

Changes in groundfish community structure and diversity in the northern Gulf of Mexico

during the last 2 decades

by

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ABSTRACT

Changes in diversity indices and community structure of the Gulf of Mexico were examined between 1987 and 2010 using univariate and multivariate statistical approaches. Trawl data were used from the National Marine Fisheries Service (NMFS) summer Southeast Assessment and Monitoring Program (SEAMAP) shrimp/bottomfish survey in the Gulf of Mexico (Gulf) between 1987 and 2010. The primary habitat sampled consisted of unstructured seafloor, including soft (sandy or muddy) bottoms or hard (shell-hash or hard-ground) bottom. Diversity and community structure was tested against temporal, spatial, or abiotic variables. Species diversity measures consisted of: number of individuals, number of species, richness, evenness, Simpson's and Shannon's diversity indices. Environmental parameters examined were depth (m), temperature ($^{\circ}\text{C}$), dissolved oxygen (mg^{-1}) (dO_2), and salinity. Diversity indices significantly increased temporally from the Mississippi River Basin to Brownsville, TX between 1987 and 2010 and spatially across the study area in a southwesterly direction. Multivariate partial least squares analysis (PLS) showed dissolved oxygen, depth, and statistical zone contributed 14.6% of the response variable. In general, the community structure between 1987 and 2010 became more consistent. Gulf-wide, the community structure was correlated with depth and DO (49%) or temperature and DO (48%). Dissolved oxygen influences community structure near the Mississippi River outfall but is less important elsewhere. Overall, the Gulf is incredibly complex and no single temporal, spatial or environmental variable completely explains the diversity or community structure. However, the Gulf may have two alternate states with respect to biodiversity and community structure.

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INTRODUCTION

Changes to biological diversity have concerned scientists for many years (Briggs, 1974; Darwin, 1859 as cited in Tittensor et al 2010; Hillebrand and Matthiessen, 2009; Worm, 2006; Worm and Duffy, 2003). Maintaining diversity can ensure an ecosystem's stability to stressors and resistance to perturbations (Worm and Duffy, 2003) but globally, the marine ecosystems are experiencing drastic declines and shifts in community structure (Pauly and Palomares, 2005; Worm, 2006). The trend in declining biodiversity is occurring throughout the world, and increasing climate change and other anthropogenic effects are theorized to increase this decline (Diaz and Rosenberg, 2008; Hiddink, et al., 2006; Pauly and Palomares, 2005; Pörtner, et al., 2005). Clearly, fishing can impact biodiversity; this has been shown in many cases (Arreguin-Sanchez, et al., ; Caillouet, et al., 1980; Pauly and Palomares, 2005; Wells, et al., 2008b). For example, as fishing pressure increased in the North Sea over the past century, size at maturity decreased in commercially fished species and community structure varied with temperature (Hofstede and Rijnsdorp, 2011). In addition, species diversity in the entire North Sea groundfish assemblage decreased over time in areas of high fishing pressure (Greenstreet, et al., 1999). Fishing pressure and low dissolved oxygen are the main contributors to the abrupt transitions in community structure between 1960 and 2000 in the Black Sea (Oguz and Gilbert, 2007).

Efforts to mitigate trends in biodiversity have included, but not been limited to, controlling invasive species, establishing marine protected areas, and implementing ecosystem based management practices (Groves, et al., 2002; Hooker and Gerber, 2004; Klein, et al., 2008; Stachowicz, et al., 2002; Trexler and Travis, 2000; Ward, et al., 1999). Invasive species can significantly alter biodiversity within ecosystems by becoming an uncontrolled predator, decreasing water quality, increasing algae blooms, or altering quantity or quality of nutrients

available to the ecosystem (Crooks, 2002; Ruiz, et al., 1997). Efforts to remove invasive species from many environments have been extensive (Hulme, 2006; Zavaleta, et al., 2001). By using a long-term database, the effects of invasive species can be better monitored throughout the Gulf of Mexico (Gulf). Marine protected areas (MPAs) can protect diversity by limiting the amount of human activities in the area. Objectives for marine protected areas are highly varied and include maintaining diversity above a particular level to halting declining trends in diversity. (Jennings, 2009). Attempting to protect multiple species with complex movement patterns combined with mitigation of human uses needs continued research; however, MPAs have been helpful protecting or maintaining diversity (Gruss, et al., 2011). For these practices to be effective MPAs must maintain or increase diversity to a level that strengthens ecosystem resiliency and maintains this resilience through time (Elmqvist, et al., 2003; Margules and Pressey, 2000; Worm and Duffy, 2003). Examining diversity in the Gulf of Mexico with a long term database will aid in better ecosystem based management practices of the Gulf and the placement of MPAs.

The Gulf has seen changes in diversity, most directly related to the effect of humans on the environment. Anthropogenic perturbations like invasive species, overfishing, trawling, dredging, gas and oil exploration, eutrophication, hypoxia, and climate change each have negatively affected species composition and altered how ecosystems function (Auster, 1998; Bianchi, et al., 2000; Jackson, 2008). Invasive species are also having a significant impact of the communities of the Gulf. For example, lionfish (*Pterois volitans*), have altered community structure and negatively influenced biodiversity in many locations in the southern Gulf (McDaniel, et al., 2000). Fishing alters species diversity by removing predatory fishes at the top of the food chain or by overfishing prey species. Overfishing leads to trophic cascades and how an ecosystem

functions (Bruno and O'Connor, 2005; Pauly and Palomares, 2005; Worm, 2006). For example, trawling can result in the homogenization of the habitat and a decrease in diversity by overfishing of targets and by-catch species (Hewitt, et al., 2008; Simon, et al., 2006). The Gulf provides a wide array of valuable resources. It yields more finfish, shrimp, and shellfish annually than the south and mid-Atlantic, Chesapeake, and New England oceanic areas combined (E.P.A, 2010). However, the harvesting of these fish has caused declines in maturing fish sizes fish populations of the targeted species (Arreguin-Sanchez, et al., ; Caillouet, et al., 1980; Gracia and Bader, ; Wells, et al., 2008a).

Another activity that alters diversity in the Gulf is petroleum exploration. Offshore platforms, created by the oil and gas industry can affect biodiversity by providing structure that would not have otherwise existed; however, platform installation, well drilling, pipe laying, and unregulated noise pollution can negatively impact and may alter surrounding communities (Driessen, 1986). Trenching the seafloor during the pipe laying process may also disturb bottom communities and noise pollution during the drilling process may also have an effect on adjacent areas (Driessen, 1986). A significant increase in the amount of petroleum production has occurred in the Gulf since 1953 (E.P.A, 2010). Although the number of barrels produced a day from the Gulf has declined over the past few years, the undiscovered resources are forecasted to increase in the future as the petroleum industry explores deeper oil exploration. Such a trend increases the importance of studying diversity now to better establish the effects this industry has on the Gulf. Because of the many ways that biodiversity can be influenced, a more complete understanding of the communities in the Gulf and the factors that influence them is critical

Eutrophication and hypoxia can also alter species and community structures. Hypoxia, defined as dissolved oxygen $< 0.2 \text{ mg l}^{-1}$, is a natural occurrence in the Gulf that has been

exacerbated by human-induced nutrient loading (Osterman, et al., 2008; Rabalais, et al., 2002b). Anthropogenic influenced hypoxia has a larger geographic extent than natural low-oxygen bottom events on the Louisiana shelf (Turner and Rabalais, 1991; Turner, et al., 2005a). Factors that contribute to hypoxic conditions are warmer temperatures, freshwater discharge, plankton blooms, eutrophication, storm activities and precipitation (Diaz, 2001; Rabalais, et al., 2002a; Turner, et al., 2005b). Although the cause of many hypoxic events are unknown, increased fertilizer use in watersheds resulting in high levels of nitrogen runoff are considered to be the major anthropogenic cause (Howarth, et al., 1996; Turner and Rabalais, 1991). High nitrogen runoff causes increased primary production that decays faster than it is consumed resulting in oxygen depletion due to high bacterial loads (Rabalais, et al., 2001a). Hypoxia can cause fish and mobile invertebrates to leave the area and cause stress or death to immobile organisms (Diaz and Rosenberg, 1995). Patterns of seasonal summer hypoxia occur off the Louisiana coast and the northeastern coast of Texas (Rabalais, et al., 2002b). Drastic declines in species richness and number of individuals have occurred because of the presence of hypoxia (Baustian, et al., 2009; Gaston and Edds, 1994; Harper, et al., 1981; Rabalais, et al., 2001b). Hypoxia off the coast of Texas is less frequent and short lived (Harper, et al., 1981; Rabalais, et al., 2001a). Analyzing a long-term database in the Gulf could lead to a better understanding of the effects of hypoxia on diversity.

On a much slower scale, climate change may also affect community structures, indirectly and directly. Of the indirect effects of global climate change in the Gulf, increasing severity and frequency of hypoxic events has been of the most concern (Conley, et al., 2009; Diaz and Rosenberg, 1995; 2008; Pörtner, et al., 2005). The Gulf of Mexico's coastal region will experience approximately 2°C temperature increase over the next decade (Karl, et al., 2009).

