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Diversity and Distribution of the Deep-Sea Ichthyofauna of the Gulf of Mexico with Outlooks On Conservation

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DIVERSITY AND DISTRIBUTION OF THE DEEP-SEA ICHTHYOFAUNA OF THE GULF OF MEXICO WITH OUTLOOKS ON CONSERVATION

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The Honors Program
in partial fulfillment of the requirements
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ABSTRACT

The ichthyofauna of the Gulf of Mexico has been fairly well documented as a consequence of the extensive fisheries activities and hydrocarbon exploration in these waters. However, the diversity and distribution of the deep-sea species remain poorly understood. This study examines the vertical distribution of fish species in the Gulf of Mexico as well as the changes in taxonomic diversity with depth. Species richness was found to decrease exponentially with depth while maximum depths species occupy closely correlates with traditional oceanic zone boundaries. The clade Percomorpha was found to account for the majority of the taxonomic diversity in the Epipelagic, below which the species richness of this clade decreases, as other taxonomic groups account for proportionally more of the diversity in the deep-sea. Conservation threats posed to deep-sea species also were investigated by examining the vertical and geographic distribution of benthic and demersal Rajiformes (skates) and Squaliformes (dogfishes) in the Gulf of Mexico. Using geographical coordinates of specimen capture and ArcGIS mapping, ranges of 33 Chondrichthyan species were examined and used to determine potential threats associated with oil and gas drilling. The results demonstrate the need for a better understanding of the biology of deep-sea species in order to accurately assess threats posed to poorly known deep-sea inhabitants.

Chapter 1: Diversity and distribution of the deep-sea ichthyofauna of the Gulf of Mexico

Introduction:

The word “ocean” brings various images to mind: waves of aquamarine water gently lapping against white sand beaches while children laugh and play happily in the calm shallow waters; or surfers swimming into the open ocean, waiting to ride the large cresting waves that come crashing and foaming onto the beach as the scent of brine floats in the sea breeze. Immediate images of bright rainbow colored, charismatic reef fish swimming around their home of colorful anemones, sponges, and corals rush to the mind of any snorkeler, scuba diver, or *Finding Nemo* watcher. For others, the word brings a more fearful image to mind: ice blue water, stretching undisturbed as far as the eye can see - an endless blue abyss. Monsters from sailors’ stories lurk unseen beneath the surface. An unmistakable grey triangle shatters the calm, desolate, glass-like surface. It undoubtedly belongs to a man eater, Jaws, waiting patiently for his next meal to fall into his watery world.

Whatever comes to mind, calm, fun, or frightening, the first thoughts of the ocean do not typically include the deep sea. It is a realm full of mystery and oddities, unrecognized by many people. A black abyss, where little to no light penetrates, is teaming with alien-like life. The deep sea and the bizarre creatures that live there remain less explored and more poorly understood than the surface of the moon. This is an investigation into some of these incredible deep-sea creatures and various aspects of their diversity, distribution, and the threats humans pose to them.

The Ocean and the Deep-Sea

The world's oceans cover 71% of the Earth's surface (NOAA, 2013), attaining an average depth of 3800 m (Nouvian, 2007). With such substantial depths, approximately 99% of Earth's potential for housing life is held in the ocean waters, 85% of which is contained in the low light or lightless waters of the deep sea (Nouvian, 2007). Approximately 68% of Earth's surface is covered with water deeper than 200 m (Angel, 1997) while waters deeper than 1000 m still account for 62% of Earth's total surface coverage (Davies et al., 2007). The waters of the deep sea hold more than 100 times the collective volume of the rest of the world's water, making the deep sea one of the largest environments in the biosphere (Haedrich, 1997; Nouvian, 2007; Ramirez-Llodra et al., 2011).

The ocean's waters are commonly divided into four zones (Fig. 1-1) determined by the intensity of light at depth in clear oceanic water along with the relationship to the base of the continental land masses (Angel, 1997; McEachran & Fechhelm, 1998; Herring, 2002; Robinson et al., 2010; Ramirez-Llodra et al., 2011). The first zone, the epipelagic, extends from the surface down to 200 m. Almost all sunlight (~99%) is scattered or absorbed by 150 m, leaving only blue wavelengths to penetrate the deeper waters (Robinson, 2004). This makes the epipelagic zone the only part of the ocean where photosynthesis can occur (Gallaway et al., 2001). Below the epipelagic zone (220 m), the deep sea begins, characterized by waters where very little or no light is found (Angel, 1997; Gallaway et al., 2001). The mesopelagic zone extends from 200 m to a depth of 1000 m and can be broken into the upper mesopelagic zone and the lower mesopelagic zone with the dividing line lying at about 600 m – 700 m (Angel, 1997). Only trace amounts of light penetrate the mesopelagic waters, resulting in twilight, or disphotic, conditions (Angel, 1997; Gallaway et al., 2001). Even in the clearest oceanic waters, virtually no light penetrates beyond 1000 m. This creates the aphotic conditions of the bathypelagic and abyssal zones (Angel, 1997; Gallway et al, 2001). The bathypelagic zone extends from 1000 m – 6000 m and can be broken into the upper bathypelagic (1200 m – 2300 m) and the lower bathypelagic (2400 m – 4000 m) zones (Robinson, 2004). Below this lies the abyssal plain, which stretches along the ocean's floor at depths greater than 6000 m. Although these distinctions in oceanic zones are well agreed upon, variations in continental margins and local bathymetry can result in differences in the zonation from place to place (Angel, 1997).

Exhibiting no viable means for primary production through photosynthesis, extremely high pressures, and very low temperatures, early scientists believed these deep ocean waters to be devoid of life. This hypothesis was disproved in 1872 with the HMS Challenger's four year circumnavigation of the globe (Van Dover, 2007; Robinson, 2009). During the Challenger Expedition, led by Sir Charles Wyville Thomson, trawls scraped the sea floor at depths up to approximately 5 miles (8047 m). Over 4000 new species were discovered and described by the expedition, revealing the previously unrecognized biodiversity of the deep sea (Van Dover, 2007). Since then, our knowledge of the deep sea has only increased, further demonstrating the diversity of the biotic communities in this ecosystem.

Deep-sea inhabitants have had to adapt to life in a very extreme environment compared to their shallow-dwelling counterparts. As depth increases, temperatures drop until they approach freezing, seasonal variability declines, and dissolved oxygen content in the water decreases. Likewise, pressure increases 1 atm with each 10 m of depth, resulting in pressures exceeding 100 atm in the bathypelagic zone (Haedrich & Merrett, 1992; Gallaway et al., 2001; Smith & Brown, 2002; Robinson, 2004; Robinson 2009). Very little, if any, light extends into the deep sea, making photosynthesis impossible and strictly limiting the amount of energy available to organisms (Pequegnat, 1983; Haedrich & Merett, 1992; Gallaway et al., 2001; Smith & Brown, 2002; Gartner et al., 2007). At 1000 m, the biomass available as energy drops to only 5% of that which is found above 200 m (Gartner et al., 1997).

Some primary production occurs at hydrothermal vents via chemoautotrophic organisms. However, the majority of deep-sea inhabitants directly or indirectly rely on energy from the epipelagic zone (Pequegnat, 1983; Haedrich & Merrett, 1992; Gartner et al., 1997; Smith & Brown, 2002; Gartner et al., 2007). Deep-sea organisms receive nutrients from the surface waters via transportation in currents or downwellings. Dissolved organic matter from the epipelagic zone also falls to the depths in the form of "marine snow," providing many deep sea organisms with a source of nutrition. Likewise, marine and terrestrial plants and animal carcasses sometimes sink to the bottom of the ocean where they become food for deep-sea benthic communities. Some deep-sea species do not wait for the organic matter to drift down from the epipelagic. Many deep-sea species of the meso- and upper bathypelagic zones feed on planktonic organisms found in the surface waters where they are more concentrated. In order to avoid predators during daylight hours when they are more visible, these species travel to the surface at night to search for food, returning to the depths of the mesopelagic zone at dawn (Herring, 2002). These daily vertical migrations are known as diel-vertical migrations and make up one of the largest migrations in the animal kingdom (Fothergill, 2001). After feeding in the epipelagic zone, the migrators carry the food down to the deep-sea, where they then excrete their gut contents in the nutrient poor oceanic zone. In this way biomass, nutrients and carbon are cycled back into deep-sea environments (Angel, 1997; Haedrich, 1997; Herring, 2002; Youngbluth, 2007).

Fish of the Deep Sea

Despite these extreme environmental conditions associated with deep-sea habitats, 10- 15 % of known fish species are found to inhabit these waters (Gartner et al., 1997) and evolutionary adaptations for living in these conditions have convergently evolved in at least 22 orders of fish (Weitzman, 1997). Some of these adaptations include reduced metabolisms, ambush predation strategies to reduce swimming distances, and increased olfaction and mechanosensory detection to account for low-light conditions (Montgomery & Pankhurst, 1997). An estimated 90% of deep-sea inhabitants are also able to produce light for communication, mating, foraging, or predator avoidance

(Robinson, 2004). These are just a few of the adaptations species have evolved for inhabiting the extreme environments of the deep-sea.

Observations that some taxonomic groups appear to be more prevalent in certain zones has led to various hypotheses about the colonization of the deep-sea. One such hypothesis observes the frequent occurrence of Perciformes, a relatively young order of teleost fish on the evolutionary time scale, in the epipelagic zone. According to this hypothesis, Perciformes colonized the epipelagic zone after being out-competed by older taxonomic groups highly specialized to life in the deep-sea (Weitzman, 1997). The general observation of Perciformes in the epipelagic leads to the prediction that the epipelagic has been colonized more recently than the deep-sea, however no quantitative data have been presented to support this conclusion.

Although relatively little is known about these deep-sea inhabitants compared to organisms in shallow water communities, researchers have found that the faunal assemblages of the deep-sea tend to vary with depth (Haedrich & Merrett, 1992; Angel, 1997; Haedrich, 1997; Moranta et al., 1998; Smith & Brown, 2002; Fujita et al., 2005; Robinson et al., 2010). Studies find a decrease in species diversity with depth but spikes in abundance and biomass in the upper bathypelagic zone (~1200 – 2300 m). Demersal fish biomass in the Atlantic Ocean was found to be the highest in the mesopelagic (at 600 m), with decreasing biomass below this depth until 1200 m, where there was a peak in biomass before further decreasing again (Haedrich & Merrett, 1992). A similar trend has been found in the Mediterranean with the maximum fish biomass found between 1000 m – 1200 m, followed by decreasing values at increasing depths (Moranta et al., 1998).

Although pelagic fish have been shown to have a low species richness below 600 m, studies have cited increased numbers of pelagic fish species in the upper bathypelagic around 1000 – 1100 m (Smith & Brown, 2002). A survey of Monterey Canyon found the highest organism abundance of bathypelagic communities in the upper bathypelagic between depths of 1500 m – 2000 m (Robinson et al., 2010). Causes for this trend are unknown but changes in photosynthetic productivity, light limitation, temperature, sediment characteristics, oxygen content, pressure, salinity, and depth have all been predicted as factors influencing zonation of deep-sea faunal assemblages (Smith & Brown, 2002; Powell & Haedrich, 2003; Fujita et al., 2005). More information is needed to reveal any broadly applicable zonation patterns in the faunal assemblages of the deep sea.

The Gulf of Mexico

This study focuses on the deep sea ichthyofauna assemblages (fishes) of the Gulf of Mexico. The Gulf of Mexico is a distinct biogeographical region (Pequegnat et al., 1990; Garner et al., 1987; McEachran & Fechhelm, 1998) bordered by Mexico, Cuba and the United States. With 4000 km of coastline and covering 1,138,980 km^2, it is the ninth largest body of water in the world. The eastern border is formed where the Caribbean Sea and the Atlantic Ocean meet, in a line from Key West to Cape Catoche. There are three geographical subregions of the Gulf of Mexico (Fig. 1-2). The Eastern subregion extends from Florida Bay to Pensicola or Mobile, the western from Pensicola or Mobile to Cape Rojo, and the southern from Cape Rojo to Cape Catoche. At its deepest, the Gulf of

Mexico extends to 3750 m, missing the abyssal zone's upper boundary by only 250 m (McEachran & Fechhelm, 1998; Ross et al., 2010). Average surface temperatures vary seasonally, ranging from 18.3 – 29° C, while bathypelagic waters remain a fairly constant 4.35 ° C (Pequegnat et al., 1990; McEachran & Fechhelm, 1998). Throughout all geographic and vertical regions, the benthos is comprised mostly of silty-clay sediment (Pequegnat et al., 1990; McEachran & Fechhelm, 1998; Gallaway et al., 2001).

Nutrient and water flow are influenced by two major systems: the Mississippi River output and the Loop Current (Pequegnat et al., 1990; McEachran & Fechhelm, 1998; Wei et al., 2012). The Mississippi River contributes 65% of the freshwater input into the area as well as 4.1 x 10^{10} tons of sediment per year, which is deposited on the northern slope and shelf (McEachran & Fechhelm, 1998). The deposits from the Mississippi River are responsible for carrying organic matter into the Gulf of Mexico (Gallaway et al., 2001). Organic matter, plants, pelagic fish and invertebrates as well as their larvae are also brought into the Gulf by the Loop Current which flows into the Gulf of Mexico from the Caribbean Sea. The current flows through the Yucatan Channel (located between the northwestern tip of the Yucatan Peninsula and Cuba) then travels north, towards the Mississippi River Delta, bends east towards Florida, and makes a final loop south where it exits the Gulf of Mexico into the Atlantic Ocean between Florida's southern tip and Cuba (Gallaway et al., 2001). This current drives the major surface circulation of the Gulf and brings warm Caribbean water into the area, affecting species distribution throughout the Gulf of Mexico (Gallaway et al., 2001).

The Gulf of Mexico is of particular interest due to the diverse array of marine organisms inhabiting the area. Although the ichthyofauna of the region is somewhat poorly known, there has been extensive biological exploration of the region because of its proximity to the United States. These began with land based surveys in the mid 1800's focusing on describing the newly discovered species of the Gulf of Mexico. The first research vessel, the *Blake*, was deployed in the Gulf by the United States Coast Survey in 1872. The *Blake*, followed by the *Albatross'* and the *Fish Hawk*'s explorations in the late 1800's, focused mainly on the research of shallow benthic environments, reefs, and invertebrates, with an emphasis on bivalves (McEachran & Fechhelm, 1998). Beginning in the early 1900's marine laboratories began popping up along the northern coast of the Gulf of Mexico, including the Gulf Biological Station in Cameron, Louisiana (1902-1910), the Marine Laboratory in Loggerhead Key, Dry Tortugas (1904), and the Louisiana State University Laboratory on Grande Isle (late 1920's – early 1950's) (McEachran & Fechhelm, 1998). At the same time, explorations in the Gulf of Mexico were focusing more on the physical aspects of the area, investigating bathymetry, oceanography, and hydrology (Moretzsohn et al., 2013). Researchers in marine laboratories associated with universities such as the University of Miami, University of Texas, and Florida State University continued to study the faunal assemblages of the Gulf of Mexico through the mid 1900's. Many of these researchers contributed to the knowledge of the fish fauna of the area. The first investigations into the fauna of the deep-sea were commissioned by Texas A&M University. The voyage of *Alaminos* in the 1960's sampled the ichthyofaunal assemblages of the slope and abyssal plains of the Gulf of Mexico (McEachran & Fechhem, 1998). The first quantitative macrofaunal sampling of the deep-sea communities began in the 1970's (Wei et al., 2012). In the 1980's the Mineral Management Service commissioned a three year survey of the northern Gulf of Mexico benthos. The research contributed to the knowledge of the benthic environment and the faunal assemblages of the northern Gulf of Mexico. Commissioned by LGL Ecological Research Associate Inc., Texas A&M University supported an exploration from 1983-1987. The mission of this exploration was the development of knowledge about the deep Gulf of Mexico fauna and its relationship to the environment (Gallaway et al., 2001). Both of the former studies were funded in light of the growing off shore oil development in the Gulf, lending to greater concerns regarding the lack of understanding about the deep sea communities in the area. In the 21st century fewer scientific explorations of the fauna have been conducted. Only recently has research in the Gulf of Mexico again been substantially conducted. After the Deepwater Horizon oil spill of 2010 released record amounts of crude oil compounds into the Gulf of Mexico, the government increased its willingness to fund scientific explorations in the Gulf to try and discover the impacts the oil will have on the environment and the organisms inhabiting areas affected by the spill (Moretzsohn et al., 2013).

From this long history of surveys, it has become apparent that the region has a relatively rich fauna, with 1,461 recorded species of fishes inhabiting the waters. Of these, 66 species are endemic to the Gulf of Mexico (McEachran & Fechhelm, 2005). While research on the pelagic midwater fauna below 200 m of the Gulf of Mexico is scarce, deep benthic communities are relatively well sampled as a result of the extensive oil exploration and drilling in the deep-sea (Ross et al., 2010). Most studies have been conducted in the northern and eastern subregions of the Gulf of Mexico, however, in these regions the ichthyofauna appears to be relatively homogeneous within depth regions (Powell & Haedrich, 2003; Ross et al., 2010). While, some studies cite higher abundance in the Mississippi Trough and DeSoto Canyon (Powell & Haedrich, 2003; Wei et al., 2012), depth appears to be more important than geography in determining the distribution of deep-sea faunal assemblages in the Gulf of Mexico (Powell & Haedrich, 2003; Ross et al., 2010).

Between about 1000 m and 1100 m not only does the light disappear entirely, but the temperatures of the Gulf of Mexico drop to 4° C, a potential explanation for the change in faunal assemblages noted by many scientists at this depth range (Gallaway et al., 2001). In the Mineral Management survey of the deep Gulf of Mexico benthos between 1983 and 1985, the fish diversity was found to increase up to 950 m in depth, and then declined steadily with depth, drastically dropping below 2300 m. While fish species richness decreased, many macrofaunal invertebrates (> 0.5 mm in size) showed increasing species richness in the bathypelagic zone (below 1000 m), especially starfish and sea cucumbers. Based on the data obtained during this study, Gulf of Mexico faunal assemblages were broken into seven discrete intervals: The shelf/slope habitat (150 – 450 m; upper mesopelagic), the Archibenthal Horizon A zone (475 – 750 m; upper mesopelagic into the lower mesopelagic), the Archibenthal Horizon B zone (775 – 950 m; lower mesopelagic), the Upper Abyssal zone (975 – 2250 m; lower mesopelagic through the upper bathypelagic), the Mesoabyssal Horizon C (2275 – 2700 m; upper bathypelagic and lower bathypelagic), Mesoabyssal Horizon D (2725 – 3200 m; lower bathypelagic), and the Lower Abyssal zone (3225 – 3850 m; lower bathypelagic) (Pequegnat, 1983).

Peaks in the abundance and density of meiofauna (> 0.05 mm in size) and megafauna (> 2.5 mm in size) have also been cited in the Gulf of Mexico's bathypelagic zone with a small peak in abundance at 1000 m (Gallaway et al., 2001). The survey also found a large peak in density in the upper mesopelagic around 300 m. Similarly, a mesopelagic spike was also shown by Powell et al. (2003) where both abundance and species richness of demersal Gulf of Mexico fish fauna were found to be greatest between 315 – 785 m and steadily decrease from there. While these studies seem to find a general trend associated with depth, the data are only representative of portions of the Gulf of Mexico and do not necessarily show the larger patterns of vertical distribution throughout the entire geographic region.

The Scope of This Study

The purpose of this study is to examine the broader distribution of the deep-sea ichthyofauna in the Gulf of Mexico. By compiling previous catch data for species in the Gulf of Mexico, this study will examine the geographical and vertical distributions of deep-sea species in the region. It is hypothesized that the species richness in the Gulf of Mexico will decline with depth, mirroring the documented patterns of density and biomass mentioned above. While many species are vertical migrants and the minimum depth is variable, species should only be able to travel to a certain depth due to environmental constraints (e.g. light, temperature, pressure, etc.). Therefore, the pattern of species richness is expected to match the maximum depth ranges of species. The study also examines the taxonomic distributions of deep-sea inhabitants of the Gulf of Mexico. Following the evolutionary hypothesis that percomorphs are of a younger evolutionary development and have been out-competed in the deep-sea by older taxa that have evolved to inhabit the harsh conditions at depth, percomorph species richness is expected to be higher in the epipelagic and decrease with depth. This study will help to provide a better understanding of the poorly understood, yet fairly well documented fish assemblages of the deep Gulf of Mexico.

Materials and Methods:

McEachran and Fechhelm's *Fishes of the Gulf of Mexico Volumes 1& 2* (1998; 2005) were used as the primary references for the documented ichthyofauna of the Gulf of Mexico. I recorded depth ranges from these volumes for all included 1,461 fish species (McEachran & Fechhelm, 1998; 2005) and input these data into a Microsoft Excel spreadsheet as integers in meters. Not all species listed are given depth ranges so data were augmented by adding depth range data from Fishbase.org (Frose & Pauly, 2013). Species known to inhabit coastal inshore areas, brackish waters, and coral reefs were assumed to live only in the upper epipelagic zone, unless reported to occur deeper, and were treated as having a maximum depth range of 100 m. The depth ranges in McEachran and Fechhelm (1998; 2005) for all deep-sea species were double checked using Fishbase.org (Frose & Pauly, 2013) by running a search on all species inhabiting the meso- and bathypelagic zone. Ranges were obtained from Fishbase.org (Frose & Pauly, 2013) for species with no documented ranges in McEachran and Fechhelm (1998; 2005) when available. Data for many deep-sea species are sparse. For this reason, even though the depth ranges of many non-endemic species included in the study are not Gulf of Mexico specific, ranges were assumed to be the same throughout each species' geographic range. Many deep-sea inhabitants have been recorded as vertical migrants. The depth ranges for these species include the migration ranges so that the minimum depth is the absolute minimum depth documented. Species with no known range distributions were excluded.

Species richness was examined using minimum and maximum depths for each species. Species were assumed to inhabit all areas in between the minimum and maximum documented depths. For the purpose of this study, maximum depth was determined to be the most important range determinant for the species, assuming that most species may migrate to the surface at night or live nearer the surface during earlier ontogenetic stages but can only travel to a certain depth before environmental constraints will restrict deeper migration. Vertical distribution patterns were determined by examining number of species with maximum depths in 100 m intervals from the surface.

Range data were used to determine species richness and taxonomic distributions of fish within varying depth intervals. Ranges were broken into four different depth intervals and species richness and compositions were compared between the four. The four intervals are listed in Table 1-1. For all four depth intervals, species were determined to inhabit each interval which fell between their minimum and maximum documented depths of occurrence. If data were missing for either the minimum or maximum depths of occurrence for a species (so that the range data were incomplete) the species was only said to inhabit the depth interval of the documented depth. Species ranges were broken up into 100 m intervals. Species were counted as inhabiting each 100 m interval between the minimum and maximum depths for their documented range. A buffer zone of 20 m was included into each range and only species with ranges falling into the interval by over 20 m were included in the depth interval. Total numbers of species inhabiting each interval was then summed to find species richness for the given interval. These data were then log transformed and plotted on a graph in Microsoft Excel. A linear regression was run on the data in PSAW Statistics 18 to test the relationship between species richness and depth.

Species richness and taxonomic distributions were examined using the other three intervals (Table 1-1). Ranges were broken into 200 m intervals up to 1000 m. Below this depth species abundance is known to drop drastically. For this reason, the remaining depths were broken only into two ranges: 1000 – 2000 m and 2000+ m. As described for the 100 m intervals, a 20 m buffer was included in the 200 m intervals as well. Species ranges were also broken into the intervals proposed by Pequegnat (1983) in his survey of the Gulf of Mexico benthos: Shelf/ slope (150 - 450 m), Archibenthal Horizon A (475 – 750 m), Archibenthal Horizon B (775 – 950 m), Upper Abyssal (975 – 2250 m), Mesoabyssal Horizon C (2275 – 2700 m) , Mesoabyssal Horizon D (2725 – 3200 m), and Lower Abyssal (3225 – 3850 m). For the purpose of this study the Mesoabyssal Horizon C, Mesoabyssal Horizon D and Lower Abyssal zones were combined into the

Mesoabyssal zone because of the low fish species abundance at these depths (Table 1-1). Following the methods of Pequegnat (1983), only species with minimum depth ranges of 150 m or maximum depth ranges exceeding 220 m were included in the Shelf/slope interval, excluding many epipelagic species from these data. A 25 m buffer is already included by Pequegnat (1983) between each interval; therefore, no additional buffer was included. Finally, ranges were divided into traditional oceanic depth zones: epipelagic (0 – 200 m), upper mesopelagic (200 – 600 m), lower mesopelagic (600 – 1000 m), upper bathypelagic (1000 – 2400 m) and lower bathypelagic (2400+ m). A 20 m buffer was included in these intervals as mentioned above for the 100 m and 200 m depth intervals.

For example, *Bathyuroconger vicinus,* has a documented range of 229 m – 1318 m. For the 100 m intervals, this species was included in all ranges between 200 – 1300 m. For the 200 m intervals, *B. vicinus* was included in all ranges besides the 0-200 m range. The species was included in the Shelf/Slope, Archibenthal Horizon A, Archibenthal Horizon B, and Upper Abyssal zones for Pequegnat's intervals and in the upper and lower mesopelagic and the upper bathypelagic zones for the traditional oceanic zones.

Taxonomic distributions were determined for these intervals by breaking species into monophyletic groups (Table 1-2) using the phylogeny of Near et al. (2012) to identify relevant clades. Species in this study are recognized in 24 different clades in the Gulf of Mexico. Where possible traditional ordinal level taxa were used, recognizable because they end in the suffix "-iformes." The exceptions are the Chondrichthys and Percomorpha. Members of the orders Carchariniformes, Chimeriformes, Hexanchiformes, Lamniformes, Myliobatiformes, Orectolobiformes, Pristiformes, Rajiformes, Squaliformes, and Topediniformes were all included in the clade Chondrichthys. The clade Percomorpha includes species from the orders Batrachoidiformes, Beloniformes, Cyprinodontiformes, Gasterosteiformes, Lophiiformes, Mugiliformes, Perciformes, Pleuronectiformes, Scorpaeniformes, and Tetraodontiformes. The use of the Percomorpha follows a more traditional usage (e.g., Nelson, 2006) rather than the recent usage of Near et al. (2012) in excluding the Ophidiiformes from the Percomopha. Because the Ophidiiformes are the sister clade to the traditional Percomorpha (Near et al., 2012), this difference is simply one in naming and not in how the basic biological entities (clades) are recognized. Taxonomic uncertainty is greatest within the Percomorpha, and these grouping ensure that all clades studies originated by approximately 100 million years ago (Near et al., 2012).

Taxonomic distribution patterns were examined by counting the number of species from each clade within the various depth intervals. The number of species in each clade was totaled for each discrete depth interval. The percentage of species representing each clade was calculated by comparing the number of species in each clade at a given depth interval to the total number of species occupying that depth interval. Taxonomic distribution patterns were compared across the three sets of depth intervals mentioned above. Patterns were identified by eye based on graphs generated using Microsoft Excel. Patterns were also visualized in a continuous form by graphing the percentage of total species in 100 m intervals for all clades that represent at least 15% of the total species richness at some depth, with the exception of the chondrichthyan clade.

Results:

Vertical distributions were examined from 1461 species known to inhabit the Gulf of Mexico. The first 100 m of the Gulf of Mexico is the most speciose. Below 100 m, the species richness decreases exponentially with increasing depths. Linear regression of log-transformed data indicate a tight fit of the data to a log-transformed linear decrease (Fig 1-3; $R^2 = 0.968$, $t = -33.369$, $p < 0.001$).

