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Authors: Farmer, Nicholas A., and Malinowski, Richard P.

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Nicholas A. Farmer* and Richard P. Malinowski

National Oceanic and Atmospheric Administration–Fisheries, Southeast Regional Office,
263 13th Avenue South, St. Petersburg, Florida 33701, USA

Mary F. McGovern

College of Charleston, 1215 Aruba Circle, Charleston, South Carolina 29412, USA

Peter J. Rubec

Florida Fish and Wildlife Conservation Commission, 100 8th Avenue Southeast, St. Petersburg,
Florida 33701, USA

Abstract

The Magnuson–Stevens Fishery Conservation and Management Act of 2006 required that regional fishery management councils implement annual catch limits and accountability measures for all federally managed stocks by 2011. Many managed species are data limited and no formal stock assessment has been done for them. One possible approach to managing unassessed species is to assign them to assemblages that are managed as units. The utility of this approach was evaluated using fishery-dependent and fishery-independent data from the Gulf of Mexico. Multivariate statistical analyses revealed several consistent assemblages among the 42 reef fish species managed by the Gulf of Mexico Fishery Management Council. Pearson correlation matrices, nodal analyses, and a weighted mean cluster association index integrated results across cluster analyses and provided additional guidance regarding the placement of rare species into groups. Productivity–susceptibility analysis and life history were also considered, as differences in productivity, vulnerability, life history, and other population-dynamic parameters for the species within complexes might imply different population responses to a similar change in fishing mortality. Identified linkages between species also provide guidance for the impacts of regulations on multispecies fisheries.

The Magnuson–Stevens Fishery Conservation and Management Act (Magnuson–Stevens Fishery Conservation and Management Reauthorization Act of 2006) required that regional fishery management councils implement annual catch limits (ACLs) and accountability measures (AMs) by 2011 to ensure that overfishing would not occur. These ACLs and AMs were required for nearly all stocks under federal management. Traditionally, management measures have been implemented based on the results of species-specific stock assessments. Unfortunately, due to limitations on funding,

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resources, and available data, many managed stocks have never been assessed. For example, in 2011 the Gulf of Mexico Fisheries Management Council (hereafter, Gulf Council) was managing 42 finfish stocks under its Reef Fish Fishery Management Plan (FMP; Table 1), yet the Gulf Council's Scientific and Statistical Committee had approved assessments for only 10 of those stocks.

Reference points for data-limited stocks can be set in a number of ways (Berkson et al. 2011; Carruthers et al. 2014). One possible approach for managing unassessed, data-limited species is to group them into stock complexes with a single ACL. A stock complex is defined as "a group of stocks that are sufficiently similar in geographic distribution, life history, and vulnerabilities to the fishery such that the impact of management actions on the stocks is similar" (USOFR 2009). Stocks may be grouped into complexes if (1) they cannot be targeted independently of one another in a multispecies fishery, (2) there are insufficient data to determine their status relative to established criteria, or (3) it is infeasible for fishermen to distinguish between individual stocks (USOFR 2009). The Gulf Council previously used stock complexes in the development of its commercial Grouper–Tilefish Individual Fishing Quota (IFQ) program.

The objectives of this study were (1) to determine whether stock complexes can be identified among the 42 managed Reef Fish FMP stocks in the Gulf of Mexico and, if so, (2) to determine whether the complexes are consistent between commercial and recreational fisheries. The results of these analyses were used to provide guidance to the Gulf Council in setting ACLs for stocks and stock complexes in their 2011 Generic Comprehensive ACL/AM Amendment (Gulf Council 2011).

METHODS

Following Lee and Sampson (2000), multiple factors and statistical techniques were used to identify species assemblages: (1) species life history, depth of occurrence, and catch history; (2) dimension reduction and hierarchical cluster analyses based on life history, abundance, and presence/absence; (3) correlation matrices, nodal analyses, and weighted mean cluster association indices; and (4) maps of species distributions. These analytical approaches are subject to different biases and limitations. Rather than focusing on a single approach, the results were synthesized across approaches to develop potential species complexes for ACL management. The analytical methods and data sources that provided the most information for each species were weighted so that they exerted more influence on the synthesized results.

Life history and catch data.—As species with similar life histories and body physiologies may respond to management measures in a similar fashion, life history and growth parameters were considered as one of the factors in species associations. Life history parameters were assembled from peer-reviewed literature, Southeast Data Assessment and Review (SEDAR) reports, unpublished data from the National Marine Fisheries Service (NMFS) Panama City Laboratory, Stock Assessment and Fishery Evaluation reports, and FishBase (Froese and Pauly 2009). Data from the Gulf of Mexico were used whenever possible. A categorical variable for taxonomic family captured aspects of body morphology and life history not described by the growth parameters in Table 1.

Commercial logbook, commercial observer, headboat logbook, recreational survey, and fishery-independent bottom longline data were used to evaluate similarities in the spatial and temporal patterns of fisheries exploitation in the Gulf of Mexico for species in the Gulf Reef Fish FMP. Commercial logbook records (Southeast Fisheries Science Center, Coastal Fisheries Logbook Program) summarize landings at the trip level, with information for each species encountered, including landings (to the nearest pound), the primary gear used, and the primary area and depth of capture (feet). Following recommendations from SEDAR-10 (2006), trip-level adjustments were made to Black Grouper *Mycteroperca bonaci* and Gag *Mycteroperca microlepis* landings to account for misidentification. Area fished was based on the 21 Gulf of Mexico commercial logbook statistical areas. A single depth of fishing is reported for each species per trip, although the species may be encountered at numerous depths during multiple sets and even within a single drifting longline set. Separate analyses were conducted for commercial longline (CLL) and commercial vertical line (CVL) gear types. Depth of capture was aggregated into atmospheric pressure bins (e.g., 33 ft = 2 atmospheres, 66 ft = 3 atmospheres, etc.). Records with no reported depth or area of capture were removed from consideration; these represented approximately 9% of the available records for both the longline and vertical line clusters. Overall, 27,566 longline and 121,767 vertical line commercial logbook records from 2005 to 2009 were evaluated.

In July 2006, the NMFS implemented a mandatory commercial reef fish observer program (RFOP) to characterize the reef fish fishery operating in the U.S. Gulf of Mexico. The RFOP provides set-level information on species encountered on trips using bottom longlines, electric (bandit) reels, and handlines. Overall, 125,368 records representing encounters (landings plus discards) by species for 7,105 observed sets in the Gulf of Mexico from 2006 to 2009 were evaluated.

The recreational headboat sector of the reef fish fishery was evaluated using Southeast Region Headboat Survey (HBS) logbook data reported by headboat operators. Headboats are large, for-hire vessels that typically accommodate 20 or more anglers on half- or full-day trips. Headboat records contain trip-level information on the number of anglers, trip duration, date, and area fished for encounters (landings and releases) of each species. Trip duration was the best available proxy for depth fished, as trips of longer duration are more likely to go farther offshore and fish deeper waters. Headboat captains fishing in multiple areas during a trip are constrained by the

TABLE 1. Life history parameters for species covered by the Gulf of Mexico Reef Fish FMP, by family (see Table A.1 in the appendix for citations). Abbreviations are as follows: a_λ = the maximum age in years, K = the Brody growth coefficient, L_∞ = the asymptotic length from the von Bertalanffy growth equation, a_0 = the scaling parameter for the theoretical age at length zero from the von Bertlanffy growth equation, W_∞ = the theoretical maximum weight (kg), L_m = length at maturity (mm), and a_m = age at maturity (months).

Species	a_λ	K	L_∞	a_0	W_∞	L_m	a_m	Depth (m)	Citation(s)
Epinephelidae									
Red Grouper	29.0	0.13	88.4	−0.19	23	572	36	2–101	12, 19
Epinephelus morio									
Rock Hind	12.0	0.16	60.1	−2.50	4	280	28	0–37	25
Epinephelus adscensionis									
Red Hind	11.0	0.09	47.1	−0.75	25	266	41	1–30	25
Epinephelus guttatus									
Yellowedge Grouper	85.0	0.06	100.5	−4.75	19	815	96	2--84	22
Hyporthodus flavolimbatus									
Snowy Grouper	28.0	0.09	132.0	−1.01	30	670	60	9–160	2, 19
Hyporthodus niveatus									
Speckled Hind	25.0	0.13	110.0	−0.98	30	503	53	8–56	27
Epinephelus drummondhayi									
Warsaw Grouper	41.0	0.05	239.4	−3.62	190	810	49	17–160	28
Hyporthodus nigritus									
Misty Grouper	41.0	0.07	163.3	−1.58	107	811	98	34–122	19
Hyporthodus mystacinus									
Nassau Grouper	29.0	0.13	76.0	−1.12	27	400	60	0–27	29
Epinephelus striatus									
Atlantic Goliath Grouper	37.0	0.13	201.0	−0.78	455	1100	48	0–30	3, 19
Epinephelus itajara									
Gag	31.0	0.14	130.0	−0.39	37	656	43	12–46	11, 19
Mycteroperca microlepis									
Black Grouper	33.0	0.14	133.4	−0.90	41	826	62	2–10	13
Mycteroperca bonaci									
Scamp	30.0	0.09	108.0	−1.36	13	353	15	9–30	26
Mycteroperca phenax									
Yellowfin Grouper	15.0	0.09	89.5	−0.75	19	540	44	1–42	7, 19
Mycteroperca venenosa									
Yellowmouth Grouper	28.0	0.06	85.4	−2.21	9	453	36	1–46	19
Mycteroperca interstitialis									
Serranidae									
Sand Perch	2.0	0.27	27.7	0.11	1	165	72	0–24	16, 15
Diplectrum formosum									
Dwarf Sand Perch	7.0	0.41	26.3	−0.42	1	157	20	0–30	16, 20
Diplectrum bivittatum									
Malacanthidae									
Blueline Tilefish (F)	43.0	0.11	63.4	−4.54	6	338	54	9–72	17, 18
Caulolatilus microps									
Blueline Tilefish (M)	43.0	0.10	75.8	−5.40	7	513	72	9–72	17, 18
Anchor Tilefish	16.0	0.18	62.2	0.77	11	341	42	9–72	16
Caulolatilus intermedius									
Blackline Tilefish	16.0	0.18	62.2	0.77	11	341	42	9–72	16
Caulolatilus cyanops									
Goldface Tilefish	16.0	0.18	62.2	0.77	11	341	42	9–72	16
Caulolatilus chrysops									

TABLE 1. Continued.

Species	a_λ	K	L_∞	a_0	W_∞	L_m	a_m	Depth (m)	Citation(s)
Tilefish (F)	50.0	0.13	112.0	−4.56	23	613	60	24–165	1, 14, 23
Lopholatilus chamaeleonticeps									
Tilefish (M)	50.0	0.15	141.5	−1.46	50	767	66	24–165	1, 14, 22
Lutjanidae									
Queen Snapper	30.0	0.61	103.0	−0.19	53	536	12	30–137	19
Etelis oculatus									
Red Snapper	57.0	0.35	100.0	−0.50	23	230	43	3–58	8
Lutjanus campechanus									
Gray Snapper	26.0	0.17	55.9	−2.23	5	233	24	2–55	31
Lutjanus griseus									
Lane Snapper	10.0	0.10	61.8	−1.73	3	205	12	3–122	30
Lutjanus synagris									
Mutton Snapper	14.5	0.16	86.9	−0.94	9	330	37	8–29	9
Lutjanus analis									
Schoolmaster	12.0	0.18	57.0	−0.45	3	148	24	1–19	19, 30
Lutjanus apodus									
Blackfin Snapper	8.2	0.35	62.0	−0.39	14	250	21	6v61	19
Lutjanus buccanella									
Cubera Snapper	22.1	0.13	105.0	−0.94	57	546	55	5–17	19
Lutjanus cyanopterus									
Dog Snapper	12.0	0.10	85.4	−1.28	10	300	74	1–12	19, 30
Lutjanus jocu									
Mahogany Snapper	28.5	0.10	49.9	−1.51	13	130	55	0–30	19
Lutjanus mahogoni									
Silk Snapper	29.0	0.10	81.2	−1.32	8	434	63	27–74	19
Lutjanus vivanus									
Yellowtail Snapper	17.0	0.17	60.0	−0.53	4	224	75	0–55	4, 32
Ocyurus chrysurus									
Wenchman	11.0	0.27	58.1	−0.52	5	321	29	7–113	16
Pristipomoides aquilonaris									
Vermilion Snapper	26.0	0.12	50.6	−3.09	3	320	24	12–91	10, 19
Rhomboplites aurorubens									
Labridae									
Hogfish	23.0	0.98	85.1	−1.38	10	169	13	1–9	24, 33
Lachnolaimus maximus									
Balistidae									
Gray Triggerfish	12.0	0.38	46.6	−0.33	6	142	12	0–110	5, 19
Balistes capriscus									
Carangidae									
Greater Amberjack	17.0	0.23	111.0	−0.79	81	788	27	0–110	6, 19, 21
Seriola dumerili									
Banded Rudderfish	10.3	0.28	77.5	−0.46	5	415	27	9–40	19
Seriola zonata									
Almaco Jack	22.2	0.13	163.3	−0.83	60	811	53	2–49	19
Seriola rivoliana									
Lesser Amberjack	10.2	0.28	67.5	−0.47	46	379	27	17–40	16
Seriola fasciata									

present data form to identify one "area fished" for the trip, which limits the spatial precision of the analysis. Area fished was aggregated at the most common reporting level (1° latitude × 1° longitude) to reduce the undesirable influence of empty bins. Records with no reported area fished (~3%) were removed from consideration. Overall, 121,334 headboat records from 2004 to 2009 were evaluated.