Combined with predictions that sea surface temperature will increase during the 21st century, hypoxia is expected to intensify. Not only will temperature increase stratification, but other climate related changes may intensify the effects of hypoxia. Because hypoxia is also related to runoff, the extent of the hypoxic zone is highest in wet years compared to dry years (Justic, 2005; Rabalais and Turner, 2001; Rabalais, et al., 1996). For instance, river inflows will be more extreme as storms and rainfall are predicted to be intense. Between these storms are thought to be more extreme droughts. In drought years, coastal environments that are affected by inflow systems like the Mississippi River, tend to higher salinities, and higher bottom dissolved oxygen concentrations (Cronin, et al., 2000; Justic, et al., 1996). In drought occurrences, hypoxia will be less intense, similar to what was seen in the Gulf of Mexico during the 1988 drought. During that year, the hypoxic zone was less intense than previous years (Justic, et al., 1996). Yet, during extremely wet seasons, hypoxic events are often more extreme. For example, as a result of the 1993 flooding event within the Mississippi River basin nutrient loading was at a high enough level to fundamentally alter nutrient cycles. The result was the doubling of the hypoxic area in the Gulf of Mexico which has maintained the same size ever since. Climate change will also significantly influence temperature and freshwater inflow, which, as stated above, are the most important factors for the hypoxic zone in the Gulf. Popular climate change models specific to the Gulf disagree on the magnitude of temperature change and freshwater discharge resulting in major differential estimates of the role of climate change on the severity of hypoxia in the future (Justic, 2005). The general circulation model (GCM) predicts the average annual runoff of the Mississippi River Basin would increase 20% if the concentration of atmospheric CO₂ doubles (Miller and Russell, 1992). However, other models vary in magnitude and direction of changes in average runoff. For example, the Canadian CGCM1

model for the Mississippi River Basin projects a 30% decrease in runoff, whereas the Hadley HADCM2 model predicts a 40% increase (Justic, 2005; Wolock and McCabe, 1999). Regardless of the model, hypoxia and temperature can alter community structure (Genner, et al., 2004; Li and Clarke, 2005) and climate change will exacerbate these effects (Burkett, et al., 2008; Moretzsohn, et al., 2011; Nance, 2000). A long-term study of the environments role on diversity would provide a better understanding of how climate change affects the community structure.

The biodiversity of many habitats within the Gulf have been measured, including estuaries, wetlands, deep-sea, corals, artificial habitats, cold water seeps and vents (Brown, et al., 2000; Cordes, et al., 2010; Gelwick, et al., 2001; Jordan-Dahlgren, 2002; Martin and Haney, 2005; Seaman, 2007; Wilson, 2008). Research within many of these habitats has been the direct result of highly visible declines in species composition or abundance. For example, within estuaries and wetlands invasive species, contaminant effects, and climate change have each influenced biodiversity (Brown, et al., 2000; Hyland, et al., 2003; Rakocinski, et al., 1997; Sosa-Lopez, et al., 2007). The diversity of coral reefs, artificial reefs, seep and vent habitats can also be influenced by anthropogenic disturbances and contaminants (Grassle, 1985; Gregg, et al., 2010; Jordan-Dahlgren, 2002; Lobegeier and Gupta, 2008; Martin and Haney, 2005; Paull, et al., 1984). Although community diversity and genetic diversity have been examined at multiple trophic levels from marine mammals to microbial communities in many of these habitats, long-term trawling studies are lacking (Gregg, et al., 2010; Hernandez, et al., 2010a; Hewson and Fuhrman, 2007; Karlsson, et al., 2009; Mullin, et al., 1991; Wu, et al., 2008). For example, increases in water temperature and currents are positively correlated to larval taxonomic diversity (Gierach, et al., 2009; Hernandez, et al., 2010b; Limouzy-Paris, et al., 1994).

Furthermore, decreasing bottom dissolved oxygen can have a negative relationship on larval settlement in coastal and estuarine habitats (Powers, 1995). Cold seeps demonstrate highly resilient, diverse microbial communities under extreme pressures (Gierach, et al., 2009; Rosano-Hernandez, et al., 2009; Wu, et al., 2008).

Despite being studied in coastal or deep sea habitats, diversity in the most abundant habitat in the Gulf of Mexico has largely been ignored (Wells, 2009). The unstructured seafloor, including soft (sandy or muddy) bottoms or hard (shell-hash or hard-ground) bottom, is the most common and least studied substrate between 30 and 360 m (Buczowski, et al., 2006; Kennicutt, et al., 1995; Link, 1997; Schroeder, et al., 1988). The equivalent of all fishable bottom of the Gulf is trawled approximately 2.5 times year⁻¹, reducing the opportunity for these areas to reach a climax community (Jackson, 2008). Overharvesting of major predators such as red snapper, tuna, and sharks can result in an altered community structure and may reduce community resilience (Christensen, et al., 2009; Gascuel and Pauly, 2009; Lombardi-Carlson, et al., 2008).

The National Marine Fisheries Service (NMFS) has been sampling the unstructured seafloor through the Southeast Data Assessment and Monitoring Program's (SEAMAP) summer shrimp/bottomfish survey. The survey started in the early 1970s to monitor commercially harvestable species abundances. This program went through substantial changes until adopting SEAMAP protocols in 1987 to standardize field techniques (Eldridge, 1988; Nichols, 2004; Service and Commission, 2001 (Revision No. 4)). The survey design is based on sample collections from *a priori* statistical zones and depth between Pensacola, FL and Brownsville, TX (National Marine Fisheries Service, 2001 (Revision No. 4); Nichols, 2004). During the survey, sites are towed with a shrimp net throughout the 24 hr period for 40 d, between June and July.

Specimens were measured, enumerated, weighed, and identified to lowest possible taxonomic level. Along with the catch data, environmental data are recorded for each site, including water temperature, dissolved oxygen, salinity, and depth. With this information, the effects that disturbances or stressors have on diversity in the Gulf can be analyzed, aiding in better ecosystem management.

The goal of this study is to determine if changes in biodiversity patterns exist in this long-term bottom trawling data set from the Gulf of Mexico and how these patterns are related to abiotic environmental parameters. Specifically, the objectives were to (1) determine if measures of biodiversity within trawls have changed between 1987 and 2010; (2) determine if relationships exist temporally or spatially between abiotic factors and biodiversity in the Gulf; (3) identify changes in community structure that have occurred using multivariate analyses; and (4) determine what temporal, spatial, and abiotic factors affect community structure. Use of long-term data sets that have exceptional spatial coverage are critical because many of the factors influencing biodiversity can take many years to decades to manifest and are often subjected to high levels of variance. Results from this study will be important for future research in the coastal northwestern Gulf of Mexico by providing a baseline analysis of biodiversity in unstructured habitat in that region.

MATERIALS AND METHODS

Data used in these analyses are limited to the period between 1987 and 2010, when SEAMAP protocols were adapted. Because the Mississippi River functions as a natural ecological divider between the eastern and western Gulf, survey samples for this study were limited to the area between Brownsville, Texas (26 °N) and the mouth of the Mississippi River

(89°W). Prior to 2006, approximately 184 sites were sampled annually across 4 geographic areas: area 1 included statistical zones 13 through 15, area 2 included statistical zones 16 and 17, area 3 included statistical zones 18 and 19, and area 4 included statistical zones 20 and 21 (Nichols, 2004; Patella, 1975) (Figure 1). Within each of these geographic areas, 46 sites were randomly selected for location and time of day so that 23 were sampled during the day and 23 were sampled at night. Trawl depths varied from 9 to 110 meters across the study area. Between 9.2 and 34.8 m depth, samples were collected for each 1.8 m of depth (15 total), 1 sample was collected between 36.6 and 40.3 m, 1 sample was collected between 40.3 and 45.8 m, between 45.8 through 82.4 m samples were collected for each 9.2 m of depth (5 samples), and a sample was collected at depths greater than 91.5m. Trawl samples were collected with a 12.19 m shrimp net with a mesh size of 4.1 cm, and 4.44 x 1.02 m chain bracketed wooden doors, without a turtle excluder device or a bycatch reduction device, at a speed of 2.5 knots. Tow duration was dependent on the amount of time required to transect a depth stratum but limited to a minimum of 10 and maximum of 55 min. If needed, multiple tows to complete the depth stratum were completed per site. Starting in 2006, the survey design was modified to sample randomly between 9.2 and 108.0 m (National Marine Fisheries Service, 2001 (Revision No. 4)). Tows were standardized to 30 minutes with tow direction determined randomly. Site selection according to depth, diurnal, and spatial allocation was also discontinued. Field operations were conducted 24 hours day⁻¹ to maintain the overall diurnal aspect of the survey.

Sampling sites were selected using bathymetric data obtained from National Oceanic and Atmospheric Administration's (NOAA) Environmental Satellite, Data, and Information Service (NESDIS). Sites were allocated based on the areal extent of the zone compared to each of the other zones identified by of the NOAA's Gulf Coast shrimp statistical zones 13-21 (Kutkuhn,

1962; Patella, 1975). If a station was determined to be ‘untrawlable’ due to obstructions such as platforms and natural hard bottom, the site was selected again until its location was in a suitable area. At each site, vertical profiles of depth (m), temperature (°C), dissolved oxygen (mg l⁻¹), and salinity were recorded with a conductivity-temperature-depth (CTD) instrument (model Seabird SBE 911+; Sea-Bird Electronics, Inc., Bellevue, Washington).

Statistical analyses

All catch data were standardized to catch-per-unit-effort (CPUE) (Murphy and Willis, 1996) and defined as number of individuals trawl⁻¹ hour⁻¹. Diversity was analyzed using 4 diversity components (1) the number of individuals (N), (2) the number of species (S), (3) species richness, and (4) species evenness. Two heterogeneous diversity indices were calculated: Simpson’s and Shannon’s diversity index. Number of species was defined as the number of species present per tow. The Margalef’s species richness index was defined as: $d=(S-1)/\text{Log}(N)$, due to its extensive use and ease of calculation (Magurran, 2004). Evenness was measured using Pielou’s evenness index ($J'=H'/\text{Log}(S)$) (Merigot, et al., 2007). Diversity indices were calculated using Primer E[®] (v.6). Measures of diversity were determined by combining all trawls within a statistical zone.

For these analyses, independent factors were year, statistical zone, depth (m), temperature (°C), dissolved oxygen (mg⁻¹), and salinity. Depth was binned in 20 m intervals starting at 9 m. Prior to analysis, outliers beyond 2 standard deviations were removed.

Patterns in diversity

To examine if changes in biodiversity have occurred between 1987 and 2010, measures of diversity were plotted over time and among statistical zones. Simple linear regression (SigmaPlot[®] (v12)) was used to identify patterns over years and among statistical zones. To test

differences among years, a nested ANOVA of statistical zone within year was used to identify patterns in biodiversity (SAS (v. 9.1)). When possible, data were transformed to meet the assumptions of linear regression using $\text{Log}(X + 1)$; however, due to the problems inherent in large-scale, multi-year data sets and the normal variability in populations of many of the organisms sampled, often the data were not able to be transformed to meet these assumptions (Hinkley and Runger, 1984). Although ANOVA analysis is not preferred, the robustness of an ANOVA based simple-linear regression allows for the identification of a general pattern (Box, 1954). To account for the variability between statistical zones or between years, a nested ANOVA was used to test for differences between dependent variables and year or statistical zone where statistical zone is nested within year or year is nested within statistical zone. Year and statistical zone were treated as independent variables, where diversity indices were treated as the dependent variables. All results were considered significant with $\alpha > 0.05$.

