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FEATURE ARTICLE

Spatial patterns in species assemblages associated with the northwestern Gulf of Mexico shrimp trawl fishery

Melissa H. Monk[1,3,4,*], Joseph E. Powers[1], Elizabeth N. Brooks[2]

[1]Department of Oceanography and Coastal Sciences, School of the Coast and Environment at Louisiana State University, Energy, Coast and Environment Building, Baton Rouge, LA 70803, USA

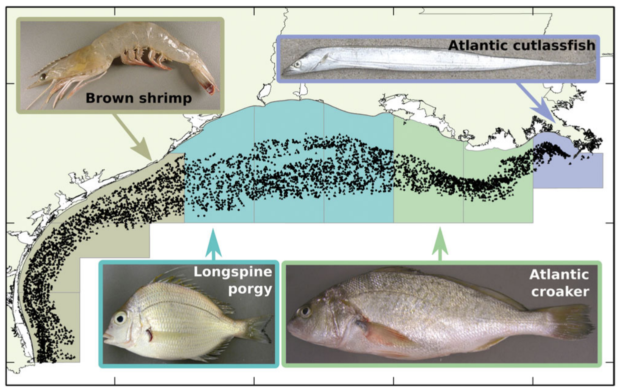
[2]Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, 166 Water St., Woods Hole, MA 02543, USA

[3]*Present address:* Center for Stock Assessment Research, Department of Applied Mathematics and Statistics, Jack Baskin School of Engineering, University of California, Santa Cruz, CA 95064, USA

[4]*Present address:* Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 110 Shaffer Road, Santa Cruz, CA 95060, USA

ABSTRACT: The shrimp trawl fishery in the Gulf of Mexico (GOM) removes a diverse community of bycatch species from the Gulf Large Marine Ecosystem (LME). A small fraction of the discarded species is economically important, and little is known about the majority of bycatch species. Large-scale fishery-independent trawl surveys from the Southeast Area Monitoring and Assessment Program (SEAMAP) were utilized to examine the spatial dynamics of the demersal fish community associated with the shrimp trawl fishery across the northwest GOM-LME. Multivariate analyses revealed 3 distinct demersal fish communities from the fall survey and 4 distinct communities from the summer survey. Shrimp Statistical Zone 13, nearest the Mississippi River, was a differentiating factor between the 2 surveys, associating with Zones 14 and 15 in the fall survey, and comprising its own dissimilar community in the summer survey. The dominant species within each zone differed between the summer and fall seasons, which can be explained by the time of spawning and seasonal ontogenetic migrations of species associated with the survey. Indicator species analysis identified species in each season and region that can be used to monitor future ecosystem changes within these regions.

KEY WORDS: SEAMAP · Fish community · Indicator species · Bycatch · Large marine ecosystem



Northwestern Gulf of Mexico demersal fish communities (DFCs) identified from SEAMAP bottom trawl surveys (points) and example indicator species.

Image: Melissa Monk (map), Brenda Bowling (fish photos)

INTRODUCTION

Ecosystem-based fisheries management (EBFM) is a process under which more holistic approaches are introduced than those considered by more traditional single-species management. EBFM is often framed at the scale of large marine ecosystems (LMEs; Pikitch et al. 2004, Link 2010). Implementation of EBFM has increased the need for data to quantify relationships among species within an ecosystem, the spatial dynamics of the system, and the impact of anthropo-

*Corresponding author: melissa.monk@noaa.gov

genic activities. An important part of the EBFM process is to evaluate community structure of major LMEs such as the US Gulf of Mexico (GOM). The GOM-LME spans the coastline of 5 states and is divided into 2 distinct systems by the Mississippi River Delta outflow. Here we focus on the spatial dynamics of the demersal fish community (DFC) associated with the northwestern GOM (Fig. 1) shrimp trawl fishery.

Shrimp trawl gear alters the physical environment of the seafloor and also catches a large biomass and diversity of bycatch species, i.e. species that are caught in trawls associated with shrimp and are subsequently discarded (Churchill 1989, Watling & Norse 1998, Duplisea et al. 2002). The removal of large volumes of bycatch species has the potential to change species biodiversity and species distribution patterns (Bohnsack 1998, Rice 2000, Board 2002, Barnes & Thomas 2005, Løkkeborg 2005). Many of the species caught as bycatch in the GOM are neither commercially nor recreationally harvested species and have not been monitored as closely as species with high economic value. Of the 199 species identified by observers in the GOM shrimp trawl fishery, only 14 were identified as recreationally, commercially, or ecologically important (13 finfish and a 'general shark' category; Scott-Denton et al. 2012). All of the commercially and recreationally important species are managed as single-species fisheries. However, an understanding of the spatial dynamics of the species along the northwestern GOM will aid in future EBFM of these species.

Few studies have examined the biodiversity and community assemblage patterns in the northwestern GOM using fisheries-independent data. Studies that were conducted focused on specific areas of the GOM, the effect of oil and gas platforms on community assemblages, and the effect of trawling on specific species (Chittenden & McEachran 1976, Stanley & Wilson 1997, Wells et al. 2008). The Southeast Area Monitoring and Assessment Program (SEAMAP), a fishery-independent trawl survey conducted in the northwestern GOM, provides a data set useful for investigating the spatial dynamics of the demersal fish community (Eldridge 1988). The trawl survey includes all species captured as bycatch in the shrimp trawl fishery, but without the potential biases introduced by using fishery-dependent data. We conducted multivariate analyses to infer the spatial structure of the demersal fish community in the northwestern GOM. Using the regions identified from the multivariate analyses, we then conducted an indicator species analysis to define a list of species that can be used to monitor the regions as part of an ecosystem approach to fisheries management.

