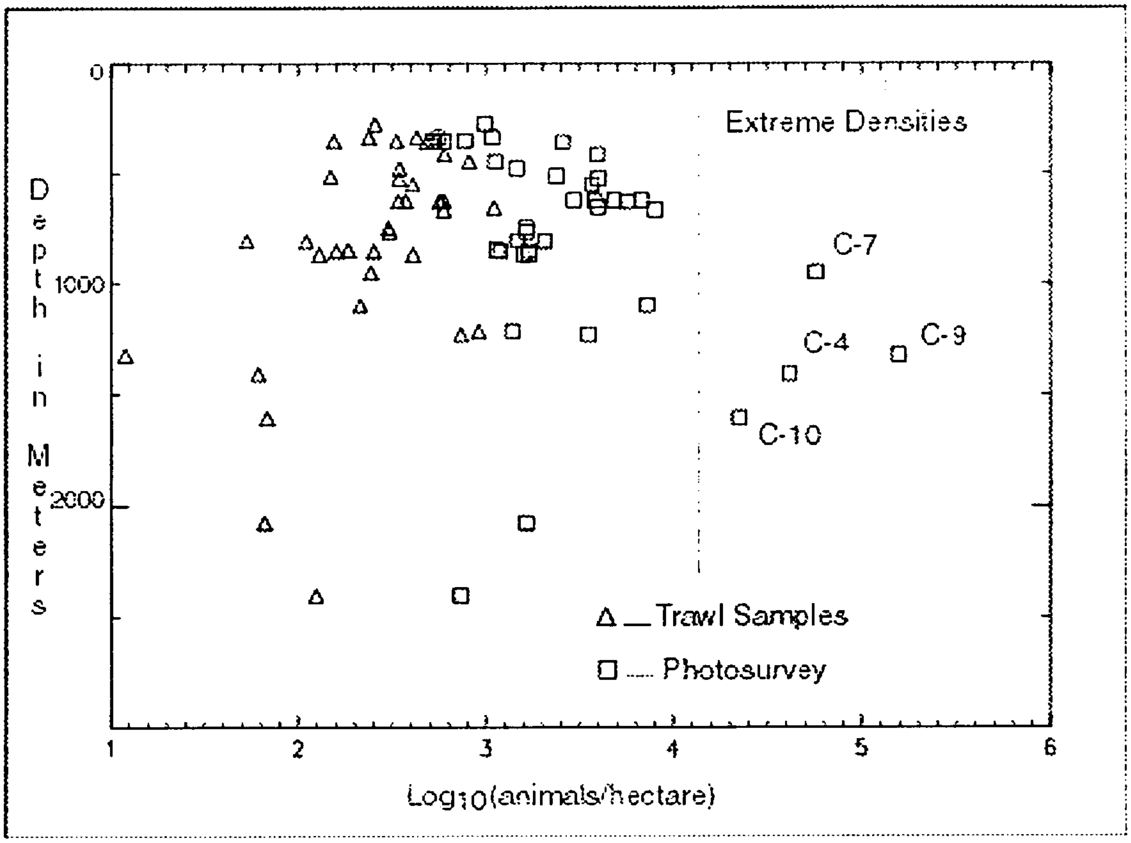


Figure 3.6. Megafauna Density Estimates Based on Photosurvey and Trawling.

On examination, it is found that only four camera stations contribute to the appearance of a mid-depth abundance increase. All in the central transect, each of these four represents a special case:

C-9 Of a reported 156,344 animals/hectare, 154,800 were the patch forming holothuroid *Peniagone.*

C-7 Of a reported 57,151 animals/hectare, 51,566 were bivalves identified as dead and possibly living vesicomyidae at a seep site.

C-4 Of a reported 41,011 animals/hectare 40,212 were again *Peniagone.*

C-10 Of a reported 22,697 animals/ hectare 16,514 were sponges.

In each of these four cases, the high densities were due to unusually high values of a single species or restricted taxa. At C-7 it is clearly associated with proximity to a chemosynthetic system. Although it is suggested in the NGMCS reports that the *Peniagone* stations might be related to seeps as well, this now seems unlikely since *Peniagone* has never been encountered during any of the subsequent manned seep dives. Rather than attempting to explain everything in terms of seeps, it seems more reasonable to consider the possibility of additional unique habitats. For instance, sponge aggregations have been observed during Alvin dives in the Gulf of Mexico below 2000 m. The tremendous topographic complexity of the continental slope in the area of the Central transect could easily give rise to such habitats. The camera survey may have sampled special topographically controlled biota. Possible mechanisms for control might be topographically enhanced and steered bottom currents, recent slumping events, or sediment instability on the slope. In these same proposed special habitats, the trawl may have failed to sample, or have successfully sampled, but then obscured the discrete nature of the habitat as it trawled over a much larger area.

3.9 Macrofauna

Macrofauna have become the primary source of faunal data for soft bottom systems. This is due to the fact that they can be sampled quantitatively, they are sampled coincidentally with the sediment they live in, and they produce sample sizes more appropriate for statistical analysis. Pequegnat (1983a) devoted little attention to this size class. Therefore, the NGMCS constitutes the primary study of deep Gulf of Mexico macrofauna. In the reanalysis undertaken, greatest emphasis was placed on diversity and density estimates since the conclusions of the NGMCS report seem to be in error. There will be no additional discussion of zonation. As stated earlier, the depth of samples was poorly suited to zonation analysis, the ANOVA suggest few macrofauna species show distinct zones, and reanalysis of zonation has shown the limited degree to which macrofauna participate in bathymetric zonation.

3.9.1 Macrofauna Diversity

The NGMCS study concluded that macrofauna diversity in the Gulf of Mexico was less than that of the ASCAR studies of the Atlantic. Additionally, the Gulf shows no depth maximum. The reanalysis of the restructured data archive reported herein, finds that the deep Gulf is markedly more species rich than the western Atlantic, but confirms the lack of a depth maximum.

The reanalysis of species diversity differed from the NGMCS study in three important ways. First, macrofauna-sized nematodes and harpacticoid copepods were included in the reanalysis. This can be expected to add many specimens to a sample count but only two taxa, lowering computed diversity. Second, counts of taxa identified only to genus were also included, increasing computed diversity. Third, the basis of comparison was Hurlbert's (1971) method of rarefaction (Hayek and Buzas 1997). By contrast, the NGMCS calculated information-based diversity (H), excluding nematodes, harpacticoids, and unresolved species.

When the macrofauna sampled on the north eastern Gulf continental slope is compared with previous shelf studies using the data archives of those studies (Carney 1993), the expected pattern of higher diversity with depth is found (Figure 3.7). Even though shelf surveys have typically produced twice to three times the 69,161 specimens of the NGMCS program, they produce only 50% to 60% of the species number. It is reasonable to conclude that diversity maintaining processes in the deep environment are different in some manner from those in shallow water. By extension, the effect of impacting agents in deepwater may not be the same as has been experienced in shallow water. In drawing this conclusion, it must be assumed that diversity differences are not simply an artifact of sieve size, 300 micrometer for deep samples versus the 500 micrometer for shallow.

Two of the shelf studies used for comparison surveyed relatively monotonous soft sediment bottoms and produced remarkably similar results of 700 to 800 macrofauna species. The best documented shelf study in the Gulf of Mexico is the South Texas Baseline Study (STBS), also called the South Texas Outer Continental Slope (STOCS) study in some references. Samples were taken 1976-77 with a $0.1 m^2$ Smith-McIntyre grab and samples sieved at 500 micrometers. An open literature publication provides the main findings (Flint and Rabalais 1981), but the final technical report (Flint and Rabalais 1980) provides the most informative detail. Complementing the STBS study and employing the same basic techniques was the Central Gulf Platform (CGP) Study in 1978-79. CGP samples were taken on the continental shelf off Louisiana in a region of oil and gas activity. The final technical report (Bedinger 1981), is the primary reference. It is interesting to note that on the southwest Florida shelf, which is a patchwork of hard and soft substrates, that higher diversities were encountered. Overall species richness was, however, lower than found on the continental slope. These data came from the Southwest Florida (SWFL) study which began in 1980. A $0.057 m^2$ box corer was used augmented by diver-collected samples, and a 500 micrometer sieve employed.

There has been a great deal of discussion focused upon the fact that the slope and rise macrofauna sampling of Sanders and Hessler found a deep diversity maximum (Rex 1983). This modal pattern is now considered one of several large scale marine and terrestrial diversity gradients where there is a maximum, parabolic diversity patterns. The NGMCS study did not report a diversity maximum. This apparent finding that the Gulf differs from the adjacent Atlantic is quite important. If valid, it would indicate that diversity maintenance in the Gulf may be unique.

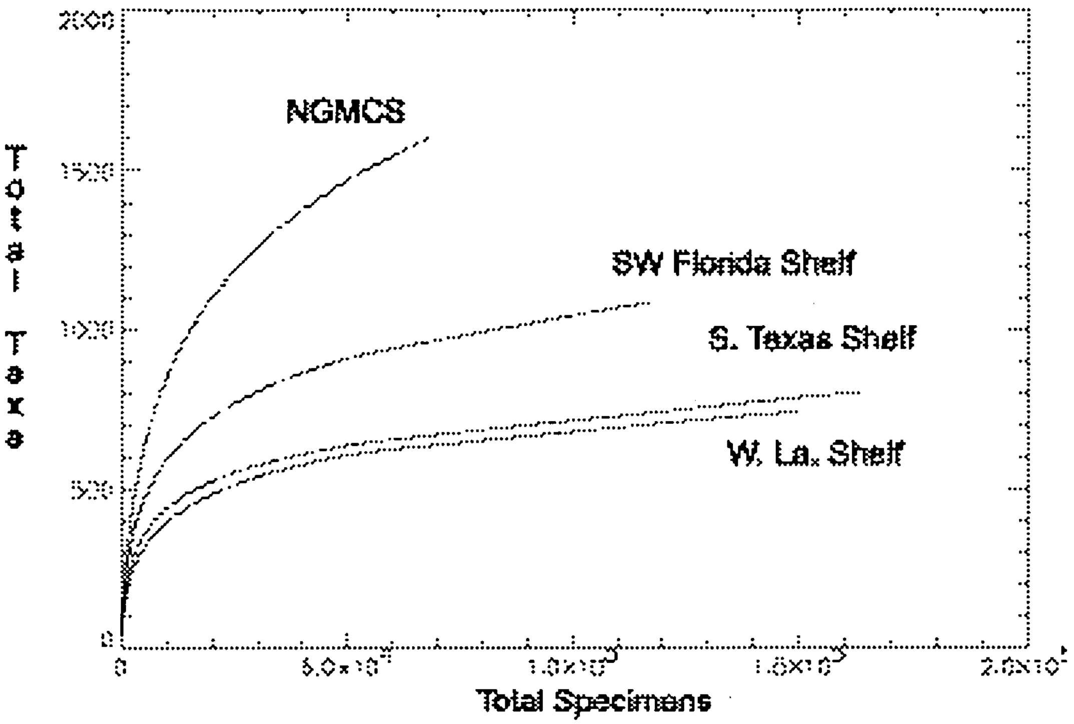


Figure 3.7. Rarefaction Curves Contrasting the Deep Macrofauna with Regional Gulf of Mexico Continental Shelf

Contrasting the NGMCS data archives with those of the ACSAR archives provided a means of checking the apparent absence of parabolic diversity in the Gulf. Since the NGMCS Study employed a 0.06 m^2 sampler rather than the more standard 0.09 m^2 sampler used in the ACSAR program there is an obvious problem of comparisons between unequal sample sizes. Conceptually and computationally complex methods of adjusting for such inequalities are rarefaction and abundification (Hayek and Buzas 1997). For our purposes however, a simpler approach is taken using the ratio taxa:specimens. This value provides a simple appreciation for how species rich a sample is (Figure 3.8).

A regionally complex parabolic diversity pattern is present. In the Southern series species:specimens increase progressively with depth and are maximum at 3000 m. The Middle series has a smaller depth range, but species:specimens increases with depth and appears to be maximum at 2000 m. The Northern series has high values with a maximum at about 2500 m. However at the 1000 m level in that series, there are also some high values which depart from the parabolic pattern.

When the NGMCS archives are considered there is no conspicuous depth trend (Figure 3.9). The apparent uniformity with depth is underscored by the fact that these 326 values have a very well defined mean of 63.57± 23.48 species per sample in spite of the fact that they spanned almost 3000 m of depth. The finding of the NGMCS study of no parabolic depth pattern seems valid. The significance of this is very hard to assess, since we do not know what causes the parabolic pattern. It may be due to an underlying pattern of unusual species depth ranges. Unfortunately, the spacing of samples does not allow for the assessment of this.