Abiotic factors affecting patterns in diversity

A partial least squares regression analysis (PLS) approach using SYSTAT (v 13.0) was used to examine abiotic factors on measures of diversity. Partial least squares regression is a technique of structural equation modeling, developed by Wold (1975). This technique creates linear combinations of variables (known as factors) constructed between predictor and response variables (Garthwaite, 1994). These created factors account for successively lower proportions of original variance (Carrascal, et al., 2009). Because of its nature, the data failed to meet both normality and variance assumptions that are associated with linear regression models. Because of the robustness of PLS, assumptions minimized, and problems such as overfit data, high collinearity, and multicollinearity are eliminated. Other advantages of this techniques are that the number of predictor variables can be greater than the number of observations, predictors can be

highly correlated, and assumptions or measurement scales are irrelevant (Fornell and Bookstein, 1982; Haenlein and Kaplan, 2004).

Spatial, temporal, and abiotic factors were considered the predictor variables for these analyses. Predictors were year, statistical zone, depth, temperature, dissolved oxygen, and salinity. Diversity indices were considered the response variables. Multivariate PLS was used to minimize type I errors. As part of the Nonlinear Iterative Partial Least Squares (NIPALS) algorithms, data was log transformed to center the data. Data were cross-validated using a random exclusion technique. The factors used in the models included all diversity indices when the R^2 from the cross-validation increased greater than 5%, with a minimum of 2 factors considered in all models (SYSTAT Software, 2009). The meaning of the factors can be interpreted by using the loadings attained by the response variables. Loadings with a value greater than 0.7 were considered very important, 0.4 through 0.7 were important, greater than 0.2 were good, and less than 0.2 had very little affect on the factors. All models were considered significant at $p = 0.05$.

Community structure

To examine temporal and spatial patterns in community structure in the Gulf of Mexico, the NMFS data were analyzed using analysis-of-similarities (ANOSIM) permutation procedure within Primer (v6) statistical package. Data were fourth root transformed to down-weight the common species relative to the rare species (Ross, et al., 2010). A Bray-Curtis similarity matrix was calculated. For analyses of temporal variations, statistical zones were nested within years and pairwise comparisons between years were calculated to test for similarities in community structure. For analysis of spatial variations, years were nested within statistical zones and pairwise comparisons between statistical zones were performed.

Abiotic factors affecting community structure

To determine the environmental parameter that best explains community structure, the BIO-ENV method (PRIMER v.6), was used. This analysis was based on the Spearman rank correlation coefficient with 0.95 as the threshold. For these analyses, all years were combined. Environmental variables used in these analyses were year, depth (m), temperature (°C), salinity, and dissolved oxygen (DO) (mg l^{-1}). For instances where the environmental data was missing (approximately 15%), the EM algorithm step within PRIMER was conducted to estimate the value. The environmental data were normalized prior to analysis.

RESULTS

The NMFS summer SEAMAP shrimp/bottomfish survey sampled 4,705 sites between 1987 and 2010, ranging from 131 to 282 sites year⁻¹. The spatial coverage of these surveys ranged between Brownsville, TX to the mouth of the Mississippi River and encompassed depths between 7.7 to 115.9 m (Figure 1).

Temperatures varied between 13.1 and 30.8 °C, with a mean temperature of 24.5 °C, (SE ± 0.12). Dissolved oxygen (DO) varied between 0 and 12.4 mg l^{-1} , a mean of 4.5 mg l^{-1} (± 0.03). Salinity was between 21.7 and 39.6, mean of 34.9 (± 0.07). A total of 683 species were collected, representing 208 families (Table 1, appendix 1). The numbers of individuals per trawl varied between 0 and 109,067 with a mean \pm standard error (S.E.) of 57.62 ± -0.372 . The number of species varied between 0 and 71 with a mean of 25.48 ± -0.156 . Species richness varied between 0 and 14.55 with a mean of 6.03 ± -0.030 . Species evenness varied between 0.812 and 1 with a mean of 0.97 ± -0.0002 . Shannon's diversity index varied between 0.563 and

4.194 with a mean of 2.99 ± -0.009 . Simpson's diversity index varied between 0.494 and 1 with a mean of 0.953 ± -0.001 .

Patterns in Diversity

Overall, there was a significant increase in diversity indices over time, throughout the northwestern Gulf of Mexico. The mean number of individuals significantly increased over time with 1988 having the lowest abundance and 2010 have the highest abundance. The mean number of species significantly increased between 1988 and 2010 (Figure 2). Pielou's evenness indices had no significant change over time; however, there may be a complex cyclical pattern within these data. Between 1994 and 2000, a steady decrease occurred in the evenness, with a sharp increase in evenness between 2000 and 2001, and another decrease in the evenness between 2001 and 2010. Species richness had a significant increase over time with the lowest richness was between 1987 and 1991 followed by a steady increase between 1992 and 2010 (Figure 2). Shannon's and Simpson's diversity indices both had positive significant increases over time (Figure 2).

Spatially, the number of individuals, mean number of species, and species richness generally increased in the southern and western directions of the northwestern Gulf (Figure 3). The mean number of individuals had a significant increase through statistical zones; however, zones 18 and 19 appeared to have a larger number than any others in the Gulf. The mean number of species and the species richness showed a significant increase through the Gulf, with statistical zones 13 and 14, close in numbers with each other and much lower than the rest and statistical zones 15 and 16 were similar to each other. However, species evenness declined significantly in the southern and western directions, with statistical zones 18 and 19 lower than all others (Figure 3). Shannon's and Simpson's indices increased significantly in the southern

and western directions with statistical zones 13 and 14 with the lowest values for each index (Figure 3). For Shannon's and Simpson's indices, statistical zones 20 and 21 had the highest values.

With the both temporal and spatial variability in biodiversity observed through the Gulf of Mexico, a nested ANOVA was calculated due to the inherent variability that occurs within statistical zones throughout time (Table 2) and within year across statistical zones (Table 2). Similar to results from the simple linear regressions, all indices were significant for temporal and spatial differences with the Gulf in the nested ANOVA.

Abiotic factors affecting patterns in diversity

A significant relationship existed between all diversity indices and all abiotic factors (multivariate PLS analysis, table 4 and 5). A total of 3,904 sites of the 4,706 (83%) of the total data set was used in this analysis due to missing values. Two significant components explained 16% of the original variance in the response variable (PLS analysis). No substantial increase occurred between factors 1 and 2; however, the *a priori* decision to include at least 2 factors in the analysis resulted in use of factors 1 and 2 (cross validation of the model, table 6). The first factor accounted for a major proportion of explained 14.9% of the variance, while the second factor accounted for 1.4%. Factor 1 was influenced by statistical zone, depth, and dissolved oxygen (loadings value > 0.4), and was moderately influenced by temperature and salinity (0.4 > loadings value > 0.2) (Table 7). Factor 2 was greatly influenced by temperature, salinity, and year (loadings value > 0.4), with temperature and salinity, again, being moderately influential. Overall statistical zone, depth, and dissolved oxygen drive the relationship of the factors in the same direction, while year drives the relationship in a direction independent of all the other

variables (Figure 4). Temperature and salinity may have the greatest effects, however were directly opposed (Figure 4).

Community structure

The community structure varied significantly between years throughout the Gulf of Mexico (ANOSIM; Global $R=0.155$, $p=0.001$). In general, between 1987 and 2010, community structure became more consistent among years. For example, 1987 was not significantly different from 1988, but was significantly different than any other year. Between 1987 and 1990, there was only 20 to 40% similarity among the concurring 5 years (Figure 5), but in 1993 through 1999, similarity among years was 80 to 100%. For example, 1997 was not significantly different compared to the next 4 out of 5 years.

Community structure varied significantly between statistical zones throughout the Gulf of Mexico (ANOSIM; Global $R=0.279$, $p=0.001$). All statistical zones were significantly different from each other (Pairwise comparisons of the statistical zones, table 8).

Abiotic factors affecting community structure

In the northwestern Gulf, community structure was best correlated with depth and DO (49%) or temperature and DO (48%) (Table 9). In fact, DO was a factor in all 11 models identified with significant correlations (appendix 2). However, examination of each individual statistical zone showed that DO had the strongest effect on community structure in areas near the Mississippi River outfall (statistical zones 13 and 14). Further away from this area, temperature and salinity were correlated drivers of community structure. For example, in statistical zone 13, directly south of the Mississippi River outfall, DO was 33% correlated with community structure, and salinity was 31% correlated. In addition, DO is present in all but one of the significant models for this zone. In statistical zone 14, DO correlated to 41% of the variation in

community structure and was present in all 10 significant models in this area. Statistical zone 15, 16 and 17 had DO as a contributor to all significant models. In this statistical zone, temperature, salinity, or depth combined with DO to explain greater than 50% of the variation in community structure. Although DO was an important factor, it was not as clearly correlated as the previous 2 statistical zones. However, off the coast of Texas, in statistical zone 18 and 19, temperature and salinity both contributed over 34% individually to each region. The role of DO was not as strongly correlated in this region of the Gulf, as it was in the more eastern regions. Statistical zone 20 had the highest correlations with both depth and temperature correlating 62% of the community individually to the area. Lastly, in the most southern region, statistical zone 21, depth alone correlated with 41% of the community structure, and combined with temperature is highest correlated to 47%.

DISCUSSION

Overall, the northwest Gulf of Mexico is a highly complex and unique system influenced by many factors. Biodiversity in the northwestern Gulf has temporal and spatial components that are influenced by depth, temperature dissolved oxygen, and salinity. No single driver completely explained the observed variation, but the Gulf may have two alternate states as related to biodiversity and community structure over the interval of 1987 to 2010. The first state includes a community with a high level of dissimilarity among years that rapidly changes to a community with a high degree of similarity among years.