Trends in maximum depths for species found below the epipelagic zone (>220 m) demonstrate an increase in the number of species' depth maxima from the 300 m (upper mesopelagic) until 600 m (the barrier between upper and lower mesopelagic). Below 600 m, the number of species' depth maxima in each interval drop until there is a peak at 1000 m (the boundary between meso-and bathypelagic), 1500 m (the upper bathypelagic), and another at 2000 m (the upper bathypelagic). Beyond 2000 m, there are less than 10 species with depth maxima in each interval (Fig. 1-4).

The 200 m depth intervals (Fig. 1-5 & 5, Tables 1-3 & 1-4) demonstrate that species richness declines substantially after the first 200 m (epipelagic zone) but has a more gradual decrease for depths below 200 m (meso- and bathypelagic zone). Percomorpha represents the majority (67%) of the high number of species in the epipelagic but the proportion of percomorphs in each depth interval decreases, representing only 33% of species in the 200 – 400 m range, 24% in the 400 – 600 m range, 17% in the 600 – 800 m range, 14 % for 800 – 1000 m and 1000 – 2000 m ranges, and 7% for depths exceeding 2000 m (Fig. 1-6). The species composition is not homogenous for all depth intervals and as the number and proportion of percomorphs decreases, other clades proportionally increase (Fig. 1-7). For example, Osmeriformes and Ophidiiformes represent only 0.5% and 1.8% of the total species composition respectively from 0 – 200 m. However, in the depths below 2000 m they represent 17.8% and 19.2% of species respectively.

Species richness and taxonomic distributions showed similar trends for Pequegnat's (1983) intervals (Fig. 1-8, Tables 1-5 & 1-6) and for traditional oceanic intervals (Fig. 1-9, Tables 1-7 & 1-8). While both zonation patterns show declining species richness with depth, Pequegnat's (1983) intervals don not appear to follow an exponential decline, but rather follow a more step-like pattern. The traditional oceanic vertical divisions show a similar trend in declining species richness as displayed by 200 m intervals. In both Pequegnat's (1983) and the traditional oceanic intervals, percomorphs compose a smaller proportion of the species in deeper intervals. For Pequegnat's (1983) intervals, Percomorpha represents 32.72% for Shelf/Slope (150 – 450 m) then drops to 21.05% for Archibenthal A (475 – 750 m), 13.57 % for Archibenthal B (775 – 950 m), 12.25% for Upper Abyssal (975 – 2250 m) and 5.36% for Mesoabyssal (2275+ m). The traditional oceanic intervals show Percomorpha declining from 66.7% (epipelagic; 0-200 m) to 30.39% (upper mesopelagic; 200-600 m), 15.60% (lower mesopelagic; 600-1000 m), 13.04% (upper bathypelagic; 1000-2400 m), and 10.64% (lower bathypelagic; 2400+ m). Osmeriformes and Ophidiiformes also show trends comparable in the 200 m intervals with values of 0.54% and 1.79% respectively in the epipelagic and values of 14.89% and 17.02% respectively in the lower bathypelagic.

Distribution patterns also show variation for individual clades with depth. Percomorpha is highly represented in the first 100 m, however after that, the number of percomorphs drops drastically and by 1000 m, there are very few representatives (Fig. 1-10). Other clades do not show such drastic declines with depth. Stomiiformes have proportionally fewer representatives than Percomorpha (Fig. 1-10) but show a much less drastic drop in species with depth (Fig. 1-11). Unlike Percomorpha, Stomiiformes show a peak in species abundance between 300 – 600 m (upper mesopelagic). This trend is mimicked by another clade of vertical migrating fishes, Myctophiformes (Fig. 1-11). Myctophiformes similarly show a peak species abundance in the upper mesopelagic around 400 – 500 m. However, the Myctophiformes also show a relatively similar species abundance between 0 – 400 m before the peak and show a much more drastic drop below 800 m and are entirely absent from depths below 2000 m.

Osmeriformes and Ophidiiformes have fewer species in the Gulf of Mexico than Percomorpha, Stomiiformes, and Myctophiformes, but show different vertical distribution patterns (Fig. 1-12). Osmeriformes have fewer species than Ophidiiformes between 0 – 400 m but have more species present than the Ophidiiformes between 400 – 1900 m. However, by 2000 m, both clades show similar declining patterns of number of species with depth.

Chondrichthyans show relatively constant values proportionally to other examined clades (Fig. 1-6, Table 1-4). Excluding 0 – 200 m, where Chondrichthyans show a value of 6.52%, and 2000+ m, where the value drops to 2.74%, Chondrichthyans represent between 11.06 and 12.35% of species for all depths between 200 – 2000 m.

However, the total number of chondrichthyan species in each depth interval is not as evenly represented (Fig. 1-13). The maximum number of Chondrichthyan species is found between 0 – 100 m, after which there is a steep decline in number species before showing another peak in species for 300 – 400 m with steadily decline with greater depth.

Discussion:

Species Richness declines exponentially with depth (Fig. 1-3). This pattern of diversity does not support the hypothesis that the species richness will show peaks in the upper bathypelagic, mirroring documented patterns of abundance and biomass in Montery Canyon's faunal communities (Robinson et al., 2010), macrofaunal communities in the Gulf of Mexico (Gallaway et al., 2001), the demersal fish assemblages of the North Atlantic (Haedrich & Merrett, 1992), and fish communities in the Mediterranean (Moranta et al., 1998). While no peaks were found in species richness in the upper bathypelagic as expected, these results are consistent with documented species richness trends in pelagic fish assemblages of the Eastern Pacific (Smith & Brown, 2002) and fish communities in the Mediterranean (Moranta et al., 1998). The species richness of the Eastern Pacific closely follows the exponential trend shown in this study with the exception of finding a maximum between 100 – 200 m instead of the 0 – 100 m maximum seen in the Gulf of Mexico (Smith & Brown, 2002). The exponential trend is not seen in the fish communities of the Mediterranean (Moranta et al., 1989) but that is explained by the fact that the sample did not include species richness in the epipelagic. Below 200 m (i.e., below the epipelagic) a linear regression line for the

Mediterranean fish communities well explained the presented species-richness data, very similar to the trend seen for the Gulf of Mexico. Alternatively, a study conducted on the demersal fish communities in the northern Gulf of Mexico found a maximum species richness in the lower mesopelagic between 315 -785 m, below which there was declining species richness (Powell & Haedrich, 2003). Some of the difference in results may be due this study's excluded portion of the epipelagic (sampling began at 188 m for the shallowest interval). However some of the depth intervals tested in the current study exclude the epipelagic, yet the trends for the other depth ranges are consistent with those including epipelagic species, further refuting the findings from the demersal fish survey of the northern Gulf of Mexico (Powel & Haedrich, 2003). This inconsistency in the data could simply be an artifact of the exclusion of pelagic fishes in the previous study. Regardless of the differences in depths of maximum species richness, there appears to be a general trend in decreasing species richness with increasing depths. This suggests that the documented peaks in biomass and density found in the upper bathypelagic zone in previous studies are not caused by diversity but rather by abundance and density of the species occupying these ranges. Future studies should be conducted examining the species composition and biomass as it relates to increasing depths to gain a better understanding of what is influencing the peaks in the upper bathypelagic zone.

Maximum depths were also examined because it was determined to be an important range determinant for species. While upper limits of many ranges are more flexible (due to ontogenic and diel-vertical migrations) the maximum documented depth is restricted by environmental factors (pressure, temperature, salinity, etc.) that likely prevent the free movement of species into deeper areas. Maximum depths were expected to follow a similar trend to species richness; however, this hypothesis was also rejected. Instead of declining with depth, the number of species-range maximums increased for depths of around 600 m, 1000 m, 1500 m and 2000 m. A previous study conducted by the Mineral Management Service found breaks in species assemblages at around 450 m, 750 m, 950 m, and 2250 m (Pequegnat, 1983). My data, however, fits more closely with traditional oceanic zonation breaks compared to the faunal assemblage breaks determined by Pequegnat (1983). The increases in maximum depth occur at the upper mesopelagic/lower mesopelagic boundary (which falls ~600 - 700 m), the boundary between the mesopelagic and bathypelagic zones (at 1000 m) and at two points within the upper bathypelagic zone (which extends to 2200 m). Sampling limitations preventing accurate estimation of maximum–depth ranges for some species but these results are consistent with trends found for pelagic fish of the Atlantic Ocean (Smith & Brown, 2002) which show peaks in the maximum-depth counts between 500 – 700 m, 1000 – 1100 m, and 1400 – 1500 m. These data suggest that the factors influencing traditional oceanic zonation, such as light and relationship to continental land masses, are also strongly affecting the vertical distribution of species.

There also appears to be taxonomic variation along the vertical gradient. It has been hypothesized that the percomorphs are a relatively young clade that never colonized deeper waters due to competition from older clades, more specialized to living in the extreme environment of the deep sea. To test this hypothesis, this study examined proportions of monophyletic taxonomic groupings at depth intervals. In support of the hypothesis, higher proportions of percomorphs were found in shallower waters. Over 75% of the species found in the epipelagic are representatives of Percomorpha. The abundance of percomorph species declines sharply below the epipelagic zone. Opposing this trend, Ophidiiformes and Osmeriformes are very poorly represented in the epipelagic (making up only 2% and 1% of total species composition of the epipelagic respectively). However, both of these groups have proportionally more representatives as depth increases, reaching maximum percentages of representative species in the bathypelagic zone. These two groups show that there are certain taxonomic clades which have become specialized for living in the deep-sea. Percomorpha has relatively few representatives in the deeper ocean, supporting the hypothesis that this clade is more specialized to life in the epipelagic zone and may also lend support to the hypothesis that percomorphs colonized the epipelagic and later moved into deeper waters.

These data also show interesting trends in several other groups, markedly in two orders known for their diel-vertical migrations: the Myctophiformes and Stomiiformes (Gartner et al., 1987; Sutton & Hopkins, 1996; Hopkins et al., 1998). Myctophiforms make up the highest percentage of the species composition in the mesopelagic. Although, the percentage of representative species in the epipelagic is markedly lower than that found in the mesopelagic, the actual number of species found in the epipelagic is almost exactly the same as that found in the mesopelagic. This confirms that most of the myctophiforms are migrating to the surface at night. Interestingly, the number of species found below the mesopelagic is much lower. This may be due to sampling errors, as many myctophiforms had no documented maximum depth. However, this group of fish may be primarily found in the mesopelagic with only few, larger individuals found in the deeper waters of the bathypelagic zone. More studies are required on these species to determine the ranges they may occupy.

Stomiiformes have also been widely suspected of being daily migrators. However, the data presented in this study does not fully agree. Like myctophiforms, the majority of the Stomiiformes appear to inhabit mesopelagic waters. However, there is a large drop in the number of species which have been found in the epipelagic. This suggests that not all stomiiform fishes migrate into the epipelagic at night. However, this may be another artifact of sampling times not accurately depicting all migrating species. Another possibility is that a large number of species of Stomiiformes occupy the lower mesopelagic or upper bathypelagic, and only migrate into the upper mesopelagic without reaching the epipelagic (Gartner et al., 1987; Sutton & Hopkins, 1996). Further studies should be conducted on these species to determine the full extent of their ranges and at which ranges migration occur.

There is an interesting trend in Chondrichthyan species richness. Unlike the previously mentioned groups, the Chondrichthyans compose a relatively stable percent of the ichthyofauna in each depth. Proportionally, the Chondrichthyans show a slight decrease in the epipelagic, but their percent composition of the ichthyofauna is constant throughout the mesopelagic and into the upper bathypelagic. There are proportionally fewer species representing Chondrichthyans in the epipelagic and lower bathypelagic zones. However, there may be more representatives at depth (such as large sleeper and gulper sharks) which have yet eluded capture in deep-sea surveys because their large size makes trawl-net capture rare. There is also a substantial decrease in the number of Chondrichthyan species between 100 – 300 m. This is very likely due to a lack of data about these species. Many pelagic sharks have documented depth ranges below 100 m. This lower species richness may be due to the fact that they are too large to be caught using standard sampling methods. More studies should be conducted to determine if epipelagic Chondrichthyans occupy deeper ranges than are currently documented. The consistent presence of Chondrichthyans throughout the ocean depth zones points to their importance in the oceanic ecosystem and suggests that these species may be important indicators of the ecosystem’s health.

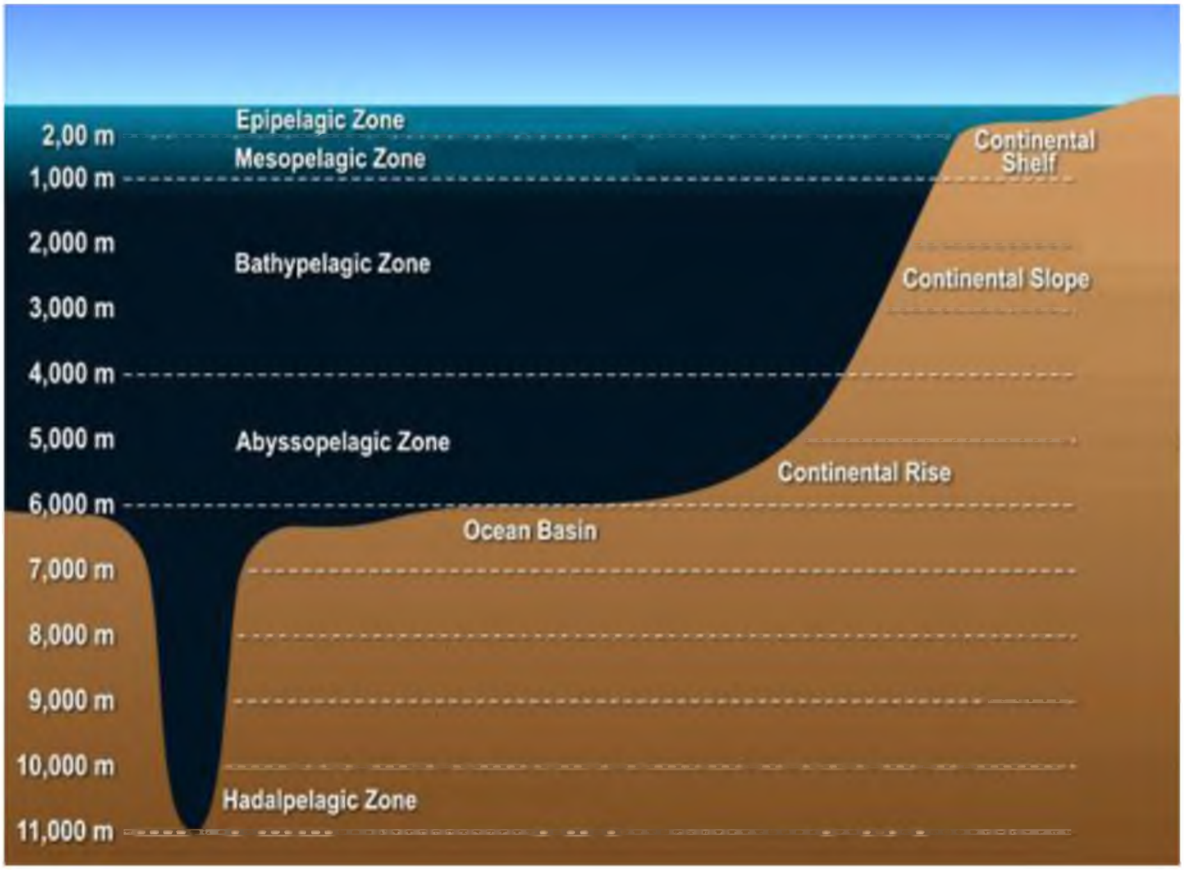

Figure 1-1: The vertical zonation of the ocean (from seasky.org). *Brown* represents the continental and oceanic crust while *blue* shows water. Labels on the crustal landmass denote changes in continental slope while labels in the water show oceanic zones and the depths associated with them.

Figure 1-2: Map of the Gulf of Mexico showing prominent bathymetric and geographical features. Basemap source: NOAA

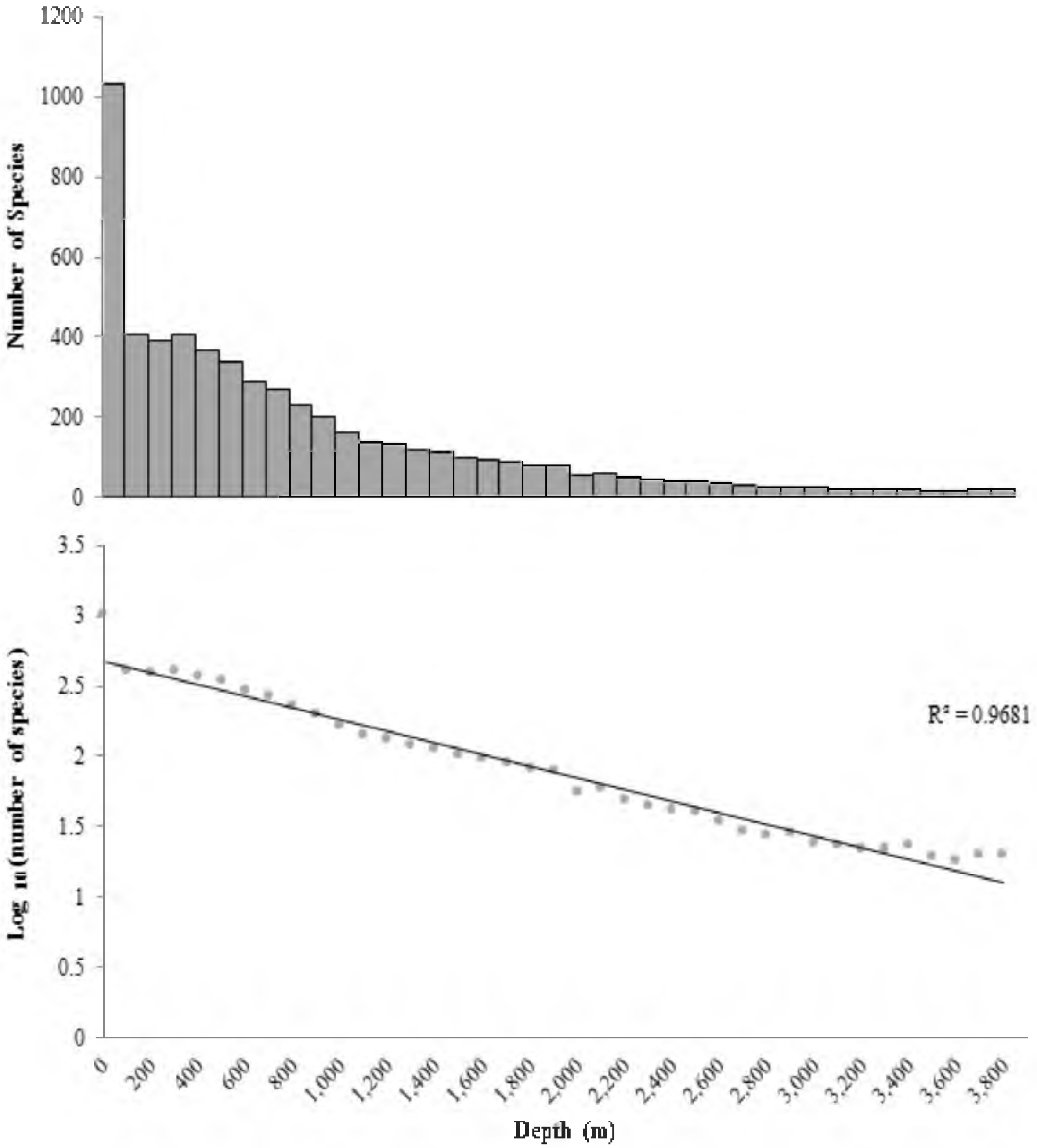

Figure1- 3: Species richness shown by the total number of species found in each depth range. Ranges are depicted in 100 m intervals. Number of species represents the total number of species documented to inhabit the range. The histogram (Top) depicts total species richness at each depth interval. The scatter plot with best fit line (bottom) depicts the log transformed number of species, indicating an exponentially declining species richness with increasing depth (R^2 = 0.968).

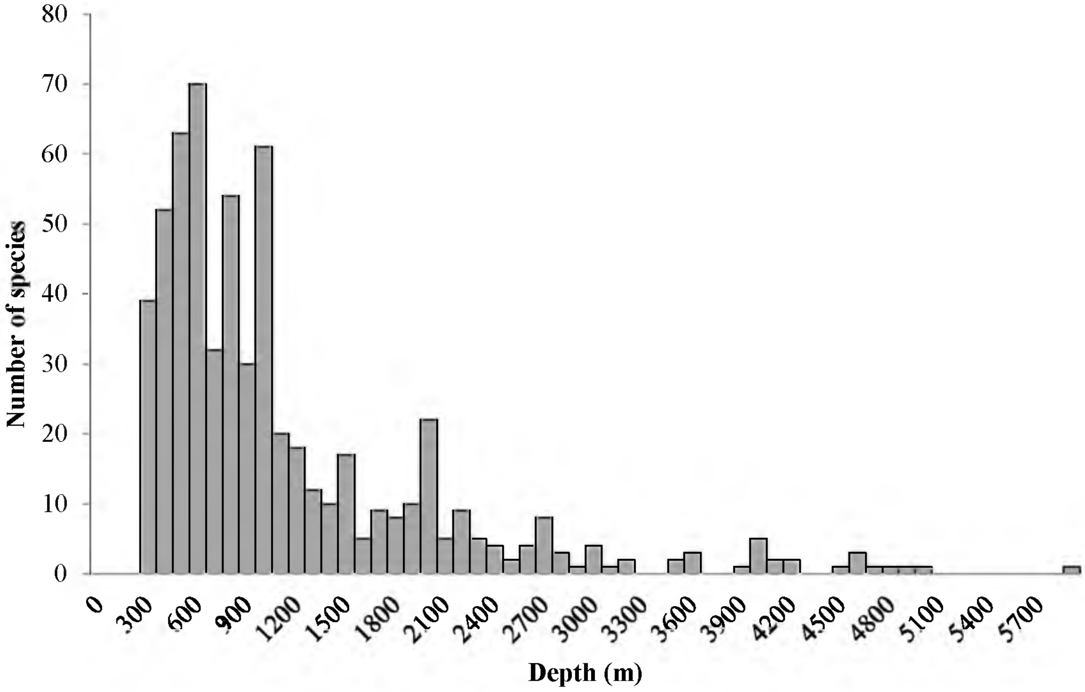

Figure 1-4: The number of species with depth range maxima in each range. Ranges are in 100 m intervals. Only species with depth maximums below 220 m are included.

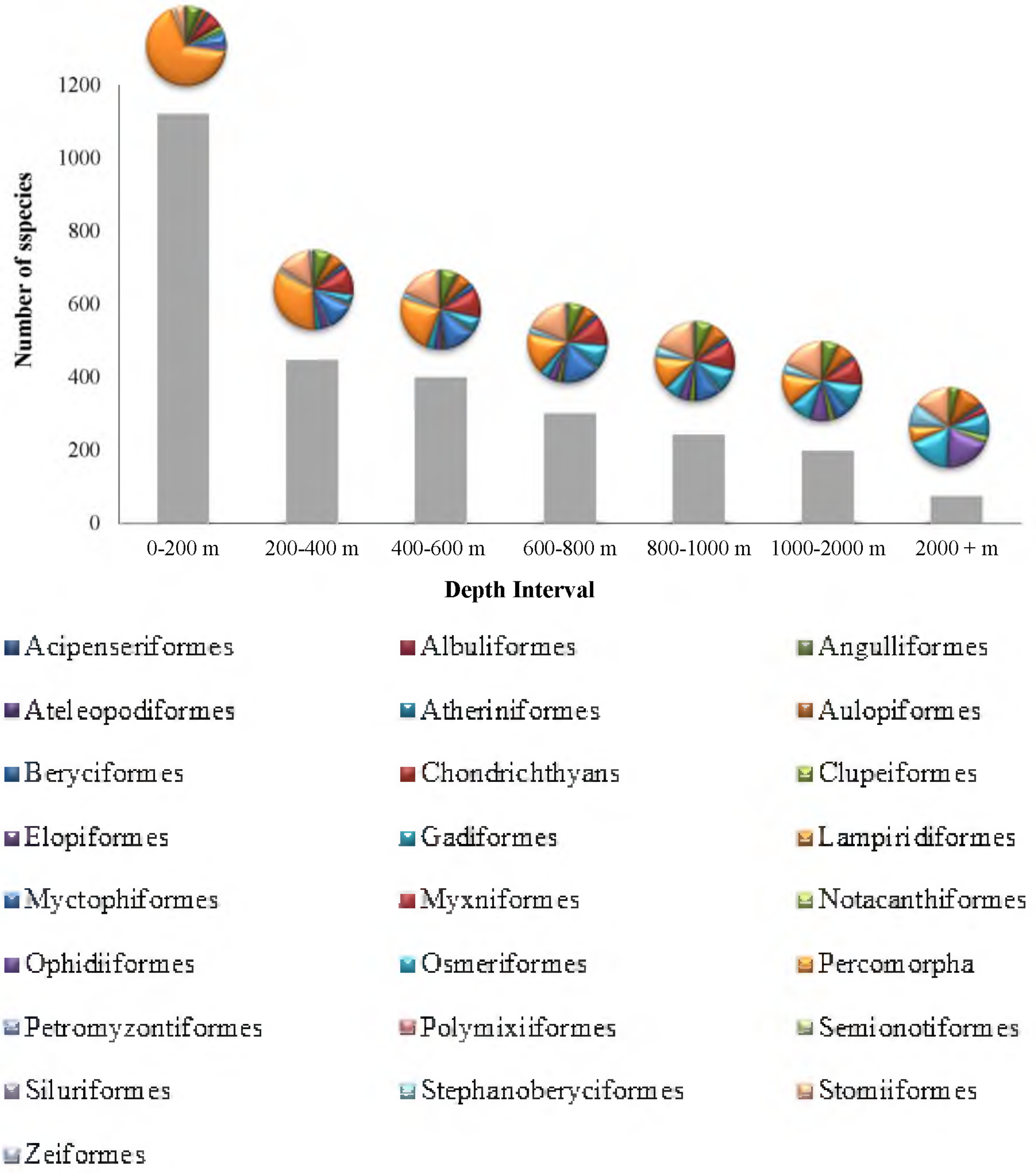

Figure 1-5: Species richness at 200 m depth intervals except for the last two which are larger intervals. The bars denote the total number of species found in each depth interval. Pie charts above each bar denote the percent species composition by clade in each depth interval.

