Spatial structure and temporal patterns in a large marine ecosystem: Exploited reef fishes of the southeast United States

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ABSTRACT

The continental shelf of the southeast United States forms one of North America's Large Marine Ecosystems (LME). Despite increased attention on ecosystem management, fisheries within this LME continue to be managed on a single stock basis, in part because interactions among species and environmental effects are poorly understood. Using fishery data from two different sources (recreational and commercial), we applied multivariate statistical techniques to elucidate spatial and temporal dynamics of reef fish assemblages. Spatial analyses of species composition revealed a zoogeographic boundary near Cape Canaveral, Florida, suggesting that management of reef fishes could be applied to the northern and southern regions with discrimination. Temporal analyses revealed, in general, gradual changes in species composition of landings, but with primary shifts in 1992 and again in 1999–2000. Chronological patterns, evident in these two independent data sets, bear the signature of one or more trending factors, which in this LME could include increased exploitation, spread of invasive species, habitat degradation, or climate change.

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1. Introduction

The desire to manage coastal ecosystems on meaningful geographic scales has led to the concept of large marine ecosystems, with fifty LMEs recognized worldwide (Sherman and Duda, 1999). Fundamental shifts in biomass, biodiversity, and productivity have been reported in LMEs around the globe, resulting from excessive fishing mortality, environmental perturbations, and coastal pollution (Sherman, 1990). Identifying these shifts within LMEs may benefit ecosystem approaches to management, and is essential for developing a synthesized understanding of pattern and process in global ecologies (Fox, 2007).

The Southeast U.S. Continental Shelf LME (SUSLME) spans Atlantic waters from the Straits of Florida to Cape Hatteras, North Carolina (Yoder, 1991). Temperate in climate, the SUSLME is considered highly productive as a result of inputs from Gulf Stream upwelling (Yoder, 1991) and from the Albemarle–Pamlico Sound, the second largest estuary in the U.S. (Aquarone, 2008). Because of its high productivity, the SUSLME supports active commercial and recreational fisheries. Much of the fishing effort targets reef fish species, such as snappers and groupers (Coleman et al., 1999).

Reef fishes within the SUSLME have previously been classified into assemblages (Chester et al., 1984; Shertzer and Williams, 2008). However, species groupings are weakly structured, as observed in other North American LMEs (Mahon et al., 1998). The lack of coherent structure in fish assemblages implies that functional relationships among species are not static across space and time. The primary goal of this study is to better understand the dynamics of reef fish assemblages in the SUSLME.

Using fishery data, we applied multivariate statistical analyses to infer both spatial and temporal patterns in reef fish assemblages. We show that species composition (1) is structured spatially within the SUSLME and (2) has varied over time, with large-scale shifts in the 1990s. We then examined through correlation analysis which species were principally responsible for the inferred spatial and temporal patterns.

2. Materials and methods

We analyzed two fishery data sets, one from the recreational sector and one from the commercial sector. The data sets and statistical techniques are fully described elsewhere (Shertzer and Williams, 2008). A synopsis follows, highlighting details specific to this study. Analyses were programmed in R (R Development Core Team, 2008).

2.1. Data sources

The recreational sector was represented by logbook data from headboat operators during 1980–2007. The commercial sector was represented by logbook data from snapper-grouper anglers using

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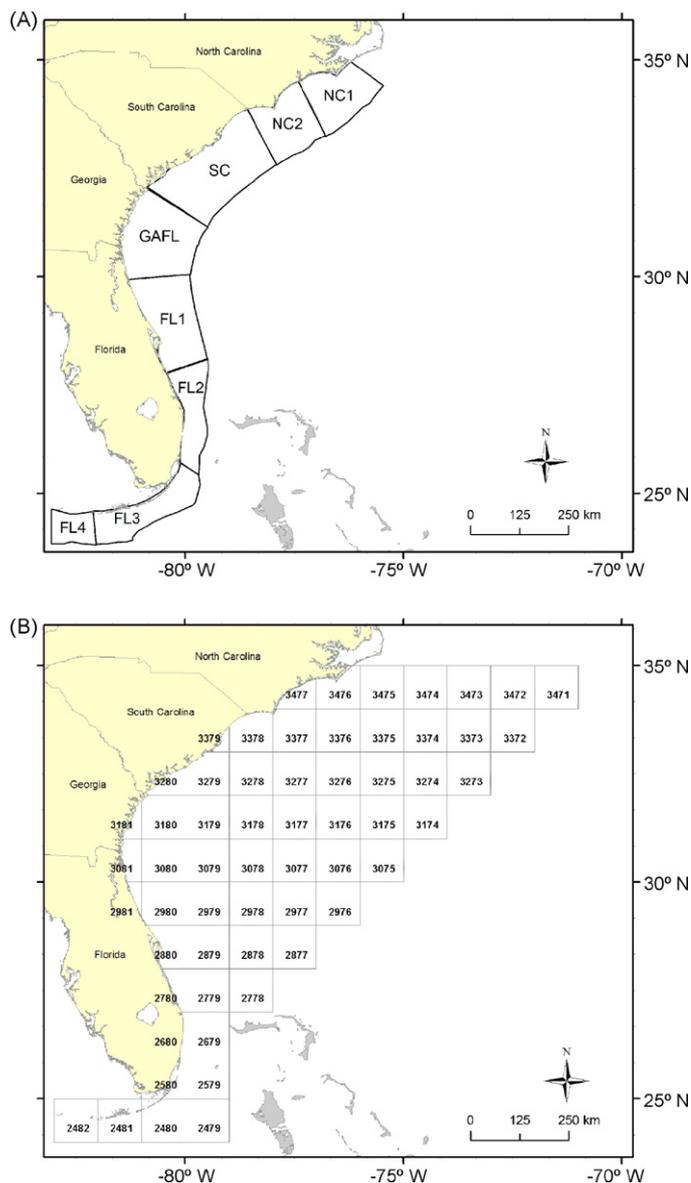E-mail address: Kyle.Shertzer@noaa.gov (K.W. Shertzer).