Between 1987 and 2010, all diversity indices increased with the exception of species evenness. This indicates that the number of species present in the Gulf increased but the number of individuals per species remained relatively constant. Inherently, with the addition of new

species, the number of individuals per species should also increase as populations become established, ultimately affecting species evenness. However, this was not the trend in the Gulf. Similarly, increases in diversity through time occurred in the English Channel and the northwest Pacific (Barry, et al., 1995; Southward, et al., 1995), but a loss in diversity was observed in some studies (Duffy, 2003; Gray, 1997; Solan, et al., 2004; Worm, 2006). In the Gulf, the increase in species could be a result of range expansion or introduction of non-native species (Fodrie, et al., 2009), which may be masked by the more dominant, stable species already present, masking the effect in species evenness. Fodrie et al. (2009) found temporal changes in fish composition of seagrass communities in the northeastern Gulf. Overall, 51 species had undergone a range shift over a 30 year period, 21 species expanded into the northern Gulf while 30 species were no longer found. Range shifts were positively related to temperature. However, the temperature changes that Fodrie et al. (2009) found in the Mobile Bay system have not been observed in the open water of the Gulf (Figure 5). Since inshore bays frequently function as nursery habitat for many of the species (e.g. Sciaenidae) found in the current study (Heck, et al., 1997), the range shifts found in the Bay system could alter the species diversity in the open ocean Gulf. Additional studies have shown similar patterns in species composition over time, with an overall net gain in diversity (Castillo-Rivera, et al., 2002; Worm and Lotze, 2009). This trend may be occurring in the northwestern Gulf of Mexico, as the community structure changed through time. The major changes to community structure occurred between 1987 and 1992, when the community was significantly different each year as compared to the subsequent 5 years. In the 1990s, the Gulf appeared to become more stable, having less change in community structure. However, the trend of change seems to be reoccurring, as community structure has started to differing again, beginning in 2004 through 2010.

The increases in diversity indices in the south and west direction were not present in species evenness. Evenness tended to decrease toward the west. With the exception of evenness, this trend in latitudinal gradients has been noted in both oceanic and terrestrial studies (Kotwicki, et al., 2005; Rosenzweig, 1995; Roy, 2000). The eastern areas of the study area (Statistical zones 13 and 14), were significantly influenced by dissolved oxygen and temperature. This area is well known for its extensive hypoxic zone, where bottom DO during the summer are 2.0 mg l^{-1} or lower. This area is also well documented with reduced species richness and low biomass (Atilla and Rabalais, 2006; Baustian and Rabalais, 2009; Rabalais, et al., 2001b; Zimmerman and Nance, 2001) . Dissolved oxygen has such a significant role in species ranges, forcing species into temperature and/or salinity ranges that they typically would not occupy (Craig and Crowder, 2005). Craig et al (2005) discovered that Atlantic croaker and brown shrimp were found in colder or warmer waters, previously not recorded, to avoid hypoxic conditions.

Hypoxia has occurred periodically on the Louisiana shelf over the last 1000 years (Osterman, et al., 2008). Natural causes of hypoxia are water temperatures and increased discharge from the Mississippi River, both which cause stratification in the water column (Rabalais, et al., 2002b). However, anthropogenic influenced hypoxia is more frequent and more extensive than natural low-oxygen bottom waters events on the Louisiana shelf (Turner and Rabalais, 1991) . Turner et al (2008) concluded that the dynamic state of the Gulf is capable of alternate states where driving forces change it nonlinearly. The driving force that triggered this change in state was the 1993 flood of the Mississippi River, when the hypoxic zone reached an all-time high and never returned to previous levels of bottom dissolved oxygen (Conley, et al., 2007; Liu, et al., 2010; Rabalais, et al., 2002a; Rabalais, et al., 1998; Turner, et al., 2008).

Moreover, returning to the previous state may be more difficult the longer the alternate state is maintained (Scheffer, et al., 2001; Turner, et al., 2008). The effects that hypoxic conditions have on biological communities has been the focus of many studies (Diaz and Rosenberg, 1995; Montagna and Froeschke, 2009; Pörtner, et al., 2005; Rabalais, et al., 2002a; Vaquer-Sunyer and Duarte, 2008). Reoccurring, large scale hypoxic events are noted to alter the community structure from the larger, slower growing, slower reproducing species to the faster growing, smaller, faster reproducing species (Conley, et al., 2009; Diaz and Rosenberg, 1995). In my study, diversity and community structure correlated with hypoxia. Following 1993, throughout the 1990s, the community structure was relatively similar between years. This sudden onset of similarity could be the response of the massive hypoxic zone in the Gulf.

With the exception of the Louisiana shoreline, oxygen has a less dominant role in structuring communities throughout the sample area. Overall, temperature and salinity had higher loading values, suggesting that their influence was stronger than DO. Water temperature is common in a range of studies, and in particular as the factor to be most influenced under many global climate change models (Genner, et al., 2004; Justic, et al., 1997; Kunkel, et al., 2008; Li and Clarke, 2005; Perry, et al., 2005; Pörtner, et al., 2005; Posey, et al., 1998; Worm and Lotze, 2009). In the open ocean of the Gulf, over the past 60 years, there have not been any changes in temperature ranges (Figure 6); however, Fodrie et al (2009) found a significant increase in temperatures in Mobile Bay since 2002. The bays and estuaries of the Gulf are much shallower systems, thus experiencing more direct effects of temperature and climate change. Because the Gulf is a much larger, deeper body of water, the effects of temperature change may not have been observed.

Temperature and dissolved oxygen are very influential abiotic factors that affect community structure, but human activities can directly intercede. Since 2002, trawling has dropped over 60% throughout the Gulf of Mexico (Figure 7). This drop in trawling pressure and disturbance may be allowing the habitat to become more established and might account for an increase in species diversity throughout the study area. Other studies have examined the effects of trawling on diversity, although conclusions vary (Auster, 1998; Bianchi, et al., 2000; Greenstreet and Hall, 1996; Jennings, et al., 2001; Thrush, et al., 2006; Wells, et al., 2008b). Two major reasons for this difference could be the amount of trawling effort in the area and bottom type. Trawling is one of the main drivers in marine systems known to cause habitat homogenization, especially over soft sediment, where the process removes habitat forming organisms (Aronson, et al., 2004; Auster, 1998; Jackson, 2001; Trush and Dayton, 2002). Frequent trawling not only removes large, slower reproducing predators and allows for the faster reproducing prey to thrive with lower predation and competition, but trawling may account for increases in nutrient recycling which increases primary production (Jennings, et al., 2001).

In addition to trawling effort, habitat type is important in diversity studies. Wells et al (2008b) concluded that diversity response to trawling differently depending on bottom types. The more complex habitats of shell-rubble were more sensitive to trawling activities than the more resilient sandy bottom habitat. In a similar study in the North Sea, trawling affected the benthic community of muddy habitats, while its effects on the shell habitat were minimal (Queirós, et al., 2006). In the current study, different habitats were not considered; therefore, subtle changes from decreases in trawling effort may not be as obvious on diversity indices.

A baseline study to determine patterns of what is currently in the Gulf of Mexico and any alterations in community structure is essential to better understand effects that climate change or

disasters have on the community structure. By examining long term databases and a range of diversity indices, ecosystem diversity and resilience could be better managed. The Gulf is currently increasing in diversity, and should not be limited to a small range of factors. In addition, community structure may have two alternate states that appear to be a legacy of hypoxia levels. Future studies need to monitor the fishing effort and sediment type, which would possibly account for more of the variance seen in this study. Continued monitoring of the Gulf of Mexico would allow for conclusive results on whether diversity in the Gulf has adjusted to the current levels of nitrogen load. Lastly, examination of the taxonomic diversity of the community structure might provide further details into how the community is changing. Monitoring species changes and habitat throughout the Gulf would give a more detailed picture as to the changes in diversity. Managers might be informed on whether species are adapting, slowly adjusting to changes by range expansions, or completely replacing each other in smaller ecosystems within the Gulf.

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TABLES

Table 1. Species with total number of individuals caught throughout the NMFS SEAMAP summer shrimp/bottomfish survey between 1987 through 2010, comprising of 1.0% or more of the total number of individuals caught for the entire study time.

Species	Total Number of Individuals Caught	Percent of Total catch	Cummulative Percent of Total Catch
<i>Micropogonias undulatus</i>	3,700,243	19.3	19.38
<i>Stenotomus caprinus</i>	2,036,276	10.6	30.04
<i>Farfantepenaeus aztecus</i>	1,508,006	7.8	37.94
<i>Chloroscombrus chrysurus</i>	1,087,059	5.6	43.63
<i>Peprilus burti</i>	1,069,065	5.5	49.23
<i>Rimapenaeus similis</i>	801,866	4.1	53.43
<i>Callinectes similis</i>	631,222	3.3	56.73
<i>Loligo plei</i>	479,726	2.5	59.24
<i>Trachurus lathami</i>	424,512	2.2	61.47
<i>Loligo pealeii</i>	298,782	1.5	63.03
<i>Squilla empusa</i>	283,431	1.4	64.52
<i>Leiostomus xanthurus</i>	282,297	1.4	65.99
<i>Prionotus longispinosus</i>	278,276	1.4	67.45
<i>Cynoscion nothus</i>	243,323	1.2	68.72
<i>Portunus spinicarpus</i>	237,576	1.2	69.97
<i>Trichiurus lepturus</i>	214,125	1.1	71.09
<i>Upeneus parvus</i>	203,392	1	72.16
<i>Sicyonia brevirostris</i>	202,359	1	73.21

Table 2. Results of nested analysis of variance of dependent variables, with statistical zones nested within years, from NMFS SEAMAP summer shrimp/bottomfish surveys between 1987 and 2010, where N is number of individuals, S is number of species, d is Margalef's species richness, J is Pielou's evenness index, H' is Shannon's diversity index, and 1- λ' is Simpson's diversity index ($\alpha=0.05$).