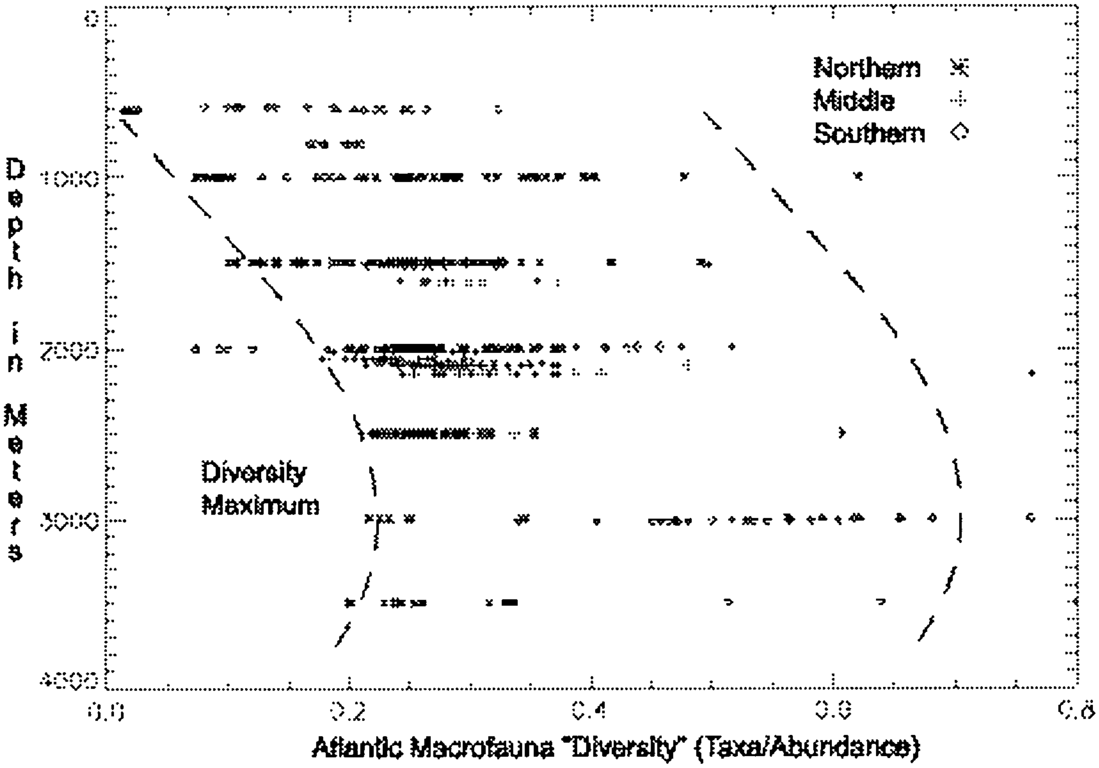


Figure 3.8. Sample-level Diversity Trends in the Western Atlantic.

Highly Diverse Deep Gulf?

A comparison of the total fauna inventory developed during the NGMCS Study with that of the ACSAR study reveals an intriguing pattern (Figure 3.10). The northern Gulf seems to have a more diverse macrofauna than the Atlantic. This is first suggested by the length of the inventories. The three regional components, North, Middle, and South, of the ACSAR Study yielded 1,233, 1,056, and 1,430 taxa respectively. NGMCS study produced 1,613. That these species richness reflect real differences is supported by the total number of specimens collected. Due to its small core size, the NGMCS Study yielded the smallest overall collection of 69,161 specimens. The components of ACSAR yielded appreciably higher values of 108,275, 99,067, and 103,719.

This result suggests that diversity control on the Gulf continental slope may be in some way different than off the East Coast. It is highly management relevant and requires careful evaluation. There are five factors which might cast doubt on the finding. However, when the consequence of each is considered only taxonomic resolution poses a serious problem.

1. Different Sampling Devices and Methods - Even though the ACSAR study used 0.09 m^2 from a 0.25 m^2 box cores and the NGMCS study used smaller

yoked 0.06 m^2 cores, this difference should not bias results in the direction observed. There is no obvious means by which a larger core would capture fewer species, and a smaller core capture more.

2. Different Processing Methods - Both projects reported similar processing methods, and any biases arising at the execution level would be biased against the observed pattern.
3. Taxonomic Resolution - The two studies utilized different taxonomic experts, and no standards exist for assessing taxonomic error.
4. Insensitivity of H' Diversity Index – The NGMCS elected to compare diversity using the information-based statistic H'. This index is most influenced by species comprising about 33% of a sample and is insensitive to rare species. It is an inappropriate choice for deep-sea samples where numerous rare species can be found in a sample.
5. Data Culling – The NGMCS study limited diversity index calculation to only those taxa fully identified to species and eliminated macrofauna-sized nematodes and harpacticoid copepods. This effectively eliminated 25% of all taxa.

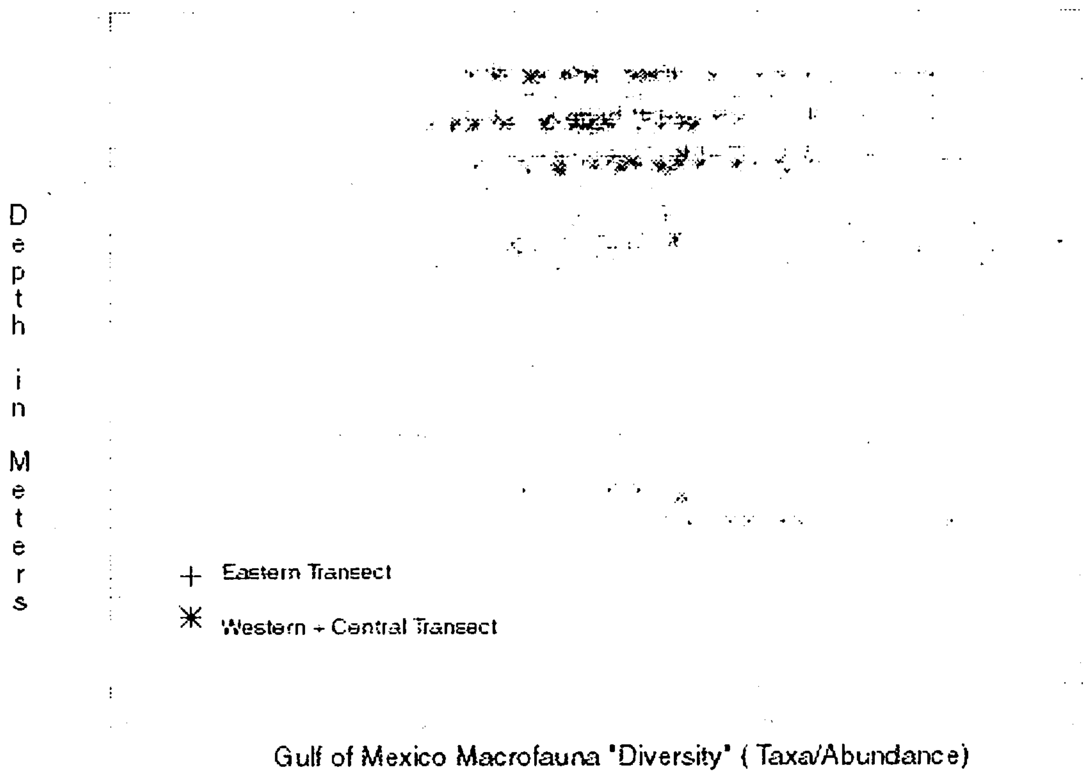


Figure 3.9. Sample-Level Diversity Trends in NGMCS Study.

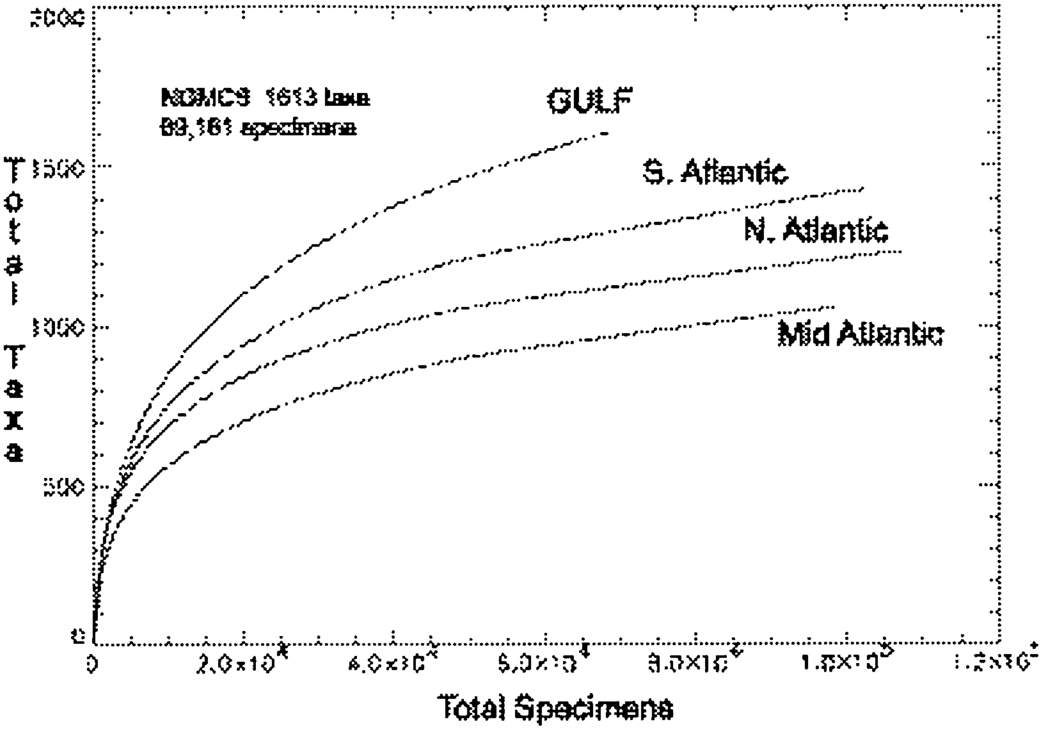


Figure 3.10. Rarefaction Curves for Gulf and Atlantic Macrofuana.

Until the issue of taxonomic resolution is resolved, the finding of higher diversity in the Gulf must be considered tentative. The best confirmation of the pattern would be to undertake comparative Gulf and Atlantic sampling using the same techniques and personnel. The extent of sampling needed, however, may be fiscally prohibitive. An adequate alternative would be resume sampling in the Gulf with the entire collection of targeted taxa, not just vouchers, sent to experts who participated in the ACSAR study. The decade that has passed since completion of ACSAR may make this difficult.

3.9.2 Macofaunal Density Comparison

It was stated by Rowe and Menzel (1971) on the basis of a few samples that the Gulf of Mexico has low standing stock macrofauna biomass when compared to other oceans. The NGMCS considered this statement and failed to reject it, but no formal comparison with other data were undertaken. If true, it could mean that the deep Gulf of Mexico experiences greater-than-usual food limitation and is especially susceptible to impact by activities which alter the detritus influx and distribution processes. Due to this potential for management relevance, a reanalysis was undertaken here.

The method of comparison is primarily graphical with statistics used for description rather than testing. Such a cautious approach is appropriate given the methodological differences in the studies compared. A comparison of the depth pattern of total faunal counts in the 326 box cores in the NGMCS data archives versus those of the 558 box cores in the ACSAR archives produces results that are difficult to interpret (Figure 3.11).

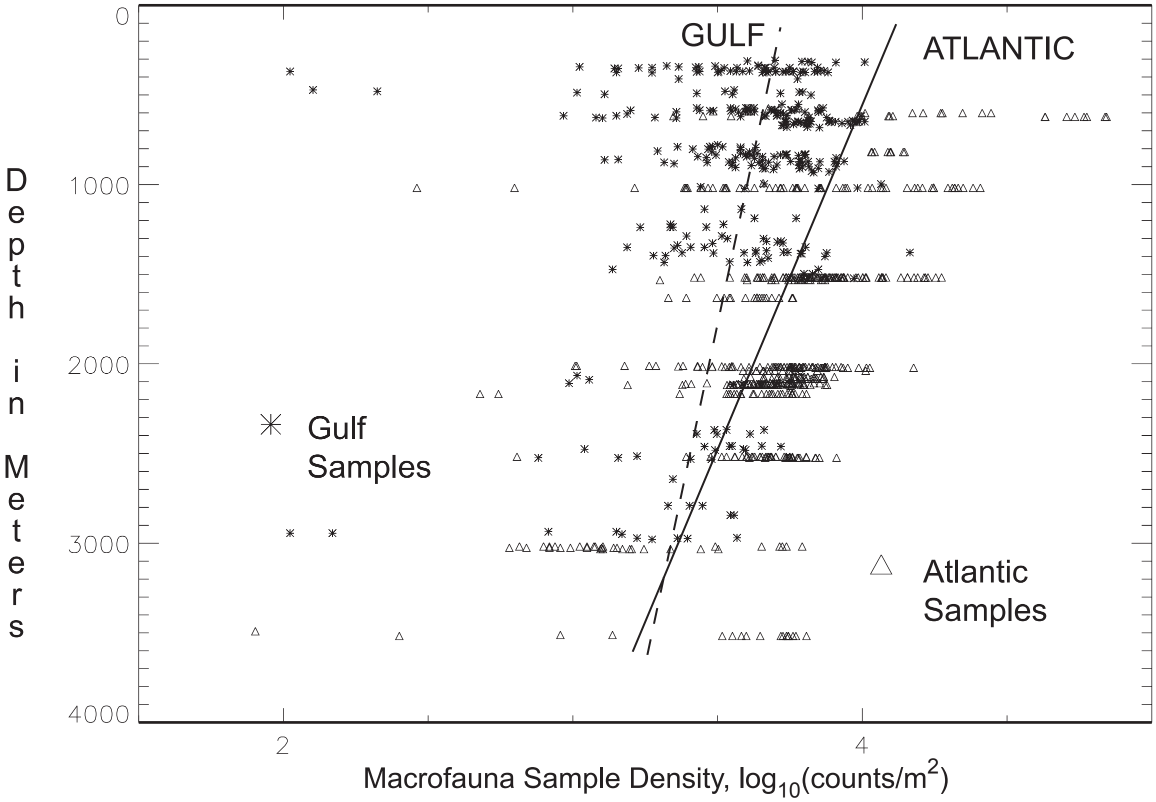


Figure 3.11. Comparative Depth Decrease of Macrofauna Densities.