(A)

(B)

Fig. 1. Geographic areas of the (A) recreational (headboat) data and (B) commercial data. In (B), each area is assigned a four digit number, in which the first two specify degrees latitude, and the second two degrees longitude; for this study, commercial areas were by degrees latitude only.

Table 1
Species used in analyses of recreational data (Recr), commercial data (Comm), or both data sets (Both).

Scientific name	Common name	Data set
Balistes capriscus	Gray triggerfish	Recr
Calamus bajonado	Jolthead porgy	Recr
Calamus leucosteus	Whitebone porgy	Recr
Calamus nodosus	Knobbed porgy	Recr
Caranx crysos	Blue runner	Both
Centropristis striatus	Black sea bass	Both
Epinephelus morio	Red grouper	Both
Epinephelus niveatus	Snowy grouper	Comm
Haemulon aurolineatum	Tomtate	Recr
Haemulon plumieri	White grunt	Both
Haemulon sciurus	Bluestriped grunt	Recr
Lutjanus analis	Mutton snapper	Both
Lutjanus campechanus	Red snapper	Recr
Lutjanus griseus	Gray snapper	Both
Lutjanus synagris	Lane snapper	Recr
Mycteroperca bonaci	Black grouper	Comm
Mycteroperca microlepis	Gag	Both
Mycteroperca phenax	Scamp	Recr
Ocyurus chrysurus	Yellowtail snapper	Both
Rhomboplites aurorubens	Vermilion snapper	Both
Seriola dumerili	Greater amberjack	Both

Species were included if present in at least 5% of all trip records.

handline gear during 1993–2007. The headboat data contained 281,887 fishing trip records, and the commercial data contained 147,731 trip records. Both data sets covered the full geographic range of the SUSLME, although the two differed in how anglers reported area fished (Fig. 1A and B). Areas reported in the commercial data are defined by degrees latitude and longitude; to avoid small sample sizes from some locations, we used latitude only. In both data sets, anglers reported landings of the 73 fish species that are federally managed under the Snapper Grouper Fishery Management Plan (SAFMC, 1983). Rare species, defined as those occurring in fewer than 5% of trip records, were excluded from analysis because they can bias the inference of patterns (Koch, 1987; Mueter and Norcross, 2000). Also excluded were red porgy, *Pagrus pagrus*, because strict harvest regulations since 1999 have substantially affected its landings, and bank sea bass, *Centropristis ocyurus*, because it was not fully reported early in the time series (Parker and Dixon, 1998). With these criteria, the analyses used 19 species from recreational data and 12 species from commercial data (Table 1).

Prior to spatial and temporal analyses, the data were prepared in a sequential four-step process. First, each data set was arranged into a matrix, in which rows represented unique combinations of year by area, and columns represented the number of trips that caught each species. Second, the rows were standardized to sum to one; this step put all year-areas (rows) on the same scale, removing possible confounding effects of fishing effort shifting among geographic areas over time. (The results of step two are invariant to whether the original matrix of step one was expressed in number or proportion of trips.) Third, the resulting rows were summed either across years for the spatial analysis or across areas for the temporal analysis, and then re-standardized. Thus, for the spatial analysis, rows of data matrix (**X**) represented geographic area fished, columns represented species caught, and elements (x_{ik}) quantified the standardized proportion of trips that caught species k in area i. For the temporal analysis, the data were arranged similarly, but matrix rows represented years. Fourth, we applied the arcsine square-root transformation, $x'_{ik} = (2/\pi) \arcsin(\sqrt{x_{ik}})$, as commonly considered appropriate for proportion data (McCune and Grace, 2002).

2.2. Multivariate statistical analyses

2.2.1. Spatial patterns

Based on composition of species, we computed dissimilarities between geographic areas using the Bray-Curtis measure of distance (McCune and Grace, 2002), a measure favored in ecological studies (e.g., Field et al., 1982; Gomes et al., 2001; Williams and Ralston, 2002). The dissimilarity (δ_{ij}) between sampling areas i and j is computed as the sum:

$$\delta_{ij} = \sum_{k=1}^{S} \delta_{ij}(k) \qquad (1)$$

where S is the number of species, and $\delta_{ij}(k)$ is the contribution of species k:

$$\delta_{ij}(k) = \frac{|x'_{ik} - x'_{jk}|}{\sum_{k=1}^{S}(x'_{ik} + x'_{jk})} \qquad (2)$$

Dissimilarities between sampling areas were then analyzed with two multivariate techniques—nonmetric multidimensional scaling (NMDS) and agglomerative hierarchical cluster analysis. For NMDS

(Kruskal, 1964), we extracted the first two dimensions of ordination space. Although the axes of NMDS are synthetic, relationships between them and explanatory variables can sometimes be identified or postulated; we examined dimension one for correlation with latitude using the Pearson correlation coefficient. For hierarchical analysis, we applied the linkage method of McQuitty (McCune and Grace, 2002) to quantify the strength of associations among geographic areas.