The private, rental, and for-hire charter sectors were evaluated using data from Marine Recreational Fisheries Statistics Survey (MRFSS) dockside intercept records. The MRFSS intercepts collect data on port agent–observed landings and angler-reported landings and discards by species, 2-month wave (wave 1 = January–February, wave 2 = March–April, etc.), state ([western] Florida, Alabama, Mississippi, or Louisiana), mode of fishing (charter, private/rental, or shore), and area fished (inland, state, or federal waters). Overall, 64,782 dockside intercept records from 2000 to 2009 were evaluated.

Since 1995, the NMFS began conducting fishery-independent bottom-longline (BLL) surveys throughout the Gulf of Mexico at depths ranging from 9 to 55 m (Grace and Henwood 1997). In 1999, the BLL survey was expanded out to depths of 366 m (Henwood et al. 2004). Study sites are randomly selected. Longline sets are made parallel to depth contours. Gangion test and length have varied between years. J-hooks were used prior to 1999, while circle hooks have been used since 1999. Soak times are always 1 h and use 100 #15/0 hooks baited with Atlantic Mackerel *Scomber scombrus*. Methods were standardized in 2001. Effort is proportionally allocated based on shelf width within 60–nautical mile statistical zones (81–82°W, 82–83°W, etc.) and stratified by depth (50%: 9–73 m, 40%: 73–183 m, 10%: 183–366 m). Overall, 851 BLL records of managed reef fish landings from 1995 to 2009 were evaluated.

Data sets were formatted as matrices, with columns representing species (i) and rows representing aggregation bins (j). Aggregation levels were chosen to minimize the number of empty bins while maximizing the spatial and temporal precision of the bin based on the available data. For commercial fisheries, species-specific landings in weight were aggregated into 3,257 CLL and 7,243 CVL year–month–area–depth bins. For the RFOP, species-specific encounters were aggregated into 7,105 set–level bins. For the HBS, species-specific encounters were aggregated into 2,615 year–month–area–trip duration bins. For the MRFSS, species-specific encounters by intercepted anglers were aggregated into 430 year–wave–mode–area bins. For the BLL, species-specific encounters were aggregated into 684 set–level bins. Each element of the matrix (c_{ij}) quantified the number of individuals of a species landed in a specific bin. No data matrix had more than one empty bin at these levels of aggregation.

Because rare species may distort inferred patterns (Koch 1987; Mueter and Norcross 2000), species were initially excluded from analyses if they appeared in less than 1% of the bins (Shertzer and Williams 2008). However, because preliminary examination suggested that the inclusion of rare species did not affect the inferred patterns in any of the cluster analyses and because one of our primary goals was to assign less abundant species to species complexes, all 42 managed species were included in the final analyses.

Prior to clustering, data were transformed using a root-root transformation, namely,

$$c_{ij}^* = \sqrt[4]{c_{ij}}. \qquad (1)$$

This transformation moderates the influence of abundant species on the resultant clusters and is recommended for density and biomass data (Field et al. 1982; Shertzer and Williams 2008).

Because the fishing effort that generated the landings data was inconsistent through time, the data may not be quantitatively comparable between collections. Additionally, while many species are heavily targeted, the catch of others is incidental. To address this concern, additional clustering was performed on binary transformations of the landings data matrices. Boesch (1977) suggests that a binary index (e.g., presence/absence) is a more appropriate measure of similarity with fisheries-dependent data. A binary index also reduces distortions caused by superabundant (headboat and commercial) and heavier (commercial) species.

Hierarchical cluster analyses and dimension reduction.— Cluster analysis and dimension reduction provide both quantitative and visual measures of association. Overall, 2 life history and 24 fishery-data clusters were generated for the stocks in the Gulf Council's Reef Fish FMP. For the life history data set (described above) and each of the six fishery catch input data sets (CLL, CVL, RFOP, HBS, MRFSS, and BLL), hierarchical cluster analysis (HCA) and dimension reduction analysis (DRA) were conducted on root-root- and presence/absence–transformed data.

The HCAs were conducted with PASW version 17.0.3 (SPSS, Chicago). Such analyses identify relatively homogeneous groups of cases (or variables) based on selected characteristics. They employ an agglomerative method that optimizes a route between individual entities to the entire set of entities through progressive fusion (Boesch 1977).

The life history parameters (Table 1) plus a categorical variable denoting taxonomic family were clustered using HCA with Ward's minimum-variance linkage method (Sneath and Sokal 1973), a Euclidean distance measure, and a Z-score transformation by variable. The Z-score transformation normalized the data by parameter, facilitating comparisons between species.

For the HCAs of the fisheries data sets (CLL, CVL, RFOP, HBS, MRFSS, and BLL), we used a chi-square measure of distance with Ward's minimum-variance linkage method. For the HCA of the binary-transformed fisheries data sets, we used

the average linkage between groups with a Sørenson measure of dissimilarity. These methods introduce little distortion into the relationships expressed in the similarity matrix and are widely used in ecology (Beals 1973; Boesch 1977; Field et al. 1982; Faith et al. 1987; McGarigal et al. 2000; Mueter and Norcross 2000; Gomes et al. 2001; Williams and Ralston 2002; Shertzer and Williams 2008; Shertzer et al. 2009).

A DRA was conducted using PROC VARCLUS in SAS version 9.2 (SAS Institute, Cary, North Carolina). This algorithm is binary and divisive: all variables start in one cluster; cluster is chosen for splitting and is split into two clusters by performing an orthoblique rotation on the first two principal components; each variable is then assigned to the rotated component with which it has the higher squared correlation. Dimension reduction analysis is nonhierarchical; variables are iteratively reassigned to clusters to maximize the variance accounted for by the cluster components. Clusters are split until 95% of the variance has been explained. Our DRA was applied identically to all input data.

Nodal analysis, correlation, and weighted mean cluster association.—As the CVL data set represented a large proportion of Gulf reef fish landings, had relatively high data resolution, and featured records for a variety of species, it was selected for nodal analysis (Sedberry and Van Dolah 1984). Percent landings by species and CVL area were tabulated and sorted by the CVL presence/absence HCA dendrogram. This nodal analysis provided a visual representation of how the spatial distribution of stocks impacted cluster output.

Pearson correlation matrices were also generated for the six catch-based input data sets. The table resulting from the co-occurrence analysis was subsequently sorted by columns according to the dendrogram from the CVL binary cluster output and by rows according to the dendrogram from the MRFSS binary cluster output. The CVL data set was selected due to its high species richness, and the MRFSS data set was selected because it represented the most contrasting sector. The cells were conditionally formatted to facilitate visual identification of the dense cells, or nodes, within the data matrix in which groups of species and groups of collections coincide between the two fisheries clusters and co-occur with high frequency between species (Williams and Lambert 1961; Lambert and Williams 1962). This nodal analysis was used to identify clusters of species that were often caught together across different sectors and to suggest cluster assignment for rare species by providing a visual reference for co-occurrence with more ubiquitous or heavily exploited species.

A weighted mean cluster association index was developed to synthesize results across the 2 life history and 24 fishery-data clusters. The cluster association matrix for each dendrogram was completed by species. For a given species in row *r*, the association level (α) with species in column *c* was computed as

$$\alpha_{r \to c} = \frac{1}{\sum \eta_r}, \qquad (2)$$

where η is the number of species lower than the species in row *r* on the branches of the dendrogram. For example, species D and E are both below species F on the branch; thus $\alpha_{F \to D} = 0.5$ and $\alpha_{F \to E} = 0.5$ in the association matrix (see Figure 1).

Unique cluster association matrices were assembled for each of the 26 dendrograms, and a weighted mean cluster association index matrix was computed. For a given species in row *r*, the weighted mean association level ($\overline{\alpha_{r \to c}}$) with species in column *c* was computed as

$$\overline{\alpha_{r \to c}} = \frac{\sum_{D=1}^{6} \left(\omega_D \sum_{m=1}^{4} \alpha_{Dm(r \to c)} \right)}{\sum_{D=1}^{6} \sum_{m=1}^{4} \omega_D}, \qquad (3)$$

where *D* is the data set under examination, *m* is the clustering method, and ω_D is the weighting term for the data set. The weighting terms were computed by data set, were based on the proportional representation of the species within bins, and were scaled to 1 as a proportion of the maximum representation of that species across the seven data sets, with life history given the maximal default value of 1 (Table 3). For example, if a species appeared in 80% of the bins in the CLL and 40% of the bins in the other data sets, its weighting term would be 1.0 for CLL ($\omega_{CLL} = 1.0$) and 0.5 for the other data sets. This weighted mean approach was employed for two reasons: (1) clusters are generally considered more reliable for species that appear frequently in the bins (Koch 1987; Mueter and Norcross 2000) and (2) management measures targeting a

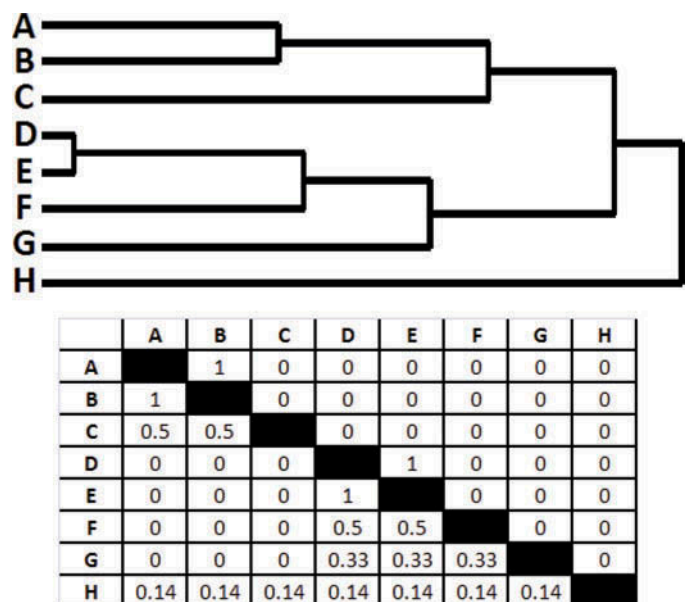|	A	B	C	D	E	F	G	H
A		1	0	0	0	0	0	0
B	1		0	0	0	0	0	0
C	0.5	0.5		0	0	0	0	0
D	0	0	0		1	0	0	0
E	0	0	0	1		0	0	0
F	0	0	0	0.5	0.5		0	0
G	0	0	0	0.33	0.33	0.33		0
H	0.14	0.14	0.14	0.14	0.14	0.14	0.14	

FIGURE 1. Example dendrogram and cluster association matrix. See the text for a more detailed explanation.

species complex would typically be expected to have a higher proportional impact on the sector that encounters the species most frequently. Sensitivity runs were performed with life history downweighted or removed from consideration.

Maps of stock distributions.—The RFOP and BLL surveys provide spatially explicit information regarding encounters with managed species in the Gulf of Mexico. These data sets were imported into ArcGIS (ESRI, Redlands, California) and displayed with respect to presence/absence on bathymetric maps of the Gulf. Trends in species distributions were used to explain inconsistencies between cluster analyses and to evaluate the "[similar] geographic distribution" requirement for stock complexes under the Magnuson–Stevens Fishery Conservation and Management Reauthorization Act of 2006. Some points were removed to protect the confidentiality of contributors to the RFOP data set.

RESULTS

Life History and Catch Data

Table 1 provides life history parameters for managed Gulf reef fish species. Because life history may be influenced by time (Shertzer et al. 2009), geography, habitat (Hoss and Engel 1996), exploitation (Hughes 1994), and climate (Holbrook et al. 1997), these point estimates may not accurately express the life history dynamics of the unexploited population or of all subpopulations. Additionally, life history data may be less reliable for data-poor species, lending uncertainty to the resultant clusters. Not surprisingly, HCA of the life history and depth of occurrence parameters in Table 1 showed clustering by family, depth of occurrence, and maximum size (Figure 2). All of these variables are highly intercorrelated ($P < 0.05$). Additionally, the von Bertalanffy growth parameters (L_∞, W_∞, a_λ, L_m, and a_m; Table 1) were significantly correlated ($P < 0.05$). A cursory examination of Table 1 and Figure 2 reveals some trends: species of the same genus often exhibit similar growth patterns, and larger and deepwater fish tend to live longer and grow more slowly.