The macrofauna counts for the box cores of the Atlantic Continental Slope and Rise study (ACSAR) provide a basis comparison of faunal density between the Atlantic slope and that of the Northern Gulf of Mexico Continental Slope study in the Gulf of Mexico. Expressed in the common form of counts m^{-2}, the Gulf appears to have dramatically lower faunal abundance.

Atlantic samples were obtained from the Battelle data archive. The Gulf of Mexico data were obtained from the restructured NGMCS data archives. Linear regression was carried out on log transformed densities, taking depth as the independent and density as the dependent value. In the oceanographic tradition, depth is plotted on the y axis. The scatter of the data overlaps, but there is an indication of different trends that can be illustrated with regression lines. The resulting lines were produced:

W. Atlantic Macrofauna Density = $4.159 - 0.00026z \pm 0.256$, n= 558

N. Gulf of Mexico Macrofauna Density = $3.712 - 0.00013z \pm 0.279$, n= 326

In the NGMCS Final Report, a similar regression was reported based on composite stations. The value of that function, which gave no variation term, was:

Station Level Macrofauna Density $= 3.52 - 0.00019z$

The differences are easily attributed to inclusion of macrofauna-sized nematodes and harpacticoids in the reanalysis.

Being cautious not to over-interpret the results, an interesting contrast can be seen. Above 2000 m the Gulf appears to have lower macrofauna density. The rate at which density declines with depth in the Gulf is apparently less than in the Atlantic. Below 2000 m densities become more similar. Food input rates and types may differ between the Gulf and the NW Atlantic. It is a possibility that should be specifically addressed.

3.10 Conclusions and Recommendations

In this final chapter the conclusions based on the reexamination and synthesis will be presented along with recommendations that come from them. Prior to presenting these new points, the recommendations presented by Pequegnat (1983a) and the NGMCS Study (Gallaway 1989) will be considered. Many of those are still quite valid.

3.10.1 Recommendations of Pequegnat

The Pequegnat report concluded with a list of recommendations for action that would minimize deep-sea impacts due to oil and gas development. He also provided a list of investigations to fill information gaps.

Pequegnat's (1983a) report concluded with a list of actions that could be voluntarily undertaken by industry or imposed by MMS. These are still worth considering, although technology development have made some outdated. Below they are classified by type, paraphrased, and commented on. The list has be reordered to give it a sense of contemporary priority. Only three of the recommended actions deal directly with ecology. Four are related to hazard reduction.

1. Ecology - Ecological monitoring should be initiated before and during specific deep development projects to provide information about effects.

   This remains an excellent recommendation made more than a decade before any development was started.

2. Ecology - Undertake surveys of the slope environment including fauna, currents, water mass properties, and studies of turbidity tolerance.

   The NGMCS study met some of these needs. Studies of the turbidity tolerance of deep animals is a good idea but poses technological challenges.

3. Ecology - Buffer zones should be provided between major areas of development to provide refuges which can be the sources for repopulation of impacted areas.

A similar provision for refuges was mandated for manganese nodule development. It is difficult to envision that deep development will be more dense than on the continental shelf, where there is no evidence of large-scale impact.

4. Geohazard - Limit leasing to areas of more stable bottom until technology of drilling is more advanced.

   Concerns about accidents associated with drilling on unstable slopes are still valid. However, there is so much technological development that a leasing prohibition is not called for at this time.

5. Geohazard - Limit drilling on unstable bottom to seasons of better weather conditions so as to minimize risks.

   Highly effective dynamic position and use of seafloor templates have effectively eliminated this concern.

6. Safety - The safest known technologies should be used.

   This is how both industry and MMS operate; no new policies are needed unless new hazards are found.

7. Blowout Control - Technology should be developed to minimize damage.

   This is still a valid suggestion. There has been substantial development in these areas.

As a framework for studies, Pequegnat felt that there should be interdisciplinary study of the Gulf stressing biological and physical data. Of particular interest to him were determination of standing stocks and secondary production using his zonation scheme as a basis for sampling. Physically, the residence time of deep water should be determined ("flushing rate"). Specifically related to oil pollution, chemical finger prints in animals and sediment should be examined. Following this general framework, specific information voids were identified. These gaps have been shortened, rephrased, and reconsidered below. Basically, all the information gaps identified in 1983 still exist.

1. Chemical - Organic detritus flux through the water and in the sediments should be measured. Measurements should included studies of benthic consumption. This information is still needed.

2. Physical - A synoptic picture of at and above bottom currents must be obtained. This would include topographic steering. This information is still needed.

3. Geological - A more extensive and geographically broader understanding of the frequency and magnitude of mass transport is needed. This geological work also needs to address natural effects on fauna.

4. Ecological - a. It was felt that megafauna had been adequately surveyed. Future surveys should focus upon macroinfauna and meiofauna but not exclude other groups. In addition the benthopelagic fauna should be considered. This is essentially how the NGMCS study was structured.

b. Surveys should focus upon specific topographic features such as DeSoto Canyon between 2250 and 2700 m, Mississippi Trough at all depths, and Alaminos Canyon. Feature-specific sampling seems highly appropriate due to the complexity of the Gulf of Mexico. Increased use of submersibles, and controlled towed instrument packages now make this more feasible.

c. Sampling in all areas should help fill the 2200-2750 m gap. This is a good recommendation, however the gap actually begins much shallower at about 1500 m.

3.10.2 Conclusions and Recommendations of the NGMCS Study

In the summary of the NGMCS study (Gallaway 1989) the conclusions were limited to the final testing of seven hypotheses. The primary evidence for a judgement of the first four hypotheses came from the multiple contrasts analyses of variance discussed in section seven of this report.

1. It was rejected that the Gulf lacked geographic regions. The eastern Gulf was thought to have greater endemism and higher biomass. The western region was distinguished by chemosynthetic communities. Physical conditions were thought to cause some of these differences.

   This reevaluation found these to be poorly supported conclusions. While east-to-west differences may occur, fewer than 1/5th of the dominant species showed any suggestion of such a pattern in the ANOVA run. The issue of endemism is greatly complicated by uneven sample designs.

2. It was concluded that there was no annual variation.

   Reevaluation found this to be an acceptable conclusion. The time-series sampled was very short.

3. It was concluded that there were seasonal fluctuations in populations.

   Reevaluation found this to be a weak conclusion found in only a few species in the ANOVA. The fall - spring contrast over just two years was too short of a sampling period.

4. It was concluded that there was significant difference in faunal composition with depth.

   This conclusion was supported by many of the multiple comparisons rather than a single strong analysis. It was consistent with what we already known about the deep sea and is most certainly correct.

5. It was concluded that there were no significant differences within faunal zones.

   Reevaluation found that the tests were unbalanced as poorly suited to detect within zone variations.

6. Is was concluded that the Gulf slope was less productive than other slopes in the ocean.

Reevaluation of macrofauna densities supports this contention above 2000 m. Below that, inter-basin densities become similar. For meiofauna, the Gulf may have very high densities.

7. It was concluded that there were atypical slope habitats, as evidenced by the chemosynthetic communities.

   Confirmation of this finding is obvious. In addition there was indication of deep sponge banks and large patches (100's m^2) of the holothuroid *Peniagone* in the NGMCS study. The Pequegnat studies found patches of unknown size where sea urchins predominated.

The primary recommendations of the NGMCS study addresses inadequacies of sampling rather than addressing more general gaps in environmental information. All the recommendations are still valid.

1. Sample sizes should be increased to improve the power of the analyses. This means larger samplers and replication.

   On reevaluation it has to be generally agreed that more replicates are better than a few. However, deep populations have so many rare species that there will never be an end to demands for more replicates. A better use of resources would be to increase size; employ a $0.25m^2$ box core, and keep replication at about five cores. Increasing trawl size is impractical, making increased replication preferred in megafuana studies. Over the range sampled, a fixed depth interval should be used that do not presume a particular zonation scheme.

2. Photosurveys of tracks and traces were concluded to be marginally useful, but image-based surveys of special habitats were seen as essential.

   On reevaluation this is still a valid consideration. Rather than abandon surveying of lebenspurren, it would be preferable to undertake development of more informative techniques.

3. Future studies should anticipate the considerable workload associated with sorting and identification of species-level samples from the deep sea.

   This is still a valid concern. It has been over ten years since MMS supported an extensive deep-sea survey, and the pool of taxonomic experts is now less than before. Either robust methods which do not require species-level work must be developed or the increasing costs of deep studies accommodated.

3.10.3 Conclusions and Recommendations of this Review

1. Megafauna - Pequegnat's conclusion that the larger fauna was well known and adequately surveyed is challenged by the fact that the NGMCS study collected many different species and produced major differences in the estimation of relative abundance. The large number of rare species in the Pequegnat and NGMCS megafuana inventories indicate that the fauna remains under sampled. This gives rise to two management concerns. First, there may be additional special habitats discovered such as chemosynthetic communities and sponge

banks. Second, there may be species encountered which attract public interest and raise environmental concerns.

2. Macrofauna - The NGMCS is the only comprehensive survey of this size group in the Gulf of Mexico. The possibility of very high species richness requires that much basic taxonomic work needs to be done in this region. The primary management concern lies in the fact that macrofauna have become the primary data source for monitoring and impact studies. Therefore a high degree of understanding of the natural variation of this group is needed.
3. Meiofauna - The meiofauna component of the NGMCS study was well designed, but only executed at a low level of taxonomic resolution and archived only at the station level. The very high densities of meiofauna, mostly nematodes and harpacticoids, warrant additional study.
4. Zonation - There is no doubt that fauna changes with depth much more than it changes along isobaths. This was well confirmed by Pequegnat, the NGMCS study, and is quite obvious from a reexamination of the data. The emphasis on a specific scheme of zonation is misdirected. Zones are very useful to management because they define regions which require specialized plans. The use of zones in understanding ecology is less well established, and efforts to carefully delineate zones by sampling quickly run into confusion as to what are meaningful and what are random patterns. Physically, there is good reason to treat the legally defined deep sea (deeper than 200 m) as having at least two major divisions. An upper zone from 200 m to 1000 m experiences physical variation and lies in the region of low oxygen. A deeper zone is physically distinct and contains a fauna that shifts progressively to deeper-dwelling species.
5. Diversity - The Gulf deep macrofauna are more diverse than the shelf environments. Based upon rarefaction, the Gulf slope has a greater species richness than the coast of the Atlantic states. This conclusion must be qualified by the fact that the compared studies differed in many important ways.
6. Abundance - The reexamination found a depth-density relationship similar to that reported in the NGMCS study. Two differences were quite important. First, Gulf macrofauna densities above 2000 m are lower than found in the ACSAR study, but become similar below that. Second, the rate of density decline with depth in the Gulf appeared to be slower, suggesting a greater influx of food to deep water. As with the diversity conclusion, it must be cautioned that this comparison looks at data from studies that differed in important ways.
7. Special Habitats - In addition to the conspicuous chemosynthetic communities there appear to be other distinct deep habitats. Megafauna show dense patches of sponges, echinoids, and holothuroids. Being sessile, it can be assumed that the sponge banks are long-term features. The persistence of the echinoderm patches is more problematic in that both echinoids and some holothuroids are capable of short-term aggregation. The view that deep fauna is homogenous is not supported.

3.10.4 Recommendations of This Review

Since this review was begun, deep oil and gas leasing has increased substantially. In response, MMS has worked with industry and the research community to identify needs and concerns. Some of these needs have been formally identified (Carney 1998) and already acted upon. The list of recommendations given here are not intended to replace those developed through other processes. They are limited to the information gaps found upon reexamination of the ecological data.

1. Maximization of Data Quality - For both the NGMCS and ACSAR studies, the required filing of NODC databases did not produce a useful and accessible archive.

   MMS should review this requirement in conjunction with NODC and adopt new procedures that accomplish that need. The archives of both studies should be recreated and updated.

2. Standardization of sampling gear - The Gulf of Mexico may emerge as the primary region of the world ocean where human impacts on deep systems are studied. It is imperative that data collected in the Gulf be comparable to the best collected elsewhere.