After inferring sampling groups (i.e., distinct zoogeographic areas), we examined which species were principally responsible for the delineations, by calculating the average contribution of each species to the overall average dissimilarity (Clarke, 1993). The overall average dissimilarity ($\bar{\delta}$) between two sampling groups was computed as the arithmetic mean of δ_{ij} from all pairs (i, j), with i in one group of zoogeographic areas and j in the other. Similarly, each species' average contribution ($\bar{\delta}_k$) to $\bar{\delta}$ was computed as the arithmetic mean of $\delta_{ij}(k)$ from all pairs (i, j). The standard deviation of each species' contribution [$SD(\delta_k)$] was used to measure consistency. As described by Clarke (1993), a good discriminating species contributes substantially to the dissimilarity (i.e., large $\bar{\delta}_k$) and does so consistently [i.e., small $SD(\delta_k)$]. By examining which species drive the inference of sampling groups, our intent was not to test hypotheses, but rather to generate them.

2.2.2. Temporal patterns

Temporal analysis focused on similarities in species composition between and among years. Otherwise, methods to quantify temporal patterns were the same as those for spatial patterns.

3. Results

3.1. Spatial patterns

Nonmetric multidimensional scaling (NMDS) revealed homogeneity of species composition within some broad geographic regions. In recreational data, areas off the Carolinas showed similarity, areas off northern Florida and Georgia showed similarity, and areas off southern Florida were each unique (Fig. 2A). Similar distinctions occurred in the commercial data, but with tighter clustering of areas off southern Florida (Fig. 2B).

Dimension one of NMDS (Fig. 2A and B) was significantly and positively correlated with the latitudinal gradient, according to one-tailed tests of Pearson $\rho \leq 0$ (recreational $P=0.001$; commercial $P=0.028$). Thus, we computed Pearson correlation coefficients to describe linear relationships between dimension one and species' relative prevalence in the data (columns of data matrix **X**, after arcsine square-root transformation). This analysis was descriptive only, and following the advice of McCune and Grace (2002), we did not calculate P-values to test if correlation coefficients were significantly different from zero. In general across data sets, species most strongly associated with northern areas were black sea bass, gag, and vermilion snapper, and species most strongly associated with southern areas were blue runner, gray snapper, mutton snapper, and yellowtail snapper (Table 2).

Cluster analysis quantified the degree of dissimilarity in species composition among areas (Fig. 3). In both data sets, primary branches of zoogeographic clusters separated near Cape Canaveral, Florida (28.39°N). The repeatability of this result, i.e., that it was common to the two different data sets, provides strong evidence that the composition of fish communities differs between northern regions (~Cape Hatteras, North Carolina to ~Cape Canaveral) and southern regions (~Cape Canaveral to ~Key West, Florida) of the SUSLME.

Species responsible for the primary branches of zoogeographic clusters (Fig. 3) were ranked by their average contributions toward
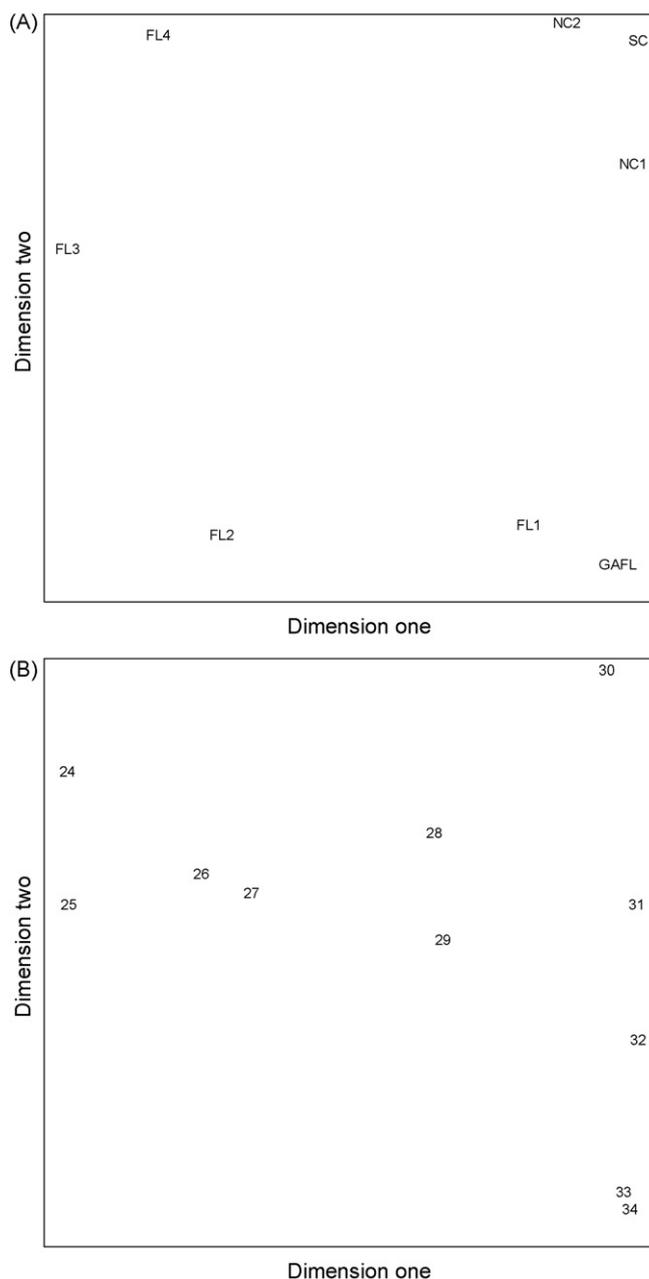

