Exploring Temporal and Spatial Variability in Nekton Community Structure in the Northern Gulf of Mexico: Unraveling the Potential Influence of Hypoxia

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ABSTRACT

The northern Gulf of Mexico supports substantial commercial and recreational fisheries. While landings have remained strong throughout recent years, the seasonal formation of hypoxic bottom waters is a threat to long-term sustainability of regional fisheries production. Because nekton are mobile, the greatest threat to fisheries resources is likely to be the effects of reduced oxygen on habitat quality, potentially forcing movement of individuals away from favorable habitat as well as altering migration pathways. As a basis for understanding potential effects of hypoxia on nekton in the northern Gulf of Mexico, we explored temporal and spatial patterns of community structure in coastal Louisiana and Mississippi. We defined community structure in terms of relative densities of sixty-six species that were either abundant, of commercial and/or recreational importance, or thought to be especially susceptible to hypoxia. Several fisheries-independent data sources were summarized to generate yearly density summaries by season (summer and fall), bathymetry (inshore, nearshore and offshore), and alongshore zones (central Louisiana and eastern Louisiana/Mississippi). Differences in community structure were most pronounced bathymetrically; densities of most species varied significantly among depths. Alongshore differences were less prominent, and were primarily driven by higher densities of bay anchovy in the eastern zone as well as higher densities of Atlantic croaker and commercially important macroinvertebrates in the central zone within inshore waters. Seasonal differences in community structure were most evident in nearshore zones as well as inshore in central Louisiana, areas historically prone to the formation of hypoxic waters. Although no substantial long-term changes in community structure were detected, temporal coverage of these data sets (1982 - 2000) may be inadequate to identify temporal alterations due to a shifted baseline. Future efforts that expand the spatial and temporal coverage of these analyses, incorporate environmental variability, and focus on areas especially susceptible to hypoxia are recommended.

KEY WORDS: Gulf of Mexico fisheries; hypoxia; nekton community structure

Explorando la Variabilidad Temporal y Espacial de la Estructura Comunitaria en el Norte del Golfo de México: Revelando la Influencia Potencial de la Hipoxia

El norte del Golfo de México mantiene pesquerías comerciales y recreacionales substanciales. Mientras los desembarques pesqueros han permanecido fuertes en los últimos años, la formación estacional de hipoxia en las aguas del fondo continúa siendo una amenaza para la sostenibilidad a largo plazo de la producción pesquera regional. Debido a la movilidad del necton, la mayor amenaza para los recursos pesqueros parece ser el efecto de la concentración reducida de oxígeno sobre la calidad del hábitat, potencialmente forzando a individuos a alejarse del hábitat favorable, así como alterando pasos migratorios. Como una base para comprender los efectos potenciales de la hipoxia sobre el necton en el norte del Golfo de México, exploramos patrones temporales y espaciales de la estructura comunitaria en las costas de Louisiana y Mississippi usando PRIMER. Definimos estructura comunitaria en términos de densidades de 66 especies que fueran ya sea abundantes, de importancia comercial y/o recreacional, o consideradas especialmente susceptibles a la hipoxia. Varias fuentes independientes de datos fueron resumidas para generar resúmenes anuales de densidad por estación (verano y otoño), batimetría (litoral interno, litoral y mar abierto) y a lo largo de las costas (centro de Louisiana y este de Louisiana/Mississippi). Diferencias en la estructura comunitaria fueron más pronunciadas batimétricamente; densidades de la mayoría de especies variaron substancialmente entre profundidades. Las diferencias a lo largo del litoral fueron menos pronunciadas, y principalmente dirigidas por las densidades altas de anchovieta en la zona este, así como densidades altas de corbina y macroinvertebrados comercialmente importantes en la zona oeste. Diferencias estacionales en la estructura comunitaria fueron más evidentes en las zonas del litoral interno y del litoral del centro de Louisiana, áreas históricamente propensas a la formación de aguas hipóxicas. Aunque no se detectaron cambios drásticos en la estructura comunitaria a largo plazo, la cobertura temporal de estos datos (1982-2000) puede ser inadecuada para identificar una estructura comunitaria alterada, debido al desfase de la línea base. Se recomiendan esfuerzos futuros que expandan la cobertura espacial y temporal de estos análisis, que incorporen la variabilidad ambiental y que se enfoquen en áreas especialmente susceptibles a la hipoxia.

PALABRAS CLAVES: Estructura communitaria, hipoxia

INTRODUCTION

The “Fertile Fisheries Crescent,” an area extending from Mississippi to eastern Texas and encompassing the region of the northern Gulf of Mexico directly influenced by discharge from the Mississippi River (Gunter 1963), is characterized by an abundance of fisheries resources that is partially driven by the prolific primary production common to the region (Houde and Rutherford 1993, Grimes 2001, Nixon and Buckley 2002). Commercial and recreational fishery landings within coastal Louisiana have exceeded those from other U.S. Gulf states in terms of biomass and value over the past several decades, and currently represent close to seventy percent of the total commercial harvest within U.S. Gulf waters (Chesney et al. 2000). During the same time frame total commercial landings within Louisiana waters have steadily increased, and as of 1996 the total bycatch produced by the various fisheries in Louisiana exceeded total fishery landings for any other Gulf state.