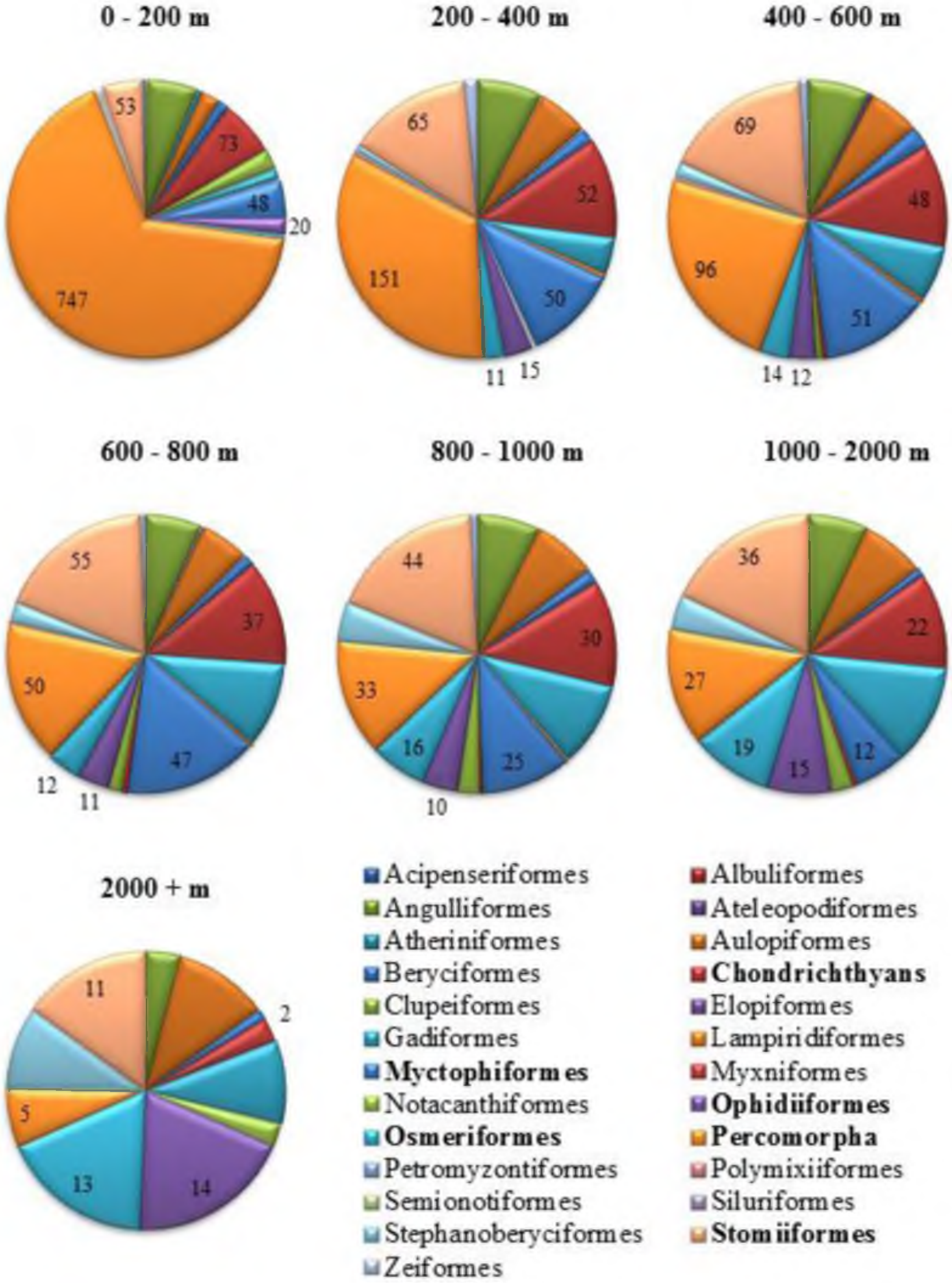

Figure 1-6: Taxonomic distribution of the Gulf of Mexico ichthyofauna in 200 m depth intervals. Each section of the pie chart represents the percentage of species for each clade at each depth interval. Numbers on sections represent the total number of species representing the clade in the given depth interval. Numbers of species are only shown for species which show prominent trends in vertical distributions. Clade names are in bold in the legend for groups which have numerical values shown in the charts.

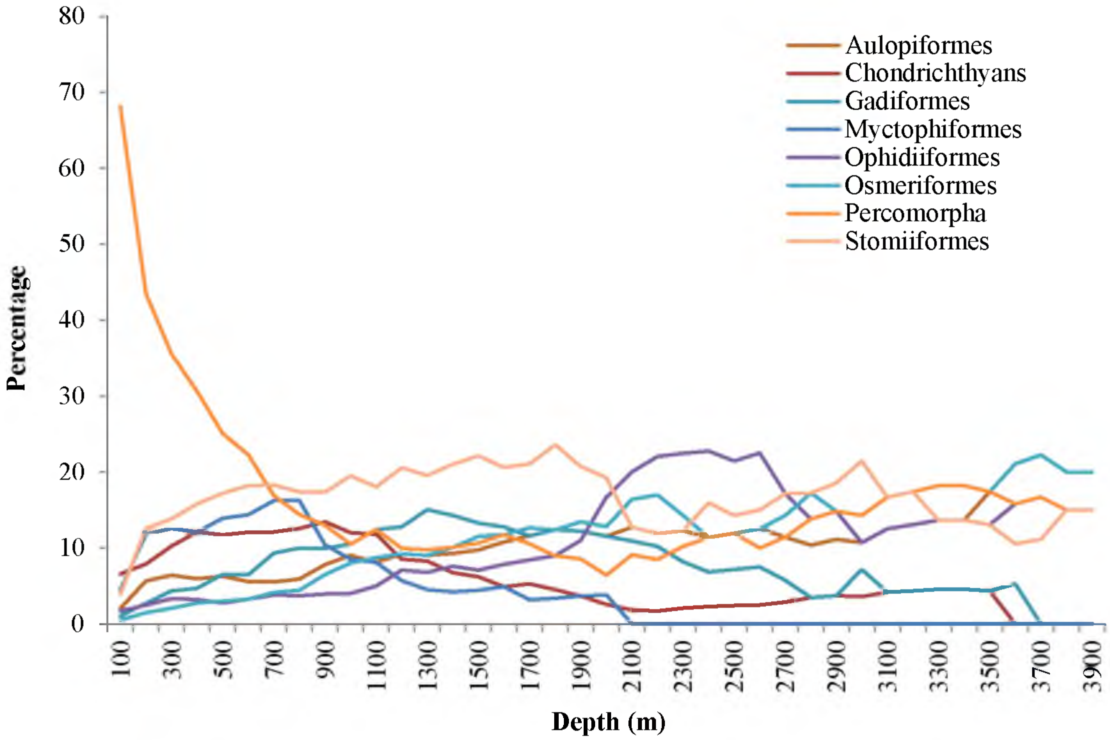

Figure 1-7: Percentage of the total species richness attributed to each clade. Clades are only included if percentage exceeds 15% for at least one depth, with the exception of Chondrichthyans.

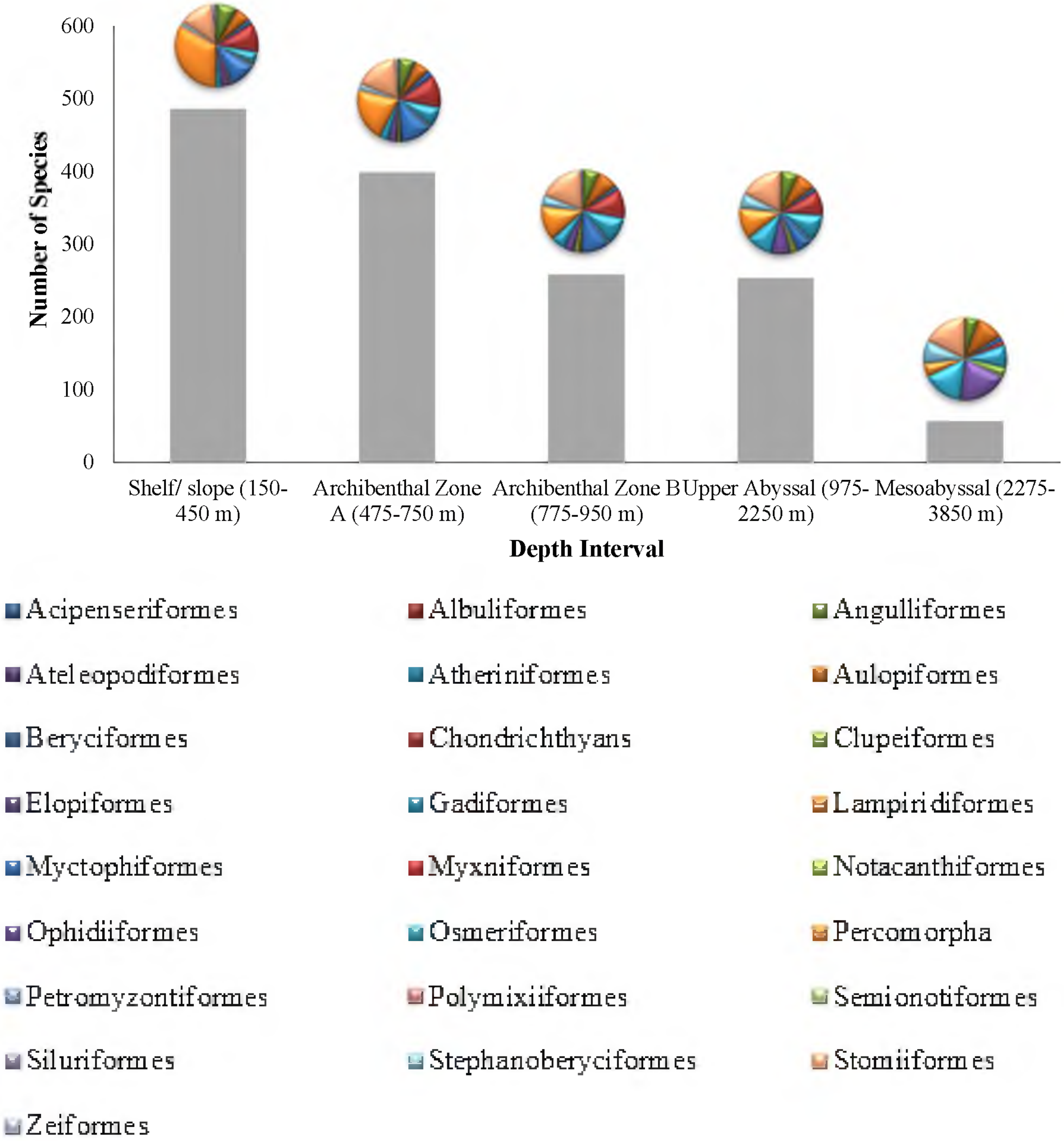

Figure 1-8: Species richness at Pequegnat's (1983) depth intervals. The bars denote the total number of species found in each depth interval. Pie charts above each bar denote the percent species composition by clade in each depth interval

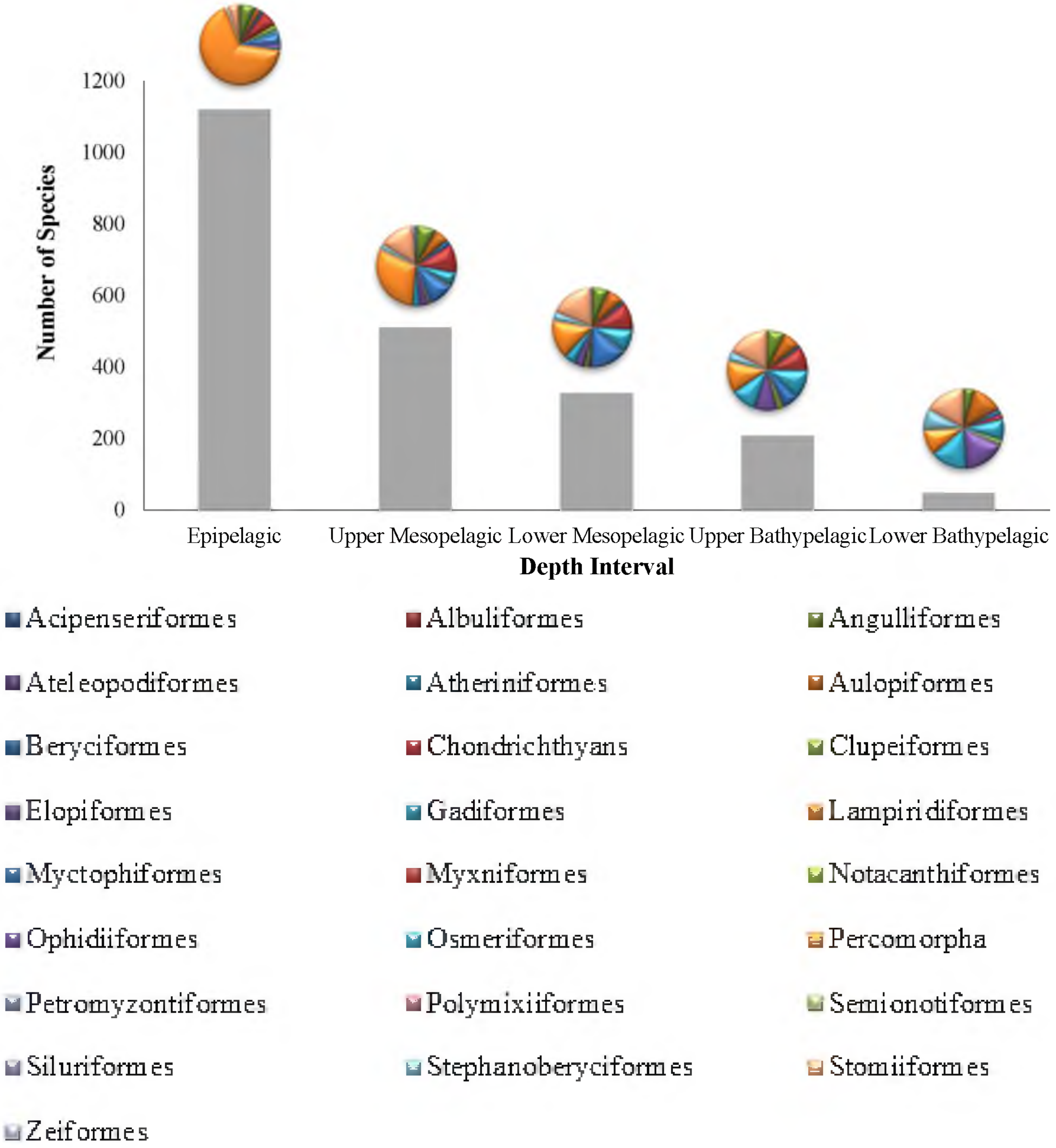

Figure 1-9: Species richness at traditional oceanic depth intervals. The Epipelagic extends from 0 – 200 m, the Upper Mesopelagic from 200 – 600 m, the Lower Mesopelagic from 600 – 1000 m, the Upper Bathypelagic from 1000 – 2400 m and the Lower Bathypelagic from 2400 m to the bottom of the Gulf. The bars denote the total number of species found in each depth interval. Pie charts above each bar denote the percent species composition by clade in each depth interval

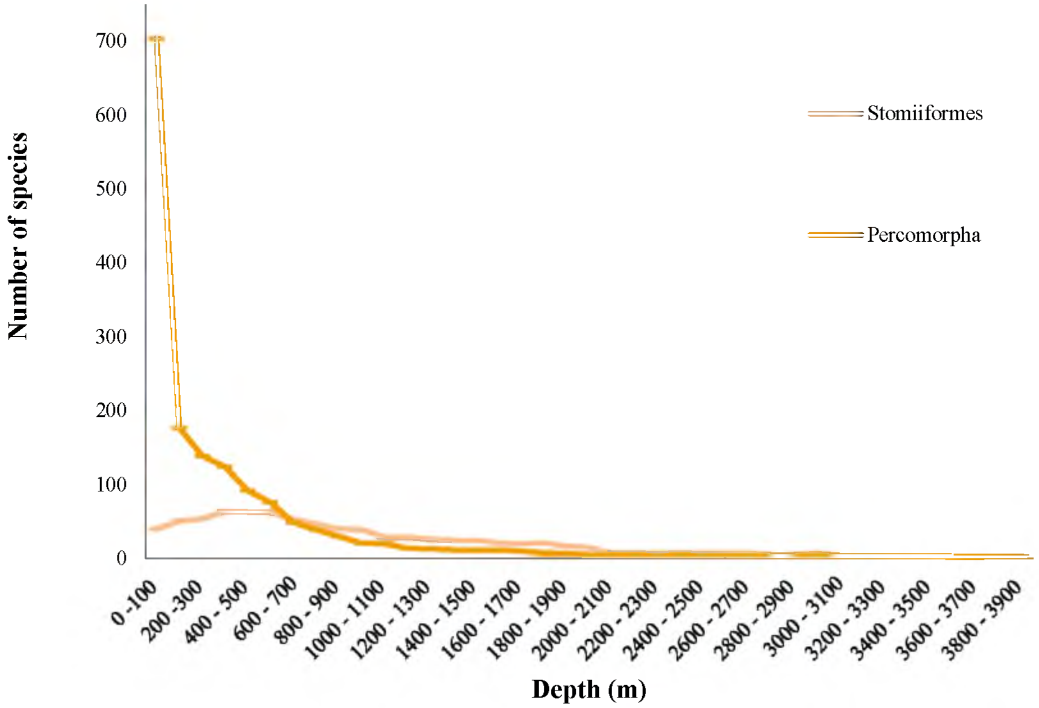

Figure 1-10: Number of species of Stomiiformes (*beige line*) and Percomorphs (*orange line*) at 100 m intervals, showing vertical distribution of each clade.

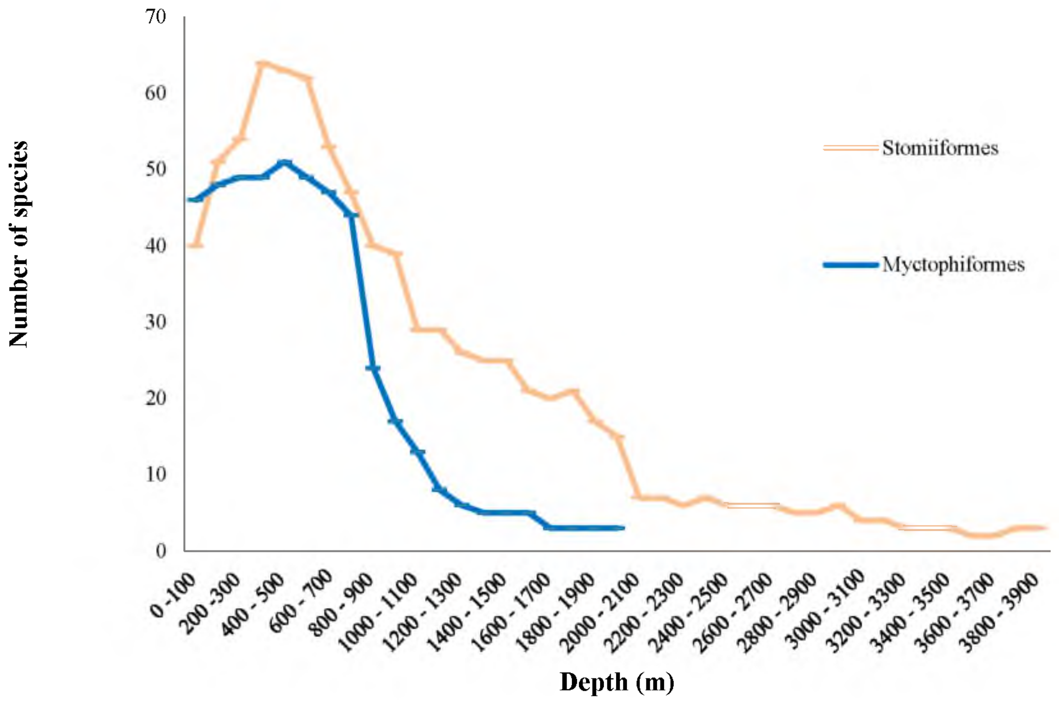

Figure 1-11: Number of species of Stomiiformes (*beige line*) and Myctophiformes (*blue line*) at 100 m intervals, showing vertical distribution of each clade.

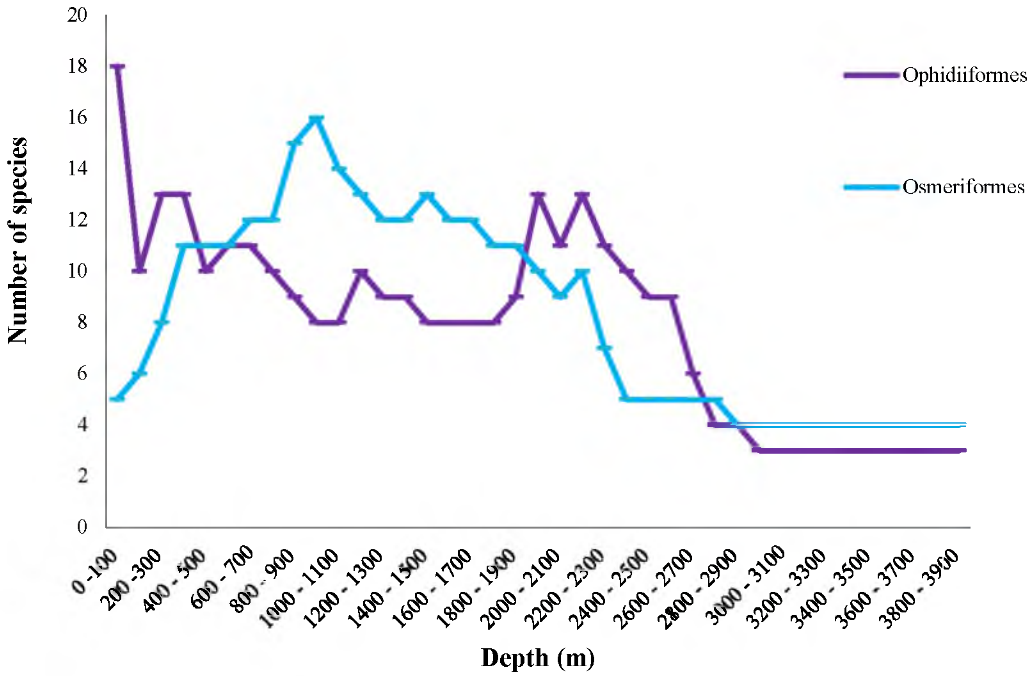

Figure 1-12: Number of species of Ophidiformes (*purple line*) and Osmeriiformes (*blue line*) at 100 m intervals, showing vertical distribution of each clade.

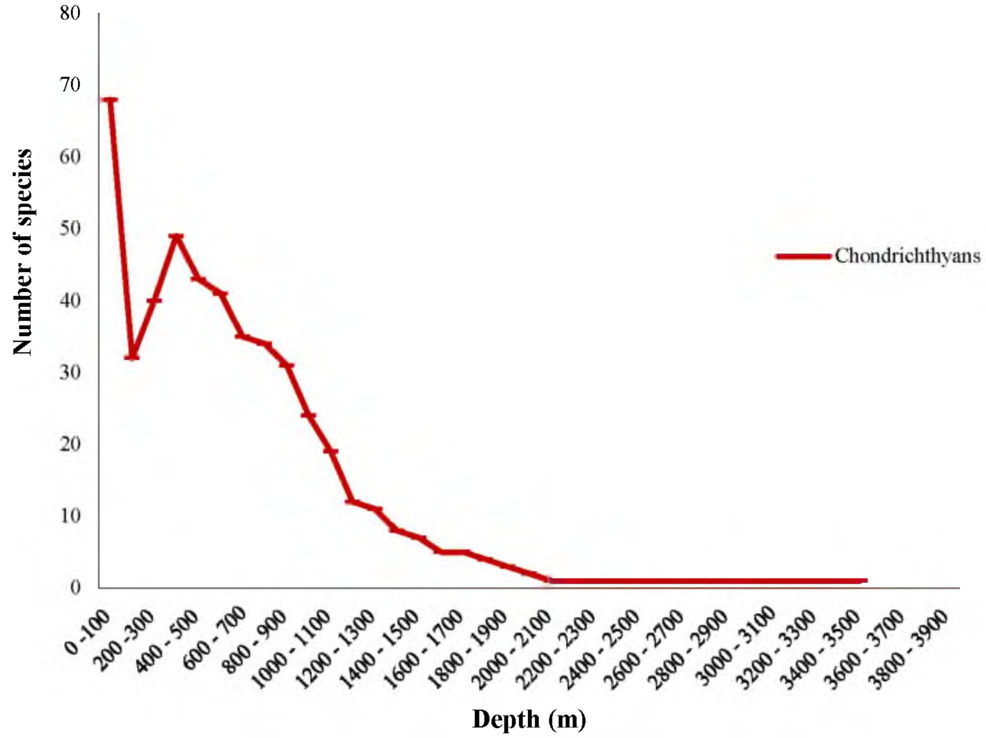

Figure 1-13: Number of species of Chondrichthyan at 100 m intervals, showing vertical distribution

Table 1-1: Depth intervals species ranges were broken into for species richness and taxonomic distribution studies

Depth Interval	Intervals Included	Buffer Included
100 m intervals	Every 100 m from 0 – 3900 m	20 m
200 m intervals (up to 1000 m)	0 – 200 m	20 m
	200 – 400 m	
	400 – 600 m	
	600 – 800 m	
	800 – 1000 m	
	1000 – 2000 m	
	2000 + m	
Pequegnat's (1983) Intervals	**Shelf / Slope**: 150 – 450 m	No extra included
	Archibenthal A: 475 – 750 m	
	Archibenthal B: 775 – 950 m	
	Upper Abyssal : 975 – 2250 m	
	Mesoabyssal : 2275 m +	
Traditional Oceanic Zones	**Epipelagic:** 0 – 200 m	20 m
	Upper Mesopelagic: 200 – 600 m	
	Lower Mesopelagic: 600 – 1000 m	
	Upper Bathypelagic: 1000 – 2400 m	
	Lower Bathypelagic: 2400 m +	

Table 1-2: Cladistic breakdown of ichthyofauna in the Gulf of Mexico used for examination of taxonomic distribution with respect to depth. Clades were determined using Near et al (2012).