Dimension Reduction and Hierarchical Cluster Analyses

The CVL and RFOP were the most representative data sets in terms of species encountered (Table 2), which is probably attributable to the broad depth ranges covered and the high levels of effort. In general, HCA and DRA outputs should be considered more reliable for species that are more prevalent in the input data matrices (Table 3). The CLL heavily weighted Red Grouper, Scamp, Gag, Yellowedge Grouper, and Snowy Grouper. The CVL heavily weighted Red Snapper, Vermilion Snapper, Scamp, Gray Triggerfish, Red Grouper, and Gag. The RFOP heavily weighted Red Grouper, Red Snapper, Vermilion Snapper, and Gag. The HBS heavily weighted Gray Triggerfish, Gag, Red Snapper, and Vermilion Snapper. The MRFSS heavily weighted Gray Snapper, Gag, Red Snapper, and Lane Snapper. The BLL

survey was the only fishery-independent data set examined. Unfortunately, the selectivity characteristic of longline gear led to low encounter rates with most reef fish species (Table 3). Only Red Snapper, Red Grouper, Yellowedge Grouper, and Tilefish were encountered in more than 5% of sets. Blueline Tilefish were landed on both sets that also landed Queen Snapper. Similarly, Tilefish was the only species landed on the only set that also landed a Goldface Tilefish. Red Snapper, Yellowedge Grouper, Warsaw Grouper, and Tilefish were all landed on sets that also landed Wenchman. The landings of Goldface Tilefish, Yellowmouth Grouper, Hogfish, Cubera Snapper, Dog Snapper, Anchor Tilefish, Schoolmaster, Nassau Grouper, Blackline Tilefish, and Mahogany Snapper were extremely low for all data sources. Other rare species were found predominantly in only one data set; for example, the Speckled Hind group assignment was heavily influenced by its CLL clustering and the Rock Hind group assignment was heavily influenced by its MRFSS clustering.

Commercial longline.—For the HCA and DRA of the CLL data, major clusters were formed by shallow-water, moderate-depth, and deepwater complexes (Figure 3). The most apparent cluster was formed by the major shallow-water grouper species (i.e., Red and Black Grouper, Gag, and Scamp). The relative lack of separation between Black Grouper and Gag in this cluster originated from the adjustment of the landings data for misidentification, which inflated the co-occurrence of these species. Within the deepwater group, Tilefish was somewhat distinct, and the deeper-water Snowy Grouper and Yellowedge Grouper were separated from the shallower-water Blueline Tilefish and Speckled Hind (Figure 3). Within the moderate-depth group, Gray Triggerfish and Vermilion Snapper were often caught together in large numbers. Queen Snapper and Wenchman both clustered with deepwater grouper and tilefish species (Figure 3). The clustering of shallow-water species was confounded because bottom longline fishing for reef fish is prohibited in waters of less than 20 fathoms (36 m; Figure 3; Table 3).

Commercial vertical line.—Cluster analyses of the CVL data provided results similar to those of the CLL data (Figure 4). Both HCA and DRA produced clusters of shallow-water grouper (Red and Black Grouper and Gag). Also apparent were moderate-depth complexes containing Silk and Blackfin Snapper and Gray Triggerfish with Vermilion, Red, and Lane Snapper. Clusters for deepwater (Yellowedge, Snowy, and Warsaw Grouper) and moderate-depth species were less clearly separated for the CVL fishery than for the CLL fishery, perhaps due to shallower average operating depths (mean = 88 m for the CLL, 50 m for the CVL) and less selective types of gear. The jacks (Greater Amberjack, Almaco Jack, Banded Rudderfish, and Lesser Amberjack) clustered relatively tightly (Figure 4). Gray Snapper clustered with the shallow-water grouper species
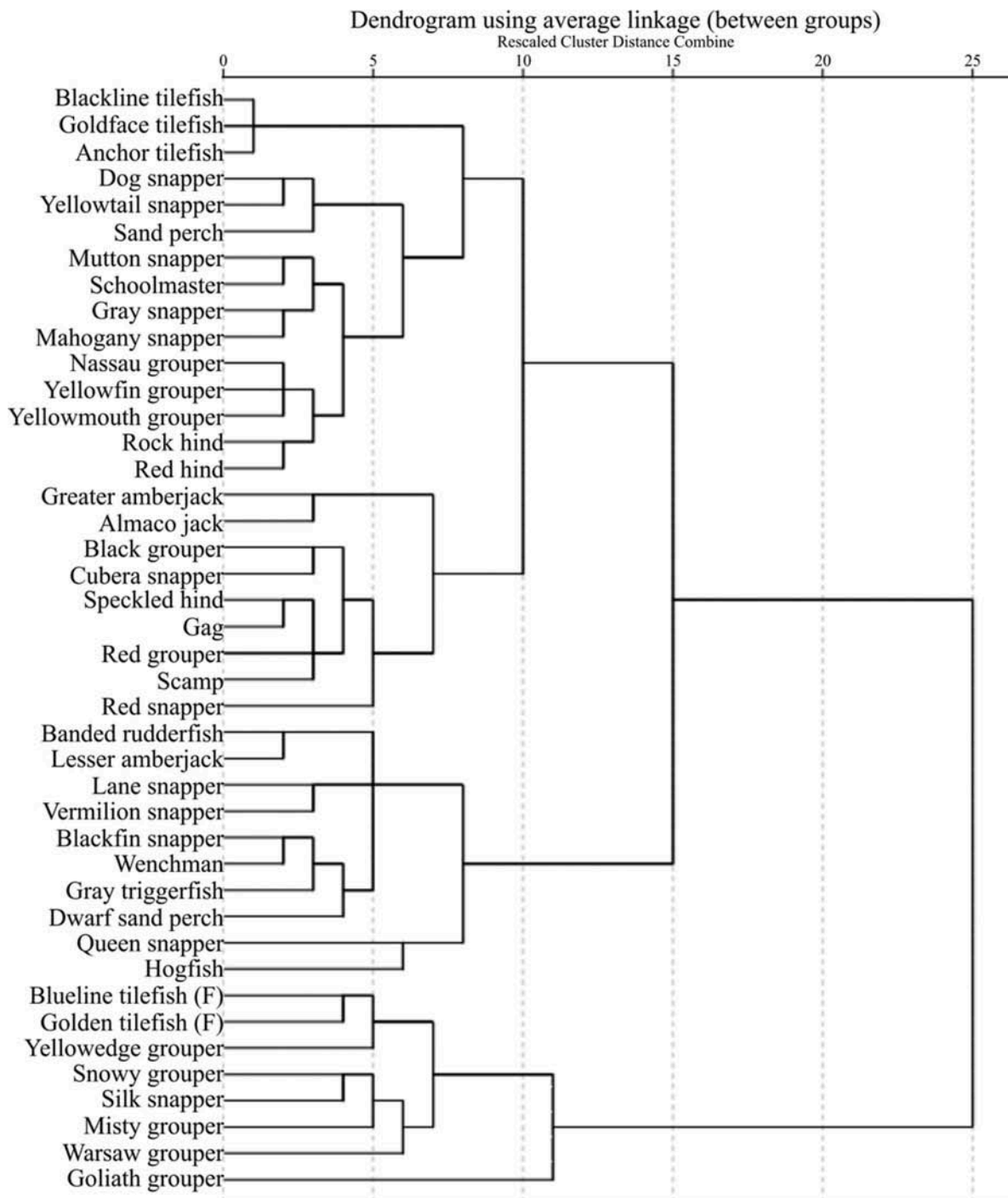
FIGURE 2. Hierarchical cluster analysis of life history parameters for managed Gulf of Mexico reef fish species with dummy code for genus (linkage: Ward's; measure: Euclidean distance; transformation: Z-score by variable). The letter "F" denotes female.

(Figure 4). Dog Snapper and Schoolmaster clustered together, as did Mutton Snapper, Yellowtail Snapper, and Hogfish (Figure 4).

Reef fish observer program.—The RFOP represents an aggregated, high-resolution subsample of the CLL and CVL data sets. Thus, it is not surprising that many of the trends observed in those clusters are repeated in the RFOP cluster (Figure 5). For example, deepwater groupers, snappers, and tilefish clustered together (i.e., Yellowedge Grouper, Blueline Tilefish, Snowy Grouper, Speckled Hind, Anchor Tilefish,

TABLE 2. Species diversity metrics for the presence of managed species in the Gulf in binned commercial longline (CLL), vertical line (CVL), reef fish observer (RFOP), headboat (HBS), Marine Recreational Fisheries Statistics Survey (MRFSS), and NMFS bottom-longline (BLL) data sets.

% Bins with species	CLL	CVL	RFOP	HBS	MRFSS	BLL
>0%	32	35	35	32	30	24
>1%	25	24	21	21	23	12
> 5%	19	12	9	15	14	4

TABLE 3. Weighting terms for the mean cluster strength matrix. Note that the life history weight = 1 for all species.

Species	Data source					
	CLL	CVL	HBS	MRFSS	BLL	RFOP
Almaco Jack	0.02	0.18	0.25	0.13	0.00	0.03
Anchor Tilefish	0.00	0.00	0.00	0.00	0.00	0.00
Banded Rudderfish	0.01	0.07	0.21	0.04	0.00	0.01
Black Grouper	0.28	0.27	0.09	0.05	0.00	0.01
Blackfin Snapper	0.08	0.04	0.01	0.00	0.00	0.00
Blackline Tilefish	0.00	0.00	0.00	0.00	0.00	0.00
Blueline Tilefish	0.17	0.10	0.01	0.00	0.04	0.04
Cubera Snapper	0.01	0.00	0.02	0.00	0.00	0.00
Dog Snapper	0.01	0.00	0.00	0.02	0.00	0.00
Dwarf Sand Perch	0.00	0.00	0.00	0.00	0.01	0.00
Gag	0.50	0.44	0.70	0.75	0.04	0.17
Goldface Tilefish	0.00	0.00	0.00	0.00	0.00	0.00
Atlantic Goliath Grouper	0.00	0.00	0.00	0.24	0.00	0.00
Gray Snapper	0.26	0.42	0.59	0.84	0.01	0.06
Gray Triggerfish	0.17	0.45	0.73	0.42	0.00	0.06
Greater Amberjack	0.29	0.32	0.43	0.31	0.02	0.06
Hogfish	0.00	0.03	0.06	0.03	0.00	0.00
Lane Snapper	0.10	0.32	0.60	0.43	0.00	0.05
Lesser Amberjack	0.06	0.09	0.03	0.01	0.00	0.01
Mahogany Snapper	0.00	0.00	0.00	0.00	0.00	0.00
Misty Grouper	0.03	0.01	0.00	0.00	0.00	0.00
Mutton Snapper	0.23	0.10	0.05	0.03	0.00	0.01
Nassau Grouper	0.00	0.00	0.00	0.00	0.00	0.00
Queen Snapper	0.05	0.05	0.00	0.00	0.00	0.00
Red Grouper	0.54	0.44	0.59	0.29	0.28	0.57
Red Hind	0.02	0.04	0.04	0.02	0.00	0.00
Red Snapper	0.16	0.58	0.63	0.60	0.33	0.43
Rock Hind	0.00	0.00	0.16	0.02	0.00	0.00
Sand Perch	0.00	0.00	0.27	0.30	0.00	0.01
Scamp	0.52	0.50	0.49	0.18	0.02	0.12
Schoolmaster	0.00	0.00	0.00	0.00	0.00	0.00
Silk Snapper	0.12	0.07	0.01	0.00	0.00	0.00
Snowy Grouper	0.34	0.12	0.06	0.03	0.03	0.04
Speckled Hind	0.19	0.06	0.06	0.00	0.01	0.03
Tilefish	0.25	0.03	0.00	0.00	0.14	0.02
Vermilion Snapper	0.13	0.54	0.61	0.30	0.01	0.20
Warsaw Grouper	0.13	0.12	0.14	0.07	0.03	0.01
Wenchman	0.00	0.00	0.00	0.00	0.01	0.00
Yellowedge Grouper	0.39	0.11	0.02	0.02	0.24	0.07
Yellowfin Grouper	0.01	0.01	0.01	0.00	0.00	0.00
Yellowmouth Grouper	0.00	0.00	0.02	0.00	0.00	0.00
Yellowtail Snapper	0.04	0.10	0.16	0.04	0.00	0.00

Queen Snapper, and Goldface Tilefish). Red Snapper and Lane Snapper clustered together, as did Scamp and Gag, Almaco Jack, and Greater Amberjack (Figure 5). Additional clusters were formed by the hinds (i.e., Red Hind and Rock Hind), as well as by Mutton and Cubera Snapper. A cluster was formed between Red Grouper and Vermilion Snapper, and Sand Perch clustered with Scamp and Gag.