Fig. 2. Nonmetric multidimensional scaling of survey areas using (A) recreational or (B) commercial data. Areas near each other in ordination space are those with similar species composition. Recreational areas are mapped in Fig. 1A, and commercial areas (degrees latitude) in Fig. 1B.

the dissimilarity (Table 3). All species played some role in determining the dissimilarity, but several dominated. As one might expect, dominant species were those abundant in one region and rare in the other. The two top-ranked species were black sea bass (associated with the north) and yellowtail snapper (associated with the south), which together accounted for ~22% of the overall dissimilarity in recreational data and ~32% in commercial data.

3.2. Temporal patterns

Nonmetric multidimensional scaling revealed changes in species composition over time (Fig. 4). In both data sets, years were located in ordination space near contiguous years, without clear distinction between sampling groups. This structure indicates that

Table 2
Species from spatial analyses, ranked by correlation (ρ) with dimension one (latitude) of nonmetric multidimensional scaling.

Recreational		Commercial	
Species	ρ	Species	ρ
Black sea bass	0.962	Black sea bass	0.975
Whitebone porgy	0.928	Vermilion snapper	0.855
Tomtate	0.880	Gag	0.843
Vermilion snapper	0.854	Red grouper	0.432
Gag	0.823	White grunt	0.430
Red snapper	0.747	Greater amberjack	−0.002
Gray triggerfish	0.721	Black grouper	−0.278
Scamp	0.592	Snowy grouper	−0.610
Greater amberjack	0.454	Gray snapper	−0.746
White grunt	−0.199	Blue runner	−0.848
Knobbed porgy	−0.419	Mutton snapper	−0.932
Red grouper	−0.634	Yellowtail snapper	−0.982
Gray snapper	−0.703		
Lane snapper	−0.704		
Jolthead porgy	−0.790		
Blue runner	−0.899		
Mutton snapper	−0.951		
Bluestriped grunt	−0.972		
Yellowtail snapper	−0.976		

Positive correlations indicate species associated with more northern latitudes.

Table 3
Contributions of reef fishes toward the distinction of zoogeographic regions in recreational and commercial data sets.

Species	$\bar{x}_{north}$	$\bar{x}_{south}$	$\bar{\delta}_k$	SD(δ_k)	$\bar{\delta}_k$/SD(δ_k)	$\sum \bar{\delta}_k$%
Recreational data set						
Black sea bass	17.52	0.90	4.81	1.30	3.68	11.26
Yellowtail snapper	0.57	15.77	4.53	0.93	4.88	21.87
Mutton snapper	0.45	12.13	4.01	0.71	5.61	31.26
Blue runner	0.39	6.98	2.65	0.60	4.44	37.47
Lane snapper	2.21	6.75	2.44	1.22	2.01	43.20
Gray snapper	3.37	8.77	2.26	1.35	1.68	48.50
Red snapper	6.62	0.92	2.15	1.16	1.86	53.55
Tomtate	8.59	2.56	2.01	1.20	1.68	58.27
Whitebone porgy	5.30	0.78	2.00	0.78	2.56	62.96
Gag	9.05	2.40	1.93	0.83	2.31	67.48
Vermilion snapper	11.37	4.26	1.87	0.96	1.95	71.87
Scamp	5.75	2.61	1.76	1.07	1.64	75.99
Bluestriped grunt	0.16	2.77	1.70	0.59	2.90	79.98
White grunt	7.25	8.28	1.68	1.11	1.51	83.91
Knobbed porgy	2.78	5.43	1.55	1.03	1.51	87.54
Gray triggerfish	9.70	5.35	1.44	0.84	1.72	90.92
Red grouper	3.04	6.75	1.37	0.93	1.47	94.13
Greater amberjack	5.02	3.44	1.26	0.61	2.05	97.08
Jolthead porgy	0.87	3.16	1.25	0.75	1.66	100.00
Commercial data set						
Yellowtail snapper	1.08	30.24	8.35	3.14	2.66	17.71
Black sea bass	20.36	0.63	6.69	2.53	2.65	31.90
Blue runner	0.33	13.46	5.46	1.68	3.25	43.48
Gag	22.49	4.91	5.08	2.32	2.19	54.26
Vermilion snapper	17.26	2.43	4.60	2.44	1.88	64.01
Mutton snapper	1.06	12.47	4.48	1.22	3.68	73.51
Gray snapper	5.37	11.30	3.26	1.91	1.71	80.41
White grunt	6.84	2.56	2.4	1.52	1.58	85.51
Red grouper	9.01	3.70	1.88	1.34	1.40	89.50
Greater amberjack	11.06	8.81	1.77	1.37	1.29	93.25
Black grouper	3.67	5.64	1.76	1.19	1.48	96.98
Snowy grouper	1.48	3.86	1.42	0.85	1.68	100.00