MATERIALS AND METHODS

Data sources

SEAMAP is a collaborative program for the collection of fisheries-independent data in the southeastern USA. We used the annual summer and fall shrimp and groundfish trawl surveys to identify changes in community composition in the northwestern GOM. We constrained the dataset to the time period prior to the fall of 2008, after which survey sampling methods changed (NOAA 2008). The summer survey is conducted in June and July, with data available from 1982 to 2008, and the fall survey is conducted in October and November and data were available from 1986 to 2007 (Eldridge 1988).

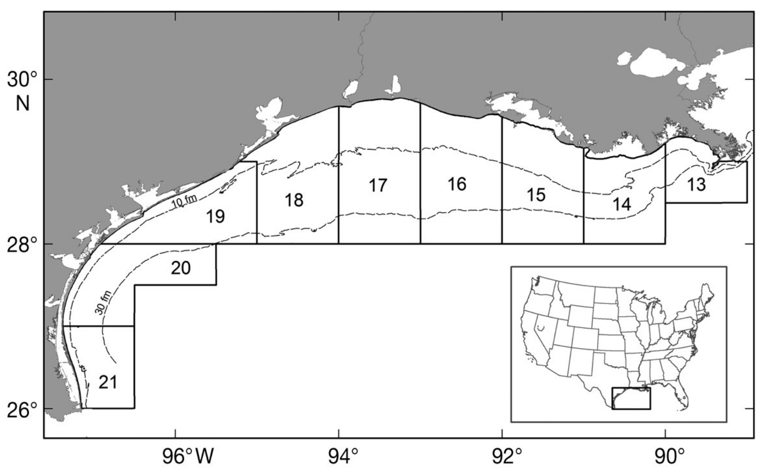


Fig. 1. Northwestern Gulf of Mexico shrimp statistical zone delineations

The SEAMAP survey was stratified by the shrimp statistical zones that are used for management of the shrimp trawl fishery (Patella 1975) (Fig. 1). We only use Zones 13 to 21 in the northwestern GOM and tows in the depth range 10 to 30 fathoms (fm; 18.3–54.9 m). In depths of less than 10 fm (18.3 m), trawls other than the SEAMAP-standard trawl 40 ft (12.2 m) headrope were common. The depth range was also chosen to reflect the depths over which the majority of the shrimp fishery effort affects economically important species, specifically red snapper *Lutjanus campechanus* (Gallaway et al. 2003). There were 2 missing years of data (1983 and 1986) for the summer survey in Zone 13.

We examined the database for errors and anomalies in individual tows. Tows using gear other than the standard SEAMAP shrimp trawl (40 ft [12.2 m] headrope) were excluded from these analyses as well as tows in which significant gear malfunctions were noted, e.g. trawl doors did not open. For stations that deployed paired tows, only 1 tow was selected for analysis to keep the samples as balanced as possible. We also constrained the data to tows falling within the standard tow times of 10 to 55 min. Trawls are towed perpendicular to the depth contour and are towed until the entire depth stratum is sampled (Eldridge 1988). We retained stations with tow times from 55 to 80 min if the standard protocols were followed, as well as stations that required 2 tows to cover the depth stratum. The maximum tow time was 70 min for the summer data and 79 min for the fall data. Details for individual cruises can be obtained in the SEAMAP environmental and biological atlases and the individual cruise reports (NOAA 2008, Rester et al. 2008).

More than 800 species were present in the SEAMAP groundfish trawl surveys. The catch, both in terms of biomass and number of individuals, was dominated by a few abundant species. Including rare species in community composition analyses has the potential to bias results (Koch 1987, Mueter & Norcross 2000). Therefore, we considered species present in fewer than 10% of all tows to be 'rare' in the survey, and excluded them from analyses. In addition, we excluded gelatinous zooplankton species due to inconsistent sampling of these species over time (J. Rester pers. comm.).

We calculated a yearly index of catch per unit effort (CPUE) prior to analysis for each species. The index of abundance was calculated from the CPUE for each zone (*z*), survey season (*s*), and year (*y*). We also calculated the index by pooling catch across years. The index multiplies the geometric mean of species *i* abundance per tow-hour (x_i), in a specific zone (*z*), season (*s*), and year (*y*, when applicable), by the proportion of tows in which a species was observed, where *n* is the number of tows in which the species was observed, and *T* is the total number of tows (Conners et al. 2002).

$$\text{Index}_{i,z,s,y} = \frac{\left(\prod_{i=1}^{n} x_{i,z,s,y}\right)^{\frac{1}{n_{i,z,s,y}}} * n_{i,z,s,y}}{T_{i,z,s,y}} \quad (1)$$

The indices of abundance were then arranged into a matrix where rows represented shrimp statistical zone/year combinations and columns represented species.

Statistical analyses

The chord distance (D_{chord}), or relative Euclidian distance, was chosen as the distance metric to use for the multivariate analyses (Legendre & Legendre 1998, McCune et al. 2002). The metric measures the dissimilarity of species composition among shrimp statistical zones by comparing the abundance index (*a*) of species *i* between pairs of shrimp statistical zones (*j* and *k*), for all *p* species, over all years.

$$D_{chord(jk)} = \delta_{jk} = \sqrt{\sum_{i=1}^{p}\left[\left(\frac{a_{ji}}{\sqrt{\sum_{i=1}^{p} a_{ji}^2}}\right)-\left(\frac{a_{ki}}{\sqrt{\sum_{i=1}^{p} a_{ki}^2}}\right)\right]^2} \quad (2)$$

The contribution of species *i* to the dissimilarity (δ) between a pair of shrimp statistical zones (j,k) is:

$$\delta_{jk}(i) = \frac{(a_{ji} - a_{ki})^2}{\delta_{jk}} \quad (3)$$

The chord distance measure is equivalent to taking the Euclidian distance after normalizing the row (shrimp statistical zone) totals so the marginal sum of squares is 1 (Orloci 1967, McCune et al. 2002). This ensures that no single species dominates the calculation of the dissimilarity matrix. This also gives the sample units (shrimp statistical zones) the same weight, making the differences in effort among those sample units irrelevant.