While moderate levels of nutrient enrichment are generally thought to enhance fisheries productivity, the input of excess nutrients, or nutrient over-enrichment, may be detrimental to fisheries resources. Scientists have long been aware of a zone of high productivity near the mouth of the Mississippi River (Riley 1937); enhanced primary production in shelf waters near the mouth of the river is positively correlated with influxes of nutrients into the Gulf of Mexico in association with seasonal peaks in freshwater discharge (Justic et al. 1993, Lohrenz et al. 1997). Over the past half century, riverine nutrient concentrations within Mississippi River waters have increased significantly due to altered land-use practices, resulting in eutrophication along the continental shelf (Turner and Rabalais 1991, Turner and Rabalais 1994, Rabalais et al. 1996). The enhanced primary productivity, coupled with strong stratification along the coast, leads to the seasonal formation of a large zone of hypoxic (≤ 2 mg/l O_2) bottom water along the Louisiana-Texas coast (Rabalais et al. 1996, Wiseman et al. 1997). Typically occurring in depths of 5 – 30 m, the areal extent of hypoxic waters has increased from 8,000 – 9,000 km^2 during the late 1980s to 16,000 – 20,000 km^2 in the late 1990s (Rabalais et al. 1996, Rabalais and Turner 2001).

The seasonal occurrence of hypoxic bottom waters in the northern Gulf of Mexico has the potential to adversely affect demersal fishery resources. In the Black Sea, long-term changes in fish abundances have been linked to eutrophication and hypoxia (Daskalov 2003), while in the northern Gulf of Mexico, abundances and distribution of penaeid shrimp and groundfish are negatively related to the relative size of the mid-summer hypoxic zone (Renaud 1985, Zimmerman and Nance 2000). Although the occurrence of hypoxia can lead to direct mortalities of sessile organisms (Burnett and Stickle 2001), most highly-mobile nekton are capable of leaving regions when dissolved oxygen concentrations drop to hypoxic levels (Breitburg et al. 2001, Rabalais et al. 2001). For most fishes and motile macroinvertebrates, the greatest threat of hypoxia is likely to be the effect of reduced oxygen on habitat quality, potentially forcing the movement of individuals away from favored habitat as well as altering migrations. While recent studies have focused on the distribution of selected species (Craig 2001) as well as overall demersal biomass (Craig et al. 2001) in relation to hypoxia, little work has focused on the effects of hypoxia on community structure in the northern Gulf of Mexico.

We explored spatial and temporal patterns in nekton community structure within coastal waters off Mississippi and Louisiana as an initial step towards understanding the potential influence of hypoxia on their patterns of distribution and abundance. Community-level analyses were conducted (1) to identify spatial differences in community structure, both alongshore and in association with changing bathymetry, and (2) to identify seasonal as well as long-term changes in community structure within given spatial zones. When differences in community structure were detected, additional analyses were conducted to identify specific taxa whose densities contributed to observed differences. Combined, these results provide valuable insight into temporal and spatial variability in community structure as well as potential community-level responses to hypoxia in the northern Gulf of Mexico.

MATERIALS AND METHODS

The northern Gulf of Mexico study area included waters off the coasts of Louisiana and Mississippi that are directly influenced by inflow from the Mississippi River (Figure 1). A total of six separate spatial zones were defined to explore spatial patterns of community structure, and these zones were constructed to account for regional hydrology as well as the occurrence of hypoxia. The study area was bisected into two alongshore zones by the Mississippi River; the central Louisiana (CLA) zone extended from the mouth of the river westward to Vermilion Bay while the eastern Louisiana/ Mississippi zone (ELA/MS) extended from the mouth of the river eastward to the Mississippi/Alabama border. Three bathymetric zones (inshore: 0 – 5 m; nearshore: 5 – 25 m; offshore: 25 – 200 m) were defined based upon areas most frequently influenced by the seasonal formation of hypoxia (Rabalais and Turner 2001).

To examine temporal and spatial patterns of community structure in the coastal waters off Louisiana and Mississippi we assembled fisheries-independent trawl data collected by the Louisiana Department of Wildlife and Fisheries (LDWF), the Mississippi Department of Marine Resources (MDMR), and the Southeast Area Monitoring and Assessment Program (SEAMAP). Because the offshore SEAMAP data is collected as part of summer and fall groundfish surveys, comparisons among areas were restricted to data collected from June through November only. For each data source, catch-per-unit-effort (CPUE) values were calculated (number 1000 m^{-2}) for sixty-six species that were selected because of their abundance, commercial and/or recreational importance, or perceived susceptibility to hypoxia. Mean CPUE values were calculated in a 2 X 3 X 2 X 19 array of alongshore zones, bathymetric zones, seasons (summer: June – August; fall: September – November) and years (1982 – 2000). When combining data from multiple sources (inshore zones only), mean CPUE values were weighted by the relative sampling effort (proportion of total area sampled) of each data source within the specified spatial zone.