Clade	Common Name	Orders Included	
Acipenseriformes	Sturgeons and Paddlefishes	Acipenseriformes	
Albuliformes	Bonefishes	Albuliformes	
Angulliformes	Eels	Anguliformes	
Atheriniformes	Silversides	Ateleopodiformes	
Aulopiformes	Lizzardfishes	Aulopiformes	
Beryciformes	Toadfishes	Beryciformes	
Chondrichthyans	Cartilaginous Fishes (sharks, skates, and rays)	Carcharhiniformes Chimeriformes Hexanchiformes Lamniformes Myliobatiformes	Orectolobiformes Pristiformes Rajiformes Squaliformes Torpediniformes
Clupeiformes	Sardines	Clupeiformes	
Elopiformes	Tarpons and Ladyfishes	Elopiformes	
Gadiformes	Cods	Gadiformes	
Lampiridiformes	Lamprids	Lampiridiformes	
Myctophiformes	Lanternfishes	Myctophiformes	
Myxniformes	Hagfishes	Myxniformes	
Notacanthiformes	Spiny eels	Notacanthiformes	
Ophidiiformes	Cusk eels	Ophidiiformes	
Osmeriformes	Smelts	Osmeriformes	
Percomorpha	Spiny-rayed fishes	Batrachoidiformes Beloniformes Cyprinodontiformes Gasterosteiformes Lophiiformes	Mugiliformes Perciformes Pleuronectiformes Scorpaeniformes Tetraodontiformes
Petromyzontiformes	Lampreys	Petromyzontiformes	
Polymixiiformes	Beardfishes	Polymixiiformes	
Semionotiformes	Holosteans	Semionotiformes	

Siluriformes	Catfishes	Siluriformes
Stephanoberyciformes	Ridgeheads	Stephanoberyciformes
Stomiiformes	Dragonfishes	Stomiiformes
Zeiformes	Dories	Zeiformes

Table 1-3: Cladistic breakdown of species richness for 200 m depth intervals

Clade	0 - 200 m	200 - 400 m	400 - 600 m	600 - 800 m	800 - 1000 m	1000 - 2000 m	2000 + m
Acipenseriformes	1	0	0	0	0	0	0
Albuliformes	1	0	0	0	0	0	0
Angulliformes	65	34	29	20	18	14	3
Ateleopodiformes	1	1	2	1	0	0	0
Atheriniformes	7	0	0	0	0	0	0
Aulopiformes	25	27	24	17	18	15	8
Beryciformes	14	8	10	4	4	2	1
Chondrichthyans	73	52	48	37	30	22	2
Clupeiformes	26	0	0	0	0	0	0
Elopiformes	2	0	0	0	0	0	0
Gadiformes	13	19	26	30	24	23	7
Lampiridiformes	2	3	2	1	1	0	0
Myctophiformes	48	50	51	47	25	12	0
Myxniformes	0	1	2	2	1	1	0
Notacanthiformes	1	1	3	5	6	5	2
Ophidiiformes	20	15	12	11	10	15	14
Osmeriformes	6	11	14	12	16	19	13
Percomorpha	747	151	96	50	33	27	5
Petromyzontiformes	1	0	0	0	0	0	0
Polymixiiformes	2	2	2	1	0	0	0
Semionotiformes	3	0	0	0	0	0	0
Siluriformes	3	0	0	0	0	0	0
Stephanoberyciformes	2	4	7	7	11	8	7
Stomiiformes	53	65	69	55	44	36	11
Zeiformes	4	7	4	2	2		0
Total	**1120**	**451**	**401**	**302**	**243**	**199**	**73**

Table 1-4: Percentage of total species richness for each 200 m depth interval accounted for by each clade

Clade	**0 - 200 m %**	**200 - 400 m %**	**400 - 600 m %**	**600 - 800 m %**	**800 - 1000 m %**	**1000 - 2000 m %**	**2000 + m %**
Acipenseriformes	0.09	0.00	0.00	0.00	0.00	0.00	0.00
Albuliformes	0.09	0.00	0.00	0.00	0.00	0.00	0.00
Angulliformes	5.80	7.54	7.23	6.62	7.41	7.04	4.11
Ateleopodiformes	0.09	0.22	0.50	0.33	0.00	0.00	0.00
Atheriniformes	0.63	0.00	0.00	0.00	0.00	0.00	0.00
Aulopiformes	2.23	5.99	5.99	5.63	7.41	7.54	10.96
Beryciformes	1.25	1.77	2.49	1.32	1.65	1.01	1.37
Chondrichthyans	6.52	11.53	11.97	12.25	12.35	11.06	2.74
Clupeiformes	2.32	0.00	0.00	0.00	0.00	0.00	0.00
Elopiformes	0.18	0.00	0.00	0.00	0.00	0.00	0.00
Gadiformes	1.16	4.21	6.48	9.93	9.88	11.56	9.59
Lampiridiformes	0.18	0.67	0.50	0.33	0.41	0.00	0.00
Myctophiformes	4.29	11.09	12.72	15.56	10.29	6.03	0.00
Myxniformes	0.00	0.22	0.50	0.66	0.41	0.50	0.00
Notacanthiformes	0.09	0.22	0.75	1.66	2.47	2.51	2.74
Ophidiiformes	1.79	3.33	2.99	3.64	4.12	7.54	19.18
Osmeriformes	0.54	2.44	3.49	3.97	6.58	9.55	17.81
Percomorpha	66.70	33.48	23.94	16.56	13.58	13.57	6.85
Petromyzontiformes	0.09	0.00	0.00	0.00	0.00	0.00	0.00
Polymixiiformes	0.18	0.44	0.50	0.33	0.00	0.00	0.00
Semionotiformes	0.27	0.00	0.00	0.00	0.00	0.00	0.00
Siluriformes	0.27	0.00	0.00	0.00	0.00	0.00	0.00
Stephanoberyciformes	0.18	0.89	1.75	2.32	4.53	4.02	9.59
Stomiiformes	4.73	14.41	17.21	18.21	18.11	18.09	15.07
Zeiformes	0.36	1.55	1.00	0.66	0.82	0.00	0.00

Table 1-5: Cladistic breakdown of species richness for Pequegnat's depth intervals

Clade	**Shelf/ slope (150-450)**	**Archibenthal Zone A (475-750)**	**Archibenthal Zone B (775-950)**	**Upper Abyssal (975-2250)**	**Mesoabyssal (2275-3850)**
Acipenseriformes	0	0	0		
Albuliformes	0	0	0	0	0
Angulliformes	39	25	17	17	3
Ateleopodiformes	2	2	0	0	0
Atheriniformes	0	0	0	0	0
Aulopiformes	29	24	21	20	6
Beryciformes	9	10	4	4	1
Chondrichthyans	55	51	30	25	1
Clupeiformes	0	0	0	0	0
Elopiformes	0	0	0	0	0
Gadiformes	25	32	28	27	5
Lampiridiformes	3	2	1	1	0
Myctophiformes	51	49	29	16	0
Myxniformes	2	2	2	1	0
Notacanthiformes	2	5	6	6	2
Ophidiiformes	16	14	10	19	11
Osmeriformes	11	14	15	27	9
Percomorpha	159	84	35	31	3
Petromyzontiformes	0	0	0	0	0
Polymixiiformes	2	2	0	0	0
Semionotiformes	0	0	0	0	0
Siluriformes	0	0	0	0	0
Stephanoberyciformes	6	8	11	15	5
Stomiiformes	68	70	47	44	10
Zeiformes	7	5	2	0	0
Total	**486**	**399**	**258**	**253**	**56**

Table 1-6: Percentage of total species richness for Pequegnat's depth intervals accounted for by each clade

Clade	Shelf/ slope (150-450) %	Archibenthal Zone A (475-750) %	Archibenthal Zone B (775-950) %	Upper Abyssal (975-2250) %	Mesoabyssal (2275-3850) %
Acipenseriformes	0.00	0.00	0.00	0.00	0.00
Albuliformes	0.00	0.00	0.00	0.00	0.00
Angulliformes	8.02	6.27	6.59	6.72	5.36
Ateleopodiformes	0.41	0.50	0.00	0.00	0.00
Atheriniformes	0.00	0.00	0.00	0.00	0.00
Aulopiformes	5.97	6.02	8.14	7.91	10.71
Beryciformes	1.85	2.51	1.55	1.58	1.79
Chondrichthyans	11.32	12.78	11.63	9.88	1.79
Clupeiformes	0.00	0.00	0.00	0.00	0.00
Elopiformes	0.00	0.00	0.00	0.00	0.00
Gadiformes	5.14	8.02	10.85	10.67	8.93
Lampiridiformes	0.62	0.50	0.39	0.40	0.00
Myctophiformes	10.49	12.28	11.24	6.32	0.00
Myxniformes	0.41	0.50	0.78	0.40	0.00
Notacanthiformes	0.41	1.25	2.33	2.37	3.57
Ophidiiformes	3.29	3.51	3.88	7.51	19.64
Osmeriformes	2.26	3.51	5.81	10.67	16.07
Percomorpha	32.72	21.05	13.57	12.25	5.36
Petromyzontiformes	0.00	0.00	0.00	0.00	0.00
Polymixiiformes	0.41	0.50	0.00	0.00	0.00
Semionotiformes	0.00	0.00	0.00	0.00	0.00
Siluriformes	0.00	0.00	0.00	0.00	0.00
Stephanoberyciformes	1.23	2.01	4.26	5.93	8.93
Stomiiformes	13.99	17.54	18.22	17.39	17.86
Zeiformes	1.44	1.25	0.78	0.00	0.00

Table 1-7: Cladistic breakdown of species richness for traditional oceanic zones

Clade	Epipelagic	Upper Mesopelagic	Lower Mesopelagic	Upper Bathypelagic	Lower Bathypelagic
Acipenseriformes	1	0	0	0	0
Albuliformes	1	0	0	0	0
Angulliformes	65	40	21	15	2
Ateleopodiformes	1	2	1	0	0
Atheriniformes	7	0	0	0	0
Aulopiformes	25	30	22	15	6
Beryciformes	14	11	4	2	1
Chondrichthyans	73	59	37	20	1
Clupeiformes	26	0	0	0	0
Elopiformes	2	0	0	0	0
Gadiformes	13	28	31	24	4
Lampiridiformes	2	3	1	0	0
Myctophiformes	48	52	49	13	0
Myxniformes	0	2	2	1	0
Notacanthiformes	1	3	6	5	1
Ophidiiformes	20	17	13	19	8
Osmeriformes	6	15	16	22	7
Percomorpha	747	155	51	27	5
Petromyzontiformes	1	0	0	0	0
Polymixiiformes	2	2	1	0	0
Semionotiformes	3	0	0	0	0
Siluriformes	3	0	0	0	0
Stephanoberyciformes	2	9	11	8	4
Stomiiformes	53	75	59	36	8
Zeiformes	4	7	2	0	0
Total	**1120**	**510**	**327**	**207**	**47**

Table 1-8: Percentage of total species richness for traditional oceanic zones accounted for by each clade

Clade	% Epipelagic	% Upper Mesopelagic	% Lower Mesopelagic	% Upper Bathypelagic	% Lower Bathypelagic
Acipenseriformes	0.09	0.00	0.00	0.00	0.00
Albuliformes	0.09	0.00	0.00	0.00	0.00
Angulliformes	5.80	7.84	6.42	7.25	4.26
Ateleopodiformes	0.09	0.39	0.31	0.00	0.00
Atheriniformes	0.63	0.00	0.00	0.00	0.00
Aulopiformes	2.23	5.88	6.73	7.25	12.77
Beryciformes	1.25	2.16	1.22	0.97	2.13
Chondrichthyans	6.52	453.85	11.31	9.66	2.13
Clupeiformes	2.32	0.00	0.00	0.00	0.00
Elopiformes	0.18	0.00	0.00	0.00	0.00
Gadiformes	1.16	155.56	9.48	11.59	8.51
Lampiridiformes	0.18	0.59	0.31	0.00	0.00
Myctophiformes	4.29	216.67	14.98	6.28	0.00
Myxniformes	0.00	0.39	0.61	0.48	0.00
Notacanthiformes	0.09	0.59	1.83	2.42	2.13
Ophidiiformes	1.79	3.33	3.98	9.18	17.02
Osmeriformes	0.54	2.94	4.89	10.63	14.89
Percomorpha	66.70	30.39	15.60	13.04	10.64
Petromyzontiformes	0.09	0.00	0.00	0.00	0.00
Polymixiiformes	0.18	0.39	0.31	0.00	0.00
Semionotiformes	0.27	0.00	0.00	0.00	0.00
Siluriformes	0.27	0.00	0.00	0.00	0.00
Stephanoberyciformes	0.18	1.76	3.36	3.86	8.51
Stomiiformes	4.73	14.71	18.04	17.39	17.02
Zeiformes	0.36	1.37	0.61	0.00	0.00

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Chapter 2: Conservation of the deep-sea: a look at deep-sea Chondrichthyans and the threats posed to them in the Gulf of Mexico

Introduction

There is no area of the ocean that is unaffected by human activity, including even the farthest reaches of the deep-sea (Ramirez-Llodra et al., 2011). Although conservation efforts have been successful in some marine ecosystems, almost all of these have focused on the protection of coastal ecosystems and near-surface waters. Unfortunately the lack of conservation attention to the deep-sea does not mean that the ecosystems are unaffected by or safe from anthropogenic disturbance.

Specific Conservation Threats

Pollution

Pollution is a substantial threat that impacts almost all marine ecosystems and organisms worldwide. Although routine dumping of certain waste materials by ships at sea was banned in 1972, over 636,000 tons of litter is dumped into the oceans by vessels annually, and an estimated 6.4 million tons of trash enters the ocean due to direct dumping or as unintentional waste each year (Ramirez-Llodra et al., 2011). A bottom survey of the northern Gulf of Mexico found multiple types of trash at all sampled depths, including the farthest reaches of the bathyal zone (Fig. 2-1). Once in the marine environment, trash causes mortalities to a range of aquatic organisms through suffocation, strangulation, and entanglement. Trash also becomes ingested by many marine organisms, which can be toxic to the organism and may result in death (Ramirez-

Llodra et al., 2011; Moore, 2011). Other pollutants, such as chemical waste and discarded pharmaceuticals make their way into marine environments as well and can disturb physiological processes or result in mortalities among marine organisms (Robinson, 2009; Moore, 2011; Ramirez- Llodra et al., 2011).

Ocean Acidification

Increasing amounts of carbon dioxide in marine environments is another cause for concern. As carbon dioxide levels in the ocean rise, the water becomes more acidic as the carbon dioxide reacts with water in the carbonate buffer system, producing bicarbonate ion and the hydrogen ions that are the basis of acidity (a process known as ocean acidification). The acidification compromises the ability of calcifying organisms (e.g. corals and crustaceans) to produce calcium carbonate hard body parts, reducing their abundance in marine ecosystems (Davies et al., 2007; Robinson, 2009; Ramirez-Llodra et al., 2011). It was modeled that the production of important planktonic calcifying organisms may decrease by as much as a 50% compared to their numbers in pre-industrial times within the next 250 years. Many of these calcifying organisms are important to marine food webs and their decline has the potential to impact the entire ecosystem (Davies et al., 2007). Furthermore, high concentrations of carbon dioxide in and the resultant acidosis have been shown to have toxic effects on organisms (Davies et al., 2007; Ramirez-Llodra et al., 2011). Sessile infauna and epifauna (immobile organisms buried in the bottom and sitting on the bottom of the ocean floor) have been shown to suffer from respiratory stress and even death due to acidosis. Although mobile species are able to avoid areas of high carbon dioxide concentration and acidification, fish swimming through carbon dioxide plumes have exhibited a loss of consciousness from the increased concentrations. Long-term exposure can cause hypercapnia, an increase in the body's acidity. This is a physiological stressor and, over time, has detrimental effects to the health of the organisms (Robinson, 2009).

Climate Change

Climate change, itself in part traceable to increased carbon dioxide levels, is another marine stressor. Ocean temperatures are predicted to rise 1.4° - 5.8° C in the next 100 years (Ramirez-Llodra et al., 2011). The warming of surface temperatures will inhibit the circulation and vertical mixing of cold, nutrient-rich water from the deep ocean which is required for photosynthesis in the epipelagic zone and may cause a redistribution of plankton away from warm tropical waters (Davies et al., 2007; Robinson, 2009; Ramirez-Llodra et al., 2011). Because deep-sea organisms rely upon the productivity of epipelagic photosynthetic and planktonic organisms, the primary producers whose energy productivity eventually is exported to the deep-sea, warming ocean temperatures will also impact the life there (Davies et al., 2007; Robinson, 2009; Ramirez-Llodra et al., 2011). The warming may even extend into the deep waters themselves. The inhabitants of the deep-sea have evolved in an environment far more stable than the environments near the surface (Devine et al., 2006; Robinson, 2009). Temperature changes in the deep sea will have unknown consequences but will likely alter physiological processes such as growth and reproductive rates (Davies et al., 2007).

Fishing

While pollution, ocean acidification, and climate change are of concern to deep-sea communities worldwide, the two most imminent threats in the Gulf of Mexico are fishing and oil and gas drilling. Fishing has always been integral to the life of the people inhabiting land near the Gulf of Mexico. Although historically not a major threat to the deep ocean, over time fishing gear has improved and allowed fishermen to exploit deeper and deeper areas of the Gulf of Mexico (Davies et al., 2007; Grace et al., 2010; Ramirez-Llodra et al., 2011). Today, deep-water fishing is a large industry in the United States, both for recreation and consumption. In 2008, commercial fishing in the Gulf of Mexico had a total catch of 1.27 billion pounds of fish and a total of 3.2 million recreational fishermen took a total of 24 million fishing trips in the area (NOAA, 2010a). Deep-water fishing only accounted for ~6.5% of total worldwide fisheries captures in 2002, a landing worth $70 – 80 billion (USD), yet both shallow water and deep-sea fisheries have significant impacts on marine ecosystems. While deep-sea fishes are not yet a frequent target of fisheries, depletion of shallow water stocks may necessitate a switch to deeper dwelling species as targets.

Examples of this have already been seen in several deep water species, such as orange roughy (*Hoplostethus atlanticus,* known as red slimehead before it was widely marketed as a food fish) which quickly became a fishery target after discovery of large-scale spawning grounds in New Zealand in the 1980's. Extensive gear (heavy duty benthic trawling nets which must be towed several thousand meters below and at least 1000 m behind the fishing vessel) is needed to harvest the fish compared to shallower dwelling species. Regardless of the increased effort required, orange roughy became a valuable fishery in New Zealand, Australia, and Nambia (Stevens, 2003). The orange roughy was originally estimated to have a lifespan of 20-30 years. However, as more became known about its habits and biology, it became apparent that orange roughy can live over 100 years and often do not reproduce until they are in their twenties. By this time fisheries had already overexploited the slow growing, deep-sea population. Biologists predict the recovery of the populations to be very slow, yet orange roughy remains one of the most valuable commercial fisheries in New Zealand (Jensen, 1997; Stevens, 2003; Monterey Bay Aquarium, 2013).

The grenadier fishery also exemplifies this same increasing use of deep-water species. Formerly discarded as unwanted by fishermen when caught incidentally, the grenadiers (deep-water fishes also known as rattails in the family Macrouridae) are now targeted by fisheries. Due to reduced population sizes and increased fishing regulations of inshore species, fisherman began catching the unregulated grenadiers off the west coast of the United States. Little is known of the biology of these fish apart from the fact that they are slow-growing and, therefore likely long lived and later reproducing like the orange roughy (Jensen, 1997; Abbott, 2006). Not only are grenadiers generally considered to be a less preferable tasting fish, but they also have an overall lower product yield (only 22-26% sellable meat per fish) compared to many other commercially targeted fish (Abbott, 2006). As humans overfish the meatier and more productive per individual fishes (e.g. groupers, bonito, tuna), fishermen are forced to catch less productive, less desirable fish like the grenadier. Globally, fishing depths have increased since the 1950's and improved technology has allowed fisheries to target deep-dwelling, long-lived species like the orange rougy and grenadiers (Grace et al., 2010). Both the orange roughy and grenadiers are currently listed as fish to avoid by the Monterey Bay Aquarium's Seafood Watch (Monterey Bay Aquarium, 2013), further demonstrating the risk of exploitation of deep-sea species. If overfishing in the epipelagic continues, more deep sea species may soon be at risk of exploitation.

Fishing also threatens species not directly targeted by commercial fisheries. Trawls are deployed for catching targeted species in the Gulf of Mexico, including, among other organisms, rock shrimp, royal red shrimp, and calico scallops. The royal red shrimp industry has the potential to be extremely detrimental to the deep sea environment. With a range between 180 – 730 m, the royal red shrimp overlaps with many species in the mesopelagic (Stiles et al., 2007). Trawling not only captures non-targeted species (bycatch) but also damages the benthic habitat as the net is dragged along the substrate, which can reduce biodiversity (Bianchi et al., 2010; Ramirez-Llodra et al., 2011). Damage to populations and environments in the deep sea are of particular concern. The species inhabiting the deep-sea have not evolved in a rapidly variable environment like those species in the epipelagic and are therefore not as adapted to dealing with environmental changes. In general, deep-sea species also tend to have a slower growth rate, reach reproductive maturity at a later age, and live longer than shallow species (Devine et al., 2006; Ramirez-Llodra et al., 2011). These traits make the deep sea inhabitants more susceptible to over exploitation. For some deep-sea fisheries, depletion of harvested populations has already been shown by reductions in catch rates. Deep-sea species in the Northwestern Atlantic, including the roundnose grenadier (*Coryphaenoides rupestris*), onion-eye grenadier (*Macrourus berglax*), blue hake (*Antimora rostrata*), spiny eel (*Notacanthus chemnitzi*), and the spinytail skate (*Bathyraja spinicauda*) experienced substantial population loses in a 17-year period due to fishery and bycatch mortalities. Because of the population declines, all five species are now categorized as critically endangered in the region according to the IUCN (Devine et al., 2006; Davies et al., 2007).

Oil and Gas Drilling

The Gulf of Mexico has a high incidence of hydrocarbons in its underlying geological formation, including very large petroleum reserves (Pequegnat et al., 1990; Gallaway et al., 2001). This has led to extensive hydrocarbon exploitation in the Gulf of Mexico, and along with it, another source of concern for the deep-sea environment. Deep-sea hydrocarbon exploitation began in the Gulf of Mexico in 1979. By 1992 there were 6 producing wells, 17 by 1997, and 118 by 2006 (Davies et al., 2007). The Gulf of Mexico has been on the forefront of deep-sea hydrocarbon drilling, and is the site of the first exploratory wells drilled into the lower bathyal zone at 3000 m deep (Davies et al., 2007; Robinson, 2009).

Drilling in the Gulf of Mexico is a very important industry, supplying about 25% of the United States' natural gas and around 18% of its oil (Franks, 2000). There are currently 110 active petroleum and gas platforms in the northern Gulf of Mexico (IHS, 2013). The drilling platforms do provide hard structure for marine organisms to use as habitat to which they can directly attach or use for shelter, acting as fish aggregation devices (Franks, 2000). While many fish use the platform structure as an artificial habitat, living near the oil and gas wells can be harmful to the health of marine organisms. Rigs release oil, gas, and toxic drilling fluids into the surrounding water during drilling and extraction (Robinson, 2009). Hydrocarbons and metals (especially silver, barium, cadmium, mercury, lead, and zinc) can be detected up to 200 m away from wells (Peterson et al., 1996). Corals growing near rigs suffer greater than 30% polyp mortality, a substantially higher rate than corals living elsewhere (Davies et al., 2007). Elevated organic carbon levels and anoxic conditions as well as more patchy distributions of benthic communities have also been found surrounding wells in the Gulf of Mexico (Ramirez-Llodra et al., 2011). Discharged hydrocarbons can be incorporated into food chains after absorption or consumption by primary consumers and may persist in sediments, chronically exposing organisms to the toxic chemicals (Peterson et al., 2012). Prolonged exposure to toxic hydrocarbons can lead to bioaccumulation in the tissues of the organisms which can lower growth, reproduction, and survival rates (Ramirez-Llodra et al., 2011; Fodrie & Heck, 2011).

While studies of bioaccumulation of crude oil components have been conducted on epipelagic organisms after oil spills, the information on deep-sea communities related to hydrocarbon exposure is limited. With such a high incidence of drilling in the deep Gulf of Mexico, it is important to assess the effects hydrocarbons have on the organisms living in areas where drilling byproducts are prevalent or oil spills are of concern. Studies have shown that other pollutants (e.g. DDT and PCB) are correlated with fish diseases such as fin rot (Peterson et al., 1996). Studies on salmon exposed to oil after the Exon Valdez oil spill suffered from bioaccumulation of pollutants, altered migration routes, and diverted spawning grounds (Wertheimer et al., 2000). Epipelagic species have been known to suffer from depleted populations after oil spills as well, making extirpations and local extinctions another concern (Chakrabarty et al., 2012). During his survey of the deep sea benthic communities, Pequegnat (1983) warns of the devastation that could occur in bathypelagic zones in the event of a deep sea blow out. He also notes that without further information on the effects of bioaccumulation of crude-oil components in this environment, it is difficult to assess the extent of damage that could be done to the ecosystem.

The Deepwater Horizon Spill

The concern for the health of deep-sea environments under exposure to crude oil components and other pollutants became obvious on April 20th, 2010 when a deep-sea oil well being drilled by BP experienced a blowout at the well head. The spill was not stopped until September 19th, 2010. Over the 84 day period, 5 million barrels of crude oil, amounting to over 200 million gallons, were released into the ocean (Fodrie & Heck, 2011). This spill was novel in several ways. First, this is the largest accidental oil spill ever to occur (Ramirez- Llodra et al., 2011). This is also the deepest oil spill yet known to have occurred, releasing oil into the environment around 1500 m deep, at the top of the bathyal zone (Chakrabarty et al., 2012). Finally, the Deepwater Horizon oil spill is the first to be extensively treated with chemical dispersants (Ramirez-Llodra et al., 2011). Over 2 million gallons of dispersants were added to the spill (Chakrabart et al., 2012). Dispersants are used to emulsify the oil, breaking it into tiny droplets that are “dispersed” in the water column. These tiny drops are too small to float up to the surface, thereby reducing the oil slick on the water’s surface and potentially reducing the direct effects in the epipelagic. The emulsified hydrocarbons are then supposed to be degraded by bacteria capable of metabolizing the chemicals (NOAA, 2010b). However, after the dispersants alter the chemistry of the hydrocarbons, the oil more readily enters larger organisms, causing a risk of toxicity and bioaccumulation (Upton, 2011).

Because dispersants were used on the spill (combined with the effects of turbulent mixing of emulsified oil particles at the well head) only half of the oil released during the blowout rose to the surface (Fodrie & Heck, 2011). Large amounts of oil remains emulsified at depth and there is a large mid-water hydrocarbon plume found around the well at 1100 m and several others found between 800 m and 1200 m (Fodrie & Heck, 2011; Peterson et al., 2012). The plume at 1100 m represents more than double the amount of hydrocarbons released by the natural seeps in the Gulf of Mexico (~10 million gallons per year) and has, as of yet, shown no evidence of substantial biodegradation (Gallaway et al., 2001; Ramirez-Llodra et al., 2011). Because extensive efforts by BP removed surface oil, the majority of the spill's impact has occurred below the ocean's surface (Fodrie & Heck, 2011; Chakrabarty et al., 2012) yet the effects on the deep sea communities remains unknown.

Unfortunately there is little information on how the chemicals in crude oil and oil treated with dispersants will react in the high pressure environment of the deep sea, making it very difficult to predict the movement, persistence, or chemical transformation of the oil in the environment. There have already been novel transformations of the crude oil witnessed by scientists that have yet to be seen by previous oil spills. Transformation of the chemical components of the oil raises the concern of chemicals' altered toxicities and prevalence in the environment (Schrope, 2011). There is potential for this oil to move into the surrounding waters in the Gulf and Atlantic and over time it may affect more than just the organisms inhabiting areas near the well head (Schrope, 2010). One year after the spill, deposits of transformed oil were found on the Gulf of Mexico sea bed as far as 130 kilometers away from the well head. The movement of other crude-oil components is unknown, especially given the novelty of the Deepwater Horizon spill (Scrope, 2011). It is particularly important to assess the impact of hydrocarbon exposure to deep sea communities which may be more susceptible to change in their normally more stable environments.

Chondrichthyans (Sharks, Skates, Rays, and Chimeras)

Larger-bodied, longer-lived organisms have a great potential to be affected by fishing and chronic exposure to toxins due to their tendency to mature later in life and produce fewer offspring. Many deep-sea organisms display these traits but chondrichthyan species are of particular interest and concern. Chondrichthyans are a group of cartilaginous fishes which include sharks, skates, rays and chimaeras. Many chondrichthyans have poorly understood life histories, but those that have been extensively studied display K-selected life history traits. They are longer-lived, have slower growth rates, reach sexual maturity later in life, and lay relatively few, large eggs or give birth to few, large offspring (Holden, 1974; Wood et al., 1979; Walker, 1998; Walker & Hislop, 1998; Baum & Myers, 2004). Chondrichthyans have also been reported to have low natural mortality rates (Holden, 1973). These traits make chondrichthyans especially susceptible to fishing and likely make them susceptible to bioaccumulations of toxins over their long life spans as well.

Sharks have been historically targeted by fisheries (Holden, 1974) and remain targets for consumption of liver, fins, skin, meat and cartilage to this day (Walker, 1998). Shark populations worldwide declined substantially between 1950 and 1990 (Walker & Hislop, 1998), attributed to their being targeted by fisheries which have been increasing catches since the 1920's (Walker, 1998). Shark landings more than tripled worldwide between 1960 and 1997. While there have been numerous restrictions and regulations put in place on shark fishing, there was only a 7.5% decline in total shark landings between

1997 and 2010 (Worm et al., 2013). Between 1980 and 1990 alone, the Mexican and US shark catches increased three fold (Bonfil, 1997) and today there is still a large shark fishery in the Mexican waters of the Gulf of Mexico (Walker, 1998). While restrictions have been placed on fishing gear and allotted catches to protect sharks in United States waters, no regulations exist in Mexican waters (Bonfil, 1997). Shark fisheries averaged 3.5% of total catches in the southern Gulf of Mexico between 1977 and 1992 (substantially larger than the world average of 0.7%; Bonfil, 1997). In addition, the majority of shark catches are due to bycatch from other fisheries, which do not get reported in total shark landings and therefore cannot be used to regulate shark populations (Walker & Hislop, 1998; Worm et al., 2013).