Headboat survey.—The HBS clusters provided results similar to those for the CLL and CVL data (Figure 6). Clusters of Red Grouper, Gag, Scamp, and Gray Snapper were observed. Moderate-depth species (Gray Triggerfish with Vermilion, Red, and Lane Snapper), and deepwater species (Yellowedge and Snowy Grouper) tended to cluster together. Greater Amberjack and Almaco Jack clustered with each other. Tropical species such as Black Grouper, Mutton Snapper, and Yellowtail Snapper clustered together. Misidentification issues may have led to the observed clustering of Yellowedge, Yellowfin, and Yellowmouth Grouper (see SEDAR-22-DW-13 2010).

Marine Recreational Fisheries Statistics Survey.—The MRFSS clusters formed few distinct groups (Figure 7). Of the deepwater species, Warsaw Grouper and Snowy Grouper clustered, as did Yellowedge Grouper and Tilefish. A moderate-depth group containing Gray Triggerfish, Red Snapper, Lane Snapper, Vermilion Snapper, Scamp, Banded Rudderfish, Greater Amberjack, Misty Grouper, and Speckled Hind was also identified. Gag and Red Grouper clustered strongly. Yellowtail Snapper and Mutton Snapper also clustered together.

Bottom longline.—The BLL survey clusters formed a few apparent groups (Figure 8). Mutton Snapper grouped strongly with Gray Snapper. Red Grouper and Gag again clustered tightly. Two deepwater complexes were identified, one containing Blueline Tilefish, Speckled Hind, Snowy Grouper, and Queen Snapper, the other containing Yellowedge Grouper, Tilefish, Warsaw Grouper, and Wenchman. Red Snapper was also loosely associated with this second deepwater complex.
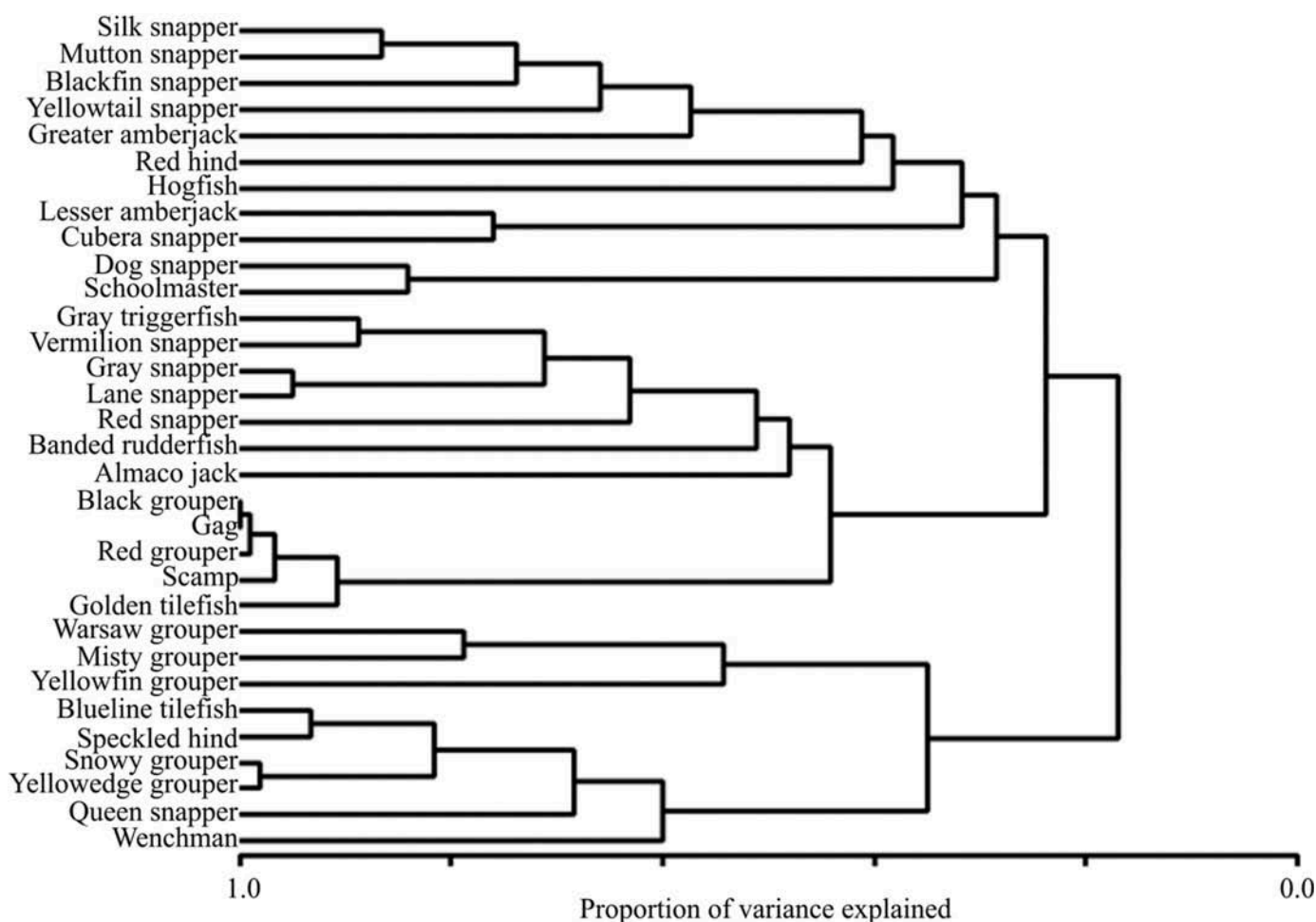
FIGURE 3. Dimension reduction cluster analysis of presence–absence for Gulf of Mexico reef fish commercial longline landings (2005–2009) aggregated by year, month, area, and depth (linkage: VARCLUS; measure: proportion variance explained; transformation: binary).

Nodal Analysis and Correlation

Geographic differences in the distribution of landings by the CVL sector explain many of the patterns observed in Figure 4. For example, Mutton Snapper, Yellowtail Snapper, and Hogfish were most frequently landed in the Florida Keys. A nodal analysis of median Pearson correlation values aggregated across the six fishery data sets provides additional validation of the observed clusters as well as guidance in the placement of rare species into complexes (Figure 9). Apparent nodes were formed by moderate-depth snapper species and jacks, deepwater snapper species and tilefish, deepwater grouper, shallow-water snapper, and grouper. Median correlation values were high between "jacks" (i.e., Almaco Jack and Banded Rudderfish), "deepwater" stocks (i.e., Queen Snapper with Blueline Tilefish and Snowy Grouper, Blackfin Snapper with Silk Snapper, Anchor Tilefish with Blueline Tilefish and Snowy Grouper, Blackline Tilefish with Yellowedge Grouper, and Wenchman with Warsaw and Yellowedge Grouper), and "shallow-water"

snapper (i.e., Cubera Snapper with Mutton Snapper and Dog Snapper with Schoolmaster)

The weighted mean cluster association index provided a quantitative approach to synthesizing the information contained in the 26 unique cluster analyses performed. Stocks were arranged by association and vulnerability to provide guidance on management complexes. Vulnerability was defined using productivity–susceptibility analysis (PSA) scores of overall risk from a MRAG Americas Gulf of Mexico Final Report (MRAG Americas 2009a). Among the 42 species analyzed, eight major complexes were identified, with some potential subgroups due to differences in life history (Table 4). The results presented in Table 4 are explored further in the Discussion.

Maps of Stock Distributions

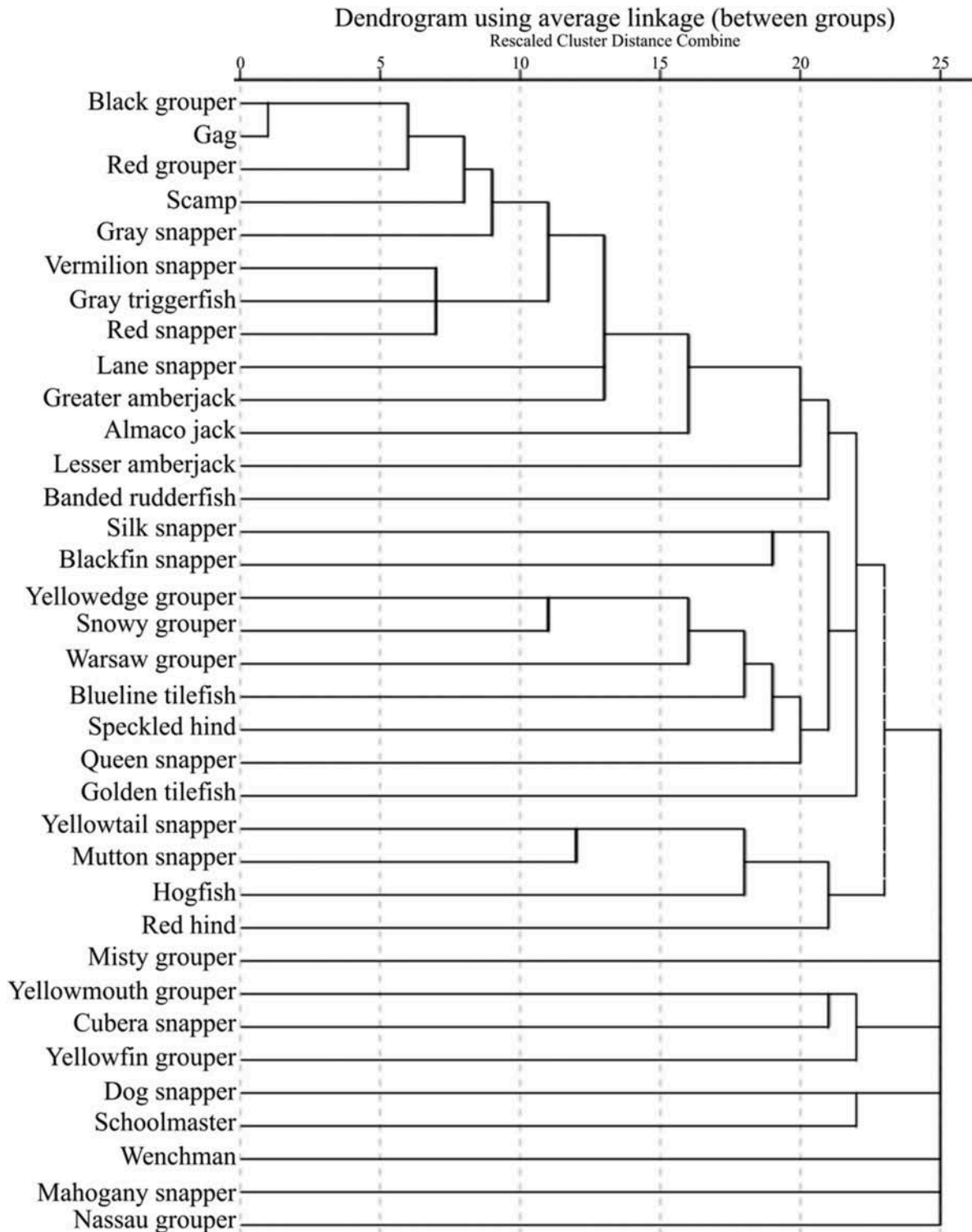Maps of the distribution of the observed BLL and RFOP interactions with managed Gulf species provide insight into

FIGURE 4. Hierarchical cluster analysis of species presence–absence in Gulf of Mexico reef fish commercial vertical line landings aggregated by year, month, area, and depth (linkage: between [average]; measure: Sørenson [binary]).