Data are summarized by the average proportion of trips ($\bar{x}$, prior to transformation) that caught species in each region, north or south, with separation near Cape Canaveral, Florida. Species are ordered by their contribution ($\bar{\delta}_k$) to the average dissimilarity ($\bar{\delta}$) between the two zoogeographic regions, reflected in the cumulative contribution ($\sum \bar{\delta}_k$%) to $\bar{\delta}$. Consistency of contribution is quantified by the standard deviation (SD). Values in first four columns were multiplied by 100.
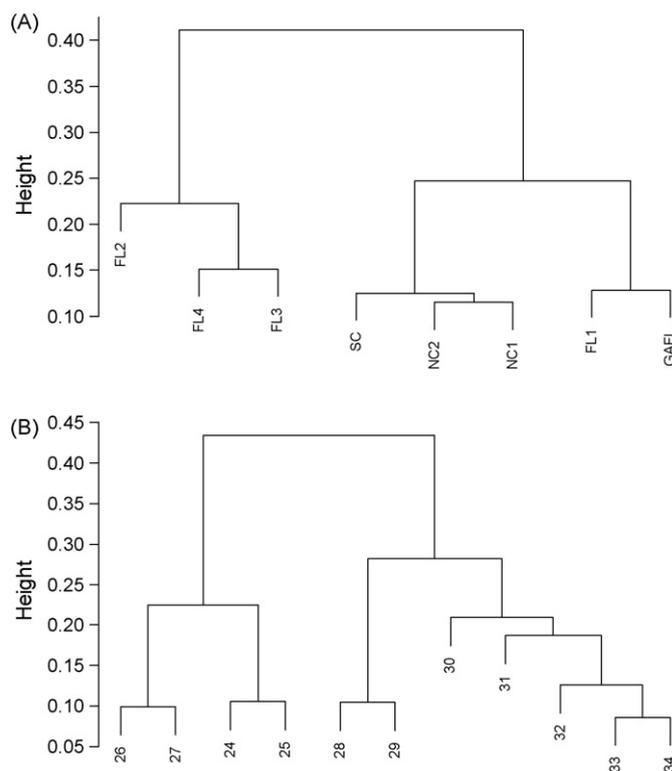

Fig. 3. Dendrograms from cluster analysis of survey areas using (A) recreational or (B) commercial data. Height measures similarity within a branch, where lower values indicate greater similarity. Recreational areas are mapped in Fig. 1A, and commercial areas (degrees latitude) in Fig. 1B.

changes in species composition occurred progressively and gradually.

Dimension one of NMDS (Fig. 4A and B) was significantly and positively correlated with chronology, according to one-tailed tests of Pearson $\rho \leq 0$ (recreational and commercial $P < 0.001$). Thus, a species' positive association with this dimension indicates increased prevalence in landings over time, and negative association indicates decreased prevalence (Table 4). Trends for some species differ between data sets, but the majority of trends agree.

Cluster analysis revealed two primary branches of years with similar species compositions. In recreational data, the primary separation occurred in 1992, and the latter branch (1992–2007) separated again in 2000 (Fig. 5A). This latter branch compares favorably to the commercial data (1993–2007), which had primary separation in 1999 (Fig. 5B). In both data sets, sampling groups contained years in chronological order. This pattern suggests gradual shifts in species compositions, possibly influenced by one or more trending factors.

Species responsible for the primary separation of years were ranked by their average contributions toward the dissimilarity (Table 5). The two top-ranked species in recreational data were tomtate (more prevalent in earlier years) and lane snapper (more prevalent in latter years), which together accounted for ∼20% of the overall dissimilarity. The two top-ranked species in commercial data were blue runner and vermilion snapper (both more prevalent in latter years), which together accounted for ∼34% of the overall dissimilarity.

4. Discussion

Reef fishes within the SUSLME have been shown to form coherent, but loosely structured, assemblages (Shertzer and Williams, 2008). Our results here demonstrate that those assemblages are

Table 4
Species from temporal analyses, ranked by correlation (ρ) with dimension one (year) of nonmetric multidimensional scaling.