Sharks are not the only chondrichthyans at risk from fisheries exploitation. Skates, flattened fish which live on the bottom of the ocean and are similar in appearance to a sting ray, have also been targeted by fisheries and are commonly caught as bycatch in bottom trawls (Walker & Hislop, 1998). Skates are currently one of the most threatened groups of all marine species, many of which have suffered little noticed declines due to fisheries exploitation until well after the populations have been substantially depleted (Stevens et al., 2000; Devine et al., 2006).

Because of their life-history traits, chondrichthyans are unable to endure the same level of harvest as shallow-water shellfish and teleost fishes can. Like other fishes, fecundity of chondrichthyan species increases with size (Holden, 1973), putting the population at even greater risk when larger individuals are preferentially captured by fisheries. Commercial landings are reported for shark and skate fisheries. However, bycatch for these species are often not catalogued (Walker, 1998; Stevens et al., 2000;

Worm et al., 2013). An estimation of the total mortalities (including both from reported landings and estimates of unreported bycatch) suggests that in the year 2000, total shark catches weighed over 1,638,000 tons and of those, 1,445,000 tons resulted in mortalities. The study estimated that the 88% mortality of sharks was equivalent to around 69,471,000 individual mortalities (Worm et al., 2013).

Many species of chondrichthyans inhabiting the deep Gulf of Mexico and are at risk of overexploitation from fisheries (Fig. 2-2). In the year 2000, there was a total landing of 5004 tons of deep water sharks reported to the United Nations Food and Agricultural Organization. Although accounting for less than 2% of the reported landings for the year (Worm et al., 2013) this shows that deep-sea species are at risk of exploitation. Extinction has already been a cause for concern in many skate species because of overexploitation through direct fishing and bycatch (Stevens et al., 2000) and other chondrichthyans may be at a similar risk considering their similar life histories.

These deep-sea species are also at risk from the deep water hydrocarbon extraction. The life-history traits of chondrichthyans put these species at substantially greater risk from chronic exposure to hydrocarbons in the environments (Peterson et al., 1996). The effect of crude oil exposure has been studied in several species of epipelagic bony fish. While teleosts have been said to have the ability to metabolize polycyclic aromatic hydrocarbons (PAHs), a major toxic compound of oil, (Metabolism of PAH by teleost, 2010) detrimental effects have still been shown in teleost species exposed to crude oil. Salmon embryos exposed to low amounts of aqueous hydrocarbons after the Exon Valdez oil spill showed substantial uptake of the chemicals resulting in reduced larval growth and survival rates, delayed effects of growth in juveniles, and straying from normal migration routes as adults (Wertheimer et al., 2000). Similarly, in a lab setting all zebrafish embryos exposed to oil mixed with dispersants in the levels expected to be present after the Deepwater Horizon oil spill showed developmental defects such as fatal heart deformities (Schrope, 2011). Despite the studies on these model organisms, the effects of crude oil contamination on most fish is unknown and is very poorly understood for deep-dwelling species, including chondrichthyan species.

The effects of deep-water toxin exposure may be greater in deep-water chondrichthyans that are at a higher risk for chronic exposure due to long life history traits and reproductive strategies. Unlike many other marine organisms which spend larval stages in the epipelagic, chondrichthyans do not undergo ontogenetic migrations into surface waters. Either few, large egg cases (known as mermaid's purses) are deposited on sediment and remain in the deep-sea until they hatch, or a few, large young are born alive at depth, where they remain for the duration of their life, putting many species at risk for exposure from the mid-water plumes found after the Deepwater Horizon oil spill. Furthermore, there has been no demonstration of metabolic pathways for PAHs in chondrichthyans, potentially increasing the exposure effects of crude oil components. More research is necessary to assess how extensive the threat of exposure to toxic crude oil and dispersant or drilling chemicals poses to these organisms.

Chondrichthyans in the Gulf of Mexico may be at a high risk of exposure to toxic chemicals released into the water during the Deepwater Horizon oil spill. There are 7 endemic species of chondrichthyans in the Gulf of Mexico that have been shown to have overlapping ranges with the spill site (Chakrabarty et al., 2012). Endemic species are at increased risk of extinction and should be monitored for population declines in light of threats. The location of dispersed oil below the surface is poorly known (Chakarbarty et al., 2012) but reports of affected species occurring throughout the water column (Schrope, 2011) suggest that the Deepwater Horizon oil spill is impacting all depth ranges from the surface to the well head. Chondrichthyans are present in relatively constant proportions throughout all depth ranges in the Gulf of Mexico (Fig. 2-2). The constant prevalence of this group of fish means that they likely play an important role throughout the marine ecosystem and also means that there may be unreported species living in ranges contaminated by the blowout.

Chondrichthyans represent important apex predators whose life traits put them at an increased risk of exploitation and chronic exposure to toxic chemicals. The recent Deepwater Horizon blowout has illuminated the damage that can be caused by future drilling accidents in the Gulf of Mexico. With such high incidents of oil and gas drilling in the northern Gulf of Mexico, it has become increasingly important to assess potential threats to species, such as chondrichthyans, at risk of exploitation, extirpations or extinctions before another devastating accident occurs. Unfortunately, little is known about chondrichthyan behaviors. This includes both geographic and vertical ranges which may increase the risk of extinction and extirpations in the Gulf of Mexico due to deep-sea drilling. This study focuses on the distribution of two orders of chondrychthyans that tend to inhabit the deep sea: Rajiformes and Squaliformes. By examining previously documented catch locations for these chondrichthyans. I hope to better identify the threats presented by extensive drilling in the northern Gulf of Mexico.

Materials and Methods:

Chondrichthyan distribution patterns were investigated using two orders of the clade: Rajiformes and Squaliformes. These orders were chosen because of the relatively large number of species representing each order in the Gulf of Mexico, the large proportion of individuals cited as having a depth range below the epipelagic zone (McEachran & Fechhelm, 1998), and the tendency for all Rajiformes and some Squaliformes to be benthic or demersal (on the bottom or associated closely with the bottom). I included all rajiforms in the study because of their known benthic behavior but I only included the squaliforms identified as benthic or demersal (McEachran & Fechhelm, 1998; Castro, 2011). Individual catch data were acquired for benthic and demersal species of these two orders using the Global Biodiversity Information Facility's web database which is connected to collections from numerous natural history museums and universities (GBIF.org, 2012). Records from Cuba, Mexico, and the United States were included in the search but out of those, only records with latitude and longitude points located within the Gulf of Mexico were used for the purpose of this study. Latitude and longitude points were input into ArcGIS version 10 (ESRI, 2011) mapping software and overlaid on a map of the Gulf of Mexico and its bathymetry. Because benthic and demersal fish are closely associated with the seabed, catch location, as documented by the records accessed through GBIF.org (2012), was used to determine the depth of occurrence. A depth range was determined for each catch record by determining which two bathymetry lines a catch record's geographical coordinates fell between on the map. Depth contours were shown in intervals of 10 m for 0 – 100 m, 100 m for 100 – 1000 m and 500 m for intervals of 1000 – 3500 m (Fig. 2-3).

Each catch record from the GBIF database (GBIF.org, 2012) was associated with a depth range using bathymetry contours in ArcGIS. These data were used to determine a minimum and maximum depth, the depth range, and the average depth for each species. Minimum and maximum depths, as well as depth ranges were compared to depths documented in McEachran and Fechhelm (1998) and on fishbase.org (Froese & Pauly, 2013). Geographic ranges were also referenced against active gas and oil drilling leases, documented platforms, and projected oil movement from the Deepwater Horizon oil spill.

Results:

There are 25 species of Rajiformes from 11 genera documented as inhabiting the Gulf of Mexico. Distribution patterns were investigated for all Rajiformes. Squaliformes have 21 species from 10 genera documented to inhabit the Gulf of Mexico. Of these, 8 are documented as benthic or demersal species and were included in the study. Of the species studied, four (three Rajiformes and one Squaliform) had no records of occurrence in the database accessed through GBIF.org (2012). ArcGIS mapping expanded the depth ranges of 21 of the 32 species compared to previously documented depth ranges (Fig 2-4; Table 2-1). Vertical ranges according to ArcGIS mapping were larger than documented ranges for 19 of the 25 rajiforms (76%) and for and 2 of the 8 squaliforms (25%). The vertical ranges of three rajiforms were reduced compared to otherwise documented ranges. Four squaliforms exhibited a decrease in the vertical range compared to both documented depth ranges while one (*Squalus mitsukurii*) had an increased range compared to McEachran & Fecchelm (1998), but a decreased range compared to the range documented by Fishbase.org (Froese & Pauly, 2013). Of the species demonstrating expansions in vertical range, 17 were due to increases in both the minimum and maximum depths, 1 was due to increase only in minimum depth, and 5 were due to increases only in maximum depths compared to previously documented depth ranges.

ArcGIS mapping demonstrates the variation in species vertical and geographic distribution patterns. *Rajella fuliginea* has a relatively even distribution throughout the Gulf of Mexico within the meso- and bathypelagic, displaying a shallower distribution in the southern portion of its range (Fig. 2-5). *Anacanthobatis folirostris* likewise has a vertical distribution primarily in the mesopelagic zone but has more records of occurrence in the northern Gulf of Mexico than in the south (Fig. 2-6). *Dipturus oregoni* has only four records of occurrence in the Gulf of Mexico, three of which are located in the northeastern and one of which is located in the southwestern Gulf. All records are found below the epipelagic zone (Fig. 2-7). *Raja texana* has both a wide geographic and vertical distribution. The majority of the records are located in the epipelagic zone in the northern and southern Gulf of Mexico but some records suggest occurrences within the meso- and bathypelagic zones as well (Fig. 2-8). Similarly, most records for *Dipturus olseni* are located within the epipelagic zone. However, several records show distribution within the meso- and bathypelagic zones as well. *D. olseni* is relatively evenly distributed around the Gulf of Mexico, with the exception of the farthest eastern borders surrounding the Yucatan Peninsula and the coast of Florida (Fig. 2-9). Conversly, *Fenestraja plutonia* is found only in a very narrow vertical range between the meso-and bathypelagic zones with a single record of occurrence within the epipelagic zone. *F. plutonia* is only recorded to occur in the eastern Gulf of Mexico near Florida (Fig. 2-10). Similar to *R. texana*, *Leucoraja lentiginosa* is distributed widely within the Gulf of Mexico. While represented throughout the vertical zones and geographic regions of the Gulf, *L.*

lentiginosa has a majority of its records in the upper mesopelagic and is more densely represented in the northeastern Gulf of Mexico, where the species has a higher occurrence in the epipelagic (Fig. 2-11). *Rajella purpuriventralis* similarly shows a wide distribution, with occurrences in the epi-, meso-, and bathypelagic. The records shown indicate distribution in the northern Gulf of Mexico extending into the southwestern Gulf (Fig. 2-12).

Similar distribution patterns are apparent for the squaliforms investigated. *Squalus cubensis* has the largest number of records in the Gulf of Mexico out of the squaliforms investigated. Geographically and vertically, *S. cubensis* appears to have a wide range, distributed throughout the Gulf of Mexico from the epipelagic down through the bathypelagic. The majority of *S. cubensis* records are shown in the upper mesopelagic near the boundary between the epi- and mesopelagic zones (which lies at 200 m). Other squaliform distribution patterns are less explicit given the small number of records in the Gulf of Mexico. *Deania profundorum* has only four records, all of which are located in the northeastern Gulf of Mexico near Louisiana. *D. profundorum*'s vertical distribution is in the mesopelagic and the upper bathypelagic (Fig. 2-14). *Etmopterus gracilipinis* has similarly few records in the Gulf of Mexico. Four are located in the meso- and bathypelagic waters of the northeastern Gulf very near Louisiana while a single record is displayed in the epipelagic, near-shore waters further east (Fig. 2-15).

These distribution patterns can be compared to locations of oil and gas extraction in order to determine potential threats posed to each species by drilling in the Gulf of Mexico. The records of oil and gas platforms in the Gulf of Mexico as of 2013 show a large, densely packed aggregation of platforms in the northern Gulf from the western boundary of the Texas coastline around to the area of the Mississippi River Delta (Fig. 2-16). This includes all platforms listed in the Bureau of Ocean Energy Management's database and depicts more platforms that are currently extracting oil (only 118 rigs are drilling in the Gulf of Mexico as of March 2013 while over 4,000 platforms are depicted on the map). Most platforms are located in inshore, epipelagic waters. However several occur at mesopelagic and bathypelagic depths. The Bureau of Ocean Energy Management's database for drilling leases as of March 2013 shows a larger number of leased plots within the meso- and bathypelagic zones and a reduced occurrence of drilling within the epipelagic (Fig. 2-17). The Deepwater Horizon well which blew out in 2010 fell within this range of densely packed bathypelagic drilling. The oil from the blowout is expected to travel into the northeastern Gulf of Mexico, radiating outward from the location of the blowout (Fig. 2-18).

Discussion:

Using ArcGIS mapping to determine species ranges, 21 of the 32 demersal chondrichthyan species (from the Orders Rajiformes and Squaliformes) showed increased vertical ranges compared to previously documented ranges (McEachran & Fechhelm, 1998; Froese & Pauly, 2013; Fig. 2-4). Of species which showed vertical range decreases, compared to documented ranges, only one species had more than six records used for range determination. The range decreases are, therefore, most likely due to low sample sizes and not indicative of a decrease in the realized niche compared to documented depth ranges. Range increases however, may indicate that the species is found in a larger vertical range than previously determined by other sampling methods. If there are errors in the geographical coordinates for specimen records or if the documented demersal species were traveling upwards in the water column at the time of capture at the given location, the depth of occurrence based on ArcGIS mapping may be inaccurate. However, assuming that all demersal species were on or near the bottom at the time of capture and assuming that the coordinates are accurate for the location of capture, the methodology used in this study may provide a more accurate vertical range depiction of poorly studied benthic or demersal species than the other examined resources.

Based on the vertical and geographic distribution patterns in conjunction with population sizes and endemism, different levels of risk can be assessed for species. Exposure to hydrocarbons is of particular interest in this study and the distribution patterns found using ArcGIS mapping can be used to determine the potential risk to different species due to hydrocarbon drilling in the Gulf of Mexico.

The rajiforms of the Gulf of Mexico show four major patterns of vertical distribution. *Rajella fuliginea* (Fig. 2-5) displays a distribution pattern mostly below the epipelagic, with most points in the lower mesopelagic and upper bathypelagic. Several points occur in the epipelagic in the southern part of the range. This species shows a range expansion and has previously only been documented to occupy the mesopelagic. *R. fuliginea* is distributed fairly evenly around the entire Gulf of Mexico and no records show occupancy of the area immediately affected by the Deepwater Horizon spill. This species is also not endemic to the Gulf of Mexico, suggesting that *R. fuliginea* is not likely at great risk of extinction or large-scale extirpation from the Gulf of Mexico from exposure to hydrocarbons, especially so given the described increase in recognized vertical rage.

Anacanthobatis folirostris (Fig. 2-6) shows a similar distribution pattern but is found almost exclusively below the epipelagic. Most points of occurrence fall within the mesopelagic and a single record shows occurrence in the epipelagic. This record may be an outlier or data error that does not represent the true species range, but without additional information to suggest error, it is treated as a valid record. Based on these data, *A. folirostris* shows an increased recognized depth range both shallower and deeper compared to previous documentation. This species is endemic to the Gulf of Mexico and most of the capture records are located in the northern Gulf of Mexico. A previous study using similar methodology involving mapping of database data (some of which came from GBIF records, as in this study), estimates that 78.95% of *A. folirostris*'s range overlaps with the Deepwater Horizon oil spill (Chakrabarty et al., 2012). High number of specimen records for this species indicates that *A. folirostris* has a large population size. However, due to the high degree of overlap with the Deepwater Horizon spill and a majority of records documenting the range in the mesopelagic, *A. folirostris* is likely at a high risk of exposure to the toxic chemicals trapped at depth from the spill, especially from mid-water plumes in the area. The very rare (or possibly inaccurate) occurrence in the epipelagic also indicates that *A. folirostris* has few or no shallow-water populations that would be away from the mid-water plumes in the meso- and bathypelagic. Thus, this species is at higher risk of dispersed hydrocarbon exposure. This species may be at high risk of extinction given its endemism and range overlap with the recent deep-water spill.

Similarly, *Dipturus oregoni* (Fig. 2-7) is exclusively located in the meso- and bathypelagic zones. There is a slight range increase compared to documented ranges for this species. The increase may be due to the limitations in the bathymetric maps used for the bathypelagic. Contours for the bathypelagic were only given in 500 m increments, giving a large range of possible depths for data points located between two contours which may be the source of range expansion in this case. *D. oregoni* is endemic to the Gulf of Mexico, yet only four records were found for the species, indicating that the species has a very small and poorly sampled range, a very small population size, or both. An estimated 80% of *D. oregoni*'s range overlaps the Deepwater Horizon oil spill (Chakrabarty et al., 2012). As mentioned for *Anacanthobatis folirostris,* the mid-water plumes present a threat to *D. oregoni.* This high overlap of a small range and a possibly small population size suggest high risk of extinction from exposure to chemicals released by the spill. *A. folirostris* and *D. oregoni* should both be considered to be candidate species for U.S. or international protection given the current threats after the Deepwater Horizon oil spill and the potential threats that may present themselves in the event of another deep-water spill in the northern Gulf of Mexico.

In contrast with the ranges of *Rajella fuliginea, Anacanthobatis folirostris,* and *Dipturus oregoni*, *Raja texana* (Fig. 2-8) is almost exclusively found in the epipelagic. However, three records indicate that *R. texana* also occurs less frequently below this range, extending into the bathypelagic. Two separate records note occurrence of *R. texana* at the bottom of the Gulf of Mexico. These two records document the same latitude and longitude and were caught separately in two different years. This suggests that *R. texana* has a substantially larger depth range than previously documented. This endemic species has a large number of records, suggesting a large population size. Only 11% of *R. texana*'s range overlaps with the Deepwater Horizon oil spill (Chakrabarty et al., 2012). Although traditionally at a higher risk of extinction due to endemism, the large range, both vertically and geographically, and the likely large population size as determined by the high incidence of catch records, demonstrates that *R. texana* is not at significant risk of extinction from the Deepwater Horizon oil spill. However, *R. texana* shows a high incidence of occurrence in the northern Gulf of Mexico, overlapping with common areas of hydrocarbon extraction (Figs. 2-16 and 2-17). While not facing an immediate threat from the Deepwater Horizon oil spill, *R. texana* may be at an increased risk in the event of future spills in the area. Given the endemism of the species in the Gulf of Mexico, precautionary regulations should be considered for this species.

Dipturus olseni (Fig. 2-9), also endemic to the Gulf of Mexico, shows a mostly epipelagic vertical distribution with few records indicating occurrence in the meso- and bathypelagic zones. This species is estimated to have a range overlap of 28.57% with the Deepwater Horizon oil spill (Chakrabaty et al., 2012). However, this species has fewer catch records than *Raja texana*, suggesting that *D. olseni* has a smaller population. Furthermore, around half of the catch records are found in the northern Gulf of Mexico, overlapping with the area of active drilling. Given the endemism in the Gulf of Mexico, smaller population size, and larger range overlap with oil and gas drilling, this species is likely at a higher risk of population declines or extinction due to exposure to chemicals from hydrocarbon extraction. *Raja eglanteria* (Appendix I), also displays this distribution pattern and has the majority of its records in the northeastern Gulf of Mexico, overlapping with drilling activity. Although not endemic to the Gulf of Mexico, the species is vulnerable to local extirpation from hydrocarbon exposure.

Very narrow vertical ranges are shown for some species, a pattern that is especially evident for *Fenestraja plutonia* (Fig. 2-10). Almost all catch records fall in a narrow range in the mesopelagic of the northeastern Gulf of Mexico, with a few records spilling into the upper bathypelagic and a single record occurring in the epipelagic. Previously documented ranges for *F. plutonia* do not show occurrence in the epipelagic. *F. plutonia* is not endemic to the Gulf of Mexico and is found away from the prominent drilling sites in the Gulf of Mexico. Narrow ranges are commonly associated with lower adaptability and therefore indicate higher vulnerability to exploitation and other disruptions. However, given *F. plutonia* does not show substantial overlap with hydrocarbon extraction, the species is not likely at considerable risk from exposure to crude oil components. This species should be watched for other threats (e.g. bottom trawling) given its narrow range. Because of its narrow range, monitoring of possible effects of oil and other chemicals from the Deepwater Horizon spill on *F. plutonia* populations may be valuable for indicating the spread of spill chemicals and their effects.

Wide ranges are exhibited by several species including *Leucoraja lentiginosa* (Fig. 2-11) and *Rajella purpuriventrals* (Fig. 2-12). *L. lentiginosa* occupies the epi-, meso-, and bathypelagic zones of the Gulf of Mexico, a large expansion of recognized vertical range in comparison to previously documented vertical ranges for the species. *L. lentiginosa* is also widely distributed throughout the Gulf of Mexico and has a large number of specimen records, which is likely indicative of a large population size. Although *L. lentiginosa* is endemic and has a 52.94% range overlap with the Deepwater

Horizon oil spill (Chakrabarty et al., 2012), there is a reduced likelihood of the species becoming extinct from hydrocarbon exposure because of the large range, both vertically and geographically. However, a large proportion of catch records of this species in the northern Gulf of Mexico, overlap with offshore oil and gas extraction. This may put the northern populations of this species at risk from chemical exposure during drilling and in the event of future oil spills.

Rajella purpuriventralis also occupies all three vertical zones in the Gulf of Mexico but is not endemic to the area. I found shallower records than the depth range documented in McEachran and Fechhelm (1998). However, no minimum depth is documented by Fishbase.org (Froese & Pauly, 2013). This indicates a poorly known range for the species and suggests that the use of ArcGIS mapping provide a more accurate depth range for the species than indicated in previous documentation. The sparse records in the Gulf of Mexico indicate that *R. purpuriventralis* likely has a small population in the Gulf of Mexico and is therefore at an increased risk of extirpation. Over 50% of the records for the Gulf of Mexico overlap with the regions of oil and gas drilling, further suggesting risk to this species in the Gulf of Mexico from hydrocarbon extraction.

Vertical distribution patterns were also examined for squaliforms; however less data on habitat preferences (i.e. benthic, demersal, or pelagic) are available for this group of chondrichthyans. For this reason, fewer species were surveyed, and of those surveyed, few had many documented catch records in the Gulf of Mexico. Despite these data limitations, similar trends in vertical distributions were apparent and ArcGIS mapping similarly determined increased ranges compared to documented ranges for some species. *Squalus cubensis* (Fig. 2-13) has the largest number of documented specimens of the squaliforms surveyed. *S. cubensis* has a range mostly localized to the upper mesopelagic with several documented captures extending into the epi- and bathypelagic zones. Previously documented ranges do not include occurrence in the bathypelagic. The range also extends into the northern Gulf of Mexico where most Gulf of Mexico oil extraction occurs. This may put *S. cubensis* at risk. However, the species is not endemic to the area, has a large range outside the Gulf of Mexico, and may have large population sizes as indicated by the relatively large number of specimen records. Relative to *S. cubensis*, *Deania profundorum* (Fig. 2-14) and *Etmopterus gracilispinis* (Fig. 2-15) are likely at increased risk due to hydrocarbon extraction within their ranges. Both species have very few specimen records in the Gulf of Mexico (five and four records respectively), indicating that the species likely has small population sizes in the area. Furthermore, the catch records have a very narrow distribution and are almost all located in the area of drilling in the northern Gulf of Mexico (Figs. 2-16 and 2-17) and very near the range of oil spilled by the Deepwater Horizon spill (Fig. 2-18). Both species may be vulnerable to extirpation.

The large proportion of species which showed an expansion in recognized depth range through use of ArcGIS mapping highlights the lack of data available for these species and demonstrates the necessity for more studies to determine more accurate ranges of chondrichthyans. Accurate ranges must be identified in order to accurately assess conservation threats posed to these species. Given the possibility of expanded ranges shown here, some species may be at risk from other sources (e.g. oil spills, chemical dumping, trawling, and fishing) that were not previously considered to be threats.

These patterns are not unique for chondrichthyans and the threats explained here also apply to other deep-sea species. ArcGIS mapping methodology can be used to determine ranges of other benthic and demersal fauna and to assess geographically identifiable threats to populations of these species. Threat assessment is very important in measuring a population or ecosystem's health and its ability to rebound from human disturbance. While healthy populations may be able to rebound from population decrease resulting from stressors such as toxin exposure or overfishing, the potential to rebound decreases as stress on the population increases. Populations, especially chondrichthyans and other long lived deep-sea species, are at increased risk of extirpation or extinction when experiencing multiple stressors (such as a combination of overfishing and exposure to the chemicals released during hydrocarbon extraction). For these species, close population monitoring is pertinent. In light of the Deepwater Horizon oil spill, regulations should be put in place to regulate threats (i.e. fishing and trawling) to these species in an effort to alleviate the potential for multiple stressors reducing population health. Endemic species are of particular concern given their localized range and increased risk of extinction after local population decline.

Importance also should be put on monitoring these species due to their potential as indicator species. As apex predators, chondrichthyans may show signs of toxic accumulation not seen in smaller, shorter-lived species. Through chronic exposure and bioaccumulation of toxins from the organisms they feed upon, chondrichthyans may show symptoms related to crude oil exposure that are not seen in the epipelagic species lower in the food chain that have previously been studied (Wertheimer et al., 2000; Schrope, 2011). Symptoms from bioaccumulation are of particular interest given the possibility that they may present themselves in humans if the species caught commercially are exposed to hydrocarbons from drilling in the Gulf of Mexico. Chondrichthyan population declines should not only be monitored to assess overall biodiversity and ecosystem health (Robinson, 2009) but also for the potential to illuminate the health of the ecosystem after toxic chemical exposure. In essence, chondrichthyans may act as a canary in a coal mine- illuminating threats posed to other organisms (including humans) before their effects are more catastrophic.

Indicator species may prove important given the recent increase in deep-sea hydrocarbon extraction which has unknown effects on the deep-sea communities or the chemical released from the wells at such high pressure. Both past and present well locations (Fig. 2-16) pose environmental threats to the area. Post drilling surveys have demonstrated poor benthic habitat surrounding wells. Furthermore, oil-based mud deposited during the process may persist for 5 or more years while benthic damage caused by anchoring may remain for more than 14 years (Continental Shelf Associates, Inc., 2006).

The shift of platform locations from predominantly in the epipelagic (Fig. 2-16) to the majority of current leases being within the meso- and bathypelagic (Fig. 2-17) highlights the increasing threats the deep-sea ecosystems. Oil and gas extraction is moving into deeper territories and exposing poorly studied deep-sea organisms to new threats. The effects are further uncertain because we have no knowledge of the behavior and biological effects of crude oil at such high pressures. Without a deeper understanding of the deep-sea environments and the organisms therein, we cannot effectively conserve them.

Conclusion:

I have become increasingly aware of the need for a deeper understanding of the deep-sea ichthyofauna and the deep-sea environment. There is surprisingly little information about the biology and life history traits of most deep-sea species. With such sparse information, it is very difficult to accurately assess the types and severity of conservation threats which may be posed to these specialized organisms.

Hydrocarbon extraction in the Gulf of Mexico makes this lack of knowledge a particularly large problem. Scientists examining the aftermath of the Deewater Horizon oil spill have no idea how the oil released will be altered by the high pressures of the deep sea, where the oil remains after emulsification by dispersants, and if it is even being naturally degraded. The extent of habitat destruction caused by the blowout (as well as the more regular drilling activities in the Gulf of Mexico) is unknown, leaving little information to assess conservation threats to the area. This issue is compounded by the fact that so little is known about the biology, life history, and distribution of many deep-sea species. With such large gaps in our knowledge of both the threats and the organisms themselves, species and habitats cannot effectively be protected through conservational efforts. The work I did in my thesis attempts to classify threats posed to a specific subset of deep-sea organisms by deep-sea drilling in the Gulf of Mexico. However, many other poorly studied species are likely in jeopardy, and may suffer population reduction, extirpation, and/or extinction as a result of the current problems they face. Without knowing exactly how oil released during the drilling process and well-head blowouts are impacting the environment, we cannot accurately determine which species are most affected and cannot therefore work on protecting them.