We analyzed the spatial patterns in species composition among shrimp statistical zones using 2 multivariate analyses: non-metric multidimensional scaling (NMDS; Shepard 1962, Kruskal 1964) and agglomerative hierarchical cluster analysis (Ward 1963). NMDS is an ordination method that performs well when data are non-normal and preserves the rank order distances from any dissimilarity measure (Clarke 1993). Stress, a goodness-of-fit statistic, was used to determine the number of retained dimensions from the NMDS. Stress is the departure from monotonicity between distances in the original dissimilarity matrix and the *k*-dimensional ordination space, with a value less than 0.3 considered acceptable (Clarke & Warwick 2001). Cluster analysis was used in parallel to corroborate the patterns observed in the NMDS analysis to classify regional groupings of species similarity among the shrimp statistical zones.

To determine which species were responsible for the regional groupings identified in the multivariate analyses, we partitioned the dissimilarity matrix and conducted an indicator species analysis (Clarke 1993). We computed the average contribution of each species to the overall average dissimilarity ($\bar{\delta}$) between 2 distinct communities identified from the multivariate analyses. The $\bar{\delta}$ is found by taking the mean of the dissimilarity between pairs of shrimp statistical zones within the 2 DFCs being compared. The average contribution of each species (δ_i) to the $\bar{\delta}$ was found by taking the mean of $\delta_{jk}(i)$ from all pairs of shrimp statistical zones in the 2 DFCs being compared. Clarke (1993) defined a species as a good discriminating species if it contributed a high proportion to $\bar{\delta}$ and had a small standard deviation (SD[δ_i]), meaning a species contributed consistently to the dissimilarities. Species were ranked by their percent contribution to the dissimilarity between any 2 DFCs, and we present the results for species contributing to the cumulative 90% difference between any 2 DFCs.

Indicator species analysis provides a metric to determine a species' affinity to a specific spatial area using the species' relative abundance (specificity) and its relative frequency (fidelity) from the sampled data (Dufrene & Legendre 1997, McCune et al. 2002). Indicator species analysis provides another metric to compare the DFCs between seasons, and we were interested to see whether species contributing the most to the dissimilarity indices could be used as indicators for a particular DFC. An indicator value, *IndVal*, was calculated for each species *i* and for each DFC *d* (pre-defined from the multivariate analysis results), according to the formula

$$IndVal_{id} = 100 \times A_{id} \times B_{id} \quad (4)$$

where A_{id} is a measure of the specificity and B_{id} is a measure of fidelity:

$$A_{id} = N\,individuals_{id} \,/\, N\,individuals_{+d} \quad (5)$$

$$B_{id} = N\,sites_{id} \,/\, N\,sites_{i+} \quad (6)$$

In this study, $N\,individuals_{id}$ represents the mean abundance of species *i* in DFC *d*, and $N\,individuals_{+d}$ is the sum of mean abundances of species *i* within all DFCs. $N\,sites_{id}$ is the number of shrimp statistical zones belonging to region *d* where species *i* is present. $N\,sites_{i+}$ is the total number of shrimp statistical zones within DFC *d*. The *IndVal* has a maximum at 100 if individuals of a species are observed in all shrimp statistical zones in a given DFC and are absent from all other zones. We considered a species to be an indicator for a particular DFC if its maximum indicator value was ≥25 (Dufrene & Legendre 1997). For each species, the region with the largest indicator value, $IndVal_{max}$, is reported. A randomization test (10 000 permutations) was used to test the statistical significance (Type I error, $p < 0.05$) of $IndVal_{max}$. Samples were randomly reassigned to shrimp statistical zones, and $IndVal_{max}$ was recalculated and compared to $IndVal_{max}$ from the data.

The NMDS and cluster analysis were programmed in R (R Core Development Team 2011) utilizing the Vegan community ecology package for the NMDS (Oksanen et al. 2010) and the cluster package for cluster analyses (Maechler et al. 2002). The indicator species analysis was conducted in PC-ORD (McCune & Mefford 2006).

RESULTS

In total, 3305 tows were retained from the summer survey (Table S1 in the Supplement, available at www.int-res.com/articles/suppl/m519p001_supp.pdf) and 2849 from the fall survey (Table S2). The 67 species found in 10% or more tows in the summer survey (Table 1) represent 13% of all species identified to the species level in the summer survey. In the fall survey, 68 species were retained for the analyses, representing 14% of all species identified in the fall survey.

A cluster analysis using all survey data revealed differences in community composition between the summer and fall surveys within zones (Fig. S1 in the Supplement). Preliminary analyses also suggested no statistically significant temporal trends in the community assemblages (Monk 2012). Therefore, we analyzed summer and fall surveys independently, and pooled data across years for the NMDS and cluster analyses. Pooling data across years also maintained sample sizes adequate for our analyses.

Summer groundfish survey

The NMDS revealed 4 distinct groups of shrimp statistical zones: Zone 13, Zones 14 and 15, Zones 16 to 18, and Zones 19 to 21 (Fig. 2a). Three axes (stress = 0.001) best explained the data, and upon visual inspection, the separation among shrimp zones was most visible in the first 2 axes.