Source	df	MS	F	P	R ²
N					
Year	23	151,213,090.00	6.44	<0.0001	0.13
StatZone(Year)	187	62,508,959.00	2.66	<0.0001	
Error	4,460	23,467,525.44			
S					
Year	23	2,035.52	22.96	<0.0001	0.23
StatZone(Year)	187	397.24	4.48	<0.0001	
Error	4,460	88.67			
d					
Year	23	26.06	17.75	<0.0001	0.21
StatZone(Year)	187	5.87	4.00	<0.0001	
Error	4,460	1.47			
J					
Year	23	0.09	3.42	<0.0001	0.09
StatZone(Year)	187	0.05	1.99	<0.0001	
Error	4,460	0.03			
H'					
Year	23	2.38	7.00	<0.0001	
StatZone(Year)	187	1.02	3.00	<0.0001	
Error	4,460	0.34			
1-λ'					
Year	23	0.17	4.65	<0.0001	0.11
StatZone(Year)	187	0.08	2.42	<0.0001	
Error	4,460	0.03			

Table 3. Results of nested analysis of variance of dependent variables, with years nested within statistical zones, from NMFS SEAMAP summer shrimp/bottomfish surveys between 1987 and 2010, where N is number of individuals, S is number of species, d is Margalef's species richness, J is Pielou's evenness index, H' is

Source	df	MS	F	P	R²
N					
StatZone	8	420,890,600.00	17.94	<0.0001	0.13
Year(StatZone)	202	58,415,602.00	2.49	<0.0001	
Error	4,460	23,467,525.44			
S					
StatZone	8	4,383.13	49.43	<0.0001	0.23
Year(StatZone)	202	425.92	4.80	<0.0001	
Error	4,460	88.66			
d					
StatZone	8	60.55	41.25	<0.0001	0.21
Year(StatZone)	202	6.01	4.09	<0.0001	
Error	4,460	1.47			
J					
StatZone	8	0.31	11.84	<0.0001	0.09
Year(StatZone)	202	0.05	1.76	<0.0001	
Error	4,460	0.03			
H'					
StatZone	8	8.82	25.95	<0.0001	0.14
Year(StatZone)	202	0.87	2.55	<0.0001	
Error	4,460	0.34			
1-λ'					
StatZone	8	0.67	19.36	<0.0001	0.11
Year(StatZone)	202	0.07	2.00	<0.0001	
Error	4,460	0.03			

Table 4. Results from multivariate partial least squares regression of spatial, temporal, and abiotic variables affecting measures of diversity from NMFS SEAMAP summer shrimp/bottomfish suveys between 1987 and 2010 ($\alpha=0.05$).

Source	df	MS	F	P
N				
Regression	2	101.77	309.07	< 0.001
Error	3,901	0.33		
S				
Regression	2	123.40	537.96	< 0.001
Error	3,901	0.23		
d				
Regression	2	79.20	597.12	< 0.001
Error	3,901	0.13		
J				
Regression	2	0.02	69.63	< 0.001
Error	3,901	0.00		
H'				
Regression	2	22.25	501.19	< 0.001
Error	3,901	0.04		
1-λ'				
Regression	2	0.51	339.44	< 0.001
Error	3,901	0.00		

Table 5. Multivariate partial least squares regression coefficients and standard error for diversity indices and spatial, temporal, and abiotic variables from NMFS SEAMAP summer shrimp/bottomfish survey between 1987 and 2010.

Regression						
Constant	2.535	1.565	0.464	-0.051	0.419	-0.143
Year	0.014	0.013	0.011	0.000	0.005	0.001
Statistical Zone	0.043	0.047	0.037	0.000	0.020	0.003
Depth	0.102	0.112	0.090	0.001	0.047	0.007
Temperature	0.001	-0.001	-0.001	0.000	-0.001	0.000
Dissolved Oxygen	0.052	0.058	0.046	0.001	0.025	0.004
Salinity	0.000	0.003	0.003	0.000	0.002	0.000
Standard Error						
Constant	0.132	0.117	0.090	0.002	0.053	0.010
Year	0.001	0.001	0.001	0.000	0.000	0.000
Statistical Zone	0.005	0.004	0.003	0.000	0.002	0.000
Depth	0.009	0.009	0.007	0.000	0.003	0.001
Temperature	0.001	0.001	0.001	0.000	0.000	0.000
Dissolved Oxygen	0.012	0.012	0.009	0.000	0.005	0.001
Salinity	0.003	0.003	0.002	0.000	0.001	0.000

Table 6. Multivariate partial least squares cross-validation statistics (predication R^2) for all possible factors throughout the Gulf of Mexico from the NMFS SEAMAP summer shrimp/bottomfish surveys between 1987 and 2010. Of the 6 possible factors, only the first 2 were used based on *a priori* decisions.

Factor	N	S	d	J	H'	1-λ'
1	0.447	0.497	0.511	0.402	0.462	0.487
2	0.475	0.521	0.533	0.422	0.51	0.514
3	0.475	0.521	0.534	0.425	0.457	0.504
4	0.465	0.512	0.526	0.447	0.486	0.507
5	0.474	0.525	0.541	0.447	0.496	0.518
6	0.468	0.514	0.529	0.423	0.469	0.503

Table 7. Loading values of the spatial, temporal, and abiotic variables for each factor from the NMFS SEAMAP summer shrimp/bottomfish surveys between 1987 and 2010.

Loadings	Factor 1	Factor 2
Year	0.104	0.517
Statistical Zone	0.495	0.163
Depth	0.507	-0.010
Temperature	-0.375	0.653
DO	0.554	0.063
SAL	0.364	-0.623

Table 8. Results from the nested ANOSIM, where year is nested within statistical zones from the NMFS SEAMAP summer shrimp/bottomfish survey between 1987 and 2010 ($\alpha=0.05$).

	Stat Zone	R Stat.	Sig. Level
13	14	0.199	0.001
	15	0.382	0.001
	16	0.445	0.001
	17	0.623	0.001
	18	0.605	0.001
	19	0.511	0.001
	20	0.633	0.001
14	21	0.646	0.001
	15	0.042	0.046
	16	0.105	0.002
	17	0.266	0.001
	18	0.292	0.001
	19	0.283	0.001
15	20	0.358	0.001
	21	0.402	0.001
	16	0.037	0.031
	17	0.233	0.001
	18	0.315	0.001
	19	0.336	0.001
16	20	0.338	0.001
	21	0.406	0.001
	17	0.069	0.002
	18	0.147	0.001
	19	0.251	0.001
	20	0.311	0.001
17	21	0.354	0.001
	18	0.043	0.024
	19	0.322	0.001
	20	0.363	0.001
18	21	0.344	0.001
	19	0.186	0.001
	20	0.325	0.001
19	21	0.278	0.001
	20	0.345	0.001
20	21	0.285	0.001
	21	0.084	0.001

Table 9. Significant results from BIO-ENV, correlating environmental variables with community structure, both Gulf wide and for each statistical zones from the NMFS SEAMAP summer shrimp/bottomfish survey between 1987 and 2010.

Gulfwide	Parameters	Correlation
Highest Correlation	Depth, Temperature, Salinity, DO	0.53
Simplest Correlations	Depth, DO	0.49
	Temperature, DO	0.48
Stat Zone		
13	Salinity, DO	0.41
14	Depth, DO	0.43
15	Temperature, Salinity, DO	0.63
16	Temperature, Salinity, DO	0.57
17	Temperature, Salinity, DO	0.58
18	Temperature, Salinity	0.48
19	Depth, Temperature, Salinity	0.42
20	Depth, DO	0.63
21	Depth, Temperature	0.47

FIGURES

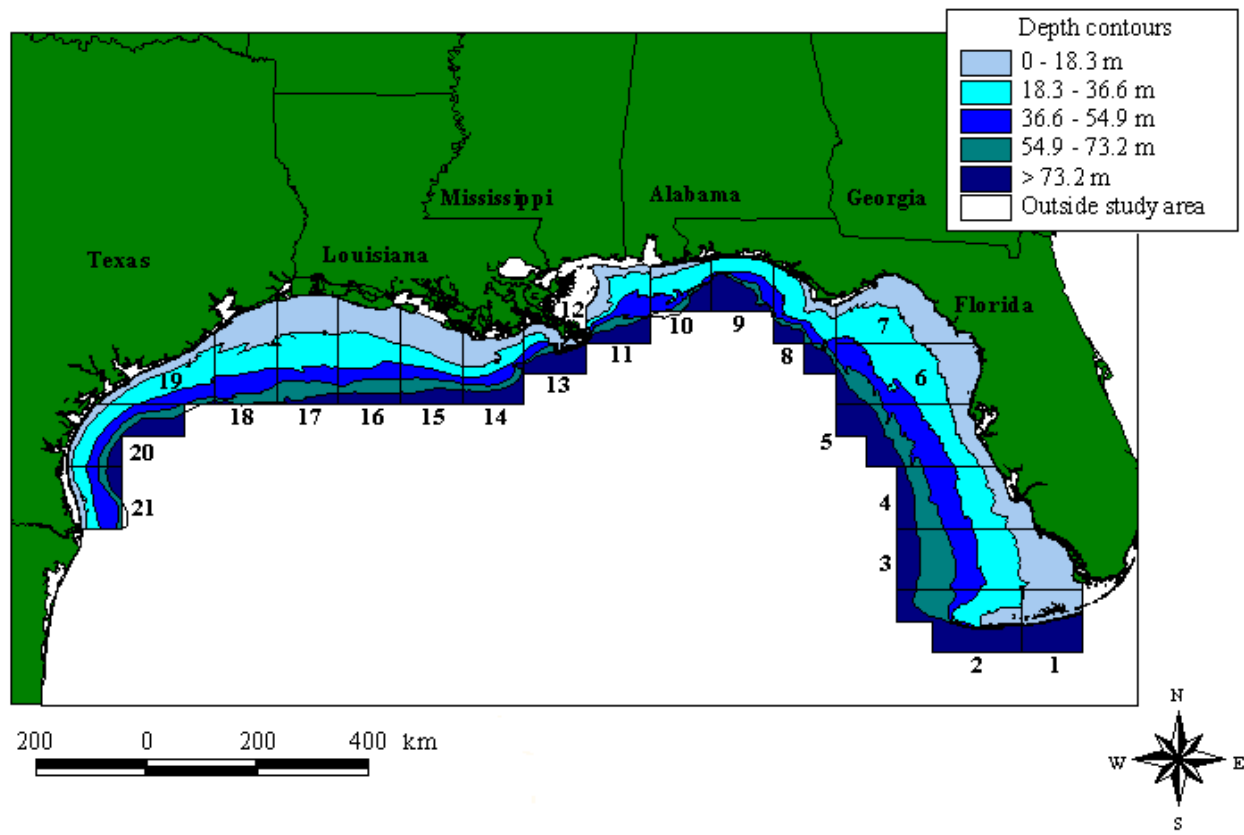


Figure 1. Shrimp Statistical Zones sampled throughout the NMFS SEAMAP summer shrimp/bottomfish surveys between 1987 and 2010. Image obtained from McDaniel et al (2000).