   The main area in deep-sea ecology where there has been some degree of standardization is macrofauna. Future sampling must make use of a 0.25 m^2 box corer. The 300 µm sieve should still be used to process the macrofauna. Any departure from this standard carries the obligation to convincingly demonstrate the value of the technology and provide a means of comparison with older data. The conclusions in this report that the Gulf is more species rich than the Atlantic and of similar biomass should be tested with appropriate gear.

3. Geographic Range of Study - MMS has a mandate only to study US waters, while the Gulf is so small that the ecology in one region may be impacted by processes in Mexican , Cuban, or even Caribbean waters.

   A means needs to be found to study basin-wide processes. The east-to-west differences proposed by Pequegnat were not adequately examined by the NGMCS study. The region east of the Mississippi should be carefully compared to the western slope of the Gulf off Texas and Mexico.

4. Bathymetric Range of Study - Deep sampling in the Gulf has been concentrated in shallower than 1500 m with most above 1000 m. Deeper than 1500 m sampling effort has been unequal.

   This lack of equal effort distorts results and leaves the recognition of faunal change at greater depths open to subjective interpretation. Future sampling should focus deeper than 1500 m. The depth sequencing of samples must not presume a given depth zonation scheme. Fixed depth intervals or randomization with bands of fixed width are preferred.

5. Special Habitats - It is obvious that the deep Gulf is a topographically, physically, and chemically complex environment with distinct habitats ranging from the obvious to the subtle.

The faunal changes associated with these features may confuse impact studies, and some habitats may warrant protection. High resolution topographic data for the northern Gulf is now being made available by the National Oceanographic Data Center, making feature specific studies feasible. Future studies should be designed to compare canyon walls and floor, topographic highs and lows, slope-prone regions and stable regions. Efforts should be made to relocate the sponge banks, holothuroid aggregations, and echinoid aggregations to determine long-term persistence.

6. Optimization of Design - Studies that frequently change the intent of sampling often end up unable to undertake convincing identification of patterns.

   The alteration of sampling to pursue arising questions result in a data set that allows few of the main questions to be answered effectively. Future sampling should target known features. Sampling should be stratified within the structure of such features testing explicit hypotheses about faunal pattern. Once a feature or series of features has been identified, and the hypotheses stated, then replication can be designed accordingly. Unfortunately, species-level analyses may require a prohibitive level of replication. In such a case, a general ecological parameter such as biomass or a process such as secondary production may be used.

4 Extension of Chemosynthetic Fauna Disturbance Monitoring

4.1 Introduction

As introduced in Chapter One, the first question facing oil and gas environmental management is how appropriate established management strategies for the continental shelf are for the deep ocean? To answer this question, we start by determining how much alike and dissimilar the environments are, and we find that in certain respects the faunae differ only by degree. There are, however, few parallels between deep-water chemosynthetic communities (VanDover 2000) and any shelf-depth assemblage. Appropriate management of these systems is a unique challenge to MMS. This chapter is different than the previous two in that it is intended to make a modest contribution of new information about chemosynthetic (more widely termed chemoautotrophic) communities, rather than review and critique previous studies. The time for a comprehensive critique from a management perspective is drawing near, but all initial results are not yet in.

The chemoautotrophic communities associated with hydrocarbon seeps of the Louisiana continental slope have been under almost continuous study since their discovery (Kennicutt et al. 1985, Rossman et al. 1987). Recognizing the "reef-like" status of these systems, MMS has sought to gain management-relevant information through a series of field studies. Initial investigations were begun as a supplemental task of the NGMCS and then expanded into the Chemosynthetic Ecosystems Study (MacDonald et al. 1995) followed by the Stability and Change in Gulf of Mexico Chemosynthetic Communities (MacDonald submitted). These studies, usually referred to as Chemo-I and Chemo-II, have been completed. A more modest effort is still ongoing under the Coastal Marine Institute Program, Improved Geohazards and Benthic Habitat Evaluations.

In terms of new information, this chapter does three things. It was the objective of this task to extend the geographic range of hydrocarbon seep sites considered by MacDonald et al. (1995) and extend the time of observation of markers left at seep community sites. Accordingly, dive tapes have been reviewed for 42 dives in 24 bottom areas studied by Roberts and Carney (1997) and collections from 13 dives sorted and identified. The status of markers left to aid recognition of long-term change was also updated to 1997.

4.1.1 The Contrast of Two Projects

In 1989, five years after the initial discovery of vent-type fauna off the Louisiana coast (Kennicutt et al.1985, Rossman et al. 1987) two largely separate groups of researchers began a decade long series of studies at hydrocarbon seep sites. The first of these, employing a strongly geochemical and ecological approach, was a multi-university project lead by the Geochemical and Environmental Research Group (GERG) of Texas A&M University. The second, lead by the Coastal Studies Institute (CSI) of Louisiana State University (LSU), took a strongly geological approach. The CSI effort examined seeps in the larger context of long-standing questions about slope dynamics and authigenic carbonate precipitation. Due to the different orientations the two programs have selected dive sites by different criteria. GERG's ecological studies required sites that could sustain repeated scientific collecting and long-term experimentation. The CSI studies had minimal biology components, and selected sites so as to sample a wide range of geological structures with few returns to the same site.

Critically examined, neither focus (largely ecology versus largely geology) by itself can provide a full picture either in terms of management or basic ecology. The needs of the GERG group have lead them to repeatedly sample systems that have been persistent enough through time to build up high population densities. These studies provide an unequalled understanding of the biology of such stable communities, but they contribute less to a broader understanding of persistence and stability. The needs of the CSI group have lead them to explore a greater variety of geological features. These explorations allow for a broader synthesis to be developed, but they lack sufficient detail to be certain that the ecological aspects of the syntheses are valid. It is the purpose of this small study to improve the ecological value of the CSI seep investigations so those results may be combined with the ecological studies of the GERG group.

4.1.2 Characterization of the Assemblage Across Sites

Previous Work and Expectations of Faunal Difference

The primary work on northern Gulf chemosynthetic communities is summarized in MacDonald et al. (1995) and MacDonald (submitted). Extensive diver observation, opportunistic sampling, and 61ANOVA-designed faunal samples (submersible scoop) determined the basic faunal patterns at four primary sites: Green Canyon 185, Bush Hill; Green Canyon 234; Green Canyon 233, Brine Pool; and Green Canyon 272. Two additional sites were sampled less extensively: Vioska Knoll 826 and Garden Banks 386. All except the Brine Pool were mixed communities of tube worms and mussels on exposed and superficially buried carbonates. During Chemo-I only mussel beds were effectively sampled. The taxonomic status of the mussels is relatively well known (Gustafson et al. 1999). Mat-forming mussels were a mono-species populations of the methane-utilizing *Bathymodiolus childressi.* Two other species were encountered in isolated clumps, *Tamu fisheri* and *Idas macdonaldi. T. fisheri* has since been found to be sulfide-utilizing and associated with tubeworm clumps. The rare *I. macdonaldi* is more problematic, its associations are not clear, and it lacks the hypertrophied gills of other seep and vent-associated mussels. While no major shifts in the species composition of mat-forming mussels were encountered on the slope above 1000 m. Deeper sites in Alaminos canyon and the west Florida escarpment were dominated by combinations of *Bathymodiolus brooksi* and *B. heckeri.* Where and why the species transition takes place is unknown.

Effective sampling of tubeworms was developed by Harbor Branch Oceanographic Institute (HBOI) and C. Fisher during Chemo-II (Fisher et al. 1997). Taxonomic work and studies of associated fauna are still in progress. Preliminary results indicates that a Lamellibrachia-like species dominates, often in mixed populations with an Escarpia-like species. As with the mussels, species composition varies little between sites above 1000 m, but a species shift is found at deeper sites.

An unexpected result of Chemo-I was that the heterotrophic associates of seeps (largely mussel beds) were relatively homogenous site-to-site shallower than 1000 m. (Carney 1995). It had be incorrectly assumed that random events would play an important role in the colonization of each site by animals from the background. Such events would cause each site to have a distinctive suite of consumers. To the contrary the consumer component, all sites above 1000 m. was dominated by the same three endemic gastropod species and two endemic crustacean species. Non-endemic species were present in comparatively lower numbers, but the same non-endemics were at all sites. As with mussels and tubeworms, major differences in composition were found were compared to the deeper sites (Hecker 1985, Carney 1994).

It can be easily appreciated that this depth dependence of results is quite management relevant. If all seep communities above 1000 m in the northern Gulf are fundamentally the same, then large populations with a high degree of dispersion are likely. Such a distributed but geneticially-linked population may be better able to recover from localized impact. However, these a resilient populations do not occupy the entire slope. At some depth on the slope there is species replacement.

There are at least three possible explanations for the observed patterns. First, seep fauna could be much like typical deep-sea organisms and show some degree of species change (zonal restrictions) with depth. Second, the individual seep organisms themselves might be capable of distribution over the entire slope, but are incapable of successfully colonizing deeper seeps due to competitive disadvantages. Third, the depth dependency of the result could be an artifact of sampling. Of the many sites that may exist above 1000 m. only a few have been sampled, and even fewer deeper sites. Therefore, limited sampling should be seriously considered.

Study Methods and Activities

Since 1989, the CSI seep group has carried out dives of the Johnson Sea-Link submersible operated by Harbor Branch Oceanographic Institution. These programs have been supported by the National Ocean and Atmospheric Administration (NOAA) National Undersea Research Program (NURP), the offshore oil and gas industry, the Louisiana Board of Regents Industrial Partnership Program, and MMS. The dive sites were selected on the basis of industry-provided high-resolution seismic records giving indications of seep conditions. These indications included:

- medium-to-high relief topography suggestive of massive carbonates aligned with fault systems,
- acoustic transparency or "wipe out zones" indicating gas charged sediments,
- apparent bubble plumes in the water column.

Dives focused on 24 lease blocks roughly clustered into three groups. A central series spanned 70 m to 700 m (Ship Shoal 286, Green Canyon 18, 53, 140,143, 180, 185, 193, 232, and 237). A western series spanned 300 to 800 m (Garden Banks171, 189, 201, 215, 304, 338, 382, and 427). An eastern-most series targeted a much narrower range, 600 to 800 m (Mississippi Canyon 709, 843, 885, and 929).

Review of 84 hours of bottom tape provided a means of assessing the gross composition of any chemosynthetic communities present. A serious limitation of such tape cataloguing is that these were not intended as systematic surveys. The geometry of the area surveyed and the spatial relationships are unknown. It is likely that some fauna are counted more than once. There is also an inherent bias towards better image coverage of exposed rock surfaces, the primary target of the geological dives. For all these limitations, data were treated qualitatively in a manner similar to MacDonald (1995). As seen in the results section, this proved adequate. In addition to tapes from twenty four lease blocks, faunal ground truth samples were collected on thirteen dives. These samples were collected in a manner similar to the faunal studies of the GERG group (Carney 1995) . The manipulator arm of the submersible was used to get one full scoop from a representative faunal patch. These scoops targeted only mussel clumps since they proved unsuitable for collecting worm clumps. This sample was stowed in the "critter gitter' on the sub. On deck, samples were sieved through a 500 µm mesh and preserved in seawater buffered 10% formaldehyde. Back in the lab samples were sorted, counted, and archived in 80% ethanol.

4.2 Markers and Recovery Experiments

4.2.1 Introduction

A modest program of long-term observation of marker rods and recovery cages initiated in 1989 was included in the Northern Gulf of Mexico Chemosynthetic Ecosystem Study (Chemo I) and reported on through 1993 (Carney 1995). This report provides an opportunity to extend the time line of these observations four additional years until 1997. This extension has resulted in four main results to be discussed in more detail below. First, recovery from disturbance (denuding the bottom of mussels) is not evident. Mussels neither migrate into the disturbed area as adults nor settle as larvae. Second, the response to new substrate (rods) was very mixed at a single site. Sometimes adult mussels became attached to a rod, but other rods remained bare. Recruitment of juveniles was extremely limited. Third, there may be major natural disruptions of the environment, a recovery cage at Green canyon 272 was first partially buried by faunal burrowing, and then completely displaced by massive hydrate movement. Fourth, (as a practical matter) long-term monitoring conflicts with investigations requiring large-scale specimen collecting. At all sites the extensive submersible activities of the past decade have dislodged and otherwise disrupted deployments. This disturbance casts some doubt upon the results of this study.

The deployment of markers of various types, although an ancillary research task, is a first step in determining a high-priority management question about hydrocarbon seep communities. What happens when they are disturbed? Presumably research sampling is a minor impact compared to the damage that might be done by careless drilling operation, but community response to small scale perturbations should increase the understanding of these systems. Are the seep communities opportunists capable of rapidly colonizing a transient seeping feature, an ecology that would make them largely impervious to industrial impact? Or, are they specialists which require narrowly restricted combinations of geochemistry and substrate? Such specialization, if true, would suggest great sensitivity to perturbation.

4.2.2 Methods

The methods have been previously reported (Carney 1995) but are repeated here for completeness. Small marker rods have been deployed since 1987 at all surveyed sites as a simple frame of reference. Each rod is 0.5 m long 3/4 inch PVC pipe sanded, deglazed, and painted with an epoxy based paint. Three primary color bands (red, blue and yellow) 10 cm wide were painted to provide scale in low resolution images and aid in determining correct color balance in video images. Rods are marked with the dive number upon deployment. The most extensive use was at the brine pool where 9 small markers were placed at roughly 2m intervals around the outer edge of the pool.