Recreational		Commercial	
Species	ρ	Species	ρ
Lane snapper	0.850	Blue runner	0.949
Gray snapper	0.844	Vermilion snapper	0.819
Red grouper	0.831	Red grouper	0.721
White grunt	0.788	Black sea bass	−0.133
Gray triggerfish	0.781	Greater amberjack	−0.204
Bluestriped grunt	0.697	White grunt	−0.367
Jolthead porgy	0.420	Gray snapper	−0.509
Whitebone porgy	0.278	Snowy grouper	−0.529
Red snapper	−0.186	Yellowtail snapper	−0.672
Vermilion snapper	−0.310	Black grouper	−0.689
Black sea bass	−0.355	Mutton snapper	−0.723
Yellowtail snapper	−0.435	Gag	−0.762
Scamp	−0.485		
Mutton snapper	−0.527		
Knobbed porgy	−0.545		
Blue runner	−0.633		
Gag	−0.641		
Greater amberjack	−0.807		
Tomtate	−0.849		

Positive values indicate increased prevalence in landings over time, and negative values indicate decreased prevalence. Recreational data span 1980–2007, and commercial data span 1993–2007.

Table 5
Contributions of reef fishes toward the distinction of time periods in recreational and commercial data sets.

Species	$\bar{x}_{period1}$	$\bar{x}_{period2}$	$\bar{\delta}_k$	$SD(\bar{\delta}_k)$	$\bar{\delta}_k/SD(\bar{\delta}_k)$	$\sum \bar{\delta}_k\%$
Recreational (period1 = 1980–1991, period2 = 1992–2007)						
Tomtate	7.97	4.90	0.76	0.41	1.87	10.52
Lane snapper	2.86	5.00	0.68	0.39	1.74	19.90
Gray triggerfish	6.55	9.03	0.56	0.33	1.71	27.58
Red grouper	3.45	5.25	0.52	0.27	1.91	34.77
Gray snapper	4.55	6.41	0.48	0.20	2.36	41.42
Black sea bass	11.80	10.20	0.47	0.34	1.41	47.95
White grunt	6.51	8.28	0.40	0.20	1.98	53.45
Greater amberjack	5.17	3.83	0.39	0.22	1.81	58.85
Blue runner	3.45	2.66	0.38	0.26	1.45	64.13
Jolthead porgy	1.48	1.97	0.33	0.24	1.40	68.69
Bluestriped grunt	0.88	1.42	0.33	0.19	1.76	73.24
Knobbed porgy	4.26	3.44	0.28	0.18	1.55	77.15
Whitebone porgy	3.23	3.74	0.27	0.21	1.32	80.90
Mutton snapper	5.54	4.76	0.27	0.19	1.41	84.58
Red snapper	4.70	4.25	0.25	0.21	1.21	88.02
Gag	6.90	6.04	0.24	0.19	1.25	91.30
Yellowtail snapper	6.95	6.37	0.23	0.16	1.37	94.41
Scamp	4.81	4.19	0.21	0.14	1.46	97.27
Vermilion snapper	8.93	8.26	0.20	0.13	1.53	100.00
Commercial (period1 = 1993–1998, period2 = 1999–2007)						
Blue runner	2.32	7.31	1.72	0.76	2.28	23.29
Vermilion snapper	9.41	12.73	0.78	0.26	2.98	33.88
Red grouper	5.60	7.79	0.78	0.46	1.68	44.38
Gag	18.17	14.34	0.77	0.35	2.16	54.75
Black grouper	5.55	3.69	0.70	0.31	2.23	64.23
Greater amberjack	10.72	10.10	0.51	0.41	1.26	71.18
Yellowtail snapper	13.44	11.68	0.45	0.27	1.65	77.28
Snowy grouper	2.72	2.20	0.42	0.31	1.36	83.02
Gray snapper	8.35	7.43	0.37	0.27	1.37	87.98
Mutton snapper	6.05	5.09	0.35	0.23	1.54	92.76
Black sea bass	12.54	12.71	0.32	0.25	1.26	97.09
White grunt	5.14	4.94	0.21	0.16	1.36	100.00

Data are summarized by the average proportion of trips ($\bar{x}$, prior to transformation) that caught species in each time period. Species are ordered by their contribution ($\bar{\delta}_k$) to the average dissimilarity ($\bar{\delta}$) between the two time periods, reflected in the cumulative contribution ($\sum \bar{\delta}_k\%$) to $\bar{\delta}$. Consistency of contribution is quantified by the standard deviation (SD). Values in first four columns were multiplied by 100.
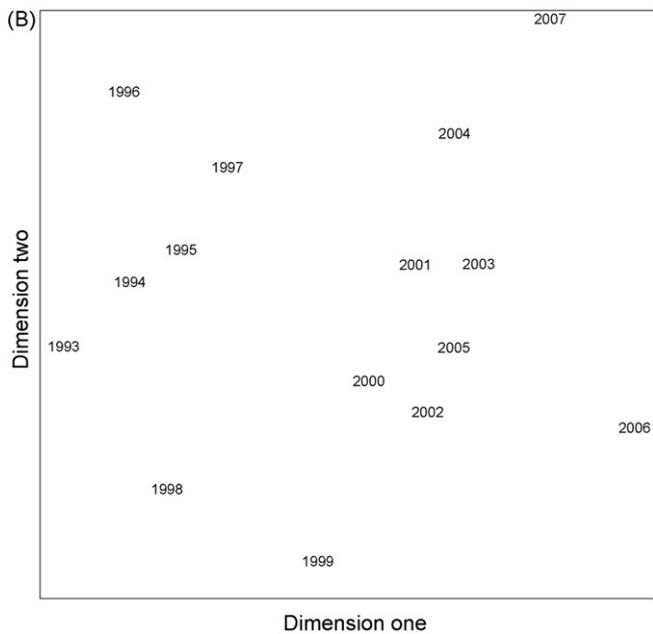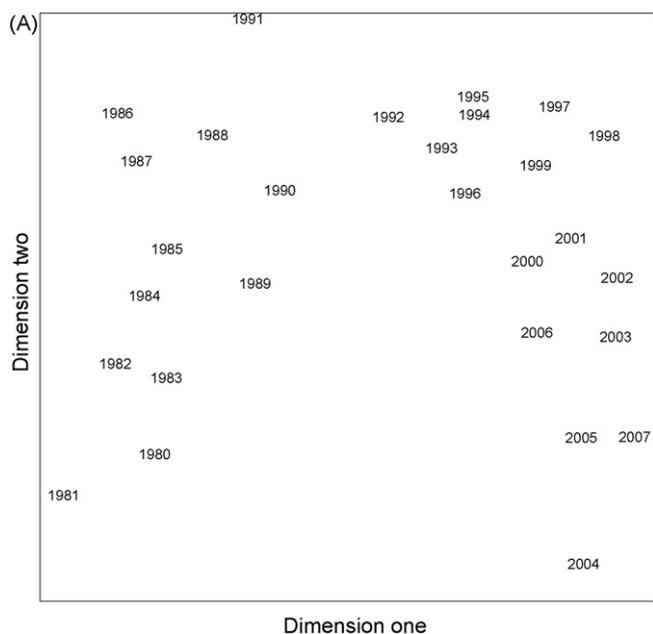