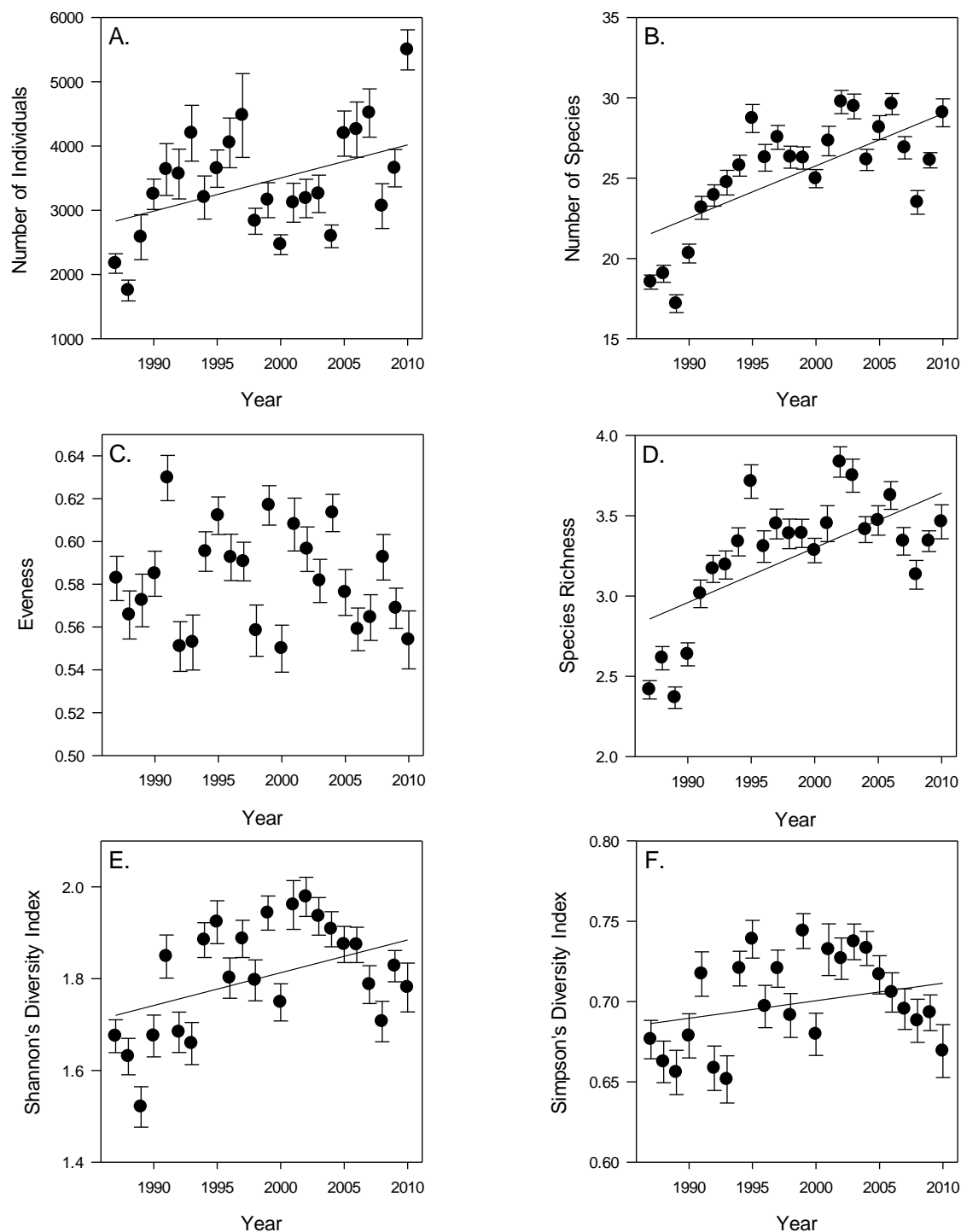


Figure 2. Patterns in biodiversity of NMFS SEAMAP summer shrimp/bottomfish surveys between 1987 and 2010 through time, where (a) is the mean number of individuals caught per site per year, (b) is the mean number of species, (c) is the mean Pielou's evenness index, (d) is the mean species richness, (e) is the mean Shannon's diversity index, and (f) is the mean Simpson's diversity index. Regression lines are displayed on graphs where there was a significant change ($\alpha=0.05$).

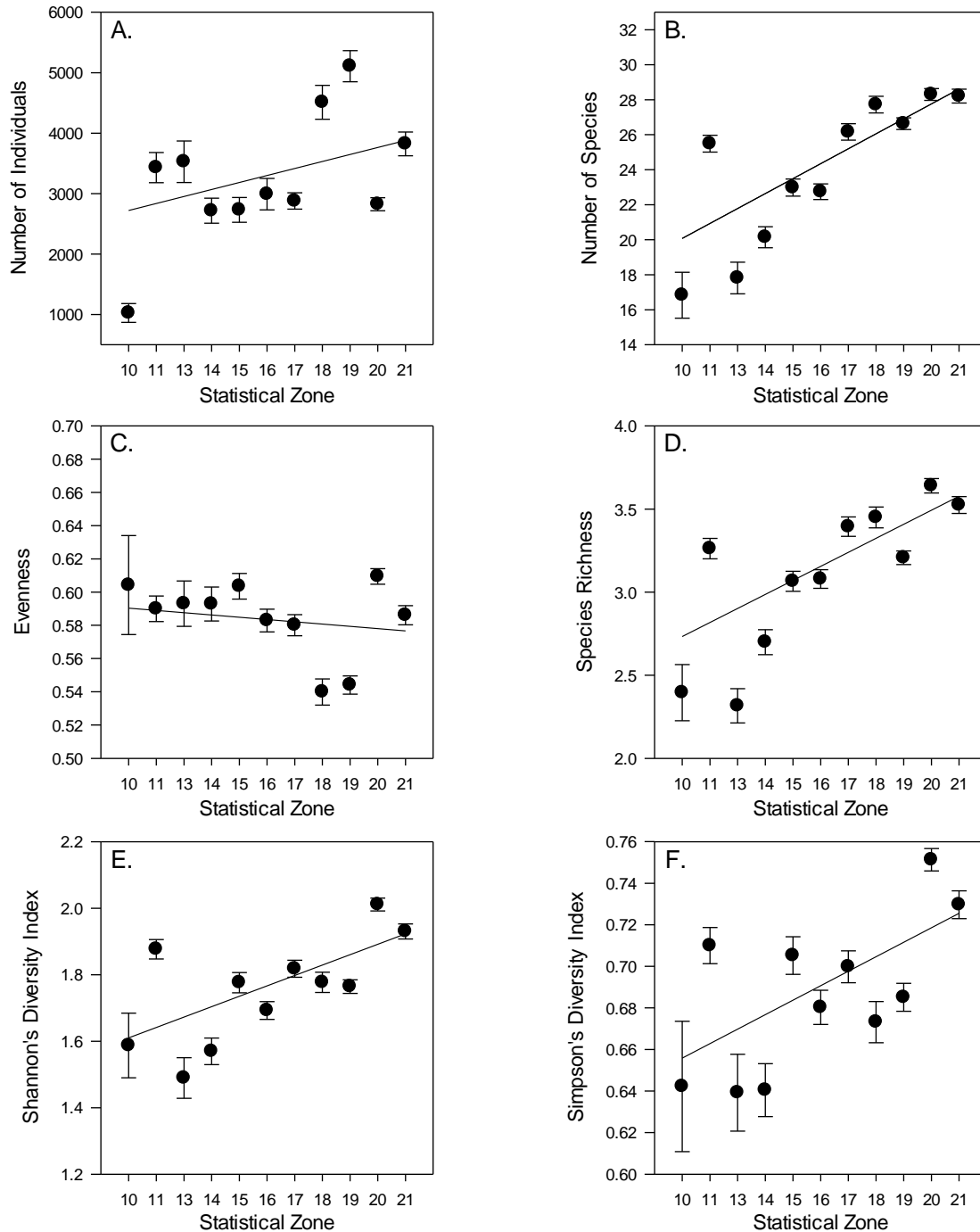


Figure 3. Patterns in biodiversity of NMFS SEAMAP summer shrimp/bottomfish surveys between 1987 and 2010 across the Gulf of Mexico where (a) is the mean number of individuals caught per site per year, (b) is the mean number of species, (c) is the mean Pielou's evenness index, (d) is the mean species richness, (e) is the mean Shannon's diversity index, and (f) is the mean Simpson's diversity index. Regression lines are displayed on graphs where there was a significant change ($\alpha=0.05$).