I focus on oil and gas drilling as a major threat in my thesis because of the high incidence of drilling in the northern Gulf of Mexico. However, this is not the only area in the world where deep-sea species are being put at risk by deep-sea hydrocarbon extraction, and oil and gas drilling is by no means the only threat that affects marine organisms. There are numerous threats that are as detrimental, if not more threatening and have likewise unknown consequences. The deep-sea has commonly been exploited both as a place to dump pollutants (trash, toxic waste, etc.) and as a place of resource acquisition (hydrocarbons, minerals, etc.) when these activities have been questioned or curtailed in nearshore coastal ecosystems (Rarmirez-Llodra et al., 2011). The philosophy of "out of sight, out of mind" seems to be applied quite literally to the deep sea as many less ethical practices are easily continued in the depths of the oceans where damage can slip by unnoticed for quite some time. We cannot continue to exploit the ocean just because the immediate consequences of our actions are not as visible as they would be in a terrestrial ecosystem. I believe we must start acting under the precautionary principle to protect these fragile and valuable deep-sea ecosystems, working to prevent exploitation before it happens rather than trying to put a band-aid over the gaping wounds we create in the environment.

Humanity has already severely damaged marine ecosystems, causing extinction of some species, such as the Caribbean monk seal, and endangering countless others. Coastal marine ecosystems, like the extremely important mangrove habitats, have been destroyed for shrimp farming and hotel construction. Whereas coral reefs have been devastated by pollution, eutrophication, bottom trawling and direct physical damage. It is heart wrenching for me to hear of the destruction caused to oceanic ecosystems I find so beautiful and to the marine organisms that enchant me. Before this intellectual journey into the deep-sea, I was unaware that these miraculous, alien-like, poorly-understood organisms were already threatened by mankind. It seems unconscionable to me that we have so substantially damaged the deep-sea environment before we have taken the time to realize the full extent of the wonder that nature has presented to us.

Despite the tragedy of destruction in the deep-sea, I remain hopeful. Our planet has proven time and time again that when left to its own devices, repairs can be made. If we act now to end the dumping of pollutants into the ocean, look for sustainable fishing options, and search for clean energy sources, the ecosystem likely will be able to rebound from the damage that has been caused. This hope is what fuels my desire to continue my explorations of the ocean and after my work on this thesis, of the deep-sea. I firmly believe that knowledge is the key to putting an end to the destruction. Only through knowledge can we discover the true extent of the damage caused and the organisms harmed and then act to correct it. I realize that change will be slow, but I hope that by researching organisms and illuminating threats posed to these species, policies can be made which will protect these organisms that I find so fascinating.

It is with this goal in mind that I continue with my research on the deep-sea. While I end here with the work specifically on the geographic and depth distribution of the deep-sea ichthyofauna of the Gulf of Mexico and the conservation threats presented in this geographical region, I will move on to researching the biology of deep-sea fish in a Master's program, with the intention of uncovering some of the many questions left unanswered about these incredible fish. I hope that this new journey will lead me down the road of conservation once again, even if that is expressed through sharing my research with others.

I firmly believe education is the most effective mode of conservation at our disposal. Only when people are made aware of the wrongs in the world can they act to change them. The more I learn about the ocean, the more beauty I find. I hope that by sharing my enthusiasm about the ocean with others they will also learn to appreciate the beauty in the creatures and habitats that lie beneath the waves, and through this appreciation, can join me in the journey of trying to protect the seas. But only by sharing my knowledge and educating the public can I even begin to redeem the world, “all of it, just as it is” (Dillard, 1999).

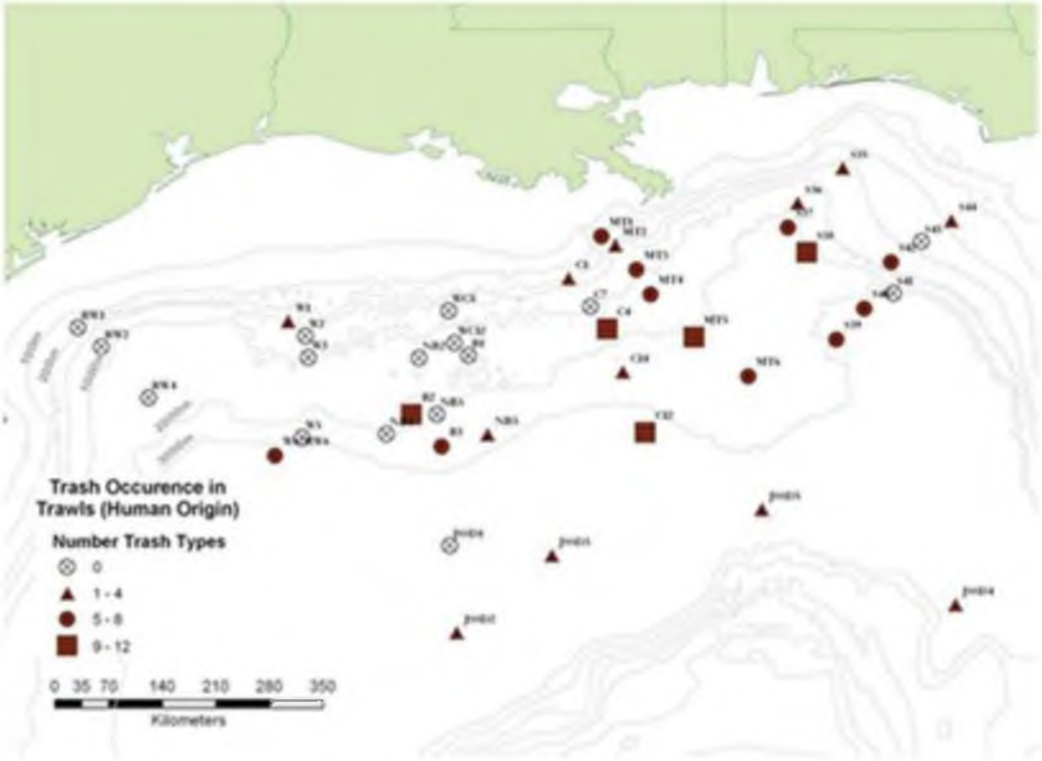

Figure 2-1: Litter occurrence in the Mississippi Trough in the Gulf of Mexico (Ramirez-Llodra et al., 2011: Fig. 3). Trawls were dominated by plastic, aluminum cans, discarded fishing gear and wood in trawls from 74 of the tested sites (n = 34).

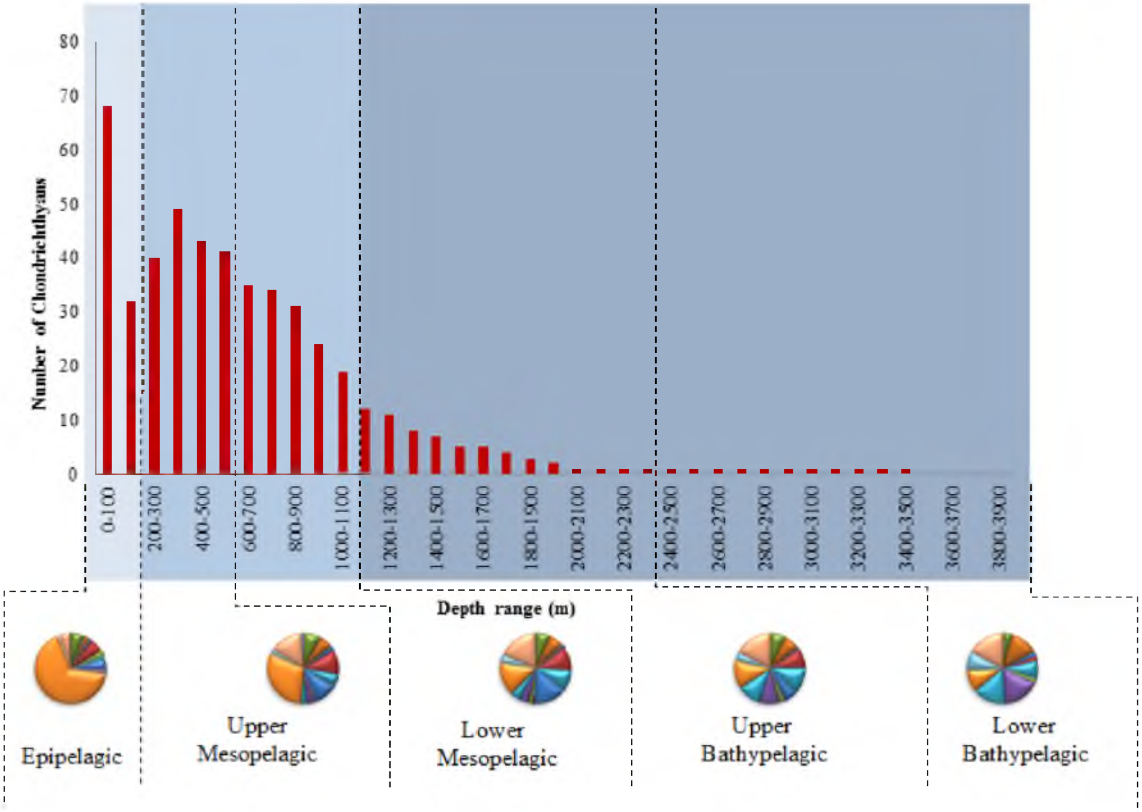

Figure 2-2: Chondrichthyan species richness along 100 m intervals in the Gulf of Mexico. *Red bars* denote the total number of chondrychthyan species at each depth interval. Pie charts below the X axis show the fish species composition at each respective depth interval. *Blue-gray shading* shows traditional oceanic zonation of the Epipelagic, Mesopelagic, and Bathypelagic. *Dashed lines* show boundaries between upper/lower oceanic zones and enclose pie charts that demonstrate the taxonomic composition for each respective zone.

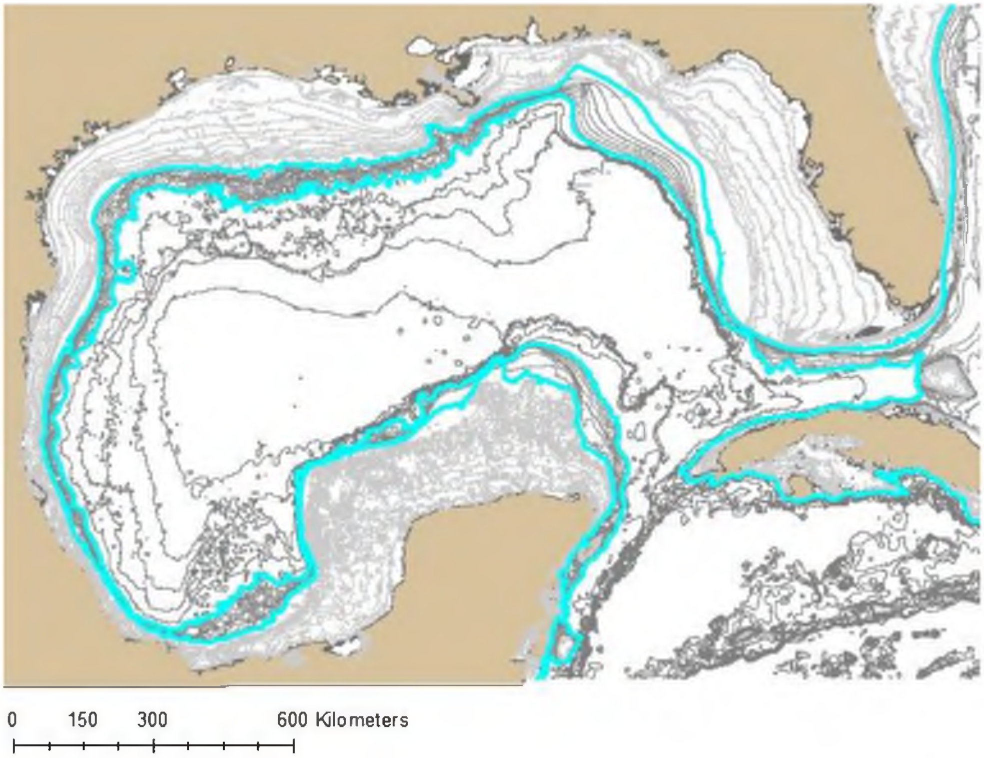

Figure 2-3: Bathymetry of the Gulf of Mexico. Highlighted blue lines show the 200 m contour (closer to shore) and the 1000 m contour (farther from shore). Lightest grey contours represent 0 – 100 m depths in 10 m intervals, medium grey contours represent 200 – 100 m depths in 100 m intervals, and darkest grey contours represent 1000 – 3500 m depths in 500 m intervals. Scale shown in kilometers.

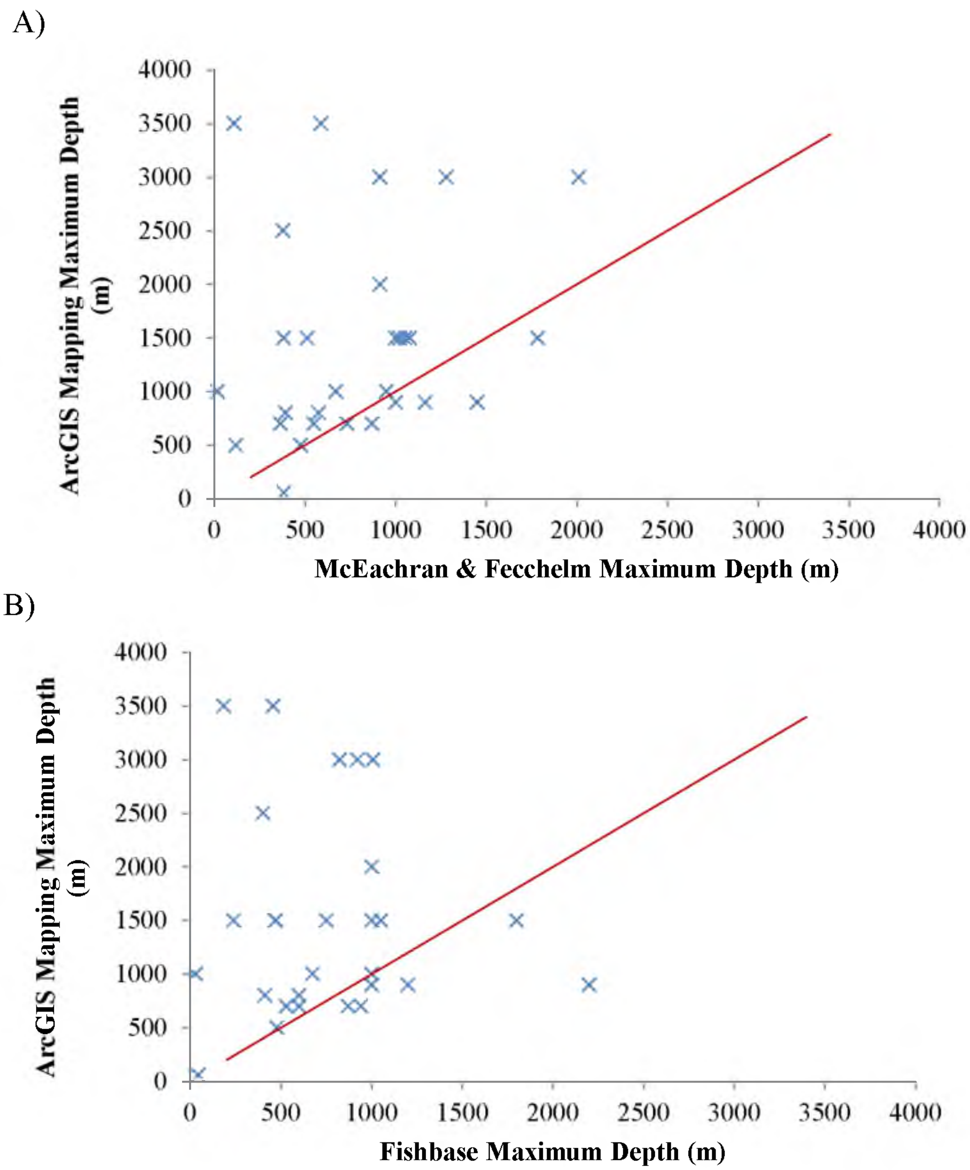

Figure 2-4: Range comparisons between maximum depths obtained using the ArcGIS mapping methodology and those (A) documented in McEachran & Fecchelm (1998) and (B) Fishbase.org (2013). *Red line* shows a 1:1 ratio for the depths. *Blue X's* denote chondrichthyan species. Data points that fall above the 1:1 line show general increases in maximum depths from the documented sources using ArcGIS mapping

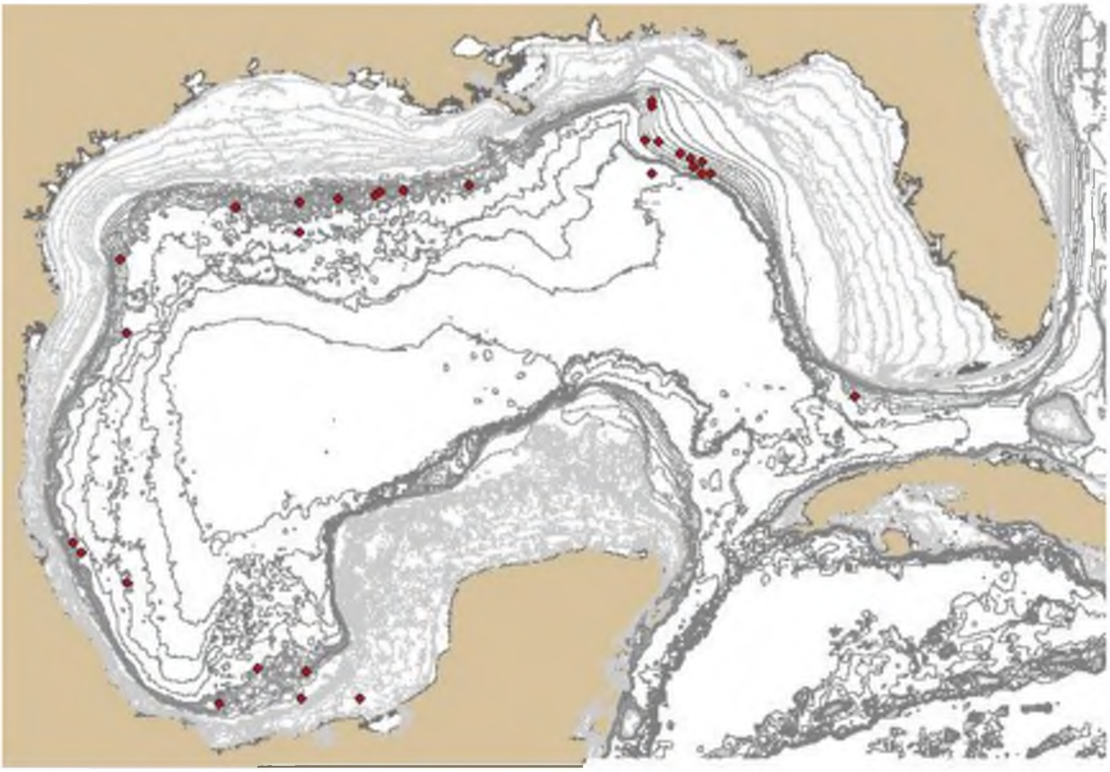

Figure 2-5: Distribution of *Rajella fuliginea* in the Gulf of Mexico. Same scale as shown in Fig. 2-3.

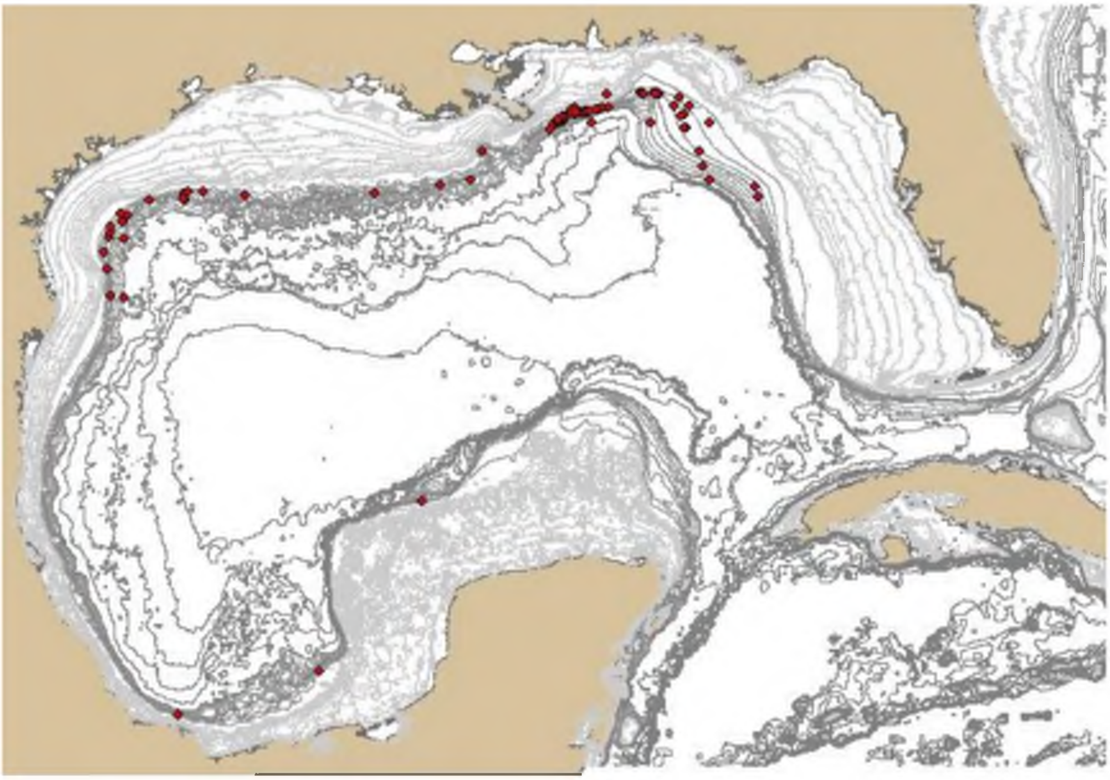

Figure 2-6: Distribution of *Anacanthobatis folirostris* in the Gulf of Mexico. Same scale as shown in Fig. 2-3.

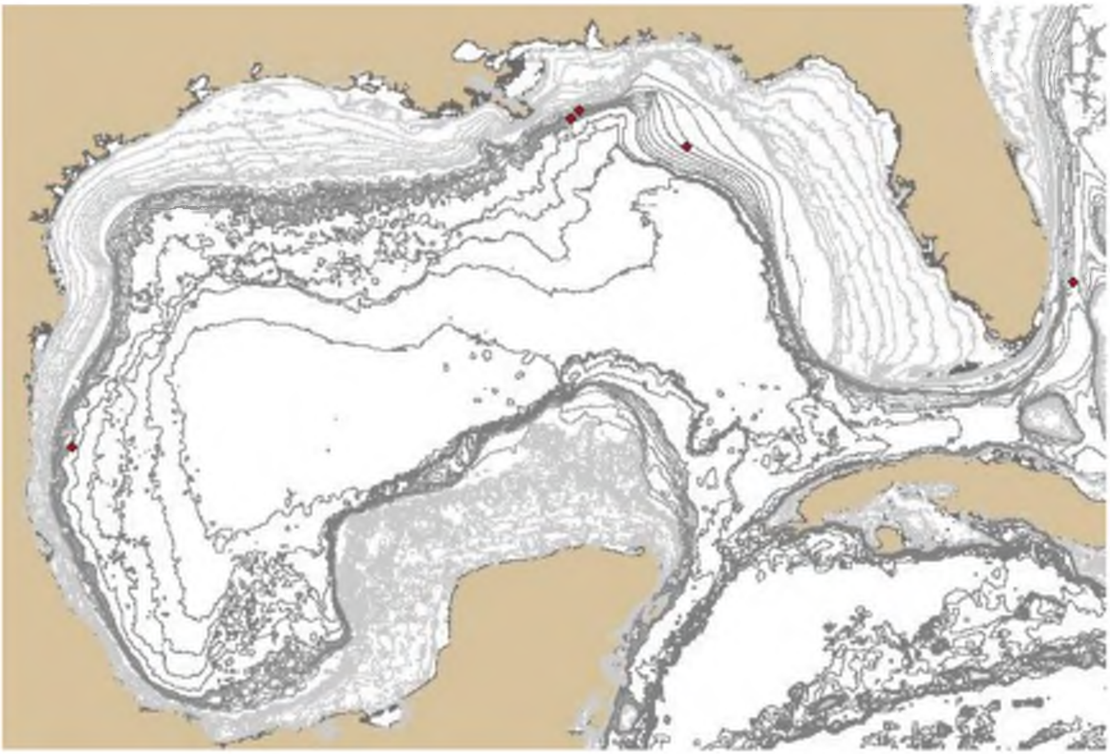

Figure 2-7: Distribution of *Dipturus oregoni* in the Gulf of Mexico. Same scale as shown in Fig. 2-3.

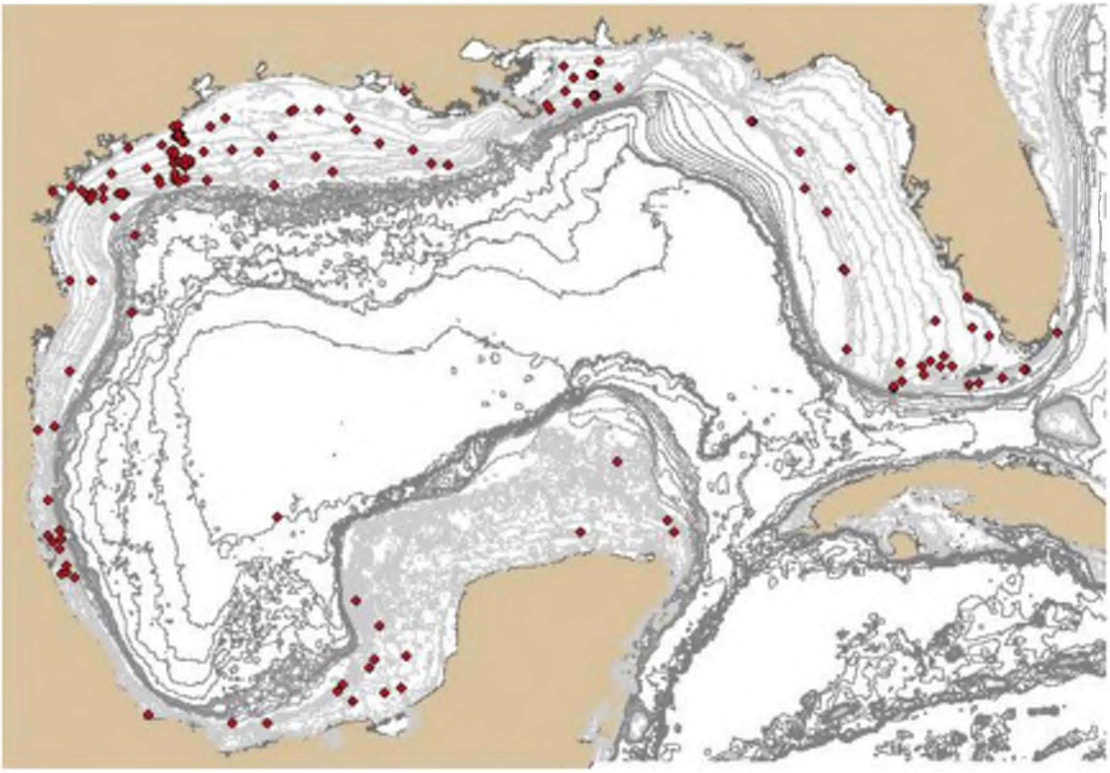

Figure 2-8: Distribution map of *Raja texana* in the Gulf of Mexico. Same scale as shown in Fig. 2-3.