In the cluster analysis, Zone 13 was again dissimilar from all other zones and formed its own branch in the dendrogram (Fig. 2b). Zones 14 to 18 formed a second distinct branch, and within that branch, Zones 14 and 15 and Zones 16 to 18 showed further separation of species composition. Zones 19 to 21 separated as a fourth unique group of species in the summer data. The repeatability of the results between the NMDS and the cluster analysis provides evidence that in the summer months, there are 4 distinct regional DFCs in the northwestern GOM. These regions represent a gradient of changing species composition starting at the mouth of the Mississippi

Table 1. Classification of species present in at least 10% of all summer or fall trawls in the northwestern Gulf of Mexico. (–) Species not present in ≥10% of trawls in that season

CLASS Order	Family	Scientific name	Common name	% trawls present Summer	Fall
OSTEICHTHYES					
Anguilliformes	Muraenesocidae	*Hoplunnis macrurus*	Freckled pike-conger	11	–
Aulopiformes	Synodontidae	*Saurida brasiliensis*	Brazilian lizardfish	52	28
		Synodus foetens	Inshore lizardfish	72	79
		Synodus poeyi	Offshore lizardfish	16	11
Batrachoidiformes	Batrachoididae	*Porichthys plectrodon*	Atlantic midshipman	33	30
Clupeiformes	Clupeidae	*Etrumeus teres*	Round herring	12	–
		Harengula jaguana	Scaled herring	20	28
		Opisthonema oglinum	Atlantic thread herring	–	20
	Engraulidae	*Anchoa hepsetus*	Broad-striped anchovy	27	18
Lophiiformes	Ogcocephalidae	*Halieutichthys aculeatus*	Pancake batfish	28	32
Ophidiiformes	Ophidiidae	*Lepophidium brevibarbe*	Shortbread cusk eel	32	28
Perciformes	Carangidae	*Caranx crysos*	Blue runner	–	18
		Chloroscombrus chrysurus	Atlantic bumper	37	57
		Selene setapinnis	Atlantic moonfish	24	21
		Trachurus lathami	Rough scad	45	28
	Ephippidae	*Chaetodipterus faber*	Atlantic spadefish	–	36
	Gerreidae	*Eucinostomus gula*	Jenny mojarra	12	34
	Gobiidae	*Bollmannia communis*	Ragged goby	16	10
	Haemulidae	*Orthopristis chrysopterus*	Pigfish	34	11
	Lutjanidae	*Lutjanus campechanus*	Northern red snapper	43	79
		Lutjanus synagris	Lane snapper	17	40
		Pristipomoides aquilonaris	Wenchman	31	–
	Mullidae	*Upeneus parvus*	Dwarf goatfish	51	32
	Sciaenidae	*Cynoscion arenarius*	Sand seatrout	33	52
		Cynoscion nothus	Silver seatrout	26	57
		Larimus fasciatus	Banded drum	–	23
		Leiostomus xanthurus	Spot croaker	21	63
		Menticirrhus americanus	Southern kingcroaker	–	10
		Micropogonias undulatus	Atlantic croaker	42	95
	Scorpaenidae	*Scorpaena calcarata*	Smoothhead scorpionfish	10	20
	Serranidae	*Centropristis philadelphicus*	Rock sea bass	65	61
		Diplectrum bivittatum	Dwarf sand perch	55	59
		Serranus atrobranchus	Blackear bass	34	26
	Sparidae	*Lagodon rhomboides*	Pinfish	–	52
		Stenotomus caprinus	Longspine porgy	86	75
	Sphyraenidae	*Sphyraena guachancho*	Guachanche barracuda	–	10
	Stromateidae	*Peprilus alepidotus*	American harvestfish	–	17
		Peprilus burti	Gulf butterfish	62	53
	Trichiuridae	*Trichiurus lepturus*	Atlantic cutlassfish	31	33
Pleuronectiformes	Archiridae	*Gymnachirus texae*	Gulf of Mexico fringed sole	–	12
	Bothidae	*Ancylopsetta quadrocellata*	Ocellated flounder species	10	15
		Cyclopsetta chittendeni	Mexican flounder	27	42
		Engyophrys senta	Spiny flounder	12	–
		Syacium gunteri	Shoal flounder	50	63
		Syacium papillosum	Dusky flounder	10	–
	Cynoglossidae	*Symphurus plagiusa*	Blackcheek tonguefish	20	13
	Paralichthyidae	*Citharichthys spilopterus*	Bay whiff	15	22
		Etropus crossotus	Fringed flounder	30	24
Scorpaeniformes	Triglidae	*Prionotus longispinosus*	Bigeye searobin	47	56
		Prionotus paralatus	Mexican searobin	25	–
		Prionotus rubio	Blackwing searobin	15	16
		Prionotus stearnsi	Shortwing searobin	28	–
Siluriformes	Ariidae	*Arius felis*	Hardhead catfish	–	22

(continued on next page)

Table 1 (continued)

CLASS Order	Family	Scientific name	Common name	% trawls present Summer	Fall
Tetraodontiformes	Balistidae	*Balistes capriscus*	Gray triggerfish	13	38
	Monacanthidae	*Monacanthus hispidus*	Planehead filefish	20	–
	Tetraodontidae	*Lagocephalus laevigatus*	Smooth puffer	29	26
		Sphoeroides parvus	Least puffer	36	31
ANTHOZOA					
Pennatulacea	Renillidae	*Renilla mulleri*	Sea pansy	11	–
ASTEROIDEA					
Paxillosida	Astropectinidae	*Astropecten duplicatus*	Two-spined star fish	17	20
BIVALVIA					
Ostreoida	Pectinidae	*Amusium papyraceum*	Paper scallop	14	10
CEPHALOPODA					
Teuthida	Loliginidae	*Loligo pealeii*	Longfin inshore squid	38	24
		Loligo pleii	Arrow squid	40	28
		Lolliguncula brevis	Atlantic brief squid	27	20
MALACOSTRACA					
Decapoda	Calappidae	*Calappa sulcata*	Yellow box crab	21	20
	Penaeidae	*Penaeus aztecus*	Brown shrimp	88	91
		Penaeus duorarum	Northern pink shrimp	23	21
		Penaeus setiferus	Northern white shrimp	16	31
		Trachypenaeus similis	Roughback shrimp	37	33
	Portunidae	*Callinectes sapidus*	Blue crab	23	12
		Callinectes similis	Lesser blue crab	80	78
		Portunus gibbesii	Iridescent swimming crab	44	55
		Portunus spinicarpus	Longspine swimming crab	21	10
		Portunus spinimanus	Blotched swimming crab	21	20
	Sicyoniidae	*Sicyonia brevirostris*	Brown rock shrimp	36	25
		Sicyonia dorsalis	Lesser rock shrimp	44	24
Stomatopoda	Squillidae	*Squilla chydaea*	Mantis shrimp	24	18
		Squilla empusa	Mantis shrimp	48	45