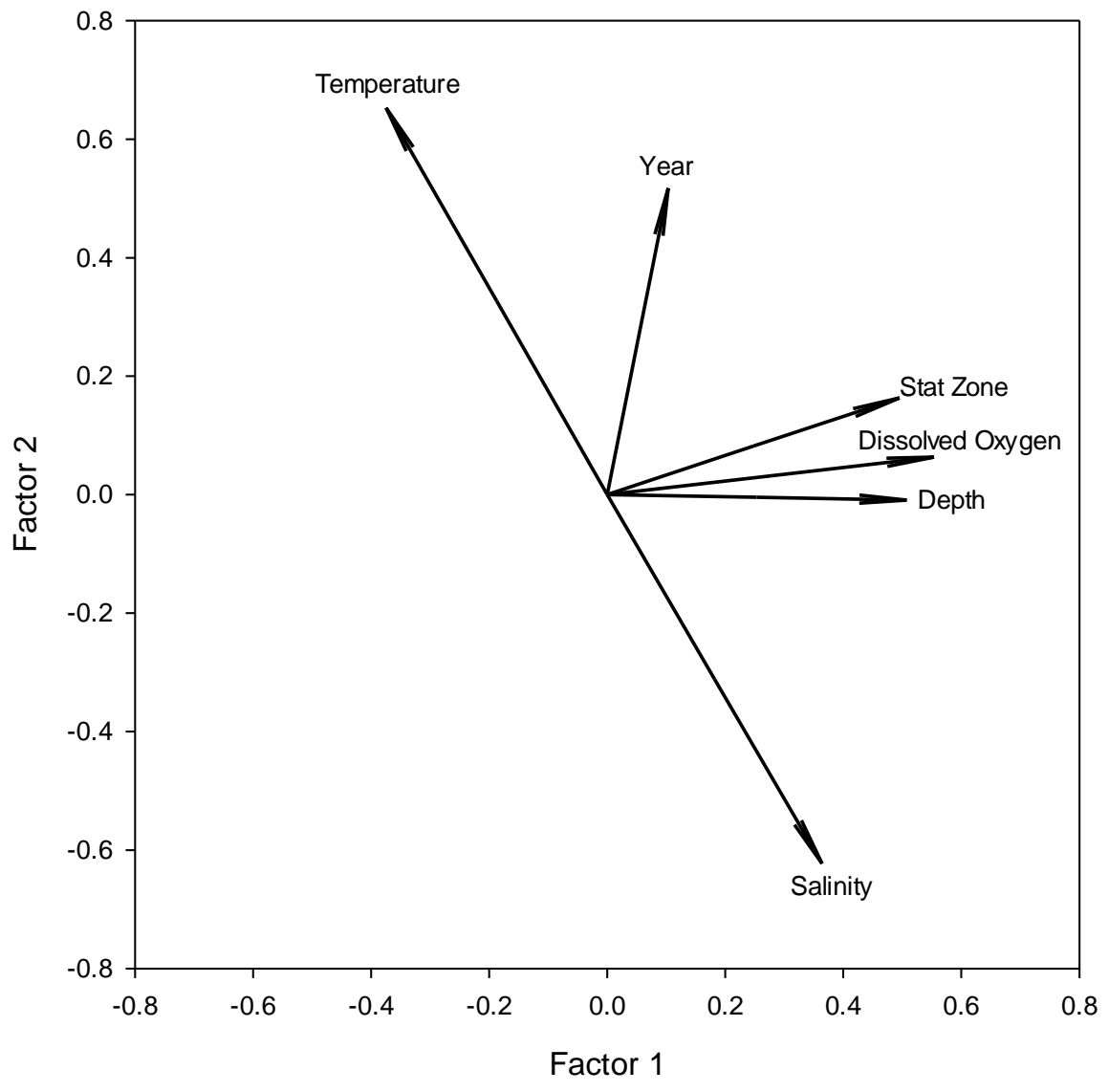


Figure 4. Ordination plot of loading values for spatial, temporal and abiotic variables affecting factors 1 and 2 from the multivariate partial least squares analysis of NMFS SEAMAP summer shrimp/bottomfish survey between 1987 and 2010.

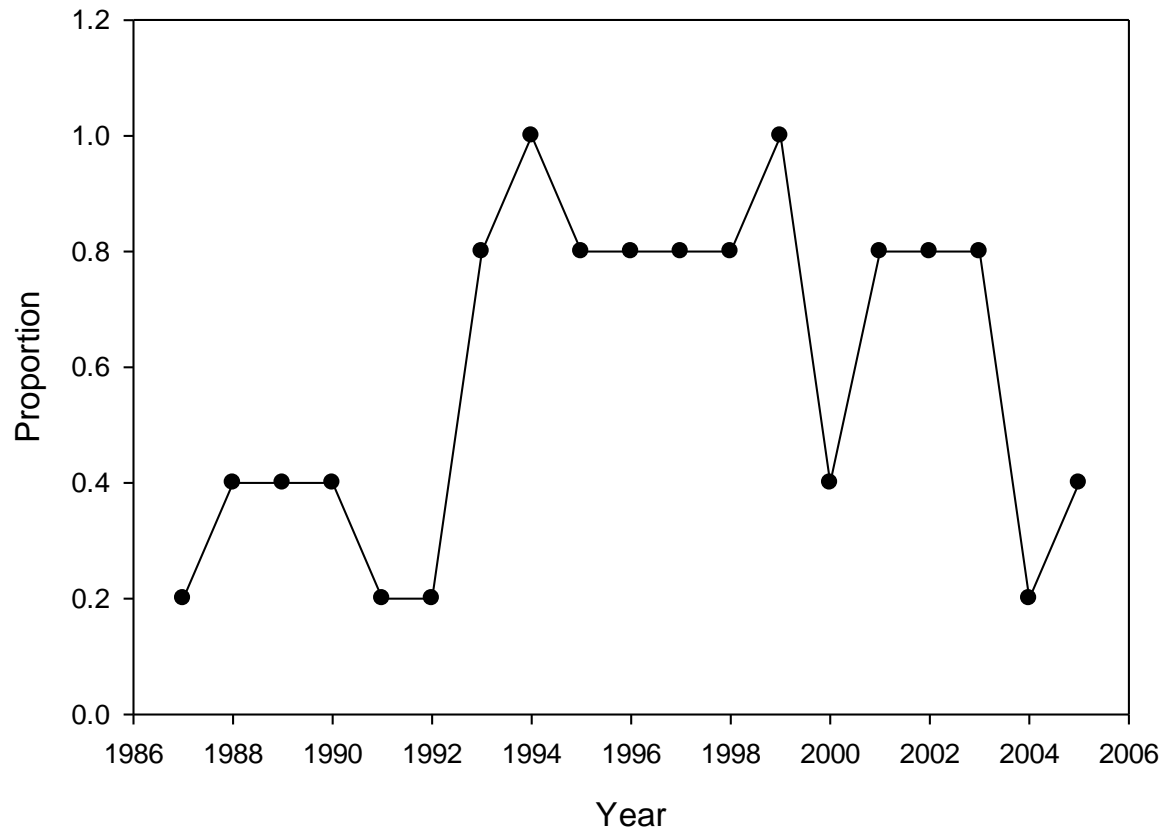


Figure 5. Proportion of similarity in community structure during 5 subsequent years for the NMFS SEAMAP summer shrimp/bottomfish survey between 1987 and 2010.

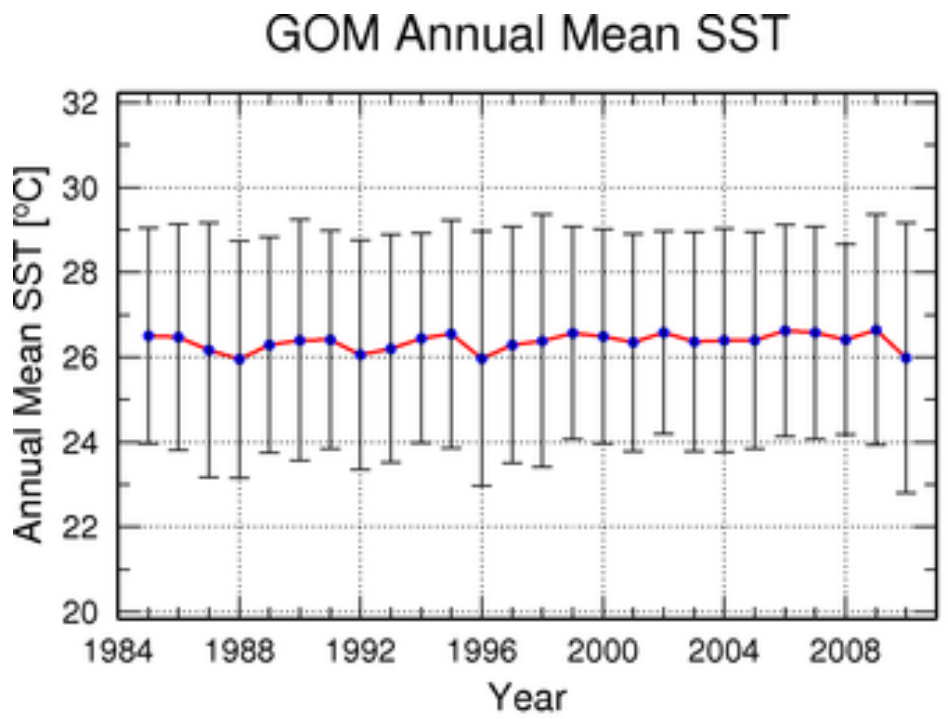


Figure 6. Mean annual sea surface temperature (SST) in the northern Gulf of Mexico between 1984 and 2009. Image obtained from: www.aoml.noaa.gov/phod/regsatprod/gom/sst_ts.php

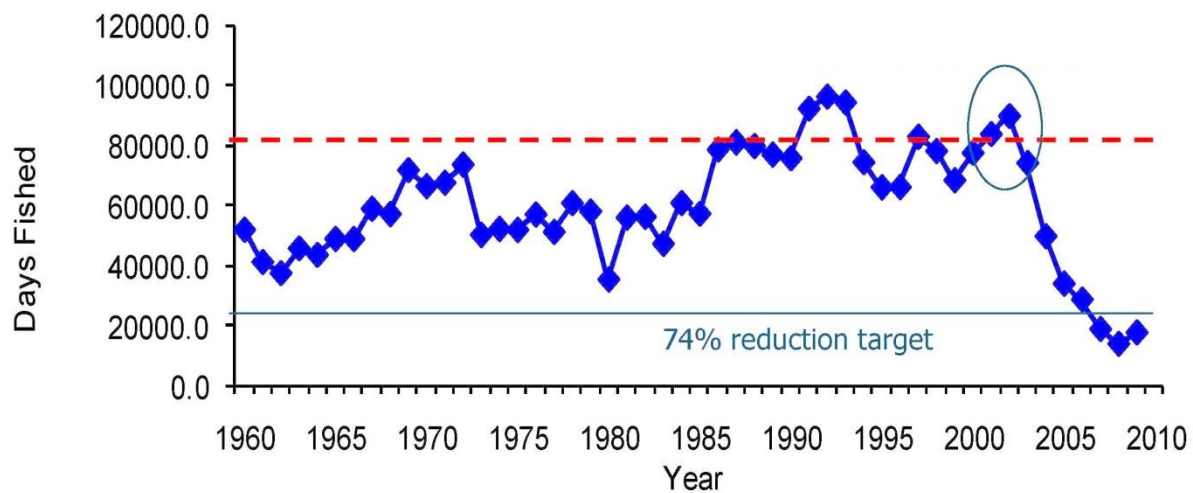


Figure 7 Shrimping effort (days fished) in the Gulf of Mexico for years 1960 through 2009. Image obtained from: sero.nmfs.noaa.gov/sf/pdfs/shrimpeffort09.pdf

APPENDICES

Appendix 1. List of Families and numbers of species collected on NMFS SEAMAP summer shrimp/bottomfish surveys between 1987 and 2010.