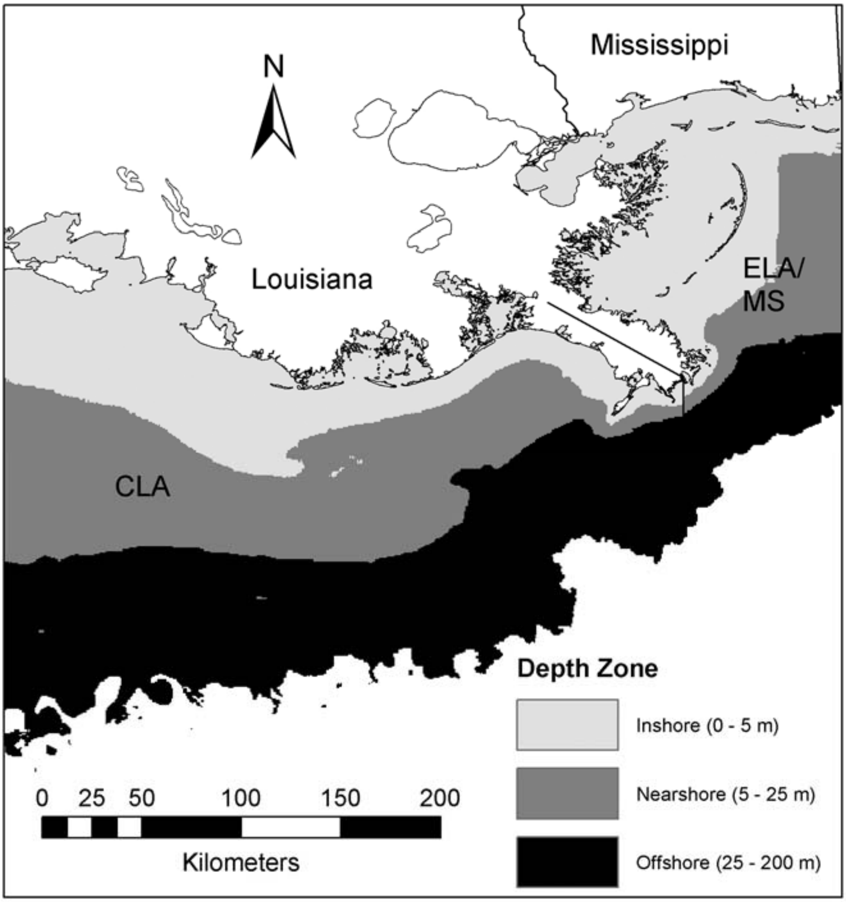

Figure 1. Study area off of Louisiana and Mississippi. Alongshore zonations (CLA: central Louisiana; ELA/MS: eastern Louisiana and Mississippi) were designated based on influence of Mississippi River plume. Bathymetric zonations (Inshore; Nearshore; Offshore) were established to isolate the Nearshore region, which is most frequently prone to hypoxia.

Spatial and temporal comparisons of community structure were conducted using the PRIMER software package (Clarke and Warwick 2001, Clarke and Gorley 2001). To minimize confounding effects and simplify interpretation of results, spatial comparisons (alongshore and bathymetric zones) were conducted seasonally, while temporal comparisons incorporating both seasonal and time-interval components (I: 1982 – 1985, II: 1986 – 1990, III: 1991 – 1995, IV: 1996 – 2000) were conducted separately for each of the six spatial zones. Ordination among samples was examined using non-metric multidimensional scaling (MDS) based upon Bray-Curtis similarities (Bray and Curtis 1957) that were calculated using square-root transformed CPUE data. For each MDS plot, stress values indicated that the amount of distortion resulting from compressing the relationships among data points to two dimensions was acceptable (i.e., as long as values did not exceed 0.3).

Spatial (alongshore zone X bathymetric zone) and temporal (season X time interval) differences in community structure were tested separately in a two-way crossed layout using the analysis of similarity (ANOSIM) procedure, a non-parametric permutation procedure applied to the Bray-Curtis similarity matrix. Testing of the null hypothesis of no difference in community structure involved a series of steps. Initially, the value of a test statistic R was calculated for the observed data based upon ranked similarities within groups and ranked similarities among groups, adjusted to range from 0 to 1. Next, a series of permutations (n = 999) were conducted in which sample labels were randomly distributed among observed values based on the null hypothesis of no difference in community structure. The observed value of R was then compared with the resulting permutation distribution to calculate a probability value. When significant differences were detected, pairwise post-hoc comparisons were conducted using the Bonferroni adjustment. Due to limitations of permutation testing, the examination of R values is generally more useful than that of p-values, and can identify whether groups were well separated (R > 0.75), were clearly separated but overlapped somewhat (0.75 ³ R > 0.5), or were barely separable (R < 0.25).

The contribution of each species to observed between-group differences was calculated using the similarity percentages (SIMPER) routine. For between-group differences (i.e., between pairs of spatial zones), the contribution of each species to Bray-Curtis dissimilarities was calculated. Bray-Curtis dissimilarities are analogous to similarities, with the exception that values range from 0 (completely similar) to 100 (completely dissimilar). Contributions were calculated by taking into account both the contribution of each species as well as the variability in overall contribution to observed dissimilarities. Due to the large number of potential comparisons, SIMPER analyses were only conducted when either significant differences were detected in ANOSIM results or the comparisons involved seasons and/or spatial zones for which hypoxic conditions are common. For the sake of brevity, only the top five species contributing to observed between-group differences were reported.

RESULTS

Distinct spatial groupings were evident seasonally (Figure 2). All three bathymetric zones were clearly separated during both seasons, while distinct separation between alongshore zones was only evident within inshore and offshore zones, primarily during fall. Community structure differed significantly among bathymetric zones during both summer (ANOSIM: R = 0.93, p < 0.001) and fall months (ANOSIM: R = 0.94, p < 0.001). Pairwise comparisons between bathymetric zones, averaged across both alongshore zones, indicated that community structure differed among all three zones during both summer (ANOSIM: R ³ 0.84) and fall (ANOSIM: R ³ 0.92). Although there was some overlap, community structure also differed significantly between alongshore zones during both summer (ANOSIM: R = 0.40, p < 0.001) and fall (ANOSIM: R = 0.48, p < 0.001).