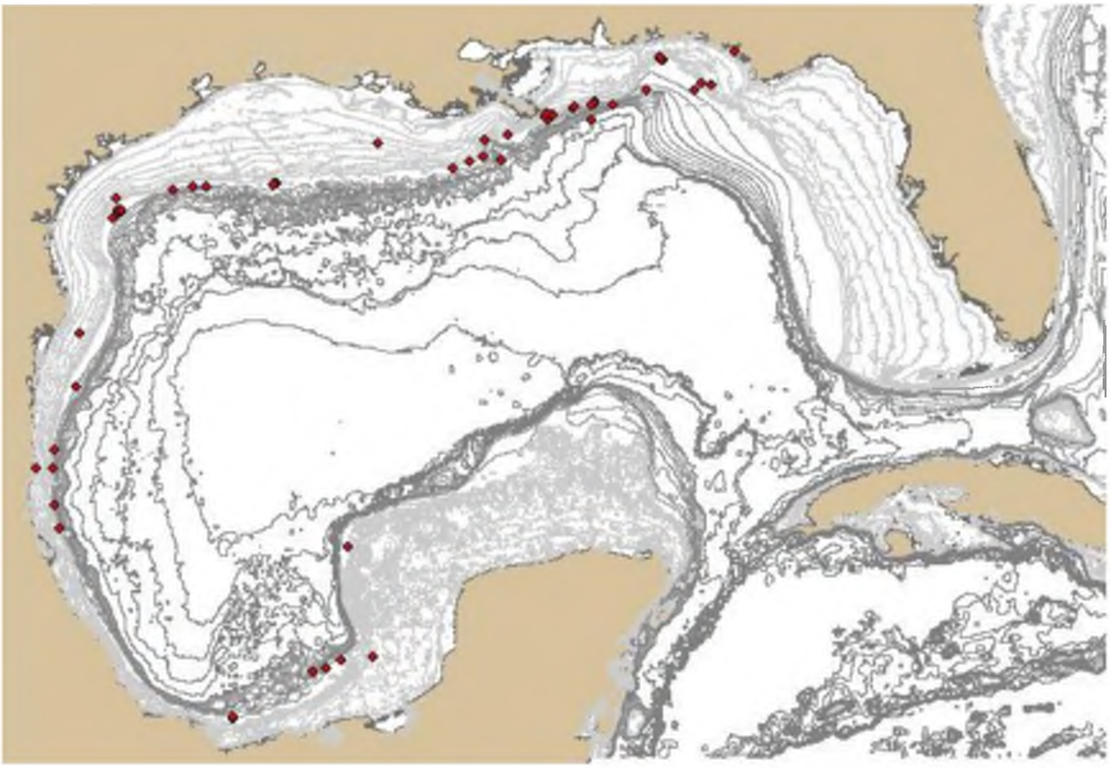

Figure 2-9: Distribution of *Dipturus olseni* in the Gulf of Mexico. Same scale as shown in Fig. 2-3.

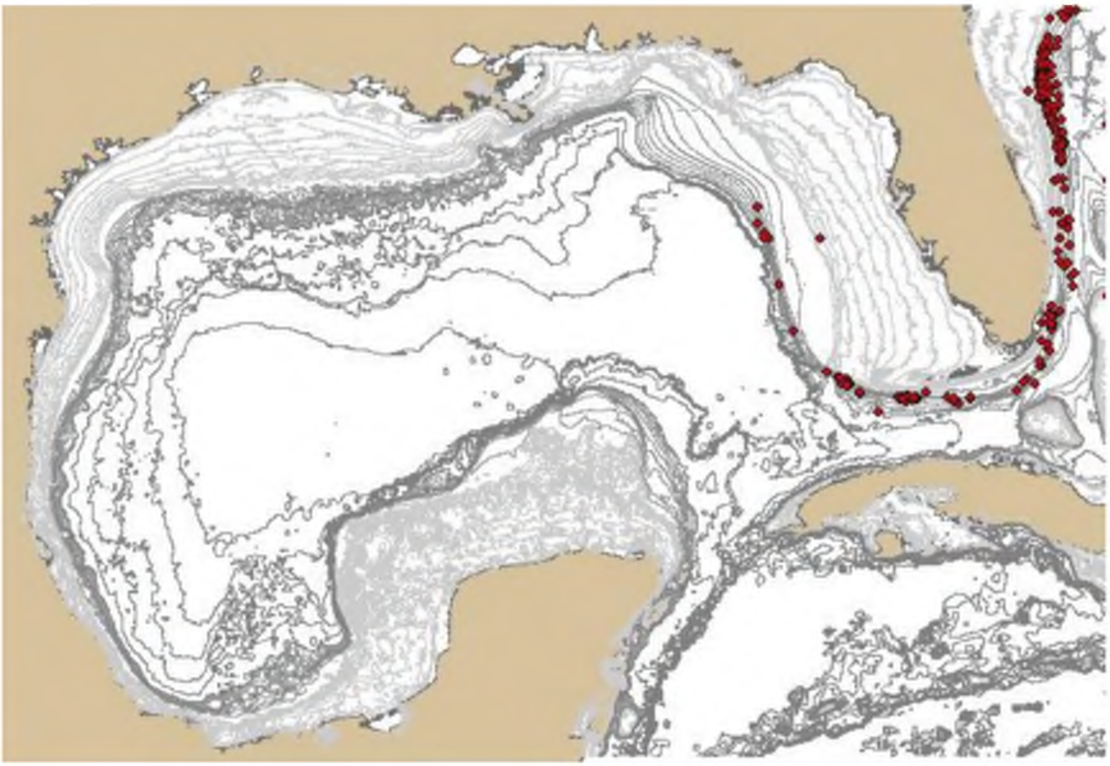

Figure 2-10: Distribution of *Fenestraja plutonia* in the Gulf of Mexico. Same scale as shown in Fig. 2-3.

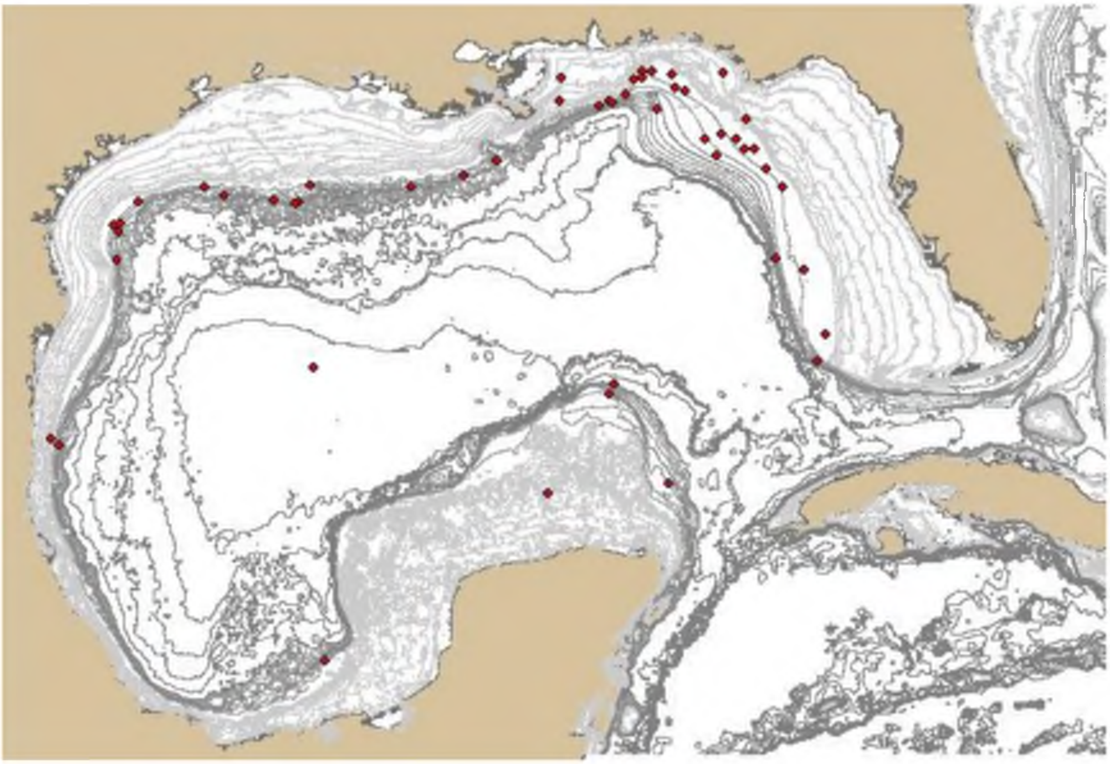

Figure 2-11: Distribution of *Leucoraja lentiginosa* in the Gulf of Mexico. Same scale as shown in Fig. 2-3.

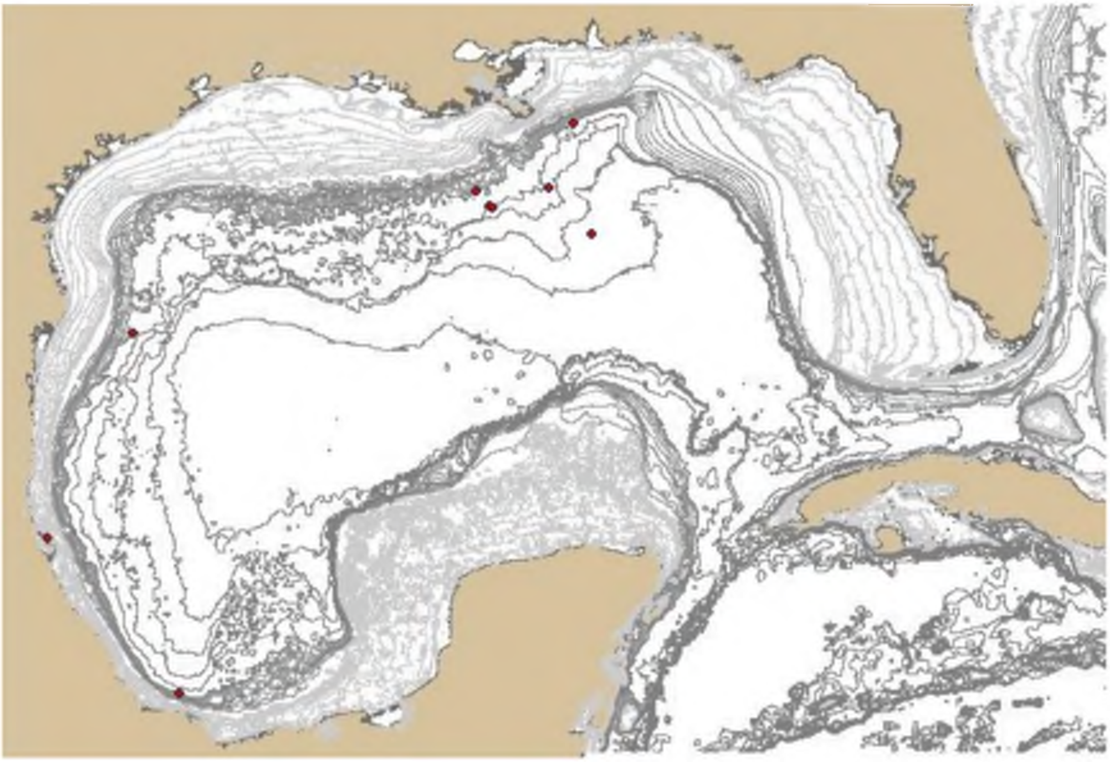

Figure 2-12: Distribution of *Rajella purpuriventralis* in the Gulf of Mexico. Same scale as shown in Fig. 2-3.

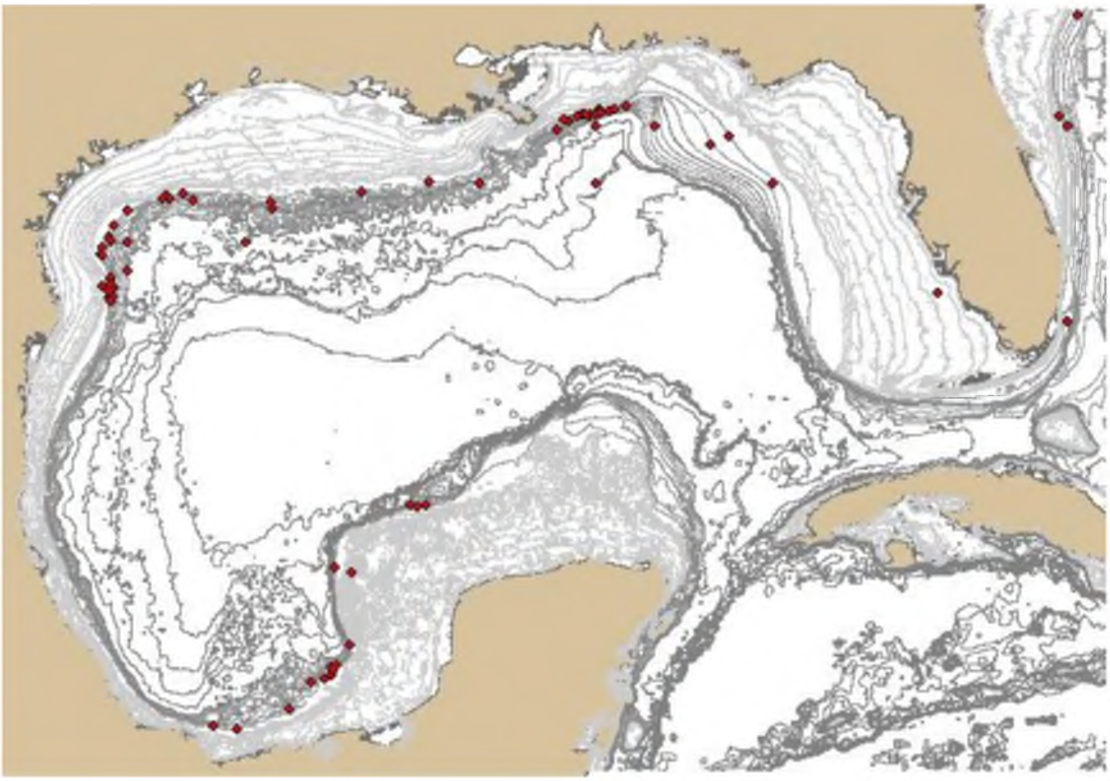

Figure 2-13: Distribution of *Squalus cubensis* in the Gulf of Mexico. Same scale as shown in Fig. 2-3.

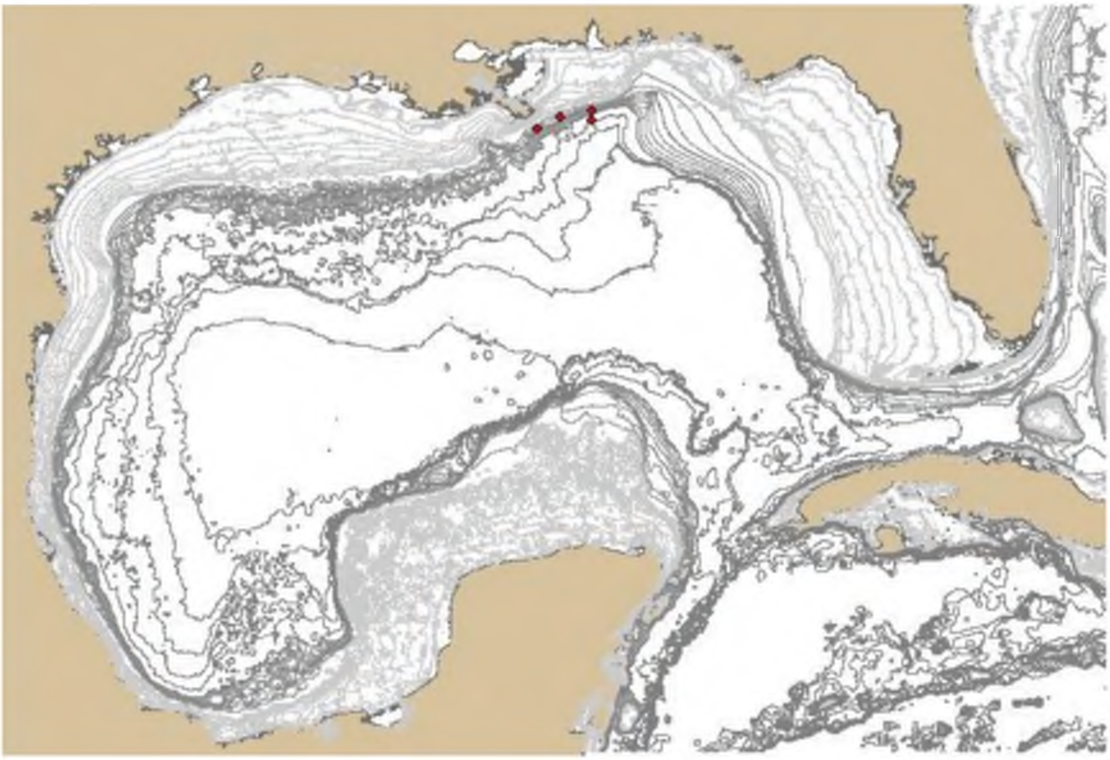

Figure 2-14: Distribution of *Deania profundorum* in the Gulf of Mexico. Same scale as shown in Fig. 2-3.

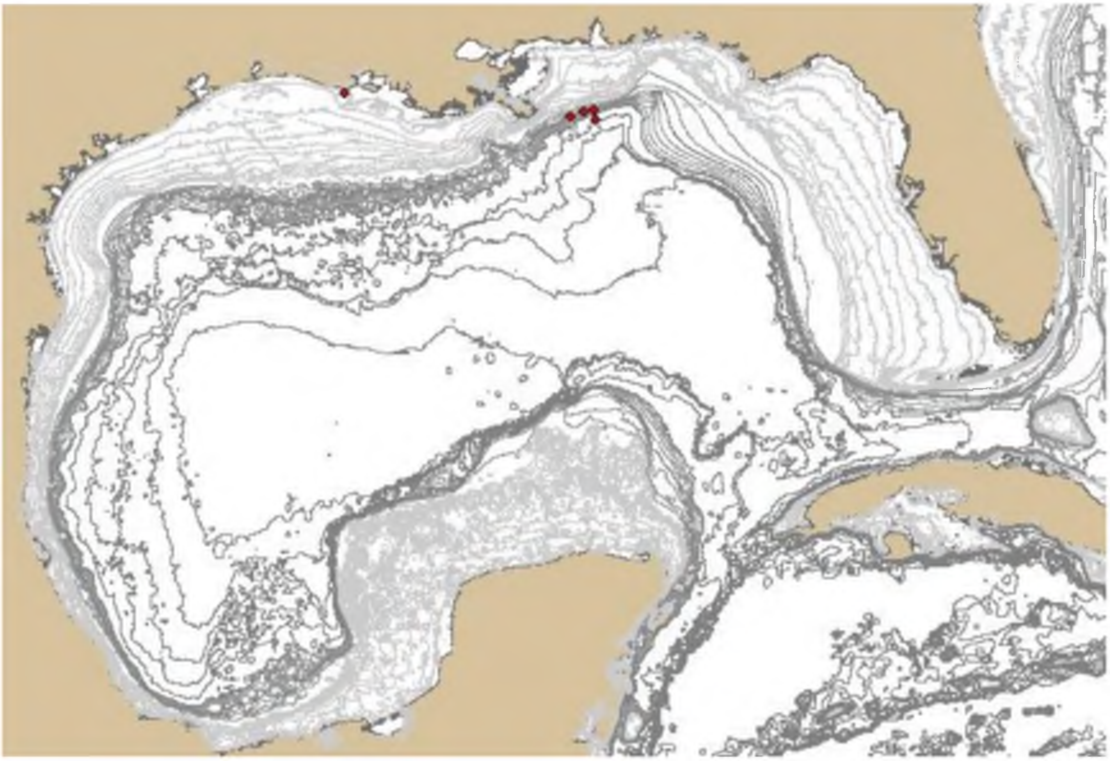

Figure 2-15: Distribution of *Etmopterus gracilispinis* in the Gulf of Mexico. Same scale as shown in Fig. 2-3.

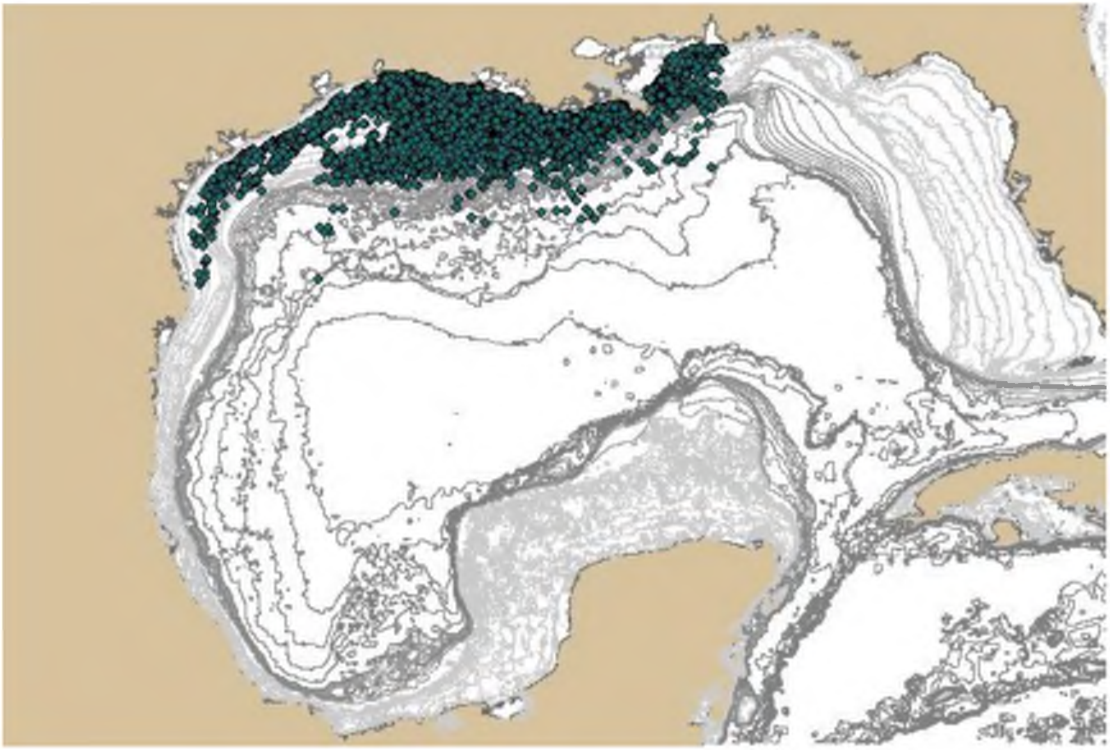

Figure 2-16: Location of oil and gas platforms in the Gulf of Mexico as of March 2013. Data provided by Bureau of Ocean Energy Management. All platforms in the BOEM's database are included in the map, active and inactive platforms. Same scale as shown in Fig. 2-3.

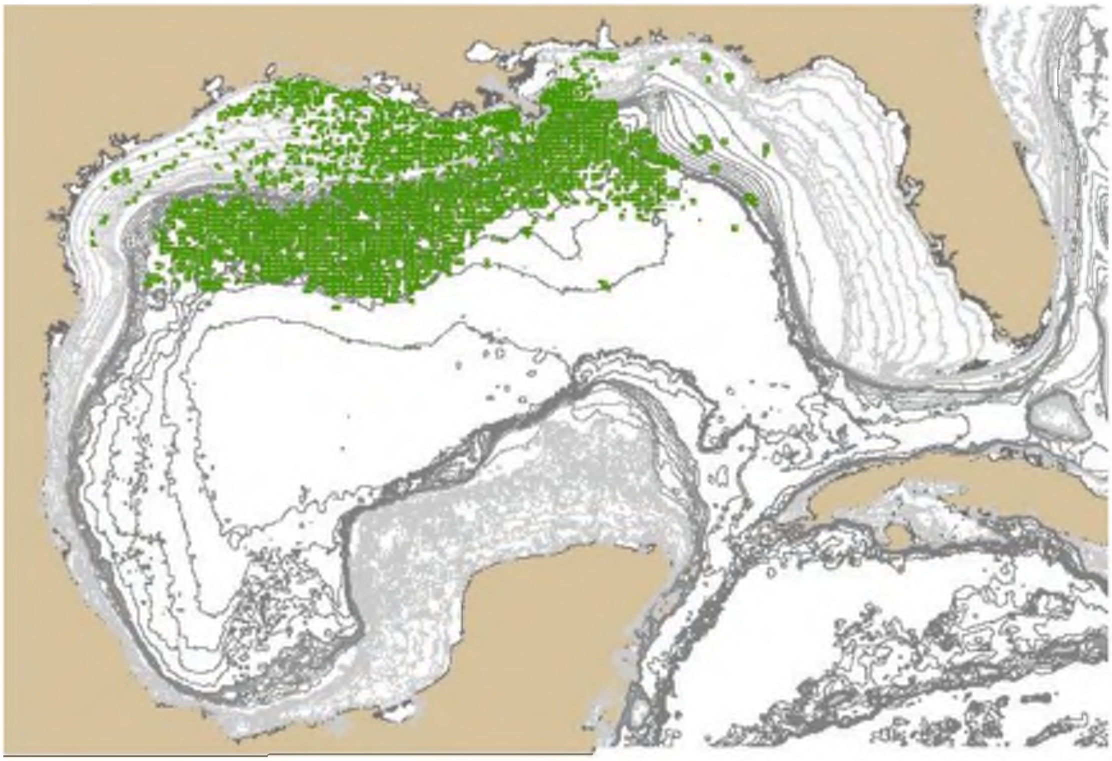

Figure 2-17: Active oil and gas drilling leases in the Gulf of Mexico as of March 2013. Information provided by Bureau of Ocean Energy Management. Same scale as shown in Fig. 2-3.

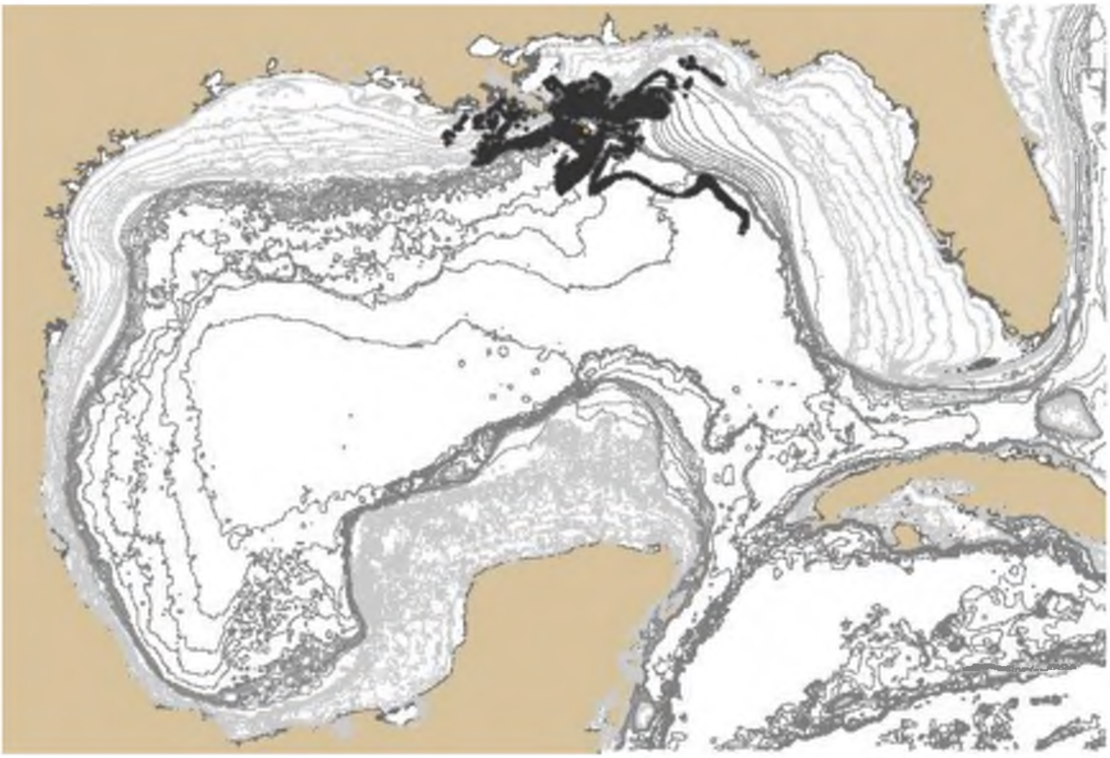

Figure 2-18: Surface area and deepwater areas affected by the oil from the Deep Water Horizon oil spill. *Orange diamond* indicates the location of the Horizon well. Same scale as shown in Fig. 2-3. Basemap source: ESRI

Table 2-1: Comparisons of species ranges from documented sources (McEachran & Fecchelm, 1998; Fishbase.org, 2013) to those determined using GBIF specimen record catch locations overlaid on a bathymetric map in ArcGIS. *Purple highlights* denote a decrease in the mapped depth when compared to both documented depths while *red highlights* indicate depth increases compared to both documented depths. *Blanks* occur when there is no data available.