Family	Number of Species	Family	Number of Species	Family	Number of Species
ACHIRIDAE	5	CLUPEIDAE	10	HOLOCENTRIDAE	2
ACROPOMATIDAE	2	CLYPEASTERIDAE	2	HORMATHIIDAE	1
ACTINOSTOLIDAE	1	COMASTERIDAE	1	INACHIDAE	4
ALPHEIDAE	1	CONGRIDAE	5	INACHOIDIDAE	4
AMPHINOMIDAE	2	CONIDAE	1	LABRIDAE	5
ANTENNARIIDAE	4	CORYPHAENIDAE	1	LAOMEDIIDAE	1
APLYSIIDAE	2	CRASSATELLIDAE	1	LEUCOSIIDAE	6
APOGONIDAE	7	CUCUMARIIDAE	2	LOLIGINIDAE	4
ARBACIIDAE	1	CYNOGLOSSIDAE	7	LOPHIIDAE	3
ARCHITECTONICIDAE	1	DACTYLOPTERIDAE	1	LUIDIIDAE	2
ARCIDAE	4	DASYATIDAE	4	LUTJANIDAE	5
ARIIDAE	2	DIADEMATIDAE	1	LYSIOSQUILLIDAE	1
ARIOMMATIDAE	1	DIODONTIDAE	4	MACROURIDAE	1
ASTROPECTINIDAE	7	DIAGENIDAE	7	MALACANTHIDAE	4
AXIIDAE	1	DORIPPIDAE	1	MASTIGIIDAE	1
BALISTIDAE	2	DROMIIDAE	3	MELLITIDAE	3
BATRACHOIDIDAE	4	ECHENEIDAE	5	MELONGENIDAE	7
BOTHIDAE	7	ECHINARACHNIIDAE	1	MENIPPIDAE	1
BREGMACEROTIDAE	2	ECHINASTERIDAE	2	MERLUCCIIDAE	1
BRISSIDAE	2	ELOPIDAE	1	MITHRACIDAE	4
BUCCINIDAE	2	ENGRAULIDAE	8	MOLPADIIDAE	2
CALAPPIDAE	4	EPHIPPIDAE	1	MONACANTHIDAE	8
CALLIANASSIDAE	1	EPIGONIDAE	2	MORIDAE	1
CALLIONYMIDAE	4	EPITONIIDAE	1	MUGILIDAE	2
CANCELLARIIDAE	1	EXOCOETIDAE	7	MULLIDAE	4
CAPITELLIDAE	1	FASCIOLARIIDAE	7	MURAENIDAE	6
CAPROIDAE	1	GEMPYLIDAE	3	MURICIDAE	9
CARANGIDAE	18	GEODIIDAE	1	MYCTOPHIDAE	1
CARAPIDAE	1	GERREIDAE	2	MYLIOBATIDAE	2
CARCHARHINIDAE	8	GINGLYMOSTOMATIDAE	1	MYTILIDAE	1
CARDIIDAE	5	GLYCERIDAE	1	NARCINIDAE	1
CARDITIDAE	1	GOBIIDAE	7	NATICIDAE	2
CARYBDEIDAE	1	GONIASTERIDAE	2	NEPHROPIDAE	1
CASSIDAE	2	GORGONIIDAE	1	NETTASTOMATIDAE	3
CAUDINIDAE	1	GORGONOCEPHALIDAE	4	NOETIIDAE	1
CHAETODONTIDAE	3	GRAPSIDAE	1	OCTOPODIDAE	4
CHAMIDAE	2	GYMNURIDAE	2	OCYPODIDAE	1
CHELONIIDAE	2	HAEMULIDAE	5	OGCOCEPHALIDAE	11
CHIROPSALMIDAE	1	HEMIRAMPHIDAE	4	OLIVIDAE	1
CIDARIDAE	2	HEPATIDAE	2	OPHICHTHIDAE	8

Appendix 1 cont.

Family	Number of Species	Family	Number of Species
OPHIDIIDAE	13	RHIZOSTOMATIDAE	1
OPHIODERMATIDAE	1	SCHIZASTERIDAE	2
OPHIONEREIDIDAE	1	SCIAENIDAE	19
OPHIOTHRICIDAE	1	SCOMBRIDAE	5
OPHIURIDAE	1	SCORPAENIDAE	9
OPISTOGNATHIDAE	3	SCYLLARIDAE	4
OSTRACIIDAE	3	SEPIOLIDAE	3
OSTREIDAE	1	SERRANIDAE	25
PAGURIDAE	6	SICYONIIDAE	6
PALAEMONIDAE	1	SOLECURTIDAE	1
PALICIDAE	1	SOLENOCERIDAE	3
PANDALIDAE	3	SPARIDAE	9
PARTHENOPIIDAE	5	SPHYRAENIDAE	4
PECTINIDAE	7	SPHYRNIDAE	2
PELAGIIDAE	1	SQUATINIDAE	1
PENAEIDAE	8	SQUILLIDAE	5
PERCOPHIDAE	2	STENOPODIDAE	1
PERIPLOMATIDAE	1	STICHAEIDAE	1
PERISTEDIIDAE	2	STROMATEIDAE	3
PERSONIDAE	1	STROMBIDAE	1
PHOLADIDAE	1	STYELIDAE	1
PHYLLOPHORIDAE	1	SYNAPHOBRANCHIDAE	1
PILUMNIDAE	3	SYNAPTIDAE	1
PINNIDAE	3	SYNGNATHIDAE	6
PISIDAE	5	SYNODONTIDAE	7
POLYNEMIDAE	1	TELLINIDAE	3
POMACENTRIDAE	2	TETRAODONTIDAE	7
POMATOMIDAE	1	TONNIDAE	2
PORCELLANIDAE	2	TORPEDINIDAE	1
PORTUNIDAE	10	TRACANTHODIDAE	1
PRIACANTHIDAE	3	TRIAKIDAE	3
PSEUDORHOMBILIDAE	2	TRICHIURIDAE	1
PTERIIDAE	1	TRIGLIDAE	15
RACHYCENTRIDAE	1	TURRIDAE	2
RAJIDAE	4	TURRITELLIDAE	1
RANINIDAE	2	ULMARIDAE	1
RENILLIDAE	2	UPOGEBIIDAE	1
RHINOBATIDAE	1	URANOSCOPIDAE	2

Appendix 2. All significant correlations between environmental variables and community structure from BIO-ENV step in PRIMER for NMFS SEAMAP summer shrimp/bottomfish surveys between 1987 and 2010. Variable numbers are: (1) year, (2) statistical zone, (3) depth, (4) temperature, (5) salinity, and (6) dissolved oxygen.

	Num. of Variables	Corr.	Variable #s		Num. of Variables	Corr.	Variable #s	
Gulf-wide	4	0.526	3-6	15 cont.	2	0.567	4,5	
	3	0.508	3,4,6		2	0.558	2,5	
	3	0.503	3,5,6		5	0.558	All	
	3	0.5	4-6		4	0.544	1,3-5	
	2	0.485	3,6		4	0.541	1,2,4,5	
	2	0.484	4,6					
	5	0.482	2-6	16	3	0.576	3-5	
	5	0.475	1,3-6		3	0.567	2,4,5	
	4	0.466	2-4,6		4	0.561	2-5	
	4	0.459	1,3,4,6		2	0.557	3,5	
Stat Zones					2	0.539	4,5	
	13	2	0.409	4,5	3	0.532	2,3,5	
		3	0.381	3-5	5	0.523	All	
		3	0.346	2,4,5	2	0.522	2,5	
		1	0.334	5	4	0.509	1,2,4,5	
		2	0.329	3,5	4	0.509	1,3-5	
		4	0.318	2-5				
		1	0.313	4	17	3	0.583	3-5
		4	0.304	1,2,4,5		4	0.565	2-5
		2	0.301	2,5		3	0.56	2,4,5
	4	0.295	1,3-5		5	0.554	All	
					4	0.548	1,3-5	
14	2	0.432	2,5		2	0.543	4,5	
	1	0.41	5		2	0.537	3,5	
	3	0.409	3-5		4	0.536	1,2,4,5	
	3	0.403	1,2,5		3	0.512	2,3,5	
	2	0.394	3,5		4	0.496	1-3,5	
	3	0.386	2,4,5					
	2	0.384	4,5	18	2	0.477	3,4	
	4	0.38	2-5		1	0.452	3	
	3	0.366	2,3,5		3	0.448	2-4	
	4	0.361	1,2,4,5		2	0.447	2,3	
				4	0.443	2-5		
15	3	0.614	3-5		3	0.442	2,3,5	
	3	0.601	2,4,5		2	0.436	2,4	
	2	0.598	3,5		4	0.425	1-3,5	
	4	0.596	2-5		5	0.424	All	
	3	0.576	2,3,5		1	0.418	2	

Appendix 2 cont.

	Num. of Variables	Corr.	Variable #s
19	3	0.42	2-4
	2	0.41	2,3
	2	0.397	2,4
	4	0.371	2-5
	1	0.369	2
	2	0.365	3,4
	3	0.36	2,3,5
	1	0.354	3
	4	0.351	1-4
	5	0.343	All
20	2	0.629	2,5
	2	0.629	3,5
	3	0.624	2,3,5
	1	0.62	2
	1	0.62	3
	2	0.62	2,3
	4	0.603	2-5
	3	0.601	2-4
	3	0.599	3-5
	3	0.599	2,4,5
21	2	0.47	2,3
	3	0.447	2-4
	3	0.439	1-3
	3	0.437	2,3,5
	4	0.426	1-4
	4	0.424	2-5
	4	0.422	1-3,5
	5	0.415	All
	2	0.409	2,4
	1	0.407	2
	5	.415	All
	2	.409	2,4
	1	.407	2