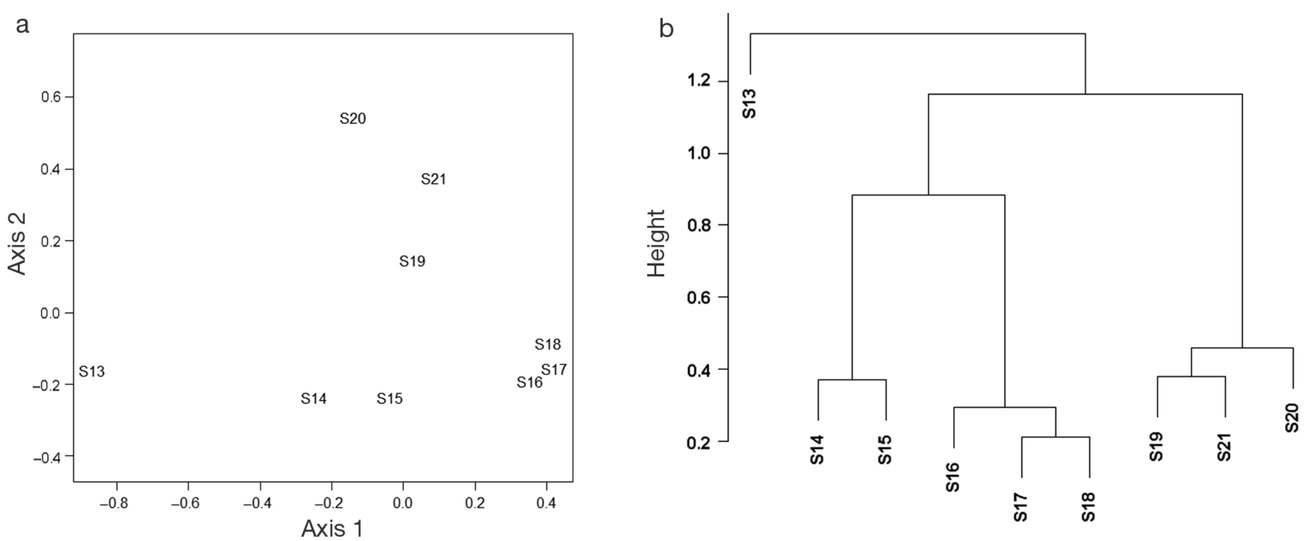


Fig. 2. (a) Nonmetric multidimensional scaling and (b) cluster analysis results for the summer groundfish trawl survey in the northwestern Gulf of Mexico. Data by year for each shrimp statistical zone were pooled to determine overall community structure among the zones. In the dendrogram (b), height measures the similarity of species composition within a branch. Smaller values indicate greater similarity

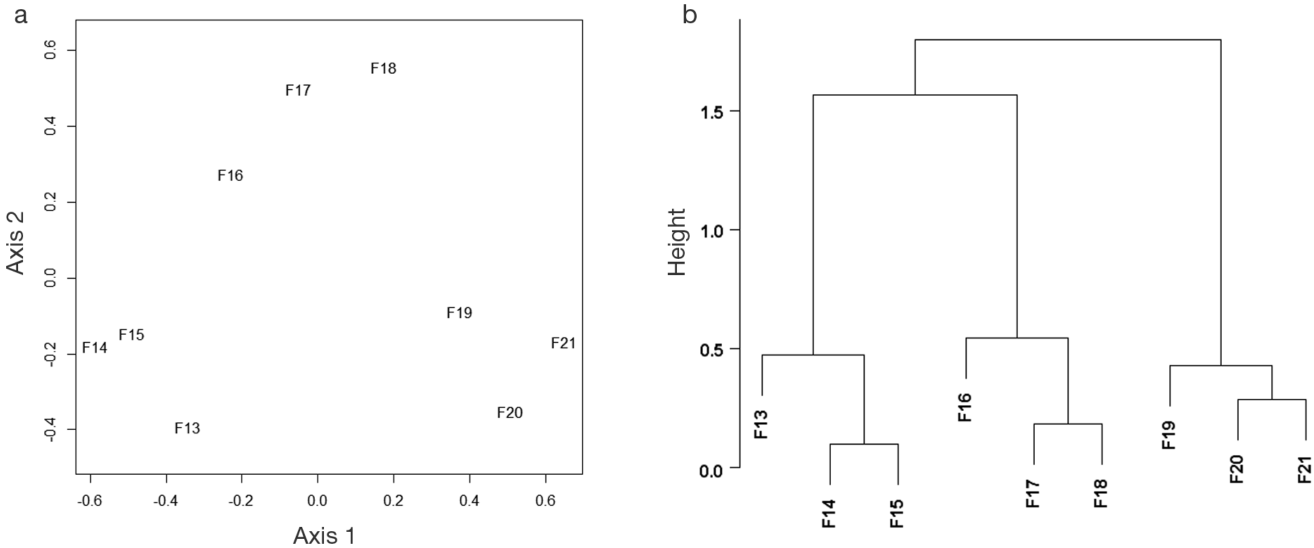


Fig. 3. (a) Nonmetric multidimensional scaling and (b) cluster analysis results for the fall groundfish trawl survey in the northwestern Gulf of Mexico. Other details as in Fig. 2

River and moving westward. The 4 DFCs will be denoted as Zone 13 DFC, East DFC (representing Zones 14 and 15), Mid DFC (representing Zones 16 to 18), and West DFC (representing Zones 19 to 21).