Large Marker Rods were made of 3m lengths of 1.0 inch PVC pipe prepared the same as the smaller rods, but painted black and white in 20 cm bands. Within the white bands, a coded series of rings were drawn to allow identification of location from a close-up image. There has been only one site marked by these large rods, the Brine Pool. Seven large rods were deployed across the long axis of the pool. Pole 2596 was laid horizontally across the mussel mat at the northern end of the pool on Sept. 13, 1989. On following dives, a rod was placed on the mat at the southern brine overflow end. The inner edge of the mat was marked near these horizontal rods by rods pushed into the bottom of the pool. These poles were within 20 cm of the inner edge of the mussel mat but not touching it. Three additional vertical rods were inserted across the length of the pool by placement in the bottom. A rod marked "B" was inserted approximately 2 meters from the northern end and "C" placed at the southern end. The third 3m long rod, "A", sank from sight when placed in the center of the pool.

In 1991, "recovery cages" were placed in areas stripped bare by massive mussel collecting in order to observe and quantify any subsequent recolonization. These collections typically removed more than 100 animals from an area of approximately 0.25 m^2. Rectangular recovery cages were constructed of 1/2 inch PVC water pipe. Fifty centimeter lengths were used to make 0.25 m^2 top and bottom sections, and the remaining sides constructed of 20 cm lengths. Corners were fastened with three-way right angle joints and commercial PVC pipe adhesive. The corners were drilled to allow for flooding of cavities. Half the interior of the cage was enclosed in 3.5 cm stretch mesh plastic fruit tree bird netting. The string of the netting is less than 1mm in diameter, is easy to see through, and its black color limits obscuring of a video image. Nylon line was stretched across the diagonal of the cage, and then netting was secured with tiewraps to these diagonal lines and adjacent sides. The 50 cm rods used had been sanded, chemically deglazed and painted white, blue, red and yellow with an epoxy based paint. The 10 cm long color bands provide visual scale, orientation, and color balance in subsequent image analysis. Cages were deployed in conjunction with massive mussel sampling during the 1991 dive series. Two cages were deployed at Bush Hill on dives JSL-3129 (Sept. 5, 1991), and JSL-3139 (Sept., 20, 1991). Single cages were deployed at Green Canyon 272 on dive JSL-3137 (Sept. 19, 1991), and Green Canyon 234 on dive JSL-3144 (Sept., 24, 1991).

4.2.3 Results to 1998

The markers at the Brine Pool were last systematically surveyed in 1996 and cursorily examined in 1998. Only four of the 12 markers placed at the outer edge of the pool could be relocated . It is assumed that the others have been pressed all the way into the sediment by the submersible during the extensive sampling at this site. In 1989, seven of nine rods were resurveyed showed no growth or retreat of the outer edge of the mat. A similar conclusion can be drawn from the resurvey of 1996 and 1998. All outer edge markers have been colonized by a short tubiculous growth, possibly hydroids. No colonization by mussels has been seen.

The large marker rods in the pool had experienced the same knocking about which has disturbed the outer edge markers. Most critically, the end markers which were separated from the mussel mat by about 20 cm were found in 1994, 1996, and 1998 to be touching the mat and lying about 10 cm deeper in the brine. With no other evidence of pool rising, it appears that they had been knocked out of position during other submersible observations and that the mat edge has been relatively stable between 1989 and 1996. Faunistically, the rods retain some unidentified tubiculous organism first noted in 1991. In the 1993 survey, two juvenile mussels, approximately 1 cm in maximum dimension were observed on the southern edge rod. This is the only evidence of recruitment found in any monitoring of a marker. These were attached at the brine pool interface, where a reddish precipitate appears to have formed on the rod. Now that the rod is touching the mussel mat, the effects of settlement and migration can no longer be separated.

The rods placed on the mat surface at the southern and northern end continue very different courses of development. By 1991, adult mussels were moving on to the northern rod, covering about 25% of the surface. In 1993 only the inner 1/2 of the rod could be seen. That end was 75% covered with adult mussels, greatly obscuring the rod. The rod could not be found in 1996 and is assumed to be lying under the mat. The southern rod continues to be moved around by bottom currents. No mussels, either juveniles or adults were observed on the rod from 1991to 1996. The mussel cover at this end of the pool is limited to discrete clumps.

Two cages had been deployed in on Bush Hill in 1991, 40 cm apart on a patch of flat bottom approximately 3 m. across ringed by exposed carbonates and mussel-tubeworm clumps. The cages were placed on sediments which had been stripped of mussels. One year later both cages had some clumping of adult mussels to the frames, but no evidence of juvenile settlement. In Cage One, approximately 15 large (greater than 7 cm) mussels occurred as a cluster in the open area of the frame. Approximately ten animals of similar size were attached to the frame of the cage on the open side. The netted side appeared to be devoid of mussels. The bottom in the open side was colored white, suggesting chemical and/or bacterial activity. The bottom on the netted side appeared to have no special coloration. The striking feature was that Cage Two had been colonized by white *Beggiatoa* The bacterial film had grown up and over the netted half. The sediment under and around it was covered with both white and red *Beggiatoa* mats. Two large mussels were attached to the outer edge of the frame, but none were in the open area. At both cages, the crustacean *Munidopsis* and *Alvinocaris* were near and/or under the cages.

The condition remained little changed up through 1998 when only a cursory survey was made. The *Beggiatoa* drape covering the second cage had become reduced by 1994 and remained restricted to a benthic mat in 1998. No additional movement of mussels on to the frame was seen. The meaning of these observations must be somewhat suspect since this site has become a station for tubeworm growth studies. During the repeated visits by the submersible, both cages have been accidentally and intentionally moved. The site must be considered a chronically disturbed site.

A single cage was deployed at GC-234 on an area of mud and exposed low relief carbonates. The site contained both dense mussel aggregations and mussel-tubeworm assemblages. The open section of the cage was whitish due to bacteria or chemical activity. Two mussels were attached to the frame in this section in 1991, and an additional five added by 1996. Again, there is no evidence of juvenile settlement. *Alvinocaris*, and *Munidopsis* have used the netted portion as a refuge since the original deployment. In 1991 and 1994 six or more of the gastropod *Buccinium* were found in the cage. This observation has not been repeated since. As with the Bush Hill site, the cage has been subject to disturbance since deployment.

The cage deployment at GC-272 exhibited the greatest changes. They were, however, due to hydrate movement rather than community change. A single cage was originally deployed in denuded area surrounded by additional mussel clumps. Rocks and tubeworm bushes surrounded this patch. In 1993, a few adult mussels were noted on the frame, but more importantly a large crab burrow (30 cm across) lay within the cage. By 1994, the cage was sitting atop a low mound approximately 1m across. In 1996, the cage had been completely displaced by exposure of a gas hydrate. The surrounding mussel mat was buried under sediment.

4.2.4 Discussion

The long-term observations of the Brine Pool produced two unexpected results about mussel beds: first, there appears to be scant new recruitment, and second, there is much repositioning of individuals in some parts of the mat. The absence of apparent recruitment is the most important result from a management standpoint. When the rods were deployed, it was suspected from the structure of the mussel bed that the brine-ocean interface provided ideal chemical conditions for mussel colonization. The mussels closest to the brine edge were tightly packed and had more small size classes. If true, any new surface placed in this environment would be quickly colonized. The meager settling observed challenges the prior assumption and raises three questions. First is the new substrate ideal (as anticipated) but that new recruitment extremely slow? Alternately, is that interface not the ideal environment? Lastly, do the results simply indicate that the plastic rod was a poor substitute of the natural substrate required by mussel larvae for settling. Due to the importance of determining recolonization rates by settlement, these questions warrant resolution in the future.

The great difference in the horizontal rods at different ends of the pool is quite interesting. At the northern end, mussels quickly climbed up on the rod in such large numbers that the rod was effectively obscured. This dramatic effect might be due to mussels climbing up to escape competition, improve their position in the methane gradient, or to escape brine and toxic levels of sulfide. Whatever the reason, it has to be assumed that the mussel mat is actually very active with much pushing and shoving as animals try to improve their position. Why the southern overflow end is so different is hard to explain. Perhaps there is no gradient-based reason to move amount, and the rod offers no extra benefit. Or, more simply, there may be less spatial competition in the relatively sparse population.

It can be postulated that when mussels are stripped from an area using the grab of the Johnson Sea-Link, that the geochemical environment of the surficial sediments undergoes a permanent change. None of the recovery cages experienced a return to pre-disturbance conditions through adult movement or settlement. Although there was some adult migration into the disturbed sites, it was limited. The transitions noted were mussel (methane) to *Beggiatoa* (sulfide) at two locations, and mussel to hydrate mound at one. What normally prevents *Beggiatoa* from enveloping mussel beds as it did the cage at Bush Hill? Is it chemical, or can the mussels suppress the bacteria? Resolution of these questions is possible, but would require experimentation that measured rates of bacterial production and consumption rather than just standing stock.

4.2.5 Conclusions Limitations and Recommendation

Within the limits of an un-replicated experiment employing artificial substrates that have been subjected to uncontrolled disturbance, the following can be suggested.

- Disturbed mussel sites do not return to their original conditions within seven years. Recruitment by settlement and adult movement appears to be very slow.
- The disturbance of denuding may irrevocably alter the geochemistry of the sediment-water interface changing the habitat value of that area.
- Mussel beds may be quite dynamic internally with the residents engaged in a struggle for a preferred position. If so, this may imply that the conditions optimal for community development may be quite narrow, and the animals have some ability to seek those optimal conditions.

More than any other investigation of seep ecology, the long-term monitoring of correctly designed and executed experimental disturbances will provide information that is of immediate management relevance. In contrast to what should be done, the work reported here is just a cursory glance at the problem. It has, however, provided interesting starting points for future work and brought to light mundane practical matters. Development of a full design is beyond the scope of this study, but some key elements can be identified. Experimental manipulation, especially manipulation employing exclusion cages, have been an extremely informative approach to marine ecology. With their growing popularity, however, it soon became obvious that there were many artifacts, confounding effects, and poor control-treatment design (Hairston 1989). Seep manipulations must consider these problems even more because poorly understood chemical gradients are involved. The factors influenced by a manipulation must be known and may include, sensory trigger to settlement, water flow, and position in a chemical gradient.

The practical recommendations are easily arrived at and all relate to the problems of submersible-based investigations.

- Priority - Experimental sites can not be "shared" with other tasks that disturb the site. Even when no samples are taken, the damage done by the submersible is unacceptable.
- Innovative Design - It must be realized that the task of site monitoring by submersible will be an additional level of disturbance. This may be addressed through a design that includes such disturbance or methodology that reduces the consequences.
- Deployed Systems - If detailed examination of an experiment site is seldom possible, it is inevitable that the effects of natural events between monitoring periods will be confounded with the experimental treatment effects. Therefore, it is preferred to maintain some form of continuous surveillance of the system. This might entail instrumented packages or moorings.

4.3 Results of Faunal Study

4.3.1 Results of Site Cataloguing

On the basis of the geological and geochemical studies undertaken by Roberts (Roberts and Carney 1997) a simple system of geological categories has been applied to all twenty four blocks. This categorization along with simple faunal description is shown in table 4.1.

Of 24 blocks containing seismic or topographic evidence of seepage, no chemosynthetic fauna was detected in five. Of the remaining 19, five had chemosynthetic fauna limited to *Beggiatoa* bacterial mats. The remaining 14 had some degree of metazoan community development beyond bacterial mats. In 11, mussels clearly predominated and in two tubeworms were clearly dominant. Tubeworm dominance (defined as the presence of numerous large bushes) seemed limited to the Green Canyon area. Limitations of the study, however, cast doubt on this finding. The mussels always appeared to be the common *Bathymodiolus childressi.* Unfortunately, there was insufficient image resolution to determine the species of tubeworms.

There can be many reasons why seep communities were absent from five sites and only bacterial mats observed at five. Most obvious is inadequacy of survey. These lease blocks are 3 nautical miles on a side and the targeted geological features extended many 100's of meters. It is highly likely that even large clumps of seep organisms could have been missed. Discounting inadequate survey, depth seems to be the most obvious factor. The five sites with mats only occurred in less than 500 m of water and the five with no seep fauna were all shallower than 600 m. It must be stressed that all these sites had strong geological evidence of seepage(surface carbonates, subsurface faults, and areas of acoustic wipeout), and the presence of the bacterial mats directly confirms the presence of sulfide.

Table 4.1 Geological and Faunal Characteristics of Lease Blocks Studies by the Coastal Studies Group. Following MacDonald et al. (1995) fauna were determined from video tapes. Abbreviations: M=mussel, V=vestimentifera, B=Beggiatoa, and L=lucinid Initials are given in apparent rank of abundance.