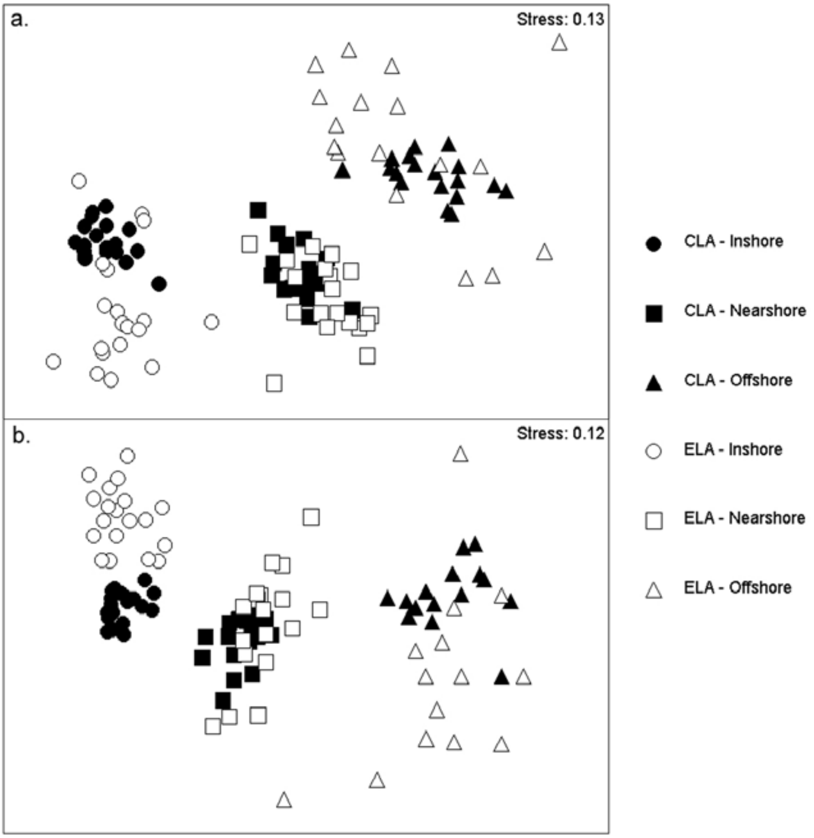

Figure 2. Spatial patterns of community structure based on non-metric multidimensional scaling for a) summer (June – August) and b) fall (September – November), respectively. Symbols represent alongshore (CLA: central Louisiana; ELA: eastern Louisiana and Mississippi) and bathymetric (Inshore: 0 – 5 m; Nearshore: 5 – 25 m; Offshore: 25 – 200 m) zonations.

Dissimilarity between bathymetric zones was high during summer, ranging from 59.0 to 80.7% (Table 1). The greatest dissimilarity was between inshore and offshore zones, and was characterized by higher abundances of *Anchoa mitchilli* within inshore zones as well as higher abundances of *Stenotomus caprinus* and *Serranus atrobranchus* within offshore zones. Nearshore and offshore communities also differed significantly, with higher abundances of *Trachypenaeus similis* and *Peprilus burti* within nearshore zones. Dissimilarity between inshore communities of central Louisiana and eastern Louisiana/Mississippi were comparable during both summer (46.3%) and fall (41.3%; Table 2). During both seasons, differences between the two zones were characterized by higher abundances of *M. undulatus* and penaeid shrimp in central Louisiana as well as higher abundances of *A. mitchilli* and *A. hepsetus* in eastern Louisiana/Mississippi.

Table 1. Bray-Curtis dissimilarity values between bathymetric zones during summer (June – Aug) in coastal Louisiana and Mississippi. Values reported include total dissimilarity (Tot.Dis), average abundance (Avg.Abund, in number 1000 m^{-2}), average dissimilarity (Avg.Dis), ratio of average dissimilarity to standard deviation of similarity (Dis/SD) and the percent contribution to the total dissimilarity (%).

			Zone I	Zone II			
Bathymetric Zones	Tot.Dis	Taxon	Avg.Abund	Avg.Abund	Avg.Dis	Dis/SD	%
Inshore - Nearshore	64.0	*A. mitchilli*	21.7	0.1	5.9	1.1	9.2
		S. caprinus	0.2	9.5	5.1	2.6	7.9
		T. similis	0.1	5.1	3.2	1.4	5.0
		P. burti	0.2	5.6	3.0	1.2	4.7
		M. undulatus	4.2	3.8	2.5	1.2	4.0
Inshore - Offshore	80.7	*A. mitchilli*	21.7	0.0	9.0	1.3	11.1
		S. caprinus	0.2	5.8	5.2	1.6	6.4
		M. undulatus	4.2	5.3	4.3	1.2	5.4
		S. atrobranchus	0.0	2.5	3.9	2.0	4.8
		A. hepsetus	3.6	0.0	3.9	1.1	4.8
Nearshore - Offshore	59.0	*T. similis*	5.1	1.1	4.0	1.3	6.8
		M. undulatus	3.8	5.3	3.5	1.1	5.9
		S. caprinus	9.5	5.8	3.3	1.4	5.6
		P. burti	5.6	1.8	3.1	1.1	5.2
		C. similis	2.9	0.3	3.1	1.7	5.2

Table 2. Bray-Curtis dissimilarity values between alongshore zones within inshore waters (0 – 5 m depth) during summer (June – Aug) and fall (Sep – Nov). Values reported include total dissimilarity (Tot.Dis), average abundance (Avg.Abund, in number 1000 m^{-2}), average dissimilarity (Avg.Dis), ratio of average dissimilarity to standard deviation of dissimilarity (Dis/SD) and the percent contribution to the total dissimilarity (%).