Fall groundfish survey

Two axes (stress = 0.004) in the NMDS explained the fall survey data. The first axis represents a longitudinal shift in community assemblages from the Mississippi River to the Texas/Mexico border (Fig. 3a). Zone 13 was the only zone that did not fall in numerical order with the other zones, but still grouped with Zones 14 and 15. The shrimp statistical zones formed 3 distinct groups, Zones 13 to 15, Zones 16 to 18, and Zones 19 to 21.

The cluster analysis from the fall survey revealed the same pattern as the NMDS with 3 regional clusters, and quantifies the differences among DFCs (Fig. 3b). Zones 13, 16, and 19 had a higher height value than other shrimp statistical zones within their respective branches of the dendrogram, which suggests these could be transition zones among fish assemblages.

Community structure and indicator species

No more than 11 species contributed to the 90% cumulative difference in dissimilarity between any 2 regions in either season, with fewer species dominating the dissimilarity in the fall survey (Tables 2 & 3). In the summer survey, Zone 13 was only compared to the collective of all other DFCs, as it formed a distinct branch in the cluster analysis (Fig. 2). All species contributing to the cumulative 90% dissimilarities also had indicator values of ≥25 for 1 of the DFCs in the fall survey (Table 4). In the summer survey, Gulf butterfish, blackear bass, and arrow squid (scientific names provided in Table 1) contributed to dissimilarity among DFCs, but were not identified as indicator species.

Longspine porgy and Atlantic croaker, 2 of the more commonly abundant species in both surveys, accounted for a total of ~91% of the dissimilarity between the East and Mid DFCs in the fall and ~28% in the summer (Table 2). Both species are indicators in both the summer and fall surveys, with Atlantic croaker identifying with the East DFC and longspine porgy with the Mid DFC.

Four of the species contributing to the difference between Zone 13 and all other DFCs were also indicator species for Zone 13 in the summer survey: roughback shrimp, bigeye searobin, a mantis shrimp (*Squilla empusa*), and Atlantic cutlassfish. Of these, roughback shrimp contributed ~22% to the dissimilarity, with the other 3 contributing an additional ~16%.

In order to compare indicator species between the summer and fall surveys, Zone 13 was separated from the East DFC in the fall indicator analysis. All of the DFCs shared at least 1 indicator species in common between the summer and fall surveys (Table 4). Species with relatively high indicator values (≥50) include the Atlantic bumper (Fall West DFC), At-

Table 2. Species accounting for 90% of the dissimilarity between any 2 demersal fish communities (DFCs) in the summer surveys of the northwestern Gulf of Mexico. The maximum group is from the indicator species analysis and is the region where the species is most prevalent. Scientific names of species are given in Table 1

Species	$\bar{\delta}_i$	$SD(\bar{\delta}_i)$	$\bar{\delta}_i / SD(\bar{\delta}_i)$	$\Sigma\bar{\delta}_i\%$
East vs. Mid DFCs				
Roughback shrimp	0.16	0.016	10.14	26.33
Longspine porgy	0.11	0.067	1.71	45.10
Bigeye searobin	0.08	0.056	1.35	57.42
Atlantic croaker	0.06	0.058	1.03	67.33
Brown rock shrimp	0.03	0.024	1.38	72.80
Gulf butterfish	0.03	0.031	0.97	77.68
Mantis shrimp (*Squilla empusa*)	0.03	0.007	3.89	82.31
Brown shrimp	0.02	0.013	1.29	85.06
Lesser blue crab	0.02	0.007	2.30	87.57
Blackear bass	0.01	0.005	1.47	88.97
Iridescent swimming crab	0.01	0.005	1.76	90.30
East vs. West DFCs				
Brown shrimp	0.24	0.109	2.23	35.96
Bigeye searobin	0.08	0.062	1.24	47.45
Atlantic croaker	0.08	0.060	1.27	58.76
Longspine porgy	0.07	0.089	0.74	68.53
Roughback shrimp	0.05	0.045	1.18	76.44
Arrow squid	0.04	0.012	3.24	82.08
Mantis shrimp (*S. empusa*)	0.02	0.010	2.21	85.15
Gulf butterfish	0.02	0.023	0.80	87.77
Lesser blue crab	0.02	0.020	0.81	90.17
Mid vs. West DFCs				
Brown shrimp	0.32	0.121	2.61	43.21
Longspine porgy	0.22	0.129	1.67	72.68
Lesser blue crab	0.04	0.029	1.50	78.73
Roughback shrimp	0.04	0.045	0.86	84.11
Brown rock shrimp	0.03	0.023	1.33	88.42
Arrow squid	0.02	0.010	2.05	91.19
Zone 13 vs. all other DFCs				
Longspine porgy	0.44	0.200	2.22	41.48
Roughback shrimp	0.23	0.089	2.61	63.23
Brown shrimp	0.08	0.127	0.66	71.06
Bigeye searobin	0.08	0.038	2.18	78.75
Mantis shrimp (*S. empusa*)	0.07	0.021	3.26	85.26
Atlantic cutlassfish	0.03	0.004	6.06	87.71
Arrow squid	0.02	0.019	1.02	89.45
Atlantic croaker	0.01	0.028	0.50	90.81

lantic croaker (Fall East DFC), Atlantic cutlassfish (Summer and Fall Zone 13 DFC), brown shrimp (Summer West DFC), dwarf goatfish (Summer West DFC), longspine porgy (Fall Mid DFC), northern white shrimp (Fall Zone 13 DFC; Table 4).