SERIES & BLOCK	DEPTH Approx.	GEOLOGICAL EVIDENCE of SEEPAGE	Seep Fauna
CENTRAL			
Ship Shoal 286	70 m	Mud Mound	None
Green Canyon 18	200 m	Large Carbonate	B only
Green Canyon 53	200 m	Complex Site, Mud Mounds, Collapse, and Carbonate Mounds	B only
Green Canyon 140	290 m	Carbonate Mounds	B only
Green Canyon 143	400 m	Mud Volcano	B only
Green Canyon 152	500 m	Fluid Expulsion	L only
Green Canyon 180	600 m	Soft Sediment Mounds	None
Green Canyon 185	600 m	Exposed Hydrates	V,M,B
Green Canyon 193	600 m	Exposed Hydrates	V,M,B
Green Canyon 237	700 m	Exposed Hydrates & Brines	M,B,V
Green Canyon 232	800 m	Exposed Hydrates	M,B,V
Green Canyon 234	800 m	Exposed Hydrates	M,B,V
WESTERN			
Garden Banks 171	300 m	Carbonate Mounds	None
Garden Banks 189	300 m	Massive Diapir	None
Garden Banks 201	400 m	Soft Sediment Mounds	B only
Garden Banks 215	500 m	Gas Charged	None
Garden Banks 382	570 m	Massive Diapir	M,B,V
Garden Banks 260	600 m	Carbonate Mounds	M,B,V
Garden Banks 338	600 m	Fluid Expulsion	M,B,V
Garden Banks 304	800 m	Complex Site, Mud Volcano, Gas vent, Carbonate mounds	M,B,V

Table 4.1 Continued.

EASTERN			
Mississippi Canyon 709	600 m	Exposed Hydrates	M,B,V
Mississippi Canyon 843	800 m	Exposed Hydrates	M,B,V
Mississippi Canyon 885	700 m	Gas Charged	M,B,V
Mississippi Canyon 929	600 m	Mineral Prone	M,B,V

Even when seep fauna was absent, authigenic carbonates were often present. These corresponded well with the deepest reef assemblage was recognized similar by Rezak (Rezak et al. 1985) for deep hardgrounds in the Gulf of Mexico. Most of the rock surface was bare, low cover was dominated by unidentified encrusting sponges. Large fauna was dominated by a gorgonian *Callogorgia* sp., a scleractinian coral *Lophelia prolifera*, and the antipatherian *Leiopathes glaberrima.* Cryptic surfaces (undersides of rock ledges) were colonized by an unidentified doriid polychaete, and brachiopods. When such rock samples were recovered they typically contained a rock-boring fauna dominated by cavity filling sponges and an unidentified sipunculid.

4.3.2 Results of Mussel Scoops

The analysis of the 13 samples is presented in table 4.2. The fauna is remarkably similar to that previously reported at the GERG-studied primary sites. There is no indication of depth or geographic trends. The sole chemosynthetic organism was the seep mussel *Bathymodiolus childressi.* The gastropod fraction of the assemblage was dominated by *Bathynerita naticoidea*, *Provanna sculpta*, and *Cataegis meroglypta.* The crustacean fraction was dominated by *Alvinocaris stactophilia* and *Munidopsis* sp. There were only two hints of any significant differences found. In a sample from Mississippi Canyon 709, the dominant gastropod was *Cataegis meroglypta* that is typically the third most abundant elsewhere. Also, a large worm, *Methanoaricia dendrobraciata*, common at Bush Hill and the Brine Pool was not sampled.

Again, interpretation is limited by the fact that there was very scant sampling. The obvious conclusion is that mussel-mat species composition above 1000 m across the northern Gulf is monotonous. In this analysis there was no appreciable evidence of founder effects or localized species groupings. The dominance of *C. meroglypta* at one site is puzzling, but the seep snails have been observed to aggregate and disperse. Our sampling may have happened to sample an aggregation. The absence of the *Methanoaricia dendrobraciata* may simply reflect the fact that most samples were taken from exposed rocks. At the Brine Pool and Bush Hill the dense worm populations are associated with a highly organic ooze directly under the mussel beds.

4.3.3 Dominant Species in the Upper Slope Seep Assemblage

Having established that a common set of species dominate upper-slope seeps, this fauna can be more formally defined and the functionality of the component species considered. The better studied mussel assemblage is predominantly a methanotrophic, bathymodiolid, bed-forming species inhabited by a suite of three browsing gastropods. These radula grazers forage extensively and may play a major role in virtually eliminating encrusting epifauna. Of roughly equal abundance are two highly mobile crustaceans that may be sub-lethal predators. Such predators take small bites of exposed mantle tissue. The mussels, the three gastropods and two crustaceans comprise the dominant endemic seep species. While their population sizes vary, they are a consistent component of the communities showing no succession or founder effect stages.

Beyond the six endemics, one habitat-forming producer and five habitat-exploiting consumers, there is an additional suite of species drawn from the slope fauna. These have been termed colonists (Carney 1994). The colonists tend to be larger predators and scavengers. The consistent members of this group include a starfish, a predatory gastropod, along with several fishes and crustaceans. An additional faunal category, vagrant, was used by Carney (1994) following Tunnicliffe (1991,1992),. These are large predators and scavengers that seem to exploit the seep environment as transients but are not especially abundant in it. This category consists of large crustaceans and fishes. In the following sections, all these major associated fauna will be considered.

Browsing Seep Endemic Gastropods

There are several species of gastropods associated with the seeps. In approximate sequence of dominance the most common species present are *Bathynerita naticoidea*, *Provanna sculpta*, and *Cataegis meroglypta*. Together they comprise the endemic browsers.

Bathynerita naticoidea Clark was the most abundant heterotrophic animal collected in association with mussel beds and sometimes exceeded even the mussels in abundance. It is a radula browser seldom larger than 1 cm in length. Considerable information on the natural history was developed by Zande (1994). Clarke (1989) produced the original description based on Bush Hill material; Warén and Bouchet (1993) extended the description based on additional material. The nerites are primarily shallow water species. *Bathynerita naticoidea* seems to be endemic to the upper slope seeps since it is only reported from the Gulf and off Barbados (Olu 1996). It has not been found at either the Alaminos canyon or the Florida Escarpment sites. A similar fossil nerite has been found at Miocene seep sites in Italy (Taviani 1994), but Warén and Bouchet point out that a lack of traits in the fossil form makes equating the two species problematic. *Bathynerita* lays small clutches of direct developing eggs in capsules attached to any suitable substrate. The shell has been found to support settlement of tubeworms and juvenile mussels.

Table 4.2. Faunal Counts for Major Taxa Contrasted with Results at Other Sites

Location	Dive	Depth ft.	*Bathymodiolus*	*Bathynerites*	*Provanna*	*Cataegis*	*Buccina*	*Alvinocaris*	*Munidopsis sp.*	*Methanoaricia*
GB-338	JSL-II-2906	1715	7	9	1	0	2	0	0	0
GB-193	JSL-II-2907	1810	18	37	2	2	2	0	0	0
GB-426	JSL-I-3567	1850	28	30	2	1	1	1	1	0
GB-237	JSL-II-2908	1870	45	103	22	5	0	3	1	0
GB-382	JSL-I-3307	1978	27	30	3	5	0	5	2	0
GB-383	JSL-I-3566	2000	6	0	0	1	0	0	1	0
GB-427	JSL-I-3305	2010	37	63	17	4	0	1	0	0
GB-427	JSL-II-2896	2010	2	1	0	0	0	0	0	0
GB-152	JSL-I-3123	1476	19	5	0	0	1	0	0	
MC-709	JSL-I-3124	2280	5	11	1	0	0	0	0	0
MC-709	JSL-I-3561	2265	42	19	2	23	0	5	1	0
MC-929	JSL-I-3309	2110	9	27	4	2	3	2	1	0
MC-929	JSL-I-3311	2110	19	2	2	5	0	2	0	0
	Average		20.31	25.92	4.31	3,69	0.69	1.46	0.62	0.0
	Std. Dev.		14.58	29.34	6.92	6.14	1.03	1.85	0.65	0.0
	N=13									
CHEMO -I Sites										
	Average		26.42	37.23	8.38	1.46	0.39	2.54	0.84	11.51
	Std. Dev.		35.70	62.78	15.83	3.56	1.55	3.77	1.31	31.98
	N=61									

*The radula browser, *Provanna sculpta* Warén and Ponder, may sometimes exceed *Bathynerita* in number. It was new to science, with the type species coming from Bush Hill (Warén and Ponder 1991). Although the genus *Provanna* has been collected away from chemosynthetic communities, its association with these systems has lead to the view that it is primarily a seep and vent endemic. Ten or more species exist associated with the chemosynthetic systems of the Pacific. *P. sculpta* seems to be the only member of the genus yet found in the Atlantic. The genus has been placed in the family Abyssochrysidae, a relict of a largely extinct group (Houbrick 1979). A comprehensive monograph of the genus *Provanna* has not yet been published, but Warén and associates have produced a series of papers describing new species from seep and vent systems and refining the description of the genus (Warén and Ponder 1991). Being small and matching mussel periostricum in color, it is largely unobserved, but very numerous. Present at all sites sampled, it is notably rare at the Brine Pool site. The shell usually shows deep dissolution pits which are often the settlement site for juvenile mussels. *Provanna* lacks a planktotrophic form, but it is not known if it has a dispersive developmental stage or not.

Cataegis meroglypta is a radular browser up to 2 cm across. It is similar to shallow water snails in that its shell is ornamented, retains color (light green) and is nacreous. Previously, *Cataegis meroglypta* McLean and Quinn has been the third most abundant gastropod found. It is now obvious that it sometimes becomes dominant. The genus was erected for two species of continental slope trochid, *C. finkli* and *C. meroglypta* that are apparently opportunistic non-seep grazers (McLean and Quinn, 1989). The former species was found at slope depths associated with seagrass falls, and the latter in the upper slope seep systems. Warén and Bouchet (1993) have reviewed current information about the species. Since *C. meroglypta* has not been reported from outside of a seep environment, it may be endemic. Larval development is unknown.

Endemic Sublethal Predatory Crustacea.

On the whole, the grab sampler of the Johnson Sea-Link is poorly suited for collecting small crustaceans capable of quickly swimming away. Therefore, it is assumed that this group has been undersampled. Crustacea living in close association with mussel mat and tube worm bushes are a common galatheid, *Munidopsis* sp., a much rarer galatheid *Eumunida picta* and the shrimp *Alvinocaris stactophila.* The first and last of these comprise the endemic crustaceans.

Hydrothermal and hydrocarbon chemosynthetic communities often have high populations of three caridean shrimp genera, *Alvinocaris*, *Rimicaris*, and *Chorocaris*. Since these genera are new to science, the taxonomic position is not well established, However, they appear to represent a distinct group with common phylogenetic affinities. Originally placed in the family Bresiliidae (Williams and Chace 1982). Subsequently, the new family Alvinocarididae was proposed (Christoffersen 1989) to contain these forms. All Alvinocarids share a large chela with a finely serrated blade edge well suited for snipping small bits of tissue. Two species of *Alvinocaris* have been found in Gulf of Mexico chemosynthetic systems. The hydrocarbon seeps on the upper continental slope are populated by *A. stactophilia* and both known deeper systems are populated by *A. muricola*. A key to the three species of *Alvinocaris* has been developed by Williams (1988) and was the basis of identification of the specimens collected in this study. It is especially noteworthy that none of the 42 benthic shrimp reported on the typical Gulf of Mexico deep-sea floor are found in the seep community. Although *Alvinocaris stactophilia* appears to have the typical caridean feeding habit of predator/scavenger, one member of the Alvinocarididae, *Rimicaris exoculata* , is specially adapted to feed upon epibiotic chemosynthetic bacteria living on its cuticle. This symbiosis involves epibiotic bacteria on the mouth parts (Van Dover, et al, 1988) and in the prebranchial chamber (Gebruck et al. 1992; Segonzac et al. 1993). A general review and detailed examination of the feeding of three species of Alvinocarididae at a mid-Atlantic ridge site has been given by (Segonzac et al. 1993).

The abundant *Munidopsis* found associated with mussel beds remain undescribed. It is somewhat larger than the *Alvinocaris*, being up to 4 cm in body length (exclusive of the chelae). The species has two large forceps-like chelae which can grasp small bits of tissue. The genus is widely distributed in the deep-sea and is often a commensal on gorgonians. Juvenile mussels less than 0.1mm across have been found clinging to the hairs on the body.

Predator and Scavenger Colonists and Vagrants

The predatory and scavenging feeding group in the seep communities are not endemic, but are come from the background fauna. The distinction between colonist and vagrant is unavoidably vague. Colonists are found in the background, but reach relatively high population levels in the seep area. As such, they are more characteristic of the seep. Two species seem to fit this description well, the predatory snail *Buccina canatae* and the predatory seastar *Sclerasterias.* In order to say that a particular animal is a vagrant, it is necessary to know that their abundance on the typical slope is similar to that in the seep. In reality, we have little information about population densities in either habitat. Seep sites are visited by more than ten fish species and a similar number of large crustacea. Some of these may better fit in the colonist category than the vagrant.