Fig. 4. Nonmetric multidimensional scaling of years using (A) recreational or (B) commercial data. Years near each other in ordination space are those with similar species composition.

heterogeneous, both in space and time, which likely accounts for their loose structure. The dynamics of reef fish communities are inextricably entwined with those of the greater food web, and thus understanding their patterns could prove useful for managing the SUSLME.

Interpretation of our results should be couched with the caveat that fishery dependent data are not collected by random sampling. Fishery independent data are often preferable for inferring patterns of biodiversity (e.g., Jay, 1996; Collie et al., 2008); however, fishery independent data sources in the SUSLME are quite limited in terms of species represented, sample sizes, and spatial coverage. None of these limitations were an issue in this study, and the extensive nature of fishery dependent data has made them useful
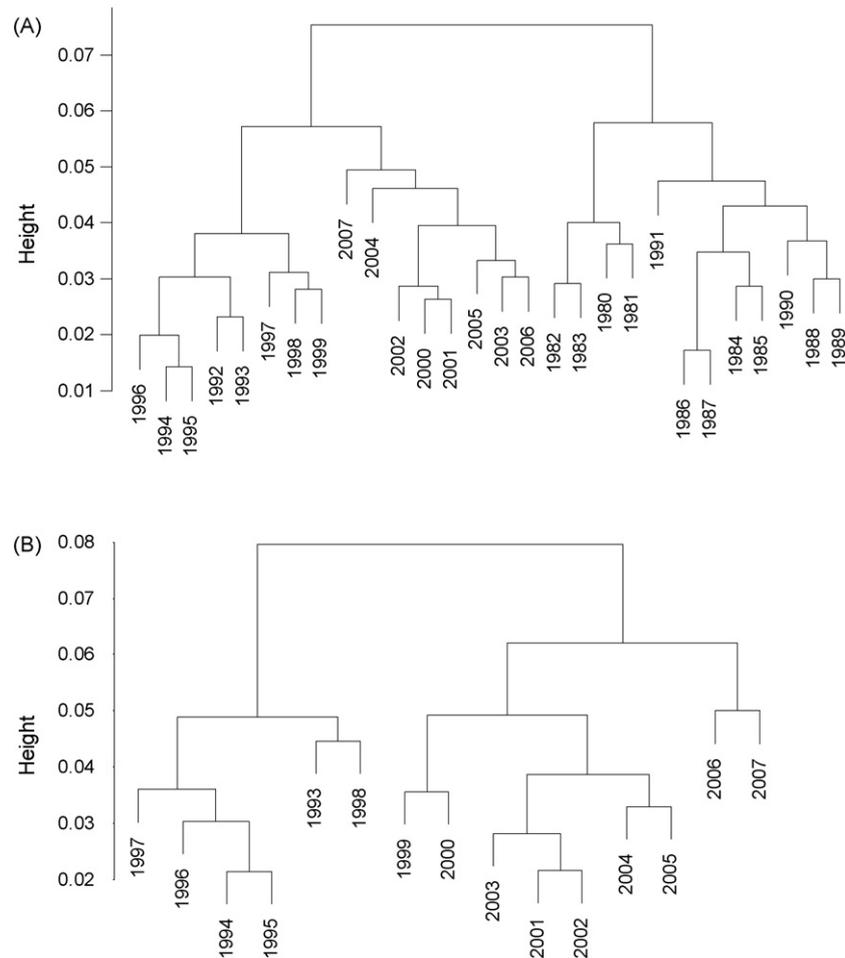
Fig. 5. Dendrograms from cluster analysis of years using (A) recreational or (B) commercial data. Height measures similarity within a branch, where lower values indicate greater similarity.

in other studies of fish assemblages (e.g., Chester et al., 1984; Lee and Sampson, 2000; Shertzer and Williams, 2008).