Four species were identified as indicator species within different DFCs between the summer and fall surveys: bigeye searobin, lesser blue crab, iridescent swimming crab, and red snapper. Except for the lesser blue crab, each species appeared as an indicator species in an adjacent DFC between the fall and summer surveys. The lesser blue crab had a significant indicator value for the West DFC in the summer survey and the Zone 13 DFC in the fall survey.

Table 3. Species accounting for 90% of the dissimilarity between any 2 demersal fish communities (DFCs) in the fall surveys of the northwestern Gulf of Mexico. Other details as in Table 2

Species	$\bar{\delta}_i$	$SD(\bar{\delta}_i)$	$\bar{\delta}_i / SD(\bar{\delta}_i)$	$\Sigma\bar{\delta}_i\%$
East vs. Mid DFCs				
Longspine porgy	0.58	0.070	8.21	61.54
Atlantic croaker	0.28	0.160	1.73	91.13
East vs. West DFCs				
Atlantic croaker	0.44	0.096	4.56	39.88
Atlantic bumper	0.33	0.048	6.92	70.15
Brown shrimp	0.08	0.044	1.80	77.32
Shoal flounder	0.04	0.015	2.86	81.27
Roughback shrimp	0.04	0.038	0.98	84.61
Longspine porgy	0.04	0.043	0.83	87.89
Dwarf sand perch	0.03	0.012	2.78	90.80
Mid vs. West DFCs				
Longspine porgy	0.35	0.151	2.29	34.70
Atlantic bumper	0.29	0.066	4.40	63.95
Atlantic croaker	0.08	0.103	0.78	72.00
Brown shrimp	0.07	0.035	2.10	79.47
Roughback shrimp	0.05	0.039	1.37	84.84
Shoal flounder	0.04	0.014	3.05	89.03
Dwarf sand perch	0.03	0.016	1.61	91.59

DISCUSSION

The demersal fish community associated with the shrimp trawl fishery in the northwestern GOM-LME exhibits spatial and seasonal structure. Four distinct DFCs were identified from the summer SEAMAP data, and 3 DFCs were identified from the fall SEAMAP data. The same shrimp statistical zones comprised the West and Mid DFCs in both fall and summer surveys. Zone 13, the shrimp statistical zone nearest the Mississippi River, was similar to Zones 14 and 15 in the fall survey, but was dissimilar to all other zones in the summer survey. The overall similarity in spatial segregation of the shrimp statistical zones between surveys, even though dominant species differ, provides strong evidence of a changing fish community along the continental shelf.

The results from this study reflect the community associated with the shrimp trawl fishery from a fisheries-independent study, and may differ from the community of bycatch in the shrimp trawl fleet. The shrimp trawl fishery participated in a voluntary observer program from 1992 to 2006 and has been subject to a mandatory observer program only since

Table 4. Species with statistically significant indicator values (≥25) for each demersal fish community (DFC). Indicator values for species appearing in both surveys are denoted as summer (S) and fall (F). Scientific names of species are given in Table 1

DFC	Summer survey	Fall survey	Both surveys
Zone 13	Bigeye searobin (37) Ragged goby (30) Rock sea bass (29)	Northern white shrimp (64) Lesser blue crab (42) Iridescent swimming crab (37) Atlantic midshipman (35) Bay whiff (31)	Atlantic cutlassfish (S: 51; F: 52) Mantis shrimp (*Squilla empusa*) (S: 41; F: 46) Sand seatrout (S: 41; F: 42) Atlantic brief squid (S: 40; F: 34) Roughback shrimp (S: 26; F: 32)
East	Iridescent swimming crab (37) Fringed flounder (27)	Bigeye searobin (34) Spot croaker (30)	Atlantic croaker (S: 25; F: 53)
Mid	Red snapper (31)	Gray triggerfish (29)	Brown rock shrimp (S: 41; F: 39) Longspine porgy (S: 35; F: 50) Inshore lizardfish (S: 27; F: 33) Lane snapper (S: 26; F: 40)
West	Dwarf goatfish (53) Lesser blue crab (32) Shortwing searobin (25)	Atlantic bumper (62) Dwarf sand perch (47) Red snapper (33) Shoal flounder (33) Two-spined star fish (31) Scaled herring (25)	Brown shrimp (S 58; F: 27) Lesser rock shrimp (S: 28; F: 29) Brazilian lizardfish (S: 25; F: 34)

2007 (GMFMC 2005). Turtle excluder devices have been required on all shrimp trawls since 1992 (US Government 1992), and bycatch reduction devices have been required in the western GOM since 1998 (US Government 1998), although neither device is used during the SEAMAP survey. The SEAMAP survey follows a stratified random sampling design, whereas the shrimp trawl fleet actively targets specific areas of known shrimp abundance. For instance, Atlantic bumper was identified as an indicator species for the fall survey West DFC and contributed strongly to the dissimilarity between DFCs, but is not listed as a documented species in the most recent shrimp trawl bycatch report (Scott-Denton et al. 2012). The same is true for bigeye searobin, which was identified as an indicator species in both surveys, and was identified as a good discriminating species in the summer survey. Nevertheless, we expect that species caught as bycatch in the shrimp fishery would be effectively monitored by the SEAMAP survey, and overall, the SEAMAP is a useful tool to understand spatial patterns of species composition and trends in the life stages sampled.

Two factors contributing to the change in dominant species communities from summer to fall are the environmental conditions in the GOM as well as species' life history characteristics and timing of spawning. In particular, Zone 13 and the East DFC are subject to unique environmental factors and are heavily influenced by their proximity to the mouth of the Mississippi and Atchafalaya Rivers (Turner & Rabalais 1994, Rabalais et al. 1996, Alexander et al. 2000). Simulations have shown that the physical drivers create a number of different circulation patterns in the Louisiana Bight, including seasonal clockwise and anticyclonic gyres (Wang & Justi 2009).