	McEachran & Fecchelm (1998)			**Fishbase.org (2013)**			ArcMapping Data				
Species	Min	max	Range	min	max	Range	min	max	Range	average	# of records
Centroscymnus cryptacanthus	400	1164	**764**	400	1200	**800**	700	900	**200**	775	2
Deania profundorum	275	1785	**1510**	205	1800	**1595**	300	1500	**1200**	608.33	6
Etmopterus bigelowi	110	1000	**890**	163	1000	**837**	200	900	**700**	506.67	45
Etmopterus gracilispinis	100	1000	**900**	70	1000	**930**	10	1500	**1490**	730.71	7
Etmopterus schultzi	348	732	**384**	200	1000	**800**					
Scymnodon squamulosus	550	1450	**900**	0	2200	**2200**	500	900	**400**	766.67	3
Squalus cubensis	60	380	**320**	60	400	**340**	50	2500	**2450**	452.27	91
Squalus mitsukurii	330	394	**64**	29	600	**571**	300	800	**500**	550	2
Rhinobatos lentiginosus	0	18	**18**	0	30	**30**	0	1000	**1000**	42.84	58
Anacanthobatis folirostris	300	512	**212**	425	472	**47**	60	1500	**1440**	432.5	114
Anacanthobatis longirostris	520	1052	**532**	530	1052	**522**	10	1500	**1490**	877.5	4
Breviraja colesi	220	415	**195**	366	522	**156**					
Breviraja spinosa	366	671	**305**	323	675	**352**	20	1000	**980**	555.45	12
Curiraja poeyi	355	870	**515**	385	870	**485**	500	700	**200**	600	1
Curiraja rugosa	366	915	**549**	366	1007	**641**	20	3000	**2980**	730.98	33
Dactylobatus armatus	338	685	**347**	300	900	**600**					0
Dactylobatus clarki	366	915	**549**	475	1000	**525**	400	2000	**1600**	720.59	22
Dipturus bullisi	183	549	**366**	200	600	**400**	100	700	**600**	407.41	14

Dipturus garricki	275	476	**201**	275	476	**201**	200	500	**300**	400	5
Dipturus olseni	55	384	**329**	91	238	**147**	20	1500	**1480**	178.59	71
Dipturus oregoni	475	1079	**604**	369	468	**99**	300	1500	**1200**	687.5	4
Dipturus teevani	320	732	**412**	320	940	**620**	5	700	**695**	436.59	24
Fenestraja ishiyamai	503	950	**447**	400	1000	**600**	900	1000	**100**	950	3
Fenestraja plutonia	293	1024	**731**	290	750	**460**	70	1500	**1430**	551.71	56
Fenestraja sinusmexicanus	59	1096	**1037**		311	**311**					0
Leucoraja garmani	66	366	**300**	55	530	**475**	10	700	**690**	262.35	45
Leucoraja lentiginosa	53	588	**535**	53	457	**404**	30	3500	**3470**	335.57	56
Pseudoraja fischeri	412	576	**164**	412	412	**0**	300	800	**500**	393.75	8
Raja ackleyi	32	384	**352**		45	**45**	40	60	**20**	50	3
Raja eglanteria	0	119	**119**	0			0	500	**500**	74.731	53
Raja texana	15	110	**95**		183	**183**	0	3500	**3500**	98.756	94
Rajella fuliginea	731	1280	**549**	732	824	**92**	30	3000	**2970**	954.16	40
Rajella purpuriventralis	732	2010	**1278**		922		0	3000	**3000**	1317.2	16

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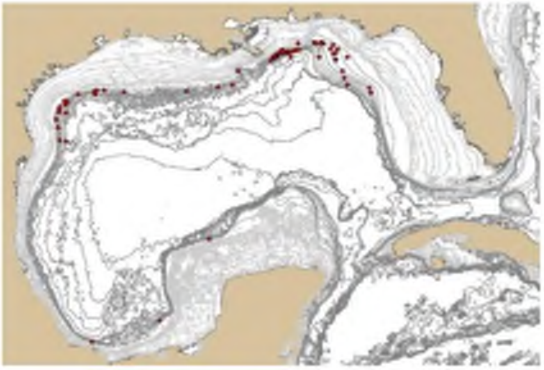
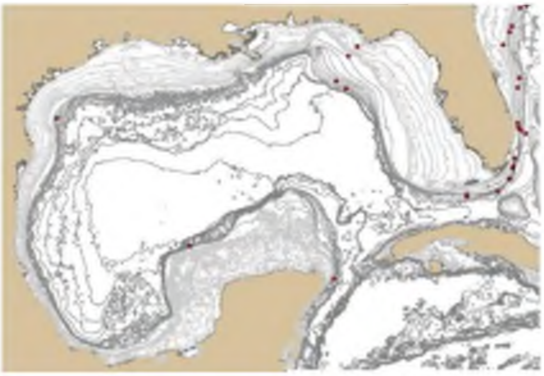
APPENDIX I

Distribution maps of all Rajiformes and Squaliformes examined in this study in alphabetical order. The genera *Centroscymnus, Deania, Etmopterus, Scymnodon,* and *Squalus* belong to the order Squaliformes. All other included taxa are in Rajiformes.



Anacanthobatis folirostris



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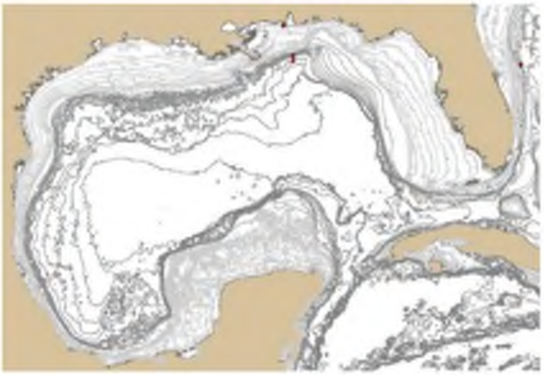

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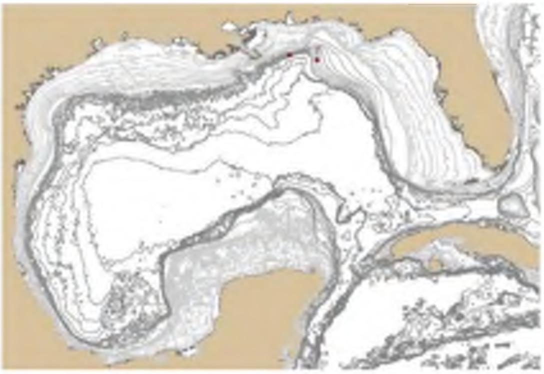
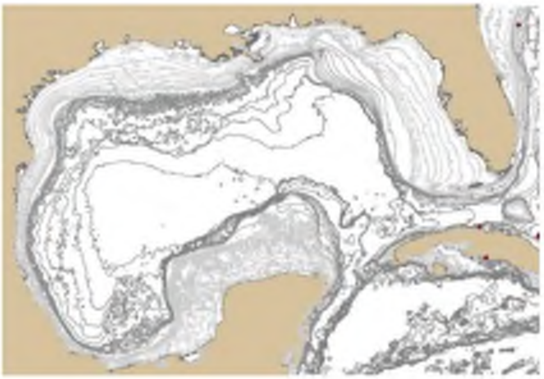
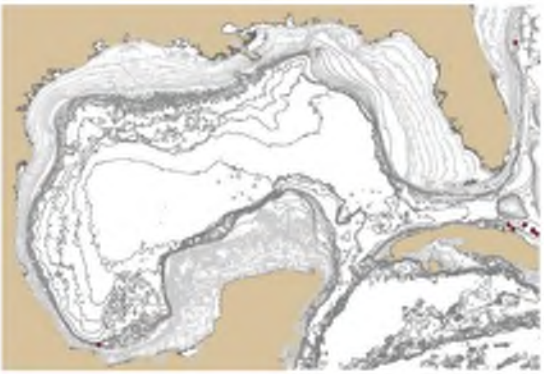


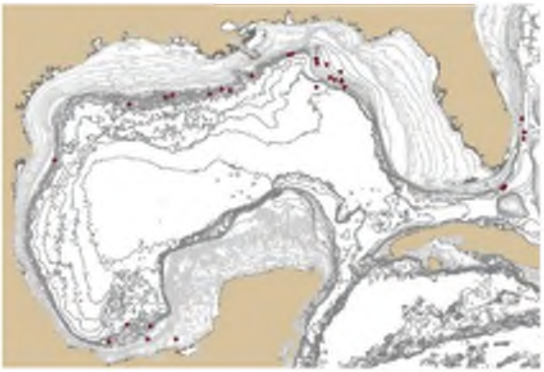
Centroscymnus cryptacanthus



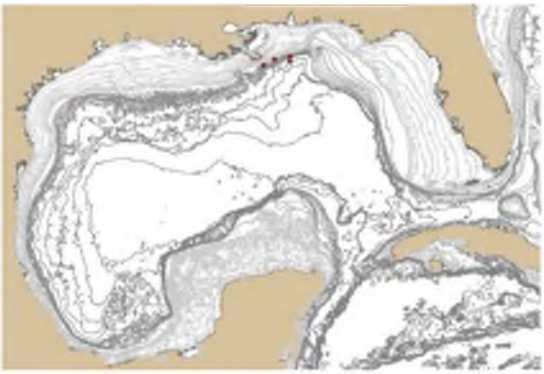
Breviraja colesi



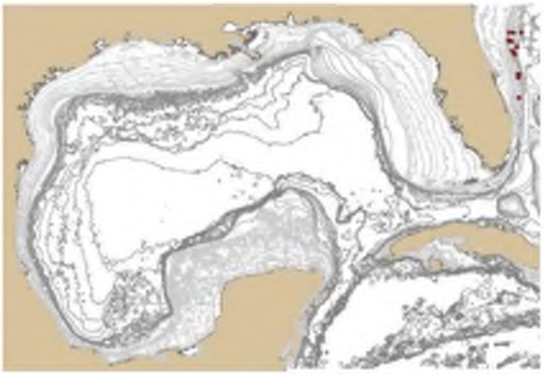
Curiraja poeyi



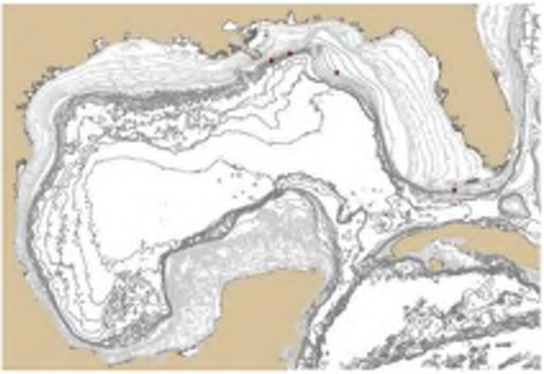
Curiraja rugosa



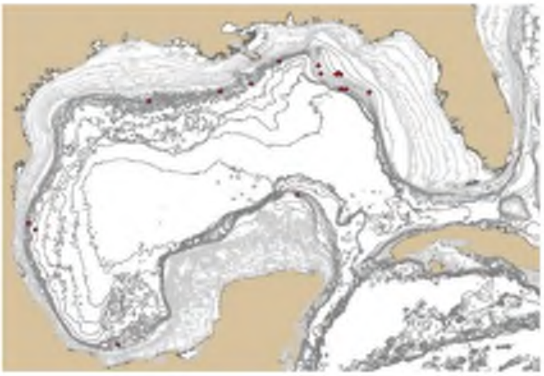
Dipturus bullisi



Dactylobatus armatus



Dipturus garricki



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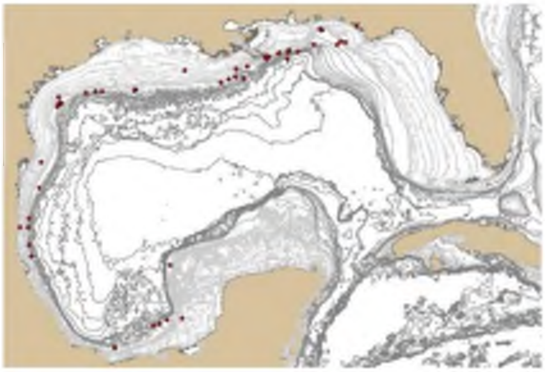
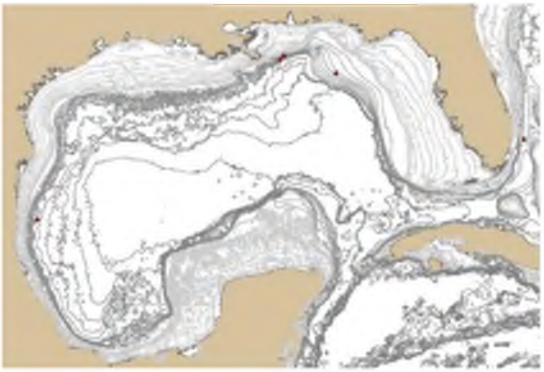


Dipturus olseni



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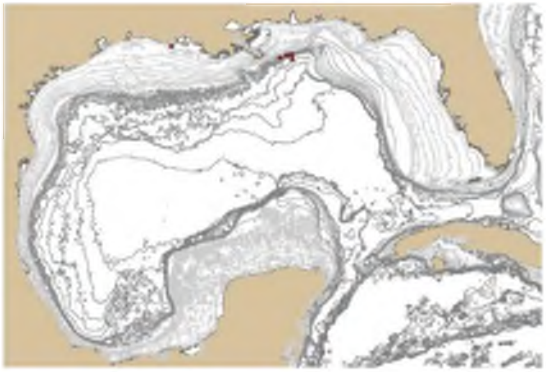

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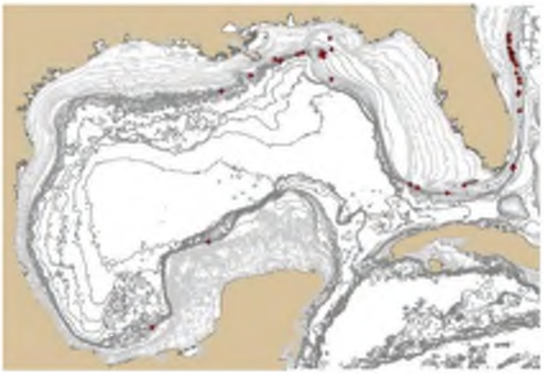
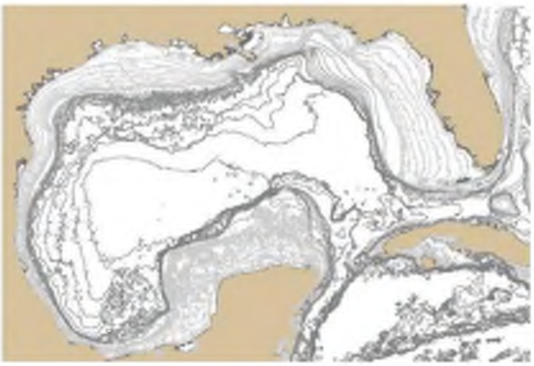
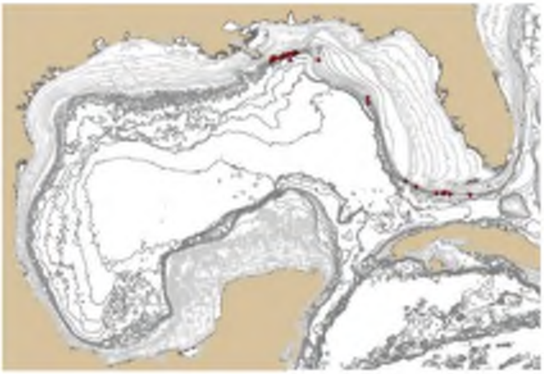


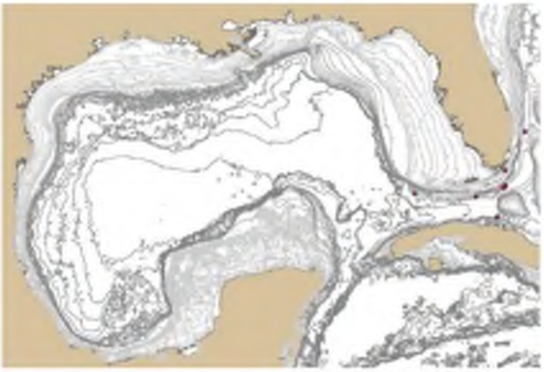
Dipturus teevani



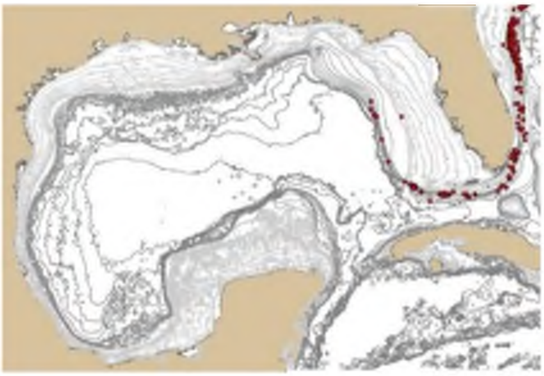
Etmopterus schultzi



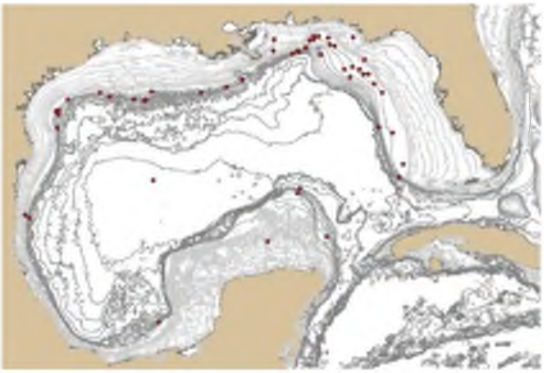
Etmopterus bigelowi



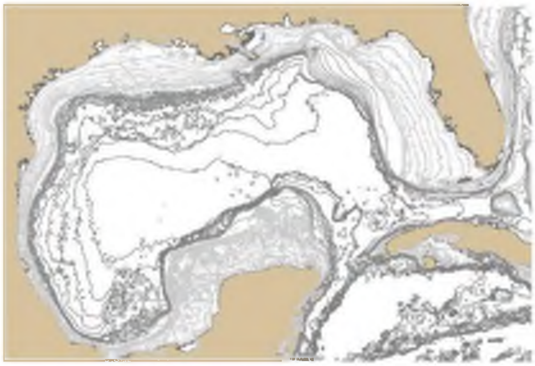
Fenestraja ishiyamai



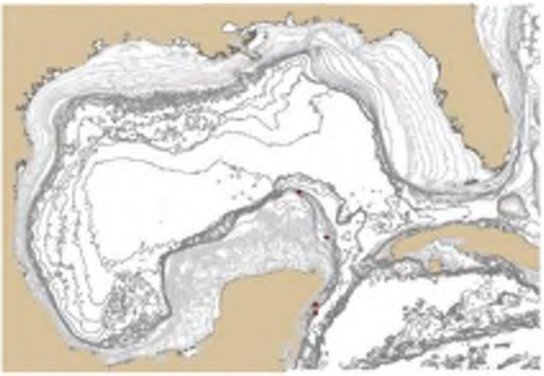
Fenestraja plutonia



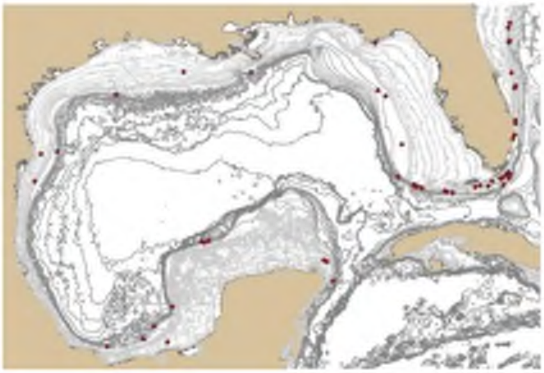
Leucoraja lentiginosa



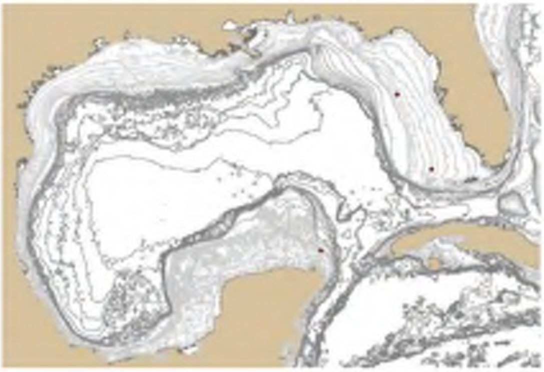
Fenestraja sinusmexicanus



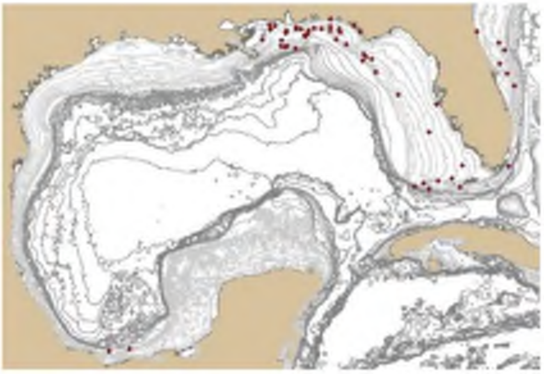
Pseudoraja fischeri



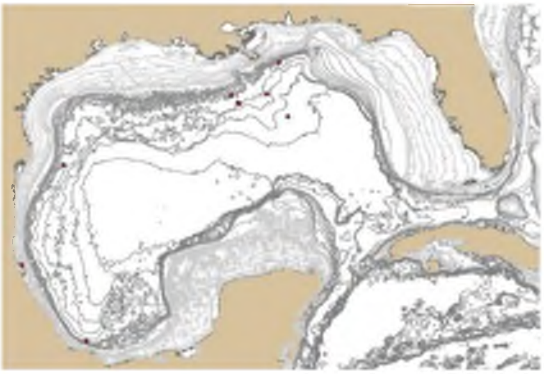
Leucoraja garmani



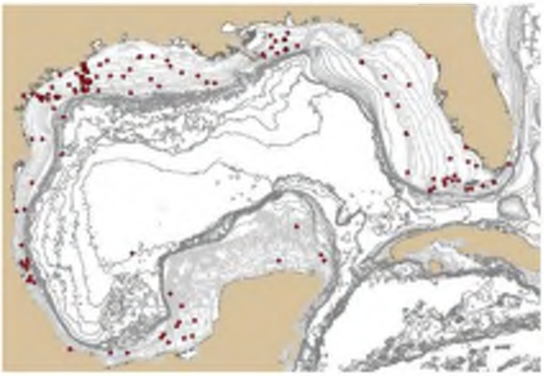
Raja ackleyi



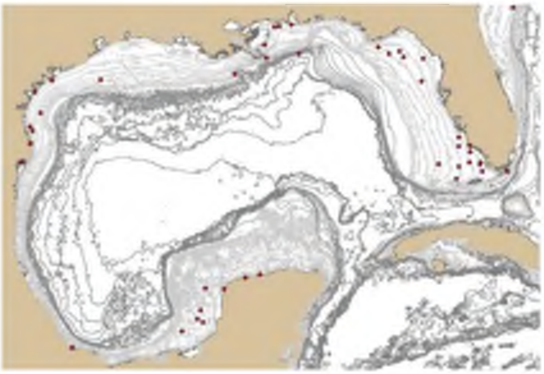
Raja eglanteria



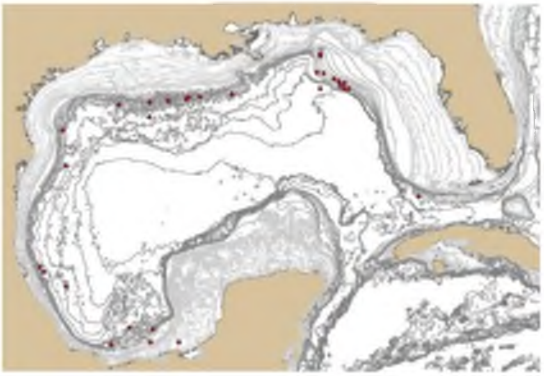
Rajella purpuriventralis



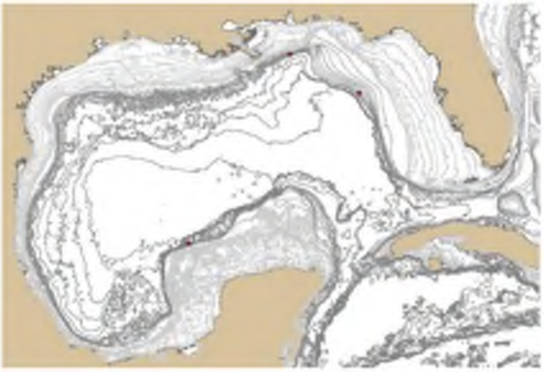
Raja texana



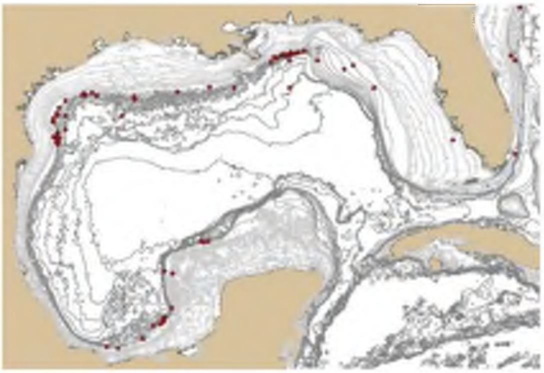
Rhinobatos lentiginosus



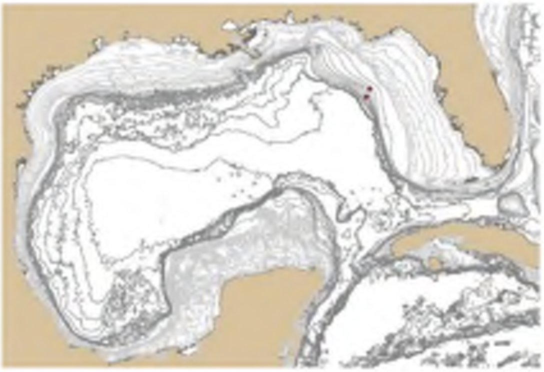
Rajella fuliginea



Scymnodon squamulosus



Squalus cubensis



Squalus mitsukurii