Season **Alongshore Zones**	**Tot.Dis**	**Taxon**	**Zone I** **Avg.Abund**	**Zone II** **Avg.Abund**	**Avg.Dis**	**Dis/SD**	**%**
Summer							
CLA – ELA/MS	46.3	*A. mitchilli*	3.9	39.5	8.0	1.4	17.3
		A. hepsetus	0.3	6.9	4.1	1.5	8.9
		M. undulatus	7.0	1.5	3.5	1.3	7.5
		C. chrysurus	2.0	1.5	1.8	1.0	3.9
		F. aztecus	3.1	1.2	1.8	1.7	3.8
Fall							
CLA – ELA/MS	41.3	*A. mitchilli*	3.8	23.8	6.8	1.8	16.6
		M. undulatus	5.3	0.9	3.1	1.3	7.6
		A. hepsetus	0.4	4.5	2.8	1.0	6.7
		C. chrysurus	2.0	3.3	2.4	1.4	5.8
		L. setiferus	3.3	1.2	1.7	1.6	4.2

Clear seasonal groupings were evident for most spatial zones, although there was little evidence of long-term changes in community structure (Figure 3). Seasonal differences were most distinct throughout central Louisiana and the nearshore zone within eastern Louisiana/Mississippi. Among seasonal comparisons, R-values ranged from 0.23 to 0.77, and there was evidence of strong seasonal differences in community structure (ANOSIM: $R > 0.52$) for all spatial zones except inshore and offshore zones within eastern Louisiana/Mississippi. Community structure did not differ strongly among time intervals for any of the six spatial zones (ANOSIM: $R \leq 0.45$). Nevertheless, subtle long-term changes in community structure may have occurred in inshore zones of central Louisiana (ANOSIM: $R = 0.45$, $p < 0.001$) and eastern Louisiana/Mississippi (ANOSIM: $R = 0.43$, $p < 0.001$). Within these two inshore zones, pairwise comparisons among time intervals indicated that community structure during the first time interval (1982 – 1985) differed from all other time intervals (1986 – 1990; 1991 – 1995; 1996 – 2000) for both central Louisiana (R ³ 0.52) and eastern Louisiana/Mississippi (R ³ 0.73).

Seasonal patterns in community structure within the nearshore zone were similar for both central Louisiana and eastern Louisiana/Mississippi (Table 3). Observed differences were driven primarily by higher abundances of *M. undulatus* during fall and higher abundances of *T. similis*, *Stenotomus caprinus* and *P. burti* during summer.

DISCUSSION

Significant spatial and temporal differences in community structure were detected within coastal waters off of Louisiana and Mississippi. Spatial differences were primarily related to bathymetry, and were similar during both summer and fall. There was also evidence of strong seasonal differences in community structure within most of the spatial zones, including nearshore zones, where similar seasonal patterns were evident in both central Louisiana and eastern Louisiana/Mississippi. We did not detect any long-term change in community structure in the northern Gulf of Mexico, although the possibility exists that hypoxia-induced changes in community structure occurred prior to the earliest data incorporated in these analyses. Alternately, the effects of hypoxia on demersal communities may be partially buffered by characteristics of the northern Gulf of Mexico ecosystem as well as the nekton themselves. Future analyses incorporating a wider spatial coverage as well as additional historical data appear warranted.

Table 3. Bray-Curtis dissimilarity values between summer (June – Aug) and fall (Sep – Nov) for nearshore zones (5 – 25 m depth) of central Louisiana (CLA) and eastern Louisiana and Mississippi (ELA/MS). Values reported include total dissimilarity (Tot.Dis), average abundance (Avg.Abund, in number 1000 m^{-2}), average dissimilarity (Avg.Dis), ratio of average dissimilarity to standard deviation of dissimilarity (Dis/SD) and the percent contribution to the total dissimilarity (%).

Alongshore Zone			**Zone I**	**Zone II**			
Season	**Tot.Dis**	**Taxon**	**Avg.Abund**	**Avg.Abund**	**Avg.Dis**	**Dis/SD**	**%**
CLA							
Summer – Fall	41.0	*M. undulatus*	4.8	17.2	4.0	1.7	9.8
		T. similis	5.7	0.6	2.8	1.6	6.8
		S. caprinus	8.4	3.0	2.1	1.2	5.1
		P. burti	4.0	0.6	2.1	1.7	5.1
		C. similis	2.1	6.2	2.0	0.8	4.8
ELA/MS							
Summer – Fall	45.3	*S. caprinus*	10.6	7.3	3.0	1.4	6.6
		T. similis	4.6	1.1	2.6	1.5	5.7
		P. burti	7.3	0.9	2.6	0.9	5.6
		M. undulatus	2.7	4.1	2.4	1.5	5.4
		C. chrysurus	0.4	3.0	2.4	1.5	5.2