the outcomes of the cluster analyses described above (Figure 10). Gray Snapper were most commonly encountered in shallow to middepth waters from central Florida to the Big Bend, with some landings off Louisiana and Texas (Figure 10A). Cubera, Dog, Mutton, and Yellowtail Snapper were most commonly encountered off southwest
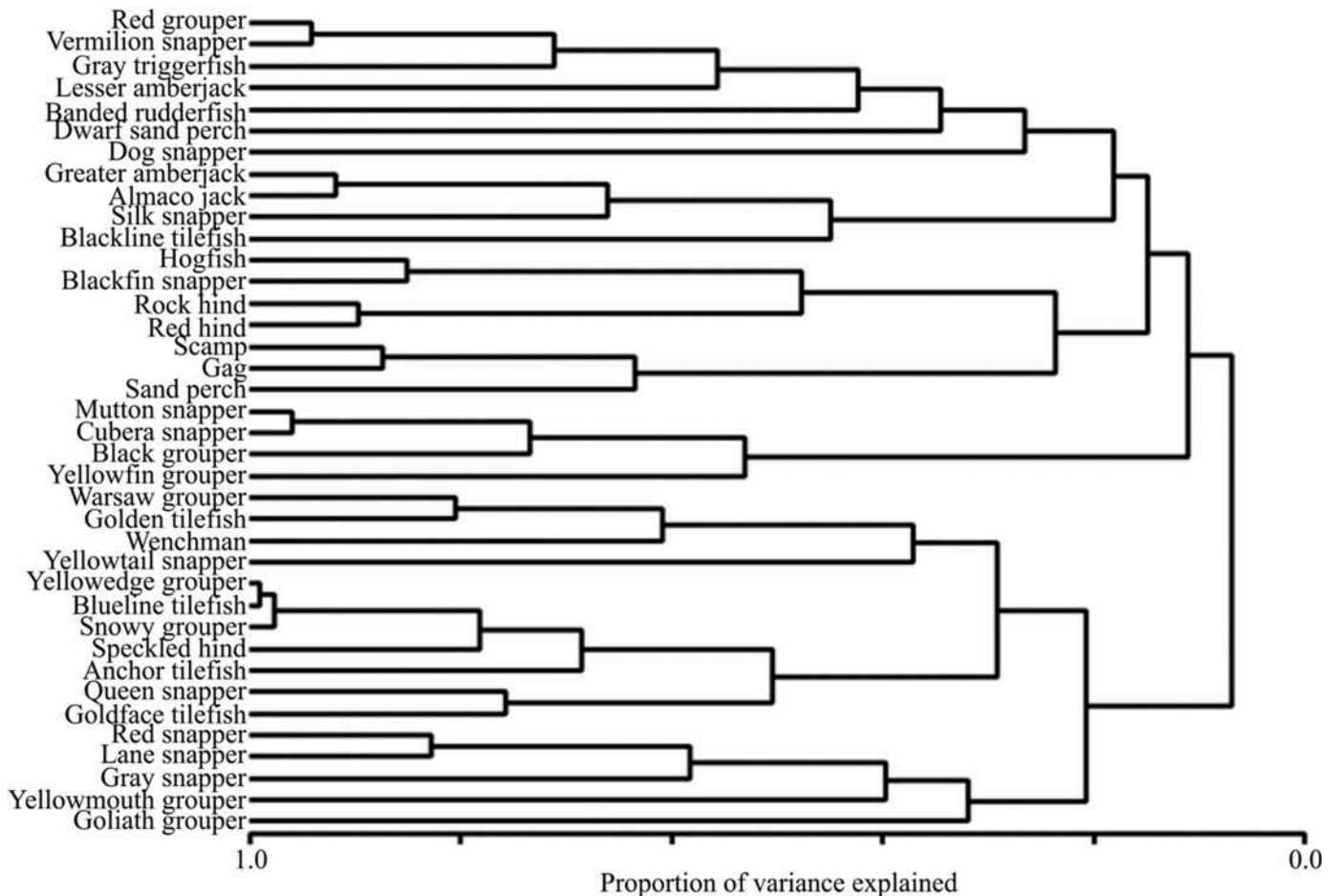
FIGURE 5. Dimension reduction cluster analysis of species presence–absence in Gulf of Mexico reef fish observer program landings aggregated at the individual set level (linkage: VARCLUS; measure: proportion variance explained).

Florida (Figure 10A). Red and Vermilion Snapper were ubiquitous in the Gulf at a broad range of depths (Figure 10B). Red Snapper co-occurred with Vermilion Snapper but also appeared inshore (Figure 10B). Silk Snapper were rarely encountered but occurred in the deeper portion of the Red and Vermilion Snapper distributions (Figure 10B). Gray Triggerfish and Lane Snapper co-occurred with Red and Vermilion Snapper; Gray Triggerfish were most common off West Florida and the Panhandle and Lane Snapper off West Florida and Louisiana (Figure 10B).

Jack stocks were encountered throughout the Gulf but less frequently off Texas (Figure 10C). Greater Amberjack encounters were broadly distributed, overlapping all other species and extending into much deeper waters off West Florida. The Lesser Amberjack and Almaco Jack distributions overlapped. Banded Rudderfish were less commonly encountered outside of Florida.

The bulk of shallow-water grouper encounters were between Red Grouper and Gag, which were heavily concentrated off West Florida at a broad range of depths

(Figure 10D). Black Grouper were most commonly encountered off southwest Florida. Red and Rock Hind occurred on the inshore portion of the Red Grouper and Gag distribution. Yellowmouth Grouper co-occurred with Red Grouper and Scamp. Scamp were observed predominantly along the deeper portion of the Gag and Red Grouper distribution off West Florida but were broadly distributed throughout the Gulf, typically at depths between 91 and 327 m. The tendency of Scamp to occasionally cluster with moderate-depth species was probably due to their high concentration off the coast of Louisiana, where there are large fisheries for Almaco Jack, Red Snapper, and Vermilion Snapper; other shallow-water grouper species are less common and longline fishing is prohibited in waters 91 m or less in depth.

The broad, overlapping distributions of Snowy and Yellowedge Grouper help explain the consistency observed in the clustering of these stocks across analyses (Figure 10E). Speckled Hind, Warsaw Grouper, and Wenchman were more broadly distributed across depths. Speckled Hind were most
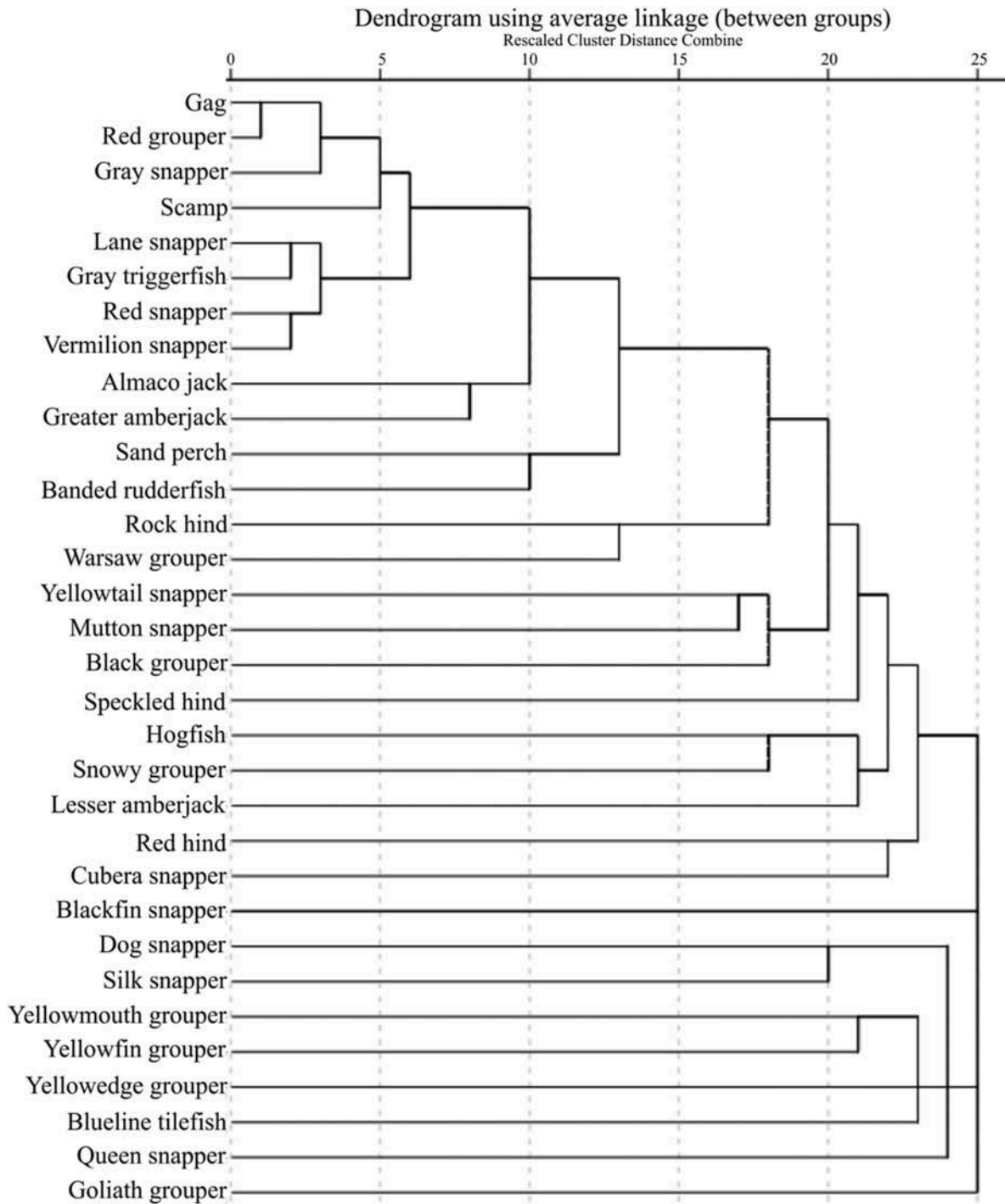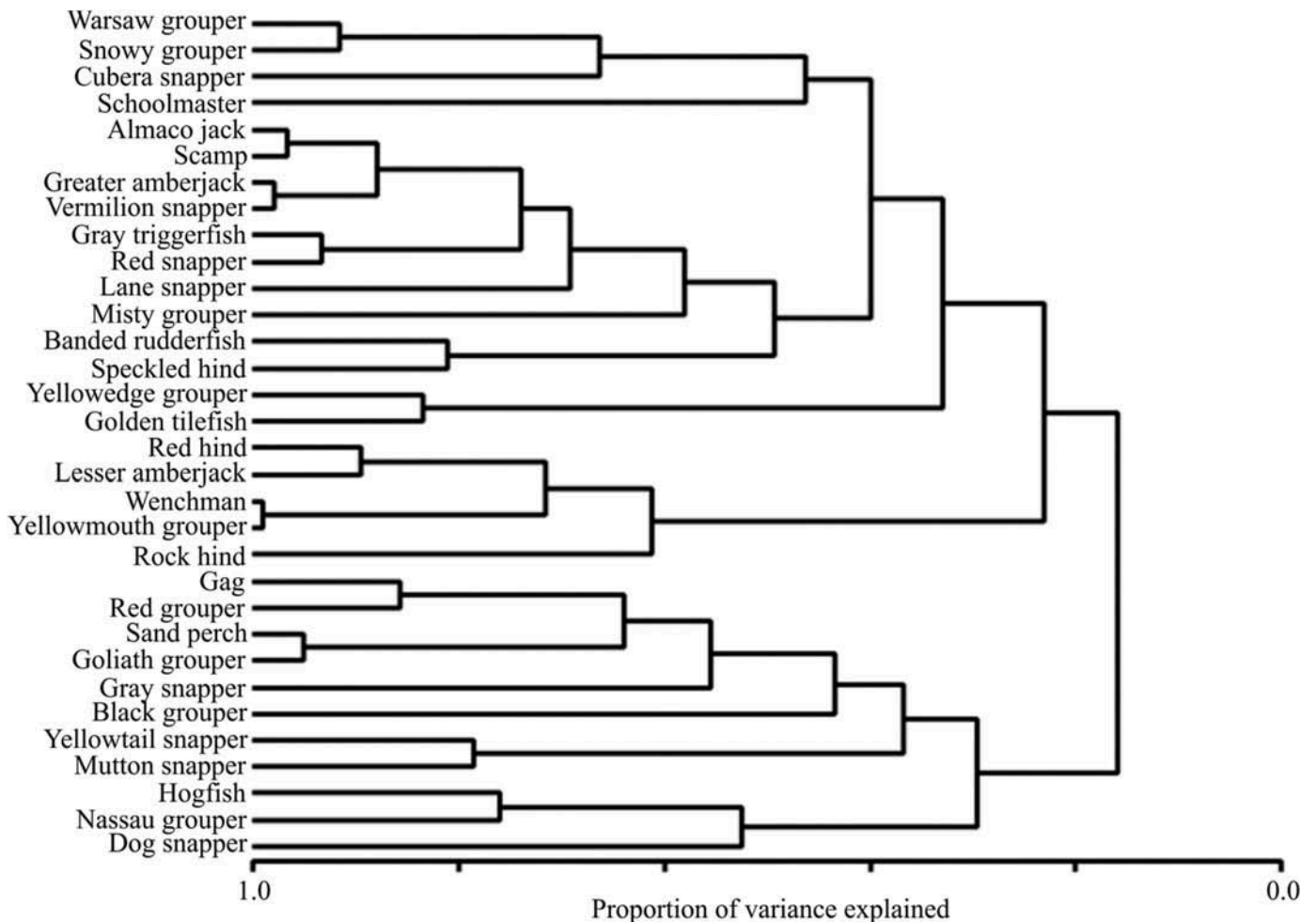
FIGURE 6. Hierarchical cluster analysis of species presence–absence in Gulf of Mexico reef fish headboat landings aggregated by year, month, trip duration, and area fished (linkage: average [between]; measure: Sørenson [binary]).

commonly encountered off West Florida. Queen Snapper were rarely encountered but co-occurred with Snowy Grouper when observed.

Tilefish were encountered in the deepest waters and were broadly distributed across the Gulf (Figure 10F). In contrast,

Blueline Tilefish co-occurred with Tilefish off Florida but were also encountered in shallower waters. Anchor, Blackline, and Goldface Tilefish were all very rare but were observed co-occurring with both Blueline Tilefish and Tilefish.

FIGURE 7. Dimension reduction cluster analysis of species presence–absence in Gulf of Mexico reef fish recreational MRFSS-reported landings aggregated by year, wave, mode of fishing, and area fished (linkage: VARCLUS; measure: proportion variance explained; transformation: binary).