Sclerasterias sp. is a predatory seastar found on the upper continental slope in the Atlantic (Clark and Downey 1991). It can be considered a colonist at seep sites in the Gulf. Pequegnat did not report any specimens of *Sclerasterias*, but the NGMCS study (Gallaway et al. 1988) did trawl one in the vicinity of a seep site. The specimens collected at seep sites most closely resemble *S. tanneri*, however, the taxonomic traits used are complex and hard to distinguish. *Sclerasterias* is a prominent feature of seep communities, but often goes unobserved, being hidden between the mussel shells and in the center of tubeworm clumps. It is a stomach everting predator and has been observed preying on both mussels and tubeworms. A keystone species regulatory role may be suspected.

Buccina canatae is a predatory neogastropod that can be considered a colonist. The genus *Buccina* is a cosmopolitan complex common on continental slopes. Both Pequegnat(1983) and NGMCS (Gallaway et al.1988) reported the genus from typical background samples. *B. canatae* has been collected from seep and non-seep environments in the Gulf of Mexico and Caribbean (Warén and Bouchet 1993). Initially observed on the sediment surface of clam areas, it appears to forage widely and form aggregations. Aggregation may be related to mating. One aggregation collected from a clam bed contained 48 individuals. During the 1992 dive series *B. canatae* were conspicuous within mussel beds at Bush Hill. The species was found at all sites.

Three crab species, *Rochina crassa, Trichopeltarion* sp. and *Nibilia antilocarpa* , have been found directly in mussel beds. Other large mobile crustacea are conspicuous in seep areas but less commonly in direct contact with vent communities. These include the decapods *Paralomis cubensis, Chaceon quinquedens*, *C. fenneri,* and the giant isopod *Bathynomus giganteus.* All of these are capable of shell crushing with jaws or chelae. As there is no reason to think that seep-area populations are especially high, they should be considered vagrants. The large fishes are much like the large crabs; it is hard to decide if they should be considered as colonists or vagrants. More than ten species of fish have been sighted during dives, but only four seem to have a close affinity for the vent communities: *Eptatretus* sp. (hagfish), *Synaphobranchus* (cutthroat eels), *Urophycis cirratus* (hake), *Hoplostethus* sp. (orange roughy), and *Chaunax suttkusi* (previously *C. pictus).*

Conclusion

While there is definite site-to-site variation in exact species composition, both the chemosynthetic species, the endemic consumers, the colonists, and vagrants are the same from Viosca Knoll in the east to Garden Banks in the west. Although there is *Beggiatoa*-colonized methane and sulfide seepage shallower, mussel and tubeworm communities are not established shallower than 400 m.

Recommendations on Future Faunal Studies

There is limited management utility in continuing to survey fauna in the northern Gulf less than 1000 m depth. The uniformity of the species composition seems adequately established. It is, however, recommended that future studies focus upon the three major remaining questions.

- Depth Patterns Deeper Than 1000 m. - In spite of the uniformity of upper slope community structure, deepest slope-base seep sites are faunally distinct. This implies that at some unsampled depth there is a transition in species composition. Finding that transition depth and describing the nature of the change may help define what conditions limit the distribution of these communities. Of direct management consequence is the possibility that seeps somewhere deeper than 1000 m may require different management strategies.
- Population Studies I- While the very uniform species composition of the upper slope suggest a community capable of dispersion over large distances, this conclusion seems in contradiction to what we know about actual dispersive capabilities. For example, the very common snail *Bathynerita* seems to lack a dispersive stage. Any future seep studies should give high priority to well designed and expertly executed population studies that assess fecundity, dispersion, and actual gene flow.
- Populations Studies II- Although the habitat-forming mussels and tubeworms are the most conspicuous component of seep communities, the vagrants and colonists comprise a group of special management relevance. As wide ranging organisms they are the component which links seeps to the background community. As large predators, these animals may be capable of regulating seep populations. Future studies should determine the actual degree of trophic transfer and the predation pressure exerted on the seep fauna by the vagrant species.

4.4 Causes of Variation in Seep Communities

In the preceding sections, it has been stressed that the species pool that contributes to seep communities remains remarkably similar across the northern Gulf between 400 to 1000 m. Therefore, the management task of detecting impact is simplified. Two types of impact can be anticipated and recognized by simple faunal comparisons. First, gross impacts may interrupt the methane/sulfide flow and cause the seep assemblage to go locally extinct. Second and more subtle, flow rates and biological interactions may cause a dominance shift in the chemosynthetic and heterotrophic components. The persistent shift from mussel to bacterial mat seen in the cage experiment might be reflective of such an impact. The natural site-to-site dominance shift of the three endemic browsing gastropods may also reflect local variation of the geochemical habitat.

As with any impact study, management's greatest problem will be establishing the causal link between an obvious community change (extinction or dominance shift) and suspected impacting activity. This will be difficult because we do not know how often either type of shift takes place naturally. Determining these "transitions" will be quite difficult, with the only practical method being dependent upon the traditional ecological approach of trading place for time. In effect, variation among many places is interpreted as being due to a common underlying process at many different stages of development.

In this section, two models of geological and chemical change at seeps are considered. Each helps to explain community difference place to place. Both are, however, still quite preliminary and conjectural. The first has appeared in the open literature (Roberts and Carney 1997). They second is still under development.

A Geological Model for Seep Development

On the basis of evidence accumulated from a variety of sources, Roberts and Carney (1997) proposed a model that considers seepage of methane and sulfide as part of a larger system of complex slope processes. Ecologically, this model serves only to help explain fauna patterns at two extreme seep environments (new seeps without a community and old seeps with extensive communities). Most areas of seepage lie in a poorly resolved “intermediate group”. It is, however, a starting point and warrants management attention. Stating the model from the perspective of the seafloor, a series of processes give rise to the creation of seepage conduits. These conduits, that allow for the persistence of seep communities, must come in many sizes, shapes, and flow rates. Accordingly, there are some long-lived seep communities associated with large persistent conduit systems, and others that survived only a brief time. Unless the natural range of seep community persistence is known, it may be confounded with oil and gas activities.

Sediment deposition is a critically important habitat-shaping process on the Gulf of Mexico continental slope, since the region has received exceptionally high amounts of sediment over geological time from the Mississippi and proto-Mississippi River. These sources have been active since the Cenozoic (Winker 1982). At the same time that the exact points of deposition have been shifting, eustatic sea-level change shifted deposition between inner and outer shelf (Pacht et al. 1990). Salt tectonics is a much more recently developed field of geology. Its influence is obvious, but much less well understood. Ultimately salt migrates in response to compression and density differences with the overlying sediment layers. Given these relations with the accumulated sediment, it is not surprising that the growth, locations, and orientations location of salt bodies is influenced by variations in sedimentation rate (Talbot 1993, Vendeville and Jackson 1993).

The regional topography of the northern Gulf is dominated by domes, canyons, and basins. This area has more than 100 basins with relief of more than 150 m, 28 domes, and eight submarine canyons of various size (Bryant et al. 1990; Bouma and Bryant 1995). There is a transition on the slope in the effect of salt tectonics. Shallower than 2,000 m, basins lie between shallow salt masses, but deeper salt sheets or nappes underlie basins. Faults in this region range from deep growth faults thousands of meters deep to small compensating faults less than a hundred meters in depth. It is this spectrum of faults that provide the conduits for fluids, gases, and sediment slurries. Superimposed on regional fault-generated patterns is a broad spectrum of smaller scale topographic features probably created by mass movement (slumping, turbidity flows, etc.). The seafloor manifestation of faults combined with mass-movements is a series of features associated with seepage ranging from rapid to slow. On the northern Gulf continental slope, seep features range from massive mud-flows and mud volcanoes (Neurauter and Bryant 1990; Kohl and Roberts 1994; Neurauter and Roberts 1994), through gas hydrate deposits (Kennicutt et al. 1985), to carbonate buildups (Roberts and Aharon 1994).

4.4.1 The Fault Conduit

In spite of the complexity of the northern Gulf continental slope, the common trait of all seepage features is association with a fault that provides the necessary conduit (Behrens 1988; Roberts 1995). The slope province in the Gulf is marked by linear seep features lying along the surface of a fault (Roberts 1995). The actual mechanics of conduit formation and seepage are currently under investigation (Roberts and Nunn 1995). Unfortunately, it is not yet possible to discuss the size and persistence spectrum of conduits and the ecological systems they support, since the controls on frequency of fault movements and flux rates are unknown. The consistent presence of natural oil slicks on the Gulf's surface suggests that seepage and venting of hydrocarbons is a widespread and ongoing process (MacDonald et al. 1993).

Conduits carrying rapid, high volume discharges may expel fluid muds with or without liquid and gas hydrocarbon. Conduits carrying slow low volume discharges are the ones typically associated with chemosynthetic communities. In the setting of very slow seepage precipitation of carbonates and barite occurs (Roberts and Aharon 1994). Most important to the development and persistence of seep communities is the observation that some seep features seem to have undergone a geological succession.

4.5 Classification of Seep Features

The Roberts and Carney model classifies all seepage areas into one of three categories.

Rapid Venting Mud-prone features

Vertical migration of gas and fluids through unconsolidated sediments may create a slurry-like mixture of sediment, gas, and water that forms conical "mud volcanoes" (Hedberg 1974). Such "volcanoes" and lower relief mud sheets have been observed in the Gulf of Mexico (Neurauter and Bryant 1990; Neurauter and Roberts, 1992, 1994). Roberts and Carney (1997) cite Green Canyon, block 143 as an example of such a mud-prone feature. This 450 to 500 m in diameter cone lies in a water depth of

335 m, and rises to a height of 35m above the surrounding sea floor. Active mud volcanoes show no sign of cementation, but dormant ones may (Neurauter and Roberts 1994). The fact that these structures reflect conduits into the deep slope sediment has been confirmed from Pleistocene and even Miocene foraminifera in the cone's expelled sediments (Kohl and Roberts 1994).

In every mud volcano so far examined, living chemosynthetic fauna is limited to *Beggiatoa* mats lying on the surface of the mud slurries. Background fauna is also absent, and the surface of mud sheets show minimal amounts of lebenspurren. The rapid expulsion of liquid and sediment produces a substrate unsuitable to colonization by epifauna and infauna. There may be scattered development of vesicomyid and lucinid clams peripheral to the unstable sediments.

Very Slow Venting Mineral Prone Features

Mineral-prone features are associated with very slow seepage rates and can be considered the opposite of mud-prone systems. The flux of fluid mud and hydrocarbons to the sea floor at such features has decreased dramatically leaving mineral-rich fluids, small amounts of gas, and perhaps traces of crude oil to affect seafloor geology and biology. Barite chimneys and crusts precipitate at local discharge sites. These mineral-prone systems are typically associated with large salt domes. The top of these domes have complex but shallow fault networks truncated by the underlying salt. Seepage is too slow to sustain a complex chemosynthetic community, but there is methane discharge and carbonate precipitation by methanotrophic bacteria. Faunal communities tend to be limited to methanotrophic mussels with only scattered tube worms and Beggiatoa mats suggesting low sulfide levels. Green Canyon 140 is cited (Roberts and Carney 1997) as an example of a mineral-prone system. Strong evidence that mineral-prone features have developed over a long time come from radiometric dating of barite chimneys which range from 194,500 to 133,000 years old (Roberts and Aharon 1994).

Slow seepage sites have a fauna similar to that of transitional areas but differ in spatial distribution (Roberts and Carney 1997). In such sites, hard substrate dominates the center and sediments are restricted to the flanks. Therefore, tube worm and mussel beds may dominate the centers. Since seepage conduits may be blocked over large areas by rock, community development is restricted to relatively small sites within the larger rocky region. Rock areas remote from seeps may be populated by typical deep reef species of sea fans, corals, and other non-chemosynthetic species.

Transitional Features Between Rapid and Slow Venting

According to the Roberts-Carney model, the most extensive development of seep communities takes place at conduits which are intermediate between the too extremes of mud-prone and mineral-prone. For these communities to thrive there seems to be three important needs, methane, sulfide, and hard substrate for attachment. Transitional flux rate sites are distinguished by a patchwork of interspersed soft and hard bottoms and can be expected to contain a relatively more diverse fauna, due to the heterogeneity of conditions. However, communities are divided into distinct patches. Bacterial mats may dot the surface of sediment areas which contain lucinids and vesycomiid clams, whereas mussels and tube worms share the same rocky areas as the more ubiquitous bacterial mats. The Bush Hill (GC185) site falls into this category and has the most extensive development of a chemosynthetic community so far found in the Gulf. Deep reef sea fans may be present with other nonseep species, but rock surfaces will tend to be populated by chemosynthetic forms.

Hard substrate is characteristic of all slower venting systems. Sea-floor lithification at seep sites ranges from isolated nodules in sediment to massive structures that may take the form of pavement-like slabs or mound-like buildups (Roberts et al. 1992). When methane and/or sulfide are present, these structures form the physical substrate to which fauna attach. These are considered authigenic carbonates composed primarily of ^{13}C-depleted calcite and aragonite produced by microbial oxidation of hydrocarbons (Ritger et al. 1987, Paull et al. 1992). The ^{13}C signature is considered the main evidence of the hydrocarbon origin. Slope carbonates from the Gulf display various amounts of ^{13}C depletion ($\delta^{13}C = -23$ to -55‰ PDB) (Roberts et al. 1992). This range of values is largely attributed to the parent source of carbonate carbon, which is interpreted as having been derived from microbial degradation of hydrocarbons ranging from crude oil to biogenic methane.