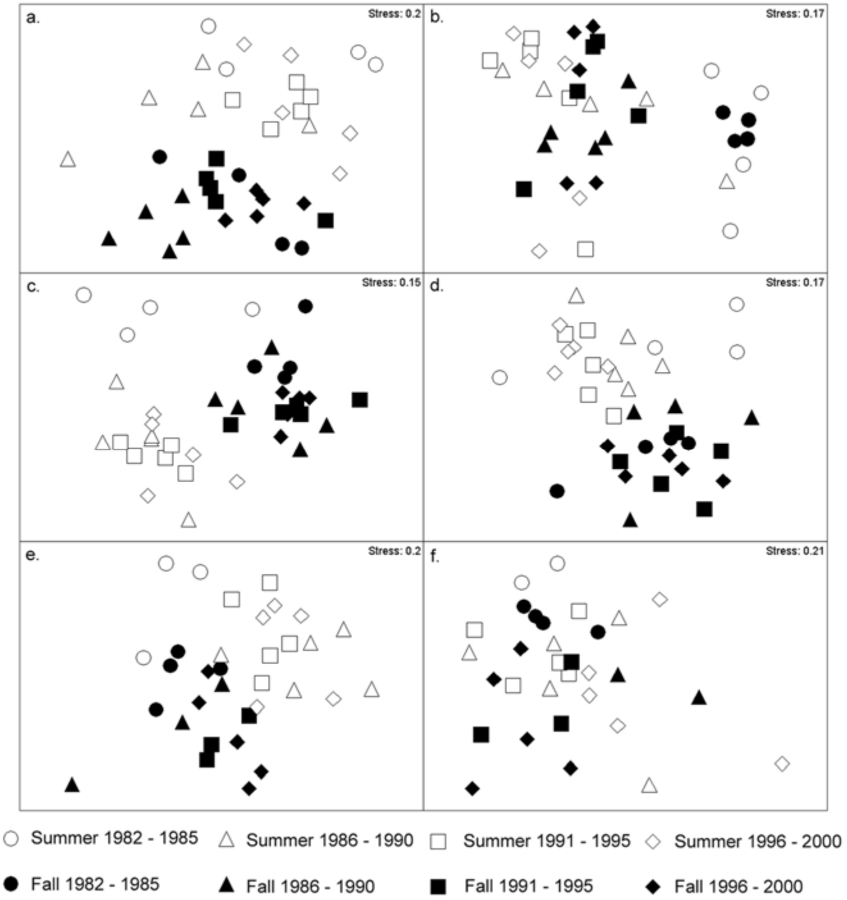

Figure 3. Temporal patterns of community structure based on non-metric multidimensional scaling for a) Inshore CLA, b) Inshore ELA/MS, c) Nearshore CLA, d) Nearshore ELA/MS, e) Offshore CLA, and f) Offshore ELA/MS, respectively.

Spatial differences in community structure were generally more pronounced than were temporal differences, and were primarily related to bathymetry and to a lesser extent alongshore position east and west of the Mississippi River. Higher abundances of anchovies (both *Anchoa mitchilli* and *A. hepsetus*) within inshore waters coupled with the virtual absence of anchovies in waters deeper than 5 m contributed to observed spatial patterns of community structure (Table 1), especially in eastern Louisiana/Mississippi (Table 2). While previous studies have also documented high abundances of anchovies within shallow, inshore waters of both Louisiana (Rakocinski et al. 1992; Baltz et al. 1993) and Mississippi (Ross et al. 1987), our results may be confounded by gear bias. Because anchovies are pelagic, observed density differences may be partially attributable to the fact that demersal trawls sample a greater proportion of the water column in shallow areas. Observed densities of *Trachypenaeus similis, Peprilis burti, Stenotomus caprinus* and *Serranus atrobranchus* also contributed to bathymetric differences in community structure, and agreed with previously-published reports regarding the distribution of these species along depth gradients (Moore et al. 1970, Brusher and Ogren 1976, Chittenden and McEachran 1976, Chittenden and Moore 1976, Geoghegan and Chittenden 1982, Murphy and Chittenden 1991). Despite clearly-defined bathymetric patterns of community structure, observed differences cannot be soley attributed to depth. We know that other factors covary with depth and may affect nekton; these include distance from shore, temperature, salinity, dissolved oxygen and chlorophyll *a* concentrations (Grimes and Finucane 1991, Rabalais et al. 1991). Future analyses need to address the relative importance of these other environmental factors on the community structure of nekton in the northern Gulf of Mexico.

Seasonal differences in community structure were evident for four of six spatial zones, including the nearshore zones of both central Louisiana and eastern Louisiana/Mississippi. Similar seasonal patterns were evident within both nearshore zones, and appear to be primarily related to ontogenetic movements of selected species. Within nearshore zones, *Micropogonias undulatus* were found in higher numbers during fall. *M. undulatus* spawn during late fall/early winter, and the fall peaks in abundance most likely represent an influx of new recruits from inshore nurseries (Gunter 1938, Moore et al. 1970). Three other species, *Trachypenaeus similis*, *Peprilus burti* and *Stenotomus caprinus*, occurred in higher numbers during summer. Summer peaks in *T. similis* abundances corresponded to those observed in coastal Florida (Brusher and Ogren 1976). Juvenile *P. burti* use nearshore waters as nurseries during summer, eventually dispersing into deeper waters as they approach 9 – 12 months of age (Murphy and Chittenden 1991). Summer peaks of *S. caprinus* most likely represent age-I individuals, since mature adults primarily spawn from January through April, with young gradually dispersing into deeper waters as they mature (Geoghegan and Chittenden 1982). Based upon these analyses, we did not detect any seasonal differences in community structure that may be directly related to the occurrence of hypoxia during summer months within nearshore waters of the northern Gulf of Mexico.