DISCUSSION

A comprehensive understanding of concurrent stock vulnerabilities to various fisheries is critical to achieving the goals of ACL/AM management. The myriad of statistical approaches explored in this study tell a relatively consistent story regarding what stocks might be impacted by similar management measures. By considering fishery and ecosystem variables such as life history, vulnerability, sector, gear, area, and depth fished, these analyses provide insights that may facilitate multispecies or place-based management. The impacts of regulatory measures for one species on associated species are more easily understood when the associations between the species have been quantified by gear and the spatial distributions of these species are better understood. For this reason, the establishment of complexes of associated species may help reduce bycatch by linking regulations to species that are frequently caught together.

Of the cluster analysis input variables, depth appeared to be the most important, and apparent shallow-water, moderate depth, and deepwater assemblages appeared in most analyses. A similar approach by Bortone et al. (1979) also found that community association was predominantly influenced by depth, with substrate, latitude, and season also playing significant roles. Identified assemblages varied slightly by data set. The HBS data set contained less information for deepwater stocks because they are farther offshore and not often targeted by limited-duration headboat trips. The CLL data set contained less information for shallow-water stocks because commercial bottom longlining is prohibited inshore of 36-m depth in the eastern Gulf of Mexico and 91-m depth in the western Gulf (e.g., west of Cape San Blas, Florida). Subtle spatial trends were also observed in assemblages. For example, in many data sets, Mutton Snapper, Red Hind, Yellowtail Snapper, and Hogfish formed a tropical assemblage due to their high landings in the Florida Keys. Genus was also important; for example, snappers and groupers were often separated. This may be due to differences in vulnerability to different gear types and fishing methods as well as to
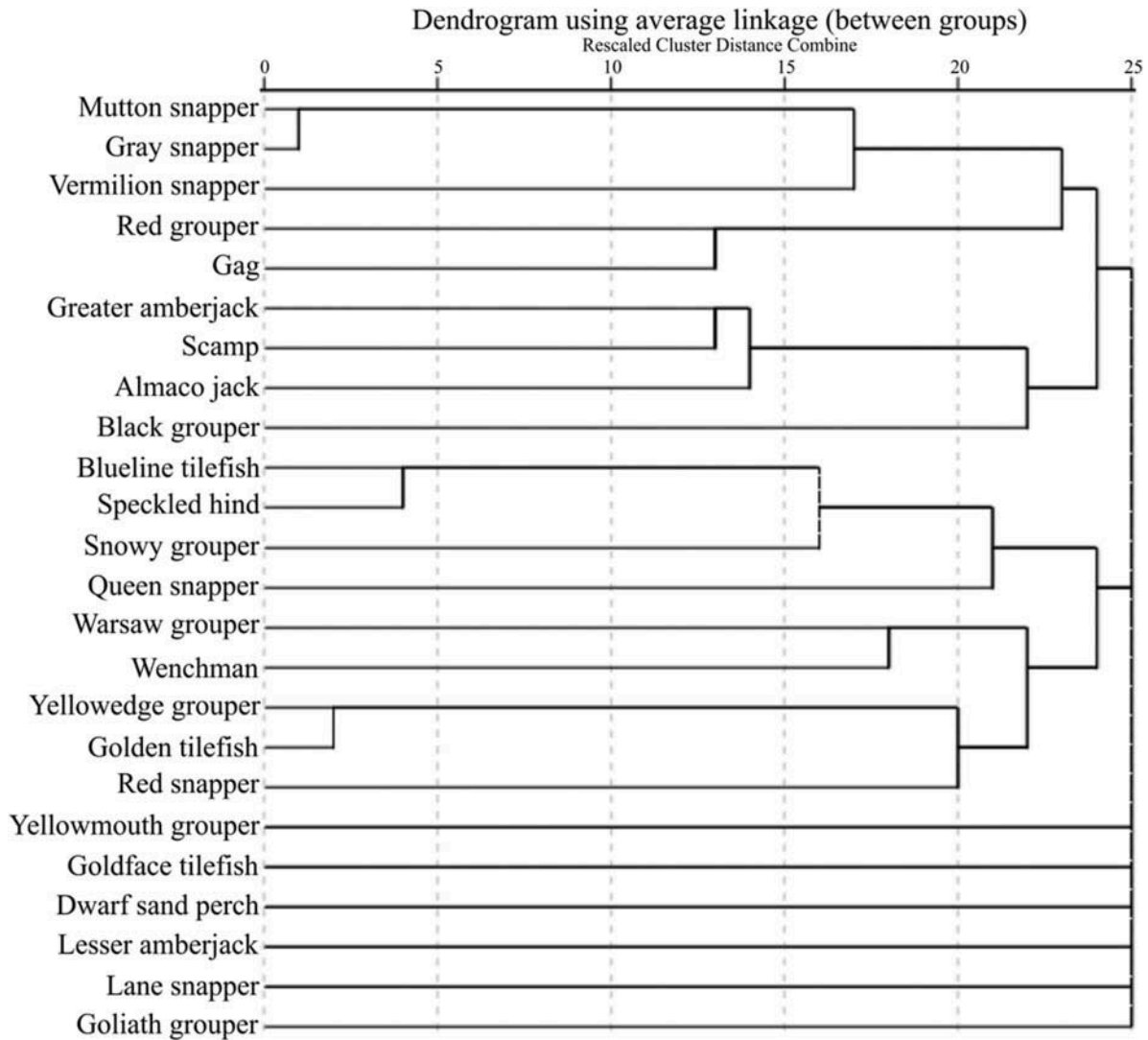
Dendrogram using average linkage (between groups)

FIGURE 8. Hierarchical cluster analysis of species presence–absence in Gulf of Mexico NMFS bottom-longline survey landings aggregated by set (linkage: average [between], measure: Sørenson [binary]).

differences in geographic and depth distributions. In addition, years of overexploitation may have altered community structure (Hughes 1994).

Although the cluster analyses were based on vulnerabilities to selective types of fishing gear, the major controlling factors included season, area, and depth; thus, some aspects of life history were included de facto in the analyses. These analyses mostly supported the Gulf Council's deepwater grouper IFQ assemblage of Yellowedge Grouper, Snowy Grouper, Warsaw Grouper, Speckled Hind, and Misty Grouper (Table 4). Due to their distance from shore and the specialized types of gear required to capture the deepwater component of these stocks, there was a low relative percentage of encounters of these species in all but the CLL and BLL data sets (Table 3). Yellowedge and Snowy Grouper stocks had extremely high weighted mean cluster association index values and have

overlapping geographic distributions (Figure 10E). The Yellowedge Grouper is extremely long-lived and highly productive compared with other members of this complex (Table 1). Warsaw Grouper is the most vulnerable member of this complex and was most highly associated with Misty and Snowy Grouper (Table 4). As with Speckled Hind, there is a substantial inshore fishery for Warsaw Grouper in addition to the core deepwater component of the stock (Figure 10E). Fishing gear rarely interacted with Misty Grouper and Speckled Hind; however, reported encounters were most often associated with other deepwater stocks such as Warsaw Grouper and various tilefish species (Table 4).

A snapper assemblage was identified for middepth to deep water that comprised Blackfin Snapper, Silk Snapper, Wenchman, and Queen Snapper. Blackfin and Silk Snapper often strongly clustered together. Queen Snapper and
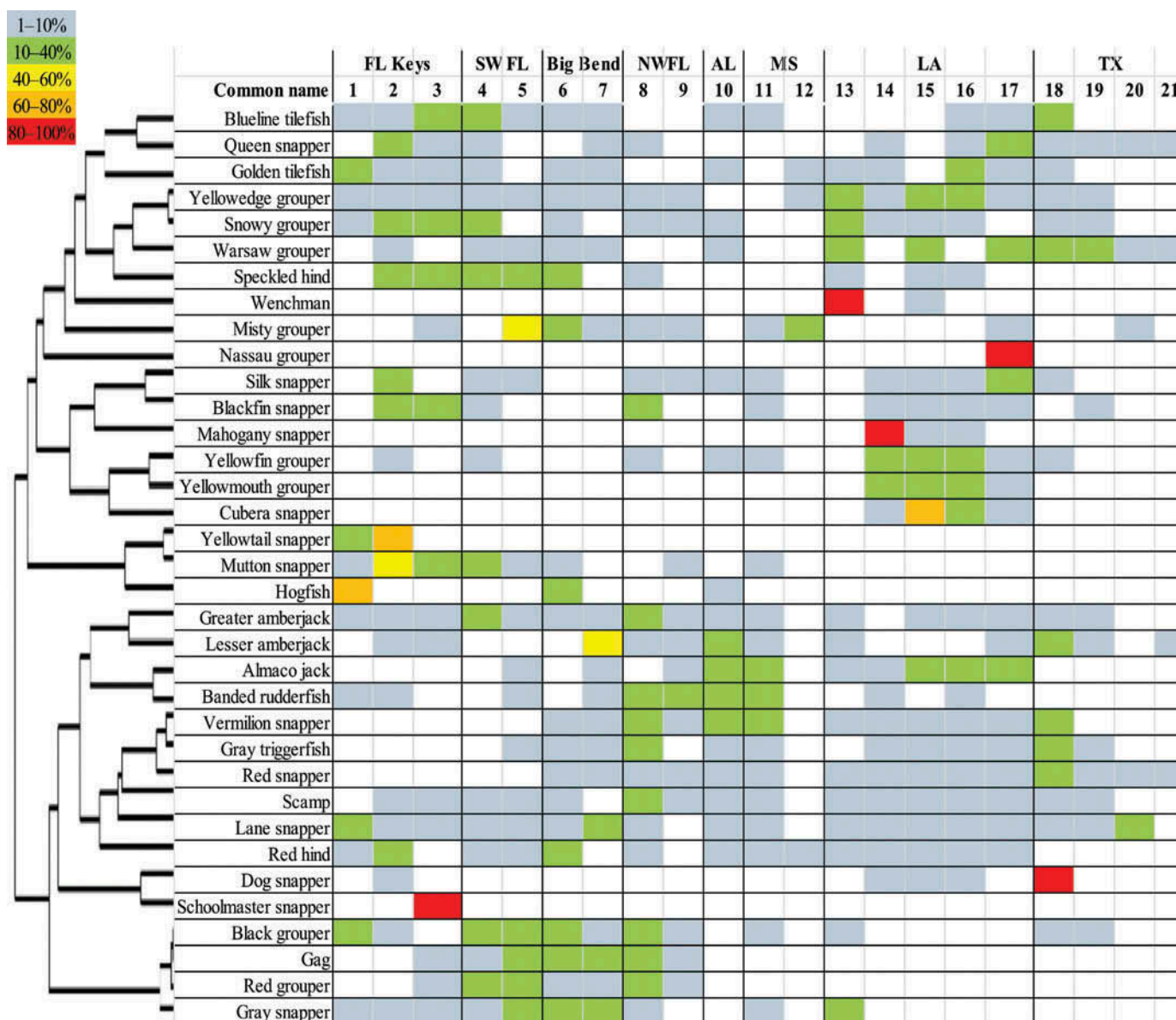
FIGURE 9. Plot of species presence–absence for Gulf of Mexico reef fish commercial vertical line landings aggregated by year, month, area, and depth (linkage: VARCLUS; measure: proportion variance explained; transformation: binary) relative to the percent of landings (2005–2009) originating from commercial logbook statistical areas 1–21. Similar color patterns in adjacent rows illustrate the importance of stock spatial distributions for the resultant clusters. Abbreviations are as follows: SW FL = southwest Florida, NWFL = northwest Florida, AL = Alabama, MS = Mississippi, LA = Louisiana, and TX = Texas.

Wenchman landings were relatively rare but the two species appeared to be loosely associated with each other and other deepwater species (Table 4).