When methane is present and seeping slowly, two special conditions can arise. First, the microbial system (Boetius et al. 2000) needed for production of hydrogen sulfide develops. Second, gas hydrates may form providing a relatively stable reservoir for methane that might mediate fluctuations in the conduit system (Carney 1994). Hydrate features may be mounds such as Bush Hill in GC 185, oblate flats (GC 180-181), or elongated along a fault line (GC 232-234). Abundant chemosynthetic communities are usually associated with combinations of hydrates, hardgrounds and massive authigenic carbonate rocks. It is suspected that development of a methane-driven hydrogen sulfide seep must require a narrow range of flow rates and duration. Seepage rate must be directly related to the delivery system, the complex of fault created conduits. In the GC 140, GC 184, and GC 185 area. With respect to duration, major seepage may have only begun in the Pleistocene (Cook and D'Onfro 1991). At that time a major thrust fault was initiated by salt movement. With respect to rates, there are sites which seem to have evolved from rapid venting (mud-prone) to slow seepage (mineral-prone). Good examples of areas in this evolution are found within GB 338 and GB 382 which overlie a subsurface salt ridge.

4.5.1 Evidence of Episodic Seepage

If seepage is episodic, then seep communities can be expected to arise and fail naturally. In order to prevent this natural process from being attributed to oil and gas operations it is important to understand the process. The Roberts-Carney model accepts that much seepage is episodic. The episodic release of fluids and gas from overpressured subsurface compartments has been recorded in mineral deposits in the Gulf Coast basin (Cathles and Smith 1983; Cathles 1990). Sulfide layers in the Winnfield salt dome (Ulrich et al. 1990) provide very good evidence. These were created by episodic release of reducing waters. Paleomagnetic dating of these sulfides indicates a frequency of around 300 yr. (Kyle et al. 1987). These results are compatible with recent numerical modeling solutions that suggest that fluid expulsion from geopressured sediments of the northern Gulf of Mexico occurs in short-lived events (Roberts and Nunn 1995). This and other studies (Ranganathan and Hanor 1989; Roberts and Nunn 1995) suggest that expulsion events create local, transient anomalies in overlying sediments in short periods of time, perhaps less than 100 yr. A recent two-dimensional finite element model of a SEI (South Eugene Island) 330 area sedimentary basin (Roberts et al. 1996) suggests that excess fluid pressures in abnormally pressured sediments would drop to approximately half of their original value after about 10,000 yr. of expulsion. They also estimate by variable fault permeability simulations, where compaction of fault zone sediments closes the fracture network, that fault permeability decreases by one to two orders of magnitude within 200 yr. after fluid expulsion begins.

4.5.2 Has Faunal Succession Been Seen?

If there is a geologically-controlled transition in seepage rates over time as reservoirs are exhausted and conduits opened and closed, is there a faunal succession? In terms of species composition and abundance the answer is a qualified yes. Rapidly seeping systems are only successfully colonized by *Beggiatoa*, indicating that hydrogen sulfide is already being produced in these early-state system. The sessile metazoans, however, require a stable substrate and can only be successful when lithifaction has had time to take place. Ultimately, as the system slows even more and becomes mineral-prone, overall population decreases, but species composition remains the same. Since no one has actually witnessed the onset of hydrocarbon seeping, we do not know the colonization sequence of the metazoans. Two lines of evidence suggest that once the inhibitory nature of rapid venting ceases, colonization can be rapid and no subsequent succession takes place.

Speed of colonization has been confirmed in direct observation of a new Pacific hydrothermal site over a 2-yr period. In the hydrothermal case, Lutz et al. (1994) dove in April 1991 on a recent eruption site in the east Pacific at about a 2,500 m depth. Thick bacterial mats were widespread but conspicuous chemosynthetic metazoans absent. Eleven months later (March 1992) the bacterial mats had retreated and one species of tube worm with tubes up to 30 cm. long had established colonies. Less than 2 yr. later (December 1993), a second tube worm species had colonized the site, reached tube lengths in excess of 1.5m and become reproductive. In the Gulf case absence of apparent succession has been noted for death assemblages at chemosynthetic sites (Powell 1995) where slumps had periodically killed communities. There was no sign of species succession during reestablishment. These results, however, only address soft bottom communities.

4.5.3 Limitations of the Model

At its present level of development, the model's ecological utility is limited to the extreme cases. Mud vents lack seep communities since they create an unstable substrate. Mineral-prone systems still retain a full suite of seep species, but community development is sparse, since the conduit system has become heavily mineralized and ineffective. Presumably it can take 1000's of years to make the transition from one state to the other. Therefore, such a fluid-to-mineral transitions are unlikely to be confused with oil and gas impacts. With additional refinement, however, the model may help identify geological structures, isotopic signatures, or mineral suites which could be used as shorter-term chronometers for assessing seep system on management-relevant time scales.

Development of a Chemical Gradient Model

On a finer scale (10's of meters) the species comprising seep communities can show dramatic, but inconsistent, segregation. Why don't the thiotrophs (tubeworms, *Tamu fisheri*, and *Beggiatoa* consistently co-occur in close proximity? Sometimes they do; often they do not. The large-scale Roberts-Carney model provides no clues.

A simple explanation for the inconsistent spatial segregation of thiotrophs may be that there is competitive displacement within the sulfide gradient. In order to examine this possibility it is necessary to carefully consider the nature of the gradient. Biogenic methane and sulfide are tightly linked by a the complex system of bacterial carbon diagenesis. The overall types and sequences of reactions generating these gases are considered to be ubiquitous but show great geographic and even greater bathymetric variation. In the typical ocean, methane-sulfide system is largely controlled by the influx of organic detritus (Janhke et al.1982). Photosynthetic detritus sinks to the sea floor and is progressively reduced in route by consumer organisms. Biological demand can be so great that oxidizing agents are totally depleted. In the anaerobic sediment, seawater-derived sulfate serves as an electron acceptor and produces sulfides. Deeper, sulfate is exhausted, methane is produced by several pathways. This detritus-driven production of sulfides and methane is characteristic of shallow marine sediments where detritus input is high (Martens and val Klump 1984). Sulfide production in typical (without seepage) deep-sea sediments is meager, and methane even lower (Bender and Heggie 1984).

Deep chemosynthetic communities are not supported directly by detritus-driven methane and sulfide production since the rates are too meager. Rather, they are dependent upon a system that may be thought of as upside down. Organics in the form of liquid petroleum and methane enter the zone for bacterial anaerobic metabolism from the bottom. As complex hydrocarbons pass through the zone of bacterial fermentation, some additional methane is produced. Above that layer, sulfate reducing bacteria are encountered that oxidize methane and other organics with sulfate coming from the overlying seawater (Boetius et al. 2000). At this point both gases needed for thiotrophic and methanotrophic organisms become present. Sulfide having been produced from the flow of methane. Of the two gases, sulfide is far more reactive and can yield substantially more energy to the organisms. Just above the sulfate reducing layer, denitrifying bacterial consume the sulfide, and at near the sediment-water interface surface aerobic bacteria consume what is left. The less reactive methane diffuses from the sediments.

The feature that distinguishes the Gulf of Mexico's methane driven system is that it has so many sources of carbon (biogenic methane, thermogenic methane, and liquid hydrocarbons). Of special interest today are the solid hydrates of methane. Hyndman and Davis (1992) have proposed that hydrates do not require the supersaturated solutions predicted from physical chemistry. Thus, even meager biogenic methane in upward migrating pore fluids may "freeze" into concentrated hydrates at the lower boundary of a pressure/temperature stability zone for the solid phase. Methane dissolving from the layer of hydrate at local points of instability could vent through the sea floor at high concentrations. Once in contact with seawater sulfate and a bacterial flora, sulfide would be generated by methane oxidation-sulfate reduction and added to the concentrated upward flow.

The manner in which bacteria, tubeworms, and mussels take up hydrogen sulfide are quite different. These differences combine with the distinctive morphology of the animals to give each a very distinctive geometry of sulfide exploitation. This geometry of exploitation may explain the exclusion of some of the biota by the others. It is known that the Gulf seep tubeworms, both *Lamellibrachia* and the *Escarpia*-like genus, have a large portion of their total length in the form of a buried narrow tube. This "root" is thinner and much more flexible than the exposed section. Increasingly, it is suspected that the "root" is the primary sulfide uptake organ (Julian et al 1999). If there is a dense clump of tubeworms, there "roots" can be buried in sulfide-rich sediment layers. Closer to the sediment-water interface, oxidation might consume upward migrating sulfide. This deep consumption and upper oxidation would preclude both bacteria and mussels from obtaining any sulfide. A bacterial mat could, similarly preclude mussels from obtaining any sulfide. Methane, however, being relatively non reactive would escape to fuel organisms at the surface.

In effect the model says that the gradients of methane and sulfide are linked in the sediment layer where they are created, but then are influenced by different biological processes. The particular species composition of the community is controlled by the final form of the gradients. Some organisms, notably the tubeworms, have a morphology that suggests that they can exploit the gradients to their benefit and to the detriment of potential competitors. If this is the case, communities shape, rather than just exploit the geochemical gradients. An initial impact upon a community can lead to alteration of the gradients that feeds back to impact the community even more severely.

In terms of the fauna, this competitive gradient utilization model is very well suited to testing. It simply requires a carefully designed mapping of the fine scale geometry of the community, describing the actual geometry of the regions of methane and sulfide uptake. Meaningful measurement of the gradients, however, will be the difficult part. Presently, the geochemical studies of the seep system are being conducted on the time and space scale convenient to the geochemist. Development of more appropriate scales and times will be a major undertaking.

4.6 Conclusions

Site-to-site and within-site variation of seep communities in the northern Gulf of Mexico between 400-1000 m involves a limited suite of species. This is true for the chemosynthetic organisms that contribute the biogenic structure of seep communities and to those consumer species that are endemics, colonists, and vagrants. The primary contribution of examining additional sites within that depth band has been: (1) confirmation of previous conclusions, and (2) refinement in our understanding of the upper depth limit of seep community occurrence. The uniformity of component species suggests the existence of large, genetically linked, populations that may be able to repopulate areas experiencing severe impact.

While the population structure of seep species may be such that repopulation is possible, the limited experiments reported herein detected little or no such recruitment over more than 5 years. That some species can disperse has been confirmed; the larvae of Lamellibrachia have been cultured (Young et al. 1996). Recruitment is either slow and sporadic, or the experiments altered the habitat to such a degree that they were no longer suitable for settlement. This latter possibility finds some support in the idea that the critical methane and sulfide gradients are shaped by the locally dominant species. Removal of one species might shift the gradients and support settlement of a different species. This would seem to imply a degree of frailty that may be of management concern.

4.7 General Recommendations

The seep systems in the Gulf of Mexico comprise one of the most extensively studied chemosynthetic communities in the ocean. As such, more is known about the distribution of the system and the biology of the component species than anywhere else. However, in the course of investigation a certain bias has crept into interpretations. The studies have gained considerable understanding of the organisms at four sites at the sacrifice of a broader understanding of place-to-place and time-to-time variation. It is the contention of this review that a good estimation of these time and place variations is of greatest management need. It is this natural variation that will set the limits of detection for man-induced impacts.

It is recommended that future investigations employ a greater geographic range focusing narrowly at wide-spread sites on issues of population recruitment and response to change. The following studies should be considered.

- Confirmation of Genetic Continuity - Estimation of genetic similarity in the chemosynthetic, endemic consumers, colonists, and vagrants should be undertaken as a major research task. Such estimation should focus upon sites selected to test specific hypotheses about depth (500 to 3500 m) and regional variation. Due to the relatively few species (15 or fewer would suffice), and the large size of the animals, it is possible to do this at the zygote (egg) level. This would eliminate confounding effects of post-zygotic selection that often limit the utility of such studies.
- Testing of Competitive Gradient Use Model - Microprobe technology should be used to map methane and sulfide gradients in the root tangle of tubeworms and under bacterial mats. Special attention should be devoted to the possibility that organisms intercept sulfide in and below the nitrate reduction zone, thus controlling the form of the overlying thiotrophic community. Once a means of fine scale mapping has been devised, well-designed experimental manipulation may provide strong tests of the model.
- Response to Controlled Impact - A program of well designed and appropriately replicated experimental impacts should be initiated. If possible, these could be carried out in cooperation with industry activity. Annual response sampling by submersible must be augmented with deployed systems. Arriving at an appropriate design will be a major intellectual task.

- Colonization of Artificial Seeps - The obverse of impacting a natural system and watching what happens is to create an artificial seep with appropriate conditions and then predicting what will happen. Such an experiment will require development of deployable methane and sulfide generators which provide suitable surfaces for settlement. Sulfide generators have been deployed and colonized by tubeworms (Carney, in preparation).

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The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The MMS **Minerals Revenue Management** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.