While we did not detect any significant long-term changes in community structure in the northern Gulf of Mexico, the temporal coverage of these data may be inadequate to detect such changes. Although continental shelf hypoxia was first reported in the early 1970s (Hanifen et al. 1997), evidence suggests that the concentration of nutrients within the Mississippi River discharge began to rise some years earlier (Turner and Rabalais 1991, Turner and Rabalais 1994). Additionally, other long-prevalent anthropogenic influences, including alterations to watershed hydrology and the impacts of fishing, may have resulted in previous alterations to community structure (Gunter 1952, Chesney et al. 2000). The potential exists that any significant changes to community structure occurred well before the earliest data included in the current analyses (1982). It is also possible that the effects of hypoxia on demersal communities have been buffered to date by characteristics of the basin, the nekton and/or the ecosystem (Chesney and Baltz 2001). Nevertheless, these analyses represent an important first step in understanding the potential effects of hypoxia as well as other anthropogenic factors on the demersal community as a whole in the northern Gulf of Mexico. Future analyses are recommended that build upon these efforts by expanding spatial coverage to include the remainder of Louisiana and Texas and by expanding temporal coverage by incorporating historical data. It will be especially important to incorporate measures of environmental variability to identify the relative effects of various environmental parameters, including dissolved oxygen, on observed patterns of community structure.

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LITERATURE CITED

Baltz, D.M., C. Rakocinski, and J.W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environmental Biology of Fishes* **36**:109-126.

Bray, J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* **27**:325-349.

Breitburg, D.L., L. Pihl, and S.E. Kolesar. 2001. Effects of low dissolved oxygen on the behavior, ecology and harvest of fishes: a comparison of the Chesapeake Bay and Baltic-Kattegat systems. Pages 241-268 in: N.N. Rabalais and R.E. Turner (eds.). *Coastal Hypoxia: Consequences for Living Resources and Ecosystems.* American Geophysical Union, Washington, D.C. USA.

Brusher, H.A. and L.H. Ogren. 1976. Distribution, abundance, and size of penaeid shrimps in the St. Andrew Bay system, Florida. *Fishery Bulletin* :158-166.

Burnett, L.E. and W.B. Stickle. 2001. Physiological responses to hypoxia. Pages 101-114 in: N.N. Rabalais and R.E. Turner (eds.). *Coastal Hypoxia: Consequences for Living Resources and Ecosystems.* American Geophysical Union, Washington, D.C. USA.

Chesney, E.J. and D.M. Baltz. 2001. The effects of hypoxia on the northern Gulf of Mexico coastal ecosystem: a fisheries perspective. Pages 321-354 in: N.N. Rabalais and R.E. Turner (eds.). *Coastal Hypoxia: Consequences for Living Resources and Ecosystems.* American Geophysical Union, Washington, D.C. USA.

Chesney, E.J., D.M. Baltz, and R.G. Thomas. 2000. Louisiana estuarine and coastal fisheries and habitats: perspectives from a fish's eye view. *Ecological Applications* **10**:350-366.

Chittenden, M.E., Jr. and J.D. McEachran. 1976. Composition, ecology, and dynamics of demersal fish communities on the northwestern Gulf of Mexico continental shelf, with a similar synopsis for the entire Gulf. Texas A&M University Sea Grant Program. Report Number 76-208. 111 pp .

Chittenden, M.E., Jr. and D. Moore. 1976. Composition of the ichthyofauna inhabiting the 110-m bathymetric contour of the Gulf of Mexico, Mississippi River to the Rio Grande. Texas A&M University Sea Grant Program. Report Number 76-210. 20 pp.

Clarke, K.R. and R.N. Gorley. 2001. *PRIMER v5: User Manual/Tutorial.* PRIMER-E, Plymouth, U.K. 91 pp.

Clarke, K.R. and R.M. Warwick. 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edition.* Natural Environment Research Council, Plymouth Marine Laboratory, Plymouth, U.K. 171 pp.

Craig, J.K., L.B. Crowder, C.D. Gray, C.J. McDaniel, T.A. Henwood, and J.G. Hanifen. 2001. Ecological effects of hypoxia on fish, sea turrles, and marine mammals in the northwestern Gulf of Mexico. Pages 269-292 in: N.N. Rabalais and R.E. Turner (eds.). *Coastal Hypoxia: Consequences for Living Resources and Ecosystems.* American Geophysical Union, Washington, D.C. USA.

Craig, K. 2001. *Effects of Large Scale Hypoxia on the Distribution of Brown Shrimp (Farfantepenaeus aztecus) and Atlantic Croaker (Micropogonias undulatus) in the Northwestern Gulf of Mexico.* Ph.D. Dissertation. Duke University, Durham, North Carolina USA. 223 pp.