Sampling by the recreational headboat fishery, despite being fishery dependent on an initial level, operates like a fishery independent survey in the sense that fishing effort is not directed at individual species, but rather targets the complex of reef fishes in general. Such nonselective effort minimizes possible confounding effects of density dependent catchability or target switching. Commercial fishermen are more likely to target individual species; thus, we consider headboat data more reliable for characterizing fish communities than are commercial data. However, in most cases, results from the two distinct data sets were in agreement, evidence that the two were tracking underlying signals in reef fish communities.

Both data sets revealed broad differences in species compositions between northern and southern regions of the SUSLME. The primary zoogeographic boundary occurred in our data near Cape Canaveral, Florida, which might be expected based on physical oceanography (Wells and Gray, 1959). This boundary is not a sharp break for all species and may occur as far south as West Palm Beach, Florida for some (Briggs, 1974), but generally, subtropical fishes occurred in the south and temperate fishes in the north. Furthermore, even species abundant in both regions may not represent a single stock. For example, white grunt caught north and south of Cape Canaveral are genetically different (Chapman et al., 1999), and they grow larger in the north (Potts, 2000). Similar differences in growth have been found for lane snapper (K. Brennan, unpub-

lished data) and gray snapper (Burton, 2001). Obviously, uniform size-limit regulations would affect the northern and southern populations differently. If resource managers were to consider dividing the SUSLME into more than one region for managing fisheries, our results suggest that a boundary might appropriately be set near Cape Canaveral.

The data used in our study contained only coarse spatial information. Finer resolution, as provided by Vessel Monitoring Systems, would facilitate more detailed analysis of species composition, allowing possible identification of environmental covariates. Indeed, several species in this study have been found to associate with particular depths or bottom habitats (Sedberry and Van Dolah, 1984; Cuellar et al., 1996; Schobernd, 2006, M.S. Thesis, College of Charleston). A comprehensive understanding of how biodiversity relates to the environment is necessary not only for understanding the spatial distribution of fish assemblages, but also for predicting the effects of environmental change on coastal marine systems (Harley et al., 2006).

Our temporal analyses revealed primary shifts in species composition in 1992 and again in 1999–2000. Because the data were fishery dependent, we cannot rule out the possibility that these shifts resulted, at least in part, from discrete-time implementation of fishing regulations. Nevertheless, our analyses also revealed a broad pattern of gradual trends in species composition. These trends are apparent in the dendrograms (Fig. 5), where branches of sampling groups contained years that were chronologically close. Such a pattern is inconsistent with the hypothesis that species

composition repeatedly reorganizes because of continual interspecific competition for suitable reef habitat. Rather, it suggests that gradual shifts in species compositions have been driven by one or more trending factors. The evidence for this chronological pattern appears strong, as it emerged independently from two different data sets.

At least four factors could be driving the observed trends in community structure. First, heavy exploitation can drastically alter communities (Hughes, 1994) and has occurred in the SUSLME for decades (Coleman et al., 1999). Several top-level predators are now rare; most conspicuous are large groupers that were once relatively common, such as speckled hind, *Epinephelus drummondhayi*, Warsaw grouper, *E. nigritis*, and yellowedge grouper, *E. favolimbatus* (Chester et al., 1984). Second, the invasive Indo-Pacific lionfish, *Pterois miles* and *P. volitans*, has become established and widespread in the SUSLME, perhaps after accidental release from aquaria (Whitfield et al., 2002). Lionfish are a rapacious consumer with few reported predators, and their effects on the ecosystem are at present unknown (Albins and Hixon, 2008). Third, habitat degradation, particularly in estuarine systems that serve as fish nurseries, has resulted from loss of wetlands (Hoss and Engel, 1996), proliferation of harmful algal blooms (Anderson et al., 2008), and increased urban, industrial, and agricultural pollution (Aquarone, 2008). Fourth, climate can influence marine communities through such forcing mechanisms as the North Atlantic Oscillation (Attrill and Power, 2002) or increased water temperatures (Genner et al., 2004; Perry et al., 2005; Collie et al., 2008), and can lead to regime shifts in reef fish assemblages (Holbrook et al., 1997). For example, on a reef off North Carolina, Parker and Dixon (1998) found that increased bottom temperatures in winter coincided with greater abundances of tropical species common to Florida and the Caribbean. Indeed, the headboat data used in our analysis, when restricted to the northern region (i.e., areas NC1, NC2, SC, GAFL, and FL1), revealed increasing incidence of bluestriped grunt, gray snapper, jolthead porgy, lane snapper, mutton snapper, and yellowtail snapper, all species with ranges that are centered south of Cape Canaveral (results not shown). Of course, all four factors – heavy exploitation, invasive lionfish, habitat degradation, and climate change – could be contributing to community shifts concurrently and interactively.

Mangel and Levin (2005) provide a cogent argument for managing fisheries on the basis of community ecology. To be operational, such an approach requires resource managers to be cognizant of pattern and process in biodiversity. This study should help advance our currently rudimentary understanding of such dynamics in the SUSLME.

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