Our analyses support the current tilefish assemblage, although there were moderately high levels of association with several deepwater groupers, which suggest that management regulations applied to stocks in either assemblage might affect stocks in the other (Table 4). Tilefish occur at depths similar to those of Yellowedge Grouper and are occasionally caught on the same set, but they are less structure affiliated, preferring soft-bottom habitats on the upper continental slope (Palmer et al. 2004; Sedberry et al. 2006). Tilefish clustered with other deepwater species but was often separated from the other members of the complex (see Figure 4). Blueline Tilefish frequently clustered with Speckled Hind, along with other deepwater stocks (Table 4). The distributions of both Blueline Tilefish and Speckled Hind extend farther inshore along the West Florida shelf than do those of the other

TABLE 4. Potential stock complexes derived from weighted mean cluster association indexes (in parentheses) indicating the top five associated species for each species. Productivity–susceptibility analysis (PSA) scores of overall risk from 15 MRAG Americas Gulf of Mexico final reports are provided when available (MRAG Americas 2009a). Solid lines separate major groups, while dashed lines show potential life history-based subgroups. Bold type indicates species for which the stock assessment includes a recommendation as to the allowable biological catch; italics indicate assessed species for which there is no recommendation. Abbreviations are as follows: GR = Grouper, Snap = Snapper, Amber = Amberjack, Rudder = Rudderfish, Tile = Tilefish, and Trigger = Triggerfish.

| Species | Top five associated species | | | | | PSA |
	1	2	3	4	5	
Misty Gr	Warsaw Gr (0.36)	Snowy Gr (0.13)	Silk Snap (0.02)	Queen Snap (0.01)	Speckled Hind (0.04)	3.66
Warsaw Gr	Misty Gr (0.48)	Snowy Gr (0.13)	Silk Snap (0.06)	Yellowedge Gr (0.04)	Warsaw Gr (0.07)	3.89
Snowy Gr	Yellowedge Gr (0.37)	Silk Snap (0.36)	Greater Amber (0.24)	Red Gr (0.23)	Warsaw Gr (0.04)	3.54
Yellowedge Gr	Snowy Gr (0.42)	Tilefish (0.28)	Blueline Tile (0.19)	Queen Snap (0.08)	Yellowmouth Gr (0.06)	3.64
Speckled Hind	Gag (0.23)	Blueline Tile (0.2)	Cubera Snap (0.13)	Banded Rudder (0.12)	Warsaw Gr (0.04)	3.42[a]
Blueline Tile	Tilefish (0.29)	Vermilion Snap (0.29)	Speckled Hind (0.23)	Yellowedge Gr (0.18)	Queen Snap (0.11)	3.4[a]
Tilefish	Blueline Tile (0.3)	Yellowedge Gr (0.29)	Wenchman (0.15)	Snowy Gr (0.05)	Warsaw Gr (0.04)	3.33
Goldface Tile	Anchor Tile (0.5)	Blackline Tile (0.5)	Queen Snap (0.03)	Dog Snap (0.01)	Atlan Goliath Gr (0.01)	
Anchor Tile	Blackline Tile (0.5)	Goldface Tile (0.5)				
Blackline Tile	Anchor Tile (0.5)	Goldface Tile (0.5)				
Gray Trigger	Red Snap (0.48)	Vermilion Snap (0.23)	Wenchman (0.23)	Lane Snap (0.18)	Blackfin Snap (0.16)	2.46[a]
Lane Snap	Gray Trigger (0.13)	Vermilion Snap (0.08)	Red Gr (0.07)	Gray Snap (0.05)	Wenchman (0.02)	2.99
Red Snap	Gray Trigger (0.23)	Vermilion Snap (0.08)	Red Gr (0.08)	Snowy Gr (0.06)	Greater Amber (0.06)	3.37
Vermilion Snap	Gray Trigger (0.29)	Greater Amber (0.21)	Lane Snap (0.18)	Blueline Tile (0.18)	Scamp (0.17)	3.07
Lesser Amber	Banded Rudder (0.61)	Greater Amber (0.04)	Vermilion Snap (0.04)	Cubera Snap (0.02)	Red Hind (0.02)	3.64
Banded Rudder	Lesser Amber (0.72)	Speckled Hind (0.04)	Almaco Jack (0.04)	Snowy Gr (0.01)	Rock Hind (0.01)	3.26[a]
Greater Amber	Almaco Jack (0.32)	Vermilion Snap (0.16)	Red Gr (0.11)	Scamp (0.08)	Red Snap (0.07)	3.23
Almaco Jack	Greater Amber (0.28)	Scamp (0.28)	Black Gr (0.21)	Banded Rudder (0.04)	Vermilion Snap (0.03)	3.35[a]
Scamp	Almaco Jack (0.31)	Gag (0.14)	Black Gr (0.1)	Red Gr (0.04)	Vermilion Snap (0.03)	3.25
Gag	Black Gr (0.46)	Red Gr (0.44)	Gray Snap (0.43)	Speckled Hind (0.23)	Tilefish (0.18)	3.52
Black Gr	Gag (0.47)	Almaco Jack (0.26)	Cubera Snap (0.23)	Scamp (0.15)	Mutton Snap (0.14)	3.48
Red Gr	Gag (0.19)	Black Gr (0.14)	Greater Amber (0.11)	Red Snap (0.11)	Yellowedge Gr (0.11)	3.28
Red Hind	Schoolmaster (0.5)	Rock Hind (0.39)	Lesser Amber (0.03)	Hogfish (0.01)	Yellowtail Snap (0.01)	3.05
Rock Hind	Red Hind (0.4)	Yellowmouth Gr (0.24)	Gray Snap (0.05)	Snowy Gr (0.04)	Warsaw Gr (0.02)	3.23[a]
Yellowfin Gr	Mutton Snap (0.27)	Yellowmouth Gr (0.25)	Nassau Gr (0.24)	Cubera Snap (0.03)	Warsaw Gr (0.01)	3.39[a]
Yellowmouth Gr	Yellowfin Gr (0.25)	Nassau Gr (0.25)	Gray Snap (0.2)	Rock Hind (0.05)	Wenchman (0.04)	3.2[a]

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TABLE 4. Continued.

| Species	Top five associated species					PSA
	1	2	3	4	5	
Atlan Goliath Gr	Yellowedge Gr (0.19)	Tilefish (0.04)	Warsaw Gr (0.03)	Misty Gr (0.01)	Red Gr (0.01)	3.42
Nassau Gr	Yellowmouth Gr (0.24)	Yellowfin Gr (0.24)	Dog Snap (0.17)	Mahogany Snap (0.16)	Yellowtail Snap (0.1)	3.3
Sand Perch	Atlan Goliath Gr (0.03)	Yellowtail Snap (0.01)	Dog Snap (0.01)	Mahogany Snap (0.01)		--
Dwarf Sand Perch	Blackfin Snap (0.39)	Gray Trigger (0.05)				--
Blackfin Snap	Dwarf Sand Perch (0.66)	Wenchman (0.48)	Silk Snap (0.21)	Mutton Snap (0.05)	Tilefish (0.01)	3.36[a]
Silk Snap	Snowy Gr (0.23)	Blackfin Snap (0.23)	Blueline Tile (0.16)	Vermilion Snap (0.08)	Mutton Snap (0.06)	3.52
Wenchman	Blackfin Snap (0.39)	Gray Trigger (0.16)	Tilefish (0.16)	Warsaw Gr (0.11)	Queen Snap (0.07)	
Queen Snap	Hogfish (0.8)	Blueline Tile (0.07)	Misty Gr (0.02)	Speckled Hind (0.01)	Yellowedge Gr (0.01)	3.08[a]
Hogfish	Queen Snap (0.82)	Nassau Gr (0.03)	Mutton Snap (0.02)	Yellowtail Snap (0.02)	Black Gr (0.01)	3.05
Mutton Snap	Yellowfin Gr (0.5)	Schoolmaster (0.48)	Yellowtail Snap (0.3)	Silk Snap (0.24)	Gray Snap (0.05)	3.27
Schoolmaster	Mutton Snap (0.4)	Red Hind (0.27)	Dog Snap (0.02)			3.49[a]
Dog Snap	Yellowtail Snap (0.41)	Nassau Gr (0.17)	Mahogany Snap (0.17)	Schoolmaster (0.17)		3.29[a]
Yellowtail Snap	Dog Snap (0.62)	Mutton Snap (0.22)	Mahogany Snap (0.17)	Nassau Gr (0.17)	Hogfish (0.17)	2.84
Mahogany Snap	Cubera Snap (0.17)	Blackfin Snap (0.15)	Yellowmouth Gr (0.1)	Silk Snap (0.09)	Dog Snap (0.06)	3.55[a]
Cubera Snap	Black Gr (0.21)	Speckled Hind (0.15)	Gag (0.04)	Snowy Gr (0.03)	Warsaw Gr (0.01)	3.92[a]
Gray Snap	Mutton Snap (0.5)	Gag (0.24)	Mahogany Snap (0.18)	Vermilion Snap (0.17)	Red Gr (0.1)	3.17

[a] MRAG Americas 2009b.

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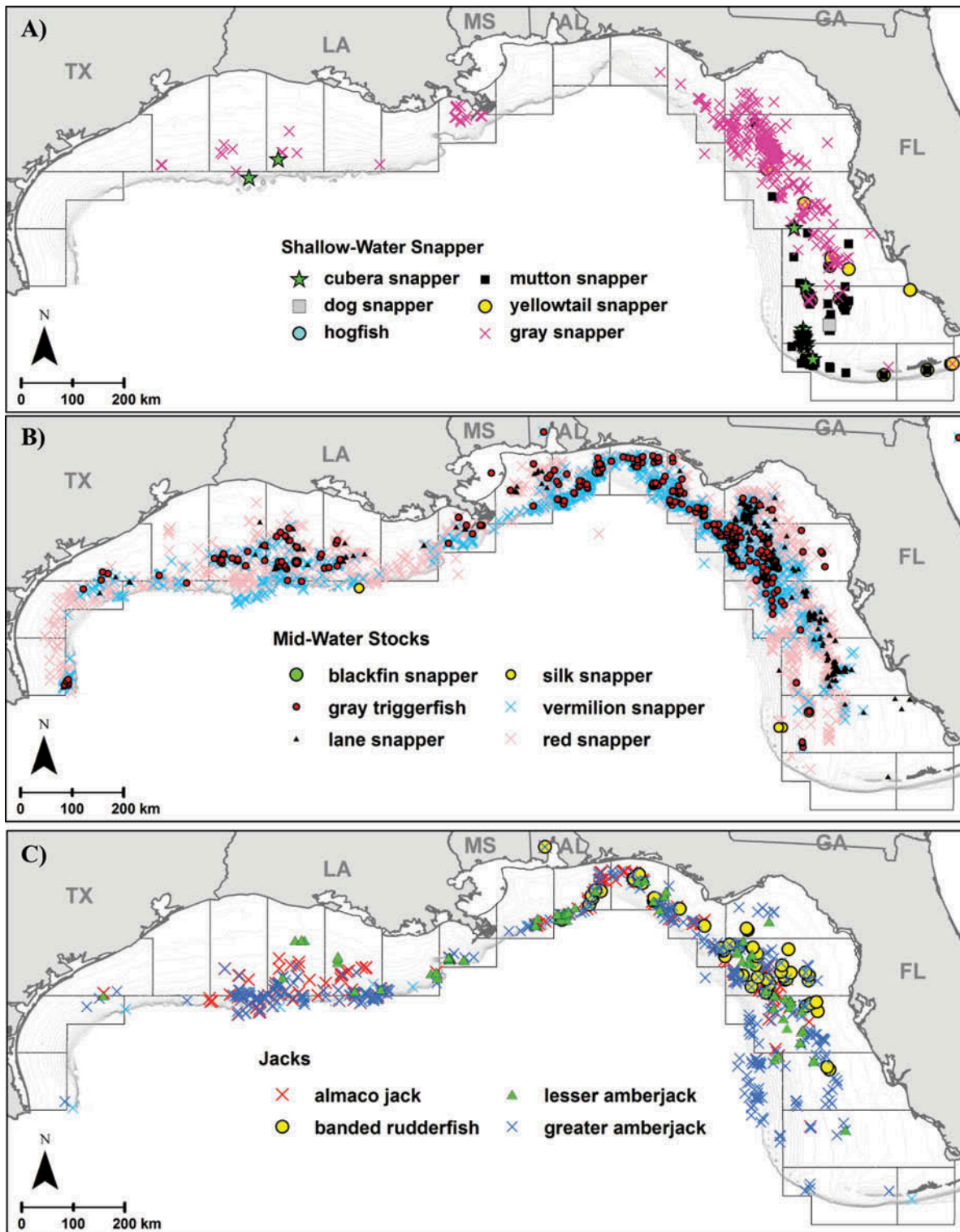
FIGURE 10. Maps of aggregated NMFS bottom-longline survey and Reef Fish Observer Program observations of **(A)** shallow-water snapper, **(B)** midwater stocks, **(C)** jacks, **(D)** shallow-water grouper, **(E)** deepwater grouper, and **(F)** tilefish groupings relative to bathymetry and commercial fishery statistical reporting areas in the Gulf of Mexico. Some observations were removed to maintain confidentiality.
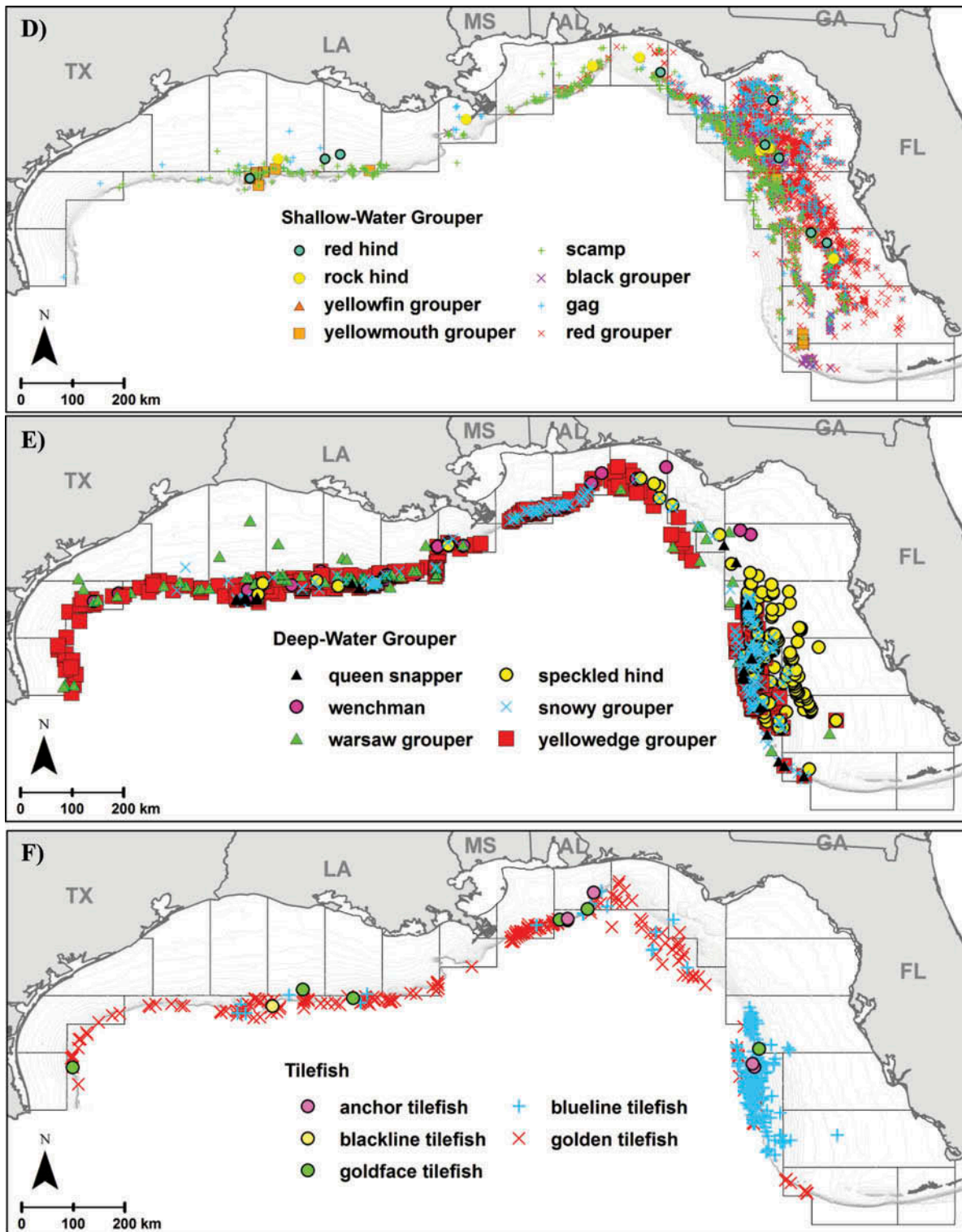
FIGURE 10. Continued.