Daskalov, G.M. 2003. Long-term changes in fish abundance and environmental indices in the Black Sea. *Marine Ecology Progress Series* **255**:259-270.

Geoghegan, P. and M.E. Chittenden, Jr. 1982. Reproduction, movements, and population dynamics of the longspine porgy, *Stenotomus caprinus*. *Fishery Bulletin* **81**:523-540.

Grimes, C.B. 2001. Fishery production and the Mississippi River discharge. *Fisheries* **26**:17-26.

Grimes, C.B. and J.H. Finucane. 1991. Spatial distribution and abundance of larval and juvenile fish, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. *Marine Ecology Progress Series* **75**:109-119.

Gunter, G. 1938. Seasonal variations in abundance of certain estuarine and marine fishes in Louisiana, with particular reference to life histories. *Ecological Monographs* **8**:314-346.

Gunter, G. 1952. Historical changes in the Mississippi River and the adjacent marine environment. *Publications of the Institute of Marine Science* 2:120-139.

Gunter, G. 1963. The fertile fisheries crescent. *Journal of the Mississippi Academy of Sciences* **9**:286-290.

Hanifen, J.G., W.S. Perret, R.P. Allemand, and T.L. Romaire. 1997. Potential impacts of hypoxia on fisheries: Louisiana's fishery-independent data. Pages 87-100 in: Proceedings Production of Northern Gulf of Mexico continental shelf waters linked to nutrient inputs from the Mississippi River. *Marine Ecology Progress Series* **155**:45-54.

Houde, E.D. and E.S. Rutherford. 1993. Recent trends in estuarine fishes: predictions of fish production and yield. *Estuaries* **16**:161-176.

Justic, D., N.N. Rabalais, R.E. Turner, and W.J. Wiseman, Jr. 1993. Seasonal coupling between riverborne nutrients, net productivity and hypoxia. *Marine Pollution Bulletin* **26**:184-189.

Lohrenz, S.E., G.L. Fahnenstiel, D.G. Redalje, G.A. Lang, X. Chen, and M.J. Dagg. 1997. Variations in primary the northern Gulf of Mexico: description, causes and change. Pages 1-36 in: N.N. Rabalais and R.E. Turner (eds.). *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*. American Geophysical Union, Washington, D.C. USA.

Moore, D., H.A. Brusher, and L. Trent. 1970. Relative abundance, seasonal distribution, and species composition of demersal fishes off Louisiana and Texas, 1962-1964. *Contributions in Marine Science* **15**:45-70.

Murphy, M.D. and M.E. Chittenden, Jr. 1991. Reproduction, age and growth, and movements of the gulf butterfish *Peprilus burti*. *Fishery Bulletin* **89**:101-116.

Nixon, S.W. and B.A. Buckley. 2002. "A strikingly rich zone" - nutrient enrichment and secondary production in coastal marine ecosystems. *Estuaries* **25**:782-796.

Rabalais, N.N., D.E. Harper, Jr., and R.E. Turner. 2001. Responses of nekton and demersal and benthic fauna to decreasing oxygen concentrations. Pages 115-128 in: N.N. Rabalais and R.E. Turner (eds.). *Coastal Hypoxia: Consequences for Living Resources and Ecosystems.* American Geophysical Union, Washington, D.C.USA.

Rabalais, N.N., W.J. Wiseman, Jr., R.E. Turner, D. Justic, B.K.S. Gupta, and Q. Dortch. 1996. Nutrient changes in the Mississippi River and system responses on the adjacent continental shelf. *Estuaries* **19**:386-407.

Rabalais, N.N. and R.E. Turner. 2001. Hypoxia in of the First Gulf of Mexico Hypoxia Management Conference, New Orleans, Louisiana USA. December 1995.

Rabalais, N.N., R.E. Turner, W.J. Wiseman, Jr., and D.F. Boesch. 1991. A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985-1988. *Geological Society Special Publication* **58**:35-47.

Rakocinski, C.F., D.M. Baltz, and J.W. Fleeger. 1992. Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. *Marine Ecology Progress Series* **80**:135-148.

Renaud, M.L. 1985. Hypoxia in Louisiana coastal waters during 1983: implications for fisheries. *Fishery Bulletin* **84**:19-26.

Riley, G.A. 1937. The significance of the Mississippi River drainage for biological conditions in the northern Gulf of Mexico. *Journal of Marine Research* **1**:60-74.

Ross, S.T., R.H. McMichael, Jr., and D.L. Ruple. 1987. Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. *Estuarine, Coastal, and Shelf Science* **25**:391-412.

Turner, R.E. and N.N. Rabalais. 1991. Changes in Mississippi River water quality this century. *BioScience* **41**:140-147.

Turner, R.E. and N.N. Rabalais. 1994. Coastal eutrophication near the Mississippi river delta. *Nature* **368**:619-621.

Wiseman, W.J., Jr., N.N. Rabalais, R.E. Turner, S.P. Dinnel, and A. MacNaughton. 1997. Seasonal and interannual variability within the Louisiana coastal current: stratification and hypoxia. *Journal of Marine Systems* **12**:237-248.

Zimmerman, R.J. and J.M. Nance. 2000. Effects of hypoxia on the shrimp fishery of Louisiana and Texas. Pages 293-310 in: N.N. Rabalais and R.E. Turner (eds.*). Coastal Hypoxia: Consequences for Living Resources and Ecosystems.* American Geophysical Union, Washington, D.C. USA.

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