The summer SEAMAP groundfish trawl survey is conducted from mid-June to the end of July, which is the peak timing for the annual hypoxia event in the northwestern GOM (Rabalais et al. 1994, 2002b). Hypoxia is defined as bottom-water oxygen levels ≤2 mg l^{-1} and occurs on the Louisiana/Texas continental shelf from May to September. Hypoxic waters were detected in all DFCs at least once. Although hypoxia off the coast of Louisiana typically occurs at depths of 5 to 30 m (Rabalais et al. 2002a), hypoxic waters were detected in 39% of summer trawls in Zone 13 and 26% of summer trawls in the East DFC (for which environmental data were available). For tows with environmental data, the average oxygen level was ≤2 mg l^{-1} in the Zone 13 summer stations in 7 survey years (1991, 1992, 1997, 2000, 2002, 2007, 2008) as well in both the summer and fall surveys in the East DFC in 1997; for yearly averages of dissolved oxygen (DO) by DFC see Fig. S2 in the Supplement. However, no significant trends were detected in community assemblages when DO was used as a covariate in the multivariate analyses. Species such as Atlantic bumper and sand seatrout exhibit markedly low DO thresholds (between 1.06 and 1.16 mg l^{-1}), which may explain the lack of significant results in this study (Craig 2012). Craig (2012) also found that Atlantic croaker and Atlantic cutlassfish (both species associating with Zone 13) have DO thresholds below 2.0 mg l^{-1}. Trends may also not have been detected because DO is only measured at one point during the SEAMAP trawl, and does not necessarily reflect the environment over an entire tow. Furthermore, trawls at 10 to 30 fm (18.3–54.9 m) are at the offshore edges of the hypoxic areas, where the bottom hypoxic layer is thin compared to inshore areas (Obenour et al. 2013). Mobile fish are also able to suspend above and behaviorally avoid the hypoxic waters (Wannamaker & Rice 2000, Bell & Eggleston 2005, Hazen et al. 2009, Craig 2012), but may still be captured in the trawl survey. Direct comparisons between the summer and fall surveys from Zone 13 incorporating additional environmental data (e.g. Mississippi River outflow, nutrient loading, upwelling/downwelling events) could explain some of the species trends observed.

The life history characteristics and time of spawning of the bycatch species also influence species susceptibility to the trawl. Northern red snapper and Atlantic croaker are 2 examples of species predominately caught as bycatch as age-0 and age-1 fish, but exhibit different life history patterns (Diamond et al. 2000, Wilson & Nieland 2001). Young-of-the-year (age-0) red snapper settle onto trawlable, low-relief habitat in the fall months, whereas age-1 fish move to more complex habitat and deeper waters in the fall (Patterson 2007). Atlantic croaker migrate to offshore waters in the late juvenile stage, which is reflected in the increased median length of fish from the summer to fall surveys (Diamond et al. 1999). The distribution of lengths revealed the same pattern for 6 other species we examined, where the summer catch was a mix of juvenile and adult fish and the fall catch was dominated by mature individuals (bigeye searobin, Gulf butterfish, inshore lizardfish, longspine porgy, sand seatrout, and silver seatrout; see Fig. S3 for length distributions of select species and Table S3 for life history information). Examining length frequencies across a broader range of depths confirms that the average size of these 6 species (except inshore lizardfish) was larger at depths greater than 30 fm (54.9 m), providing more evidence for the ontogenetic shifts occurring in these species. The ontogenetic shifts in habitat use and seasonal migrations of species add a level of complexity to disentangling patterns in species biomass from the natural variability in juvenile population sizes. This also confounds the ability to assess population level changes and the effect of the shrimp trawl bycatch mortality on population trajectories simply from the survey index. A more synoptic picture that included surveys covering the entire species spatial range as well as information about all removals (catch, bycatch) would be needed to understand the population dynamics of the various species.

Basic life history information, including length-at-maturity, time of spawning, maximum age, and maximum size, is lacking for the majority of bycatch species. Fewer than 5% of the species encountered in the survey are considered economically or ecologically important, as defined by Scott-Denton et al. (2012). Eight of the 32 indicator species identified in this study are harvested in the GOM. Formal stock assessments have only been conducted for red snapper, lane snapper, and gray triggerfish, in addition to the shrimp species. Other economically and ecologically important species identified as indicators were Atlantic croaker, longspine porgy, and sand seatrout.

As we move towards EBFM, additional research is needed to understand the dynamics of species and communities that are not currently well studied. The SEAMAP groundfish survey is the only long-term fisheries-independent survey available in the GOM-LME. In addition to fisheries stock assessments, the SEAMAP survey data are used to inform ecosystem models for the GOM (Walters et al. 2008, Drexler & Ainsworth 2013, Grüss et al. 2014). The importance of defining the spatial community dynamics of a system has become apparent as we move towards EBFM (Mangel & Levin 2005). The regional and seasonal demersal fish communities identified in this study can be used to monitor the GOM-LME, aid in marine spatial planning, and be incorporated in ecological models. Studies on both the west coast (Jay 1996, Williams & Ralston 2002, Tolimieri & Levin 2006) and east coast (Shertzer & Williams 2008, Auster & Link 2009, Shertzer et al. 2009) of the USA have examined the spatial and temporal variability in fish assemblages. Depending on the orientation of the study area, these studies found either latitudinal or longitudinal (Aleutian Islands; Logerwell & Aydin 2005) gradients for species assemblages. On Georges Bank, species compositions have shifted, but trophic guilds have remained relatively consistent through time (Garrison & Link 2000). In the Chesapeake Bay, which is driven by the Susquehanna River outflow (much like Zone 13 in our study), species assemblages have a spatial and seasonal component but have been resilient to environmental perturbations (Jung & Houde 2003). These studies all contribute to the baseline understanding of species assemblages and their contribution to EBFM. In the GOM, the assemblages identified can be used as a baseline to monitor future changes resulting from shrimp fishery effort reduction or any other physical and environmental drivers.

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