deepwater stocks (Figure 10D–F). Blueline Tilefish prefer irregular, rocky bottom from the outer shelf edge to the upper slope (Struhsaker 1969; Ross 1978; Ross and Huntsman 1982; Parker and Ross 1986; Harris et al. 2004). Blueline Tilefish, Snowy Grouper, Warsaw Grouper, Speckled Hind, Yellowedge Grouper, and Greater Amberjack have all been documented to co-occur on the top edge of sinkholes (Reed et al. 2005). Little is known about Anchor, Blackline, and Goldface Tilefish, but they may co-occur and even share burrows with Blueline Tilefish and Tilefish (Able et al. 1987).

The four managed jack species (Greater Amberjack, Lesser Amberjack, Banded Rudderfish, and Almaco Jack) were highly associated (Table 4) and were most frequently encountered by the HBS and CLL sectors (Table 3). SEDAR-15 (2008) concluded that Lesser Amberjack and Almaco Jack were correctly identified in most instances, but smaller Greater Amberjack and Banded Rudderfish were often misidentified. Misidentifications might lead to problems computing single-species ACLs for these species unless the rate of misidentification is quantifiable or has been constant through time. Encounters off the West Florida Shelf beyond 236 m were almost exclusively with Greater Amberjack; thus, regulatory changes on the deepwater component of any jacks complex might impact only Greater Amberjack (Figure 10C). Managing these jacks as a complex would mitigate issues with species identification.

Several species occurring at moderate depths consistently clustered together: Gray Triggerfish and Vermilion, Red, and Lane Snapper (Table 4). Their clusters often overlapped with some of the more broadly distributed shallow-water species, such as Gray Snapper, Scamp, Red Grouper, and Mutton Snapper. Gray Triggerfish and Vermilion, Red, and Lane Snapper were most consistently encountered in the HBS data (Table 3) and were strongly associated in this data set (Figure 6). Among the snappers, the strongest association was between Red and Vermilion Snapper (Table 4). Although Gray Triggerfish clustered with these snapper species, it may be desirable to manage it separately due to differences in its life history (Table 1). Red and Vermilion Snapper are both highly productive stocks and are ubiquitously distributed throughout the Gulf (Figure 10B).

Our analyses partly support the Gulf IFQ program's shallow-water grouper complex of Red, Black, Yellowmouth, and Yellowfin Grouper, Red and Rock Hind, Scamp, and Gag (Table 4). Red Grouper and Gag consistently clustered together and were often clustered with Scamp and Black Grouper (Table 4). Black Grouper and Gag were highly associated in the CLL and CVL clusters, but this is likely an artifact of the misidentification adjustment that was applied. These species were separated in the HBS clusters (Figure 6). Although these species overlap in their distributions and are vulnerable to the same gear types and fishing techniques, the core of the Black Grouper distribution is in the Florida Keys, whereas the Gag is nearly ubiquitous across the eastern Gulf (Figure 10D). Red Hind, Rock Hind, Yellowfin Grouper, and

Yellowmouth Grouper were rarely encountered but were associated with each other when they were (Table 4). An assessed species (Gag) is the most vulnerable species in the complex (Table 4).

The clustering for shallow-water snappers (i.e., Gray, Mutton, Yellowtail, Cubera, Dog, and Mahogany Snapper and Schoolmaster) was reasonably tight (Table 4). These stocks are primarily found on the West Florida Shelf (Figure 10A). Of these, Gray, Mutton, and Yellowtail Snapper are abundant, but encounters with other shallow-water snapper species are rare (Table 3). Gray Snapper was most commonly encountered in the MRFSS and formed a somewhat distinct cluster (Table 3; Figure 7). Gray Snapper is common in Florida waters, especially in the Florida Keys, where it co-occurs to some extent with Mutton Snapper; but it also has a sizeable fishery on the offshore reefs and oil rigs in the western Gulf of Mexico. This may explain why Gray Snapper sometimes clustered with shallow-water groupers (i.e., Gag and Scamp) and moderate-depth snapper species (i.e., Lane and Red Snapper).

Yellowtail Snapper was most common in the CVL data set, where it clustered with Mutton Snapper and Hogfish. Yellowtail Snapper was most highly correlated and associated with Dog and Mutton Snapper (Table 4). Mutton Snapper was associated with Schoolmaster and Yellowtail and Gray Snapper. Gulf landings of Hogfish, Mutton Snapper, and Yellowtail Snapper are predominantly concentrated in southwest Florida and the Florida Keys (Figure 10A). The unique fishing techniques used to land Yellowtail Snapper (surface chumming and unweighted lines) and Hogfish (spearfishing) may make them good candidates for species-specific ACLs.

Clustering the rare snapper species was done primarily through an examination of the nodal analysis and weighted mean cluster association index output (Figure 9; Table 4). Schoolmaster was highly correlated with Dog and Mutton Snapper and highly associated with Mutton, Dog, Yellowtail, and Cubera Snapper. Cubera Snapper has a life history similar to that of Mutton Snapper (Figure 2). Dog Snapper was highly correlated and associated with Yellowtail Snapper (Table 4). Mahogany Snapper was only recorded in the CVL data set, and every trip landing a Mahogany Snapper also landed a Gray Snapper. Mahogany Snapper was associated with Cubera Snapper (Table 4).

The Magnuson–Stevens Fishery Conservation and Management Reauthorizatoin Act of 2006 requires that fishery management plans "establish a mechanism for specifying annual catch limits . . . at a level such that overfishing does not occur in the fishery." Setting stock-specific ACLs for many unassessed stocks may be unrealistic because data are inadequate for determining stock status relative to established status determination criteria. Many of these stocks are data poor, difficult to identify, or experience extreme fluctuations in relative landings due to their large year-classes, rarity, inadequate data collection procedures, or

lack of targeted fishing effort. Using stock complexes to set ACLs may be the best management option when formal stock assessments are unavailable and the data requirements (e.g., a stable catch for several years and reliable estimates of natural mortality) of other methods (such as depletion-adjusted average catch; MacCall 2007) are not met. Using stock complexes for ACL/AM management reduces the management burden for quota monitoring and may help mitigate the impacts of uncertainty in landings data or species identification by pooling data-poor species. Another option would be to use assessed stocks as indicator species; however, the use of an indicator species implicitly assumes that the population trends of that species reflect those of others in the assemblage (Simberloff 1998; Zacharias and Roff 2001; Carignan and Villard 2002)—an assumption that is often violated in practice (Niemi et al. 1997). For an assessed stock to be an appropriate indicator stock for a stock complex, assessed stocks and unassessed stocks in the complex should show similar trends in population abundance in response to environmental forcing, fishing pressure, and fisheries management regulations. Unfortunately, it is extremely difficult to separate out these signals for Gulf stocks given the absence of fishery-independent data (e.g., Jay 1996; Collie et al. 2008).

Using fishery-dependent data as a proxy for trends in population abundance introduces several layers of bias (e.g., gear, spatial, temporal, and depth) into any evaluation of indices of abundance. These biases might generate spurious correlations that would be difficult to separate from actual population trends (May and MacArthur 1972; Landres et al. 1988; Leibold 1995; Niemi et al. 1997; Shaul et al. 2007; Shertzer and Williams 2008). In the absence of a fully resolved analysis of indices of abundance that adequately controls for the confounding variability introduced by environmental forcing, fishing pressure, and fisheries management regulations, a comprehensive understanding of co-occurrence in the catch across sectors is critical to simplifying ACL/AM management. Simberloff (1998) recommends identifying keystone species instead, which might not be assessed or even appropriate targets for management but whose activities govern the well-being of many other species. Unfortunately, keystone species are difficult to identify. More recently, the establishment of fully protected areas in representative habitats has been suggested as a way to restore natural ecosystem dynamics and protect a portion of the reproductive stock (Bohnsack et al. 2004; Lindenmayer et al. 2006).

In establishing stock complexes, managers should consider the geographic and depth distribution of species, along with their life history characteristics, exploitation patterns, and vulnerabilities. As new information and understanding of species linkages and complexes arises, managers should adapt their management strategies. This will allow for proactive management that accounts for ecosystem-based management considerations (such as temporal fluctuations in stock abundance due to environmental forcing or multispecies interactions) as well as comprehensive assessments of the impacts of regulations on associated species. For this approach to succeed, data collection will need to aim at developing a high-resolution map of the biogeographic distribution of fish stocks and the spatial distribution of fishing effort as well as improved estimation of life history parameters and the trophic linkages between species. This approach is especially relevant given that community structure may change through time (Shertzer et al. 2009) due to heavy exploitation (Hughes 1994; McClenachan 2009), invasive species (Albins and Hixon 2008), habitat degradation (Hoss and Engel 1996; Anderson et al. 2008), and climate change (Holbrook et al. 1997; Attrill and Power 2002; Genner et al. 2004; Perry et al. 2005; Collie et al. 2008). Similarly, the structure of stock complexes may change through time if the fishery begins operating more heavily in different areas, using different gear types, or targeting different species. Complexes derived from methods such as those explored in this study should be revisited periodically and supplemented with fishery-independent indices of abundance or ecosystem-based approaches.

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Appendix: Life History Parameter Information Sources

TABLE A.1. References for life history parameters (see Table 1). Abbreviations are as follows: SEDAR = Southeast Data Assessment and Review, SAR = Stock Assessment Report.

Reference	Source
1	Northeast Fisheries Science Center. 1999. Essential fish habitat source document: Tilefish, *Lopholatilus chamaeleonticeps*, life history and habitat characteristics. NOAA Technical Memorandum NFMS-NE-152.
2	SEDAR-4-SAR1. 2004. Deepwater snapper–grouper complex in the South Atlantic. SEDAR, Charleston, South Carolina.
3	SEDAR-6-SAR1. 2004. Goliath Grouper. SEDAR, Charleston, South Carolina.
4	SEDAR-8-SAR1. 2005. Caribbean Yellowtail Snapper. SEDAR, Charleston, South Carolina.
5	SEDAR-9-SAR1. 2005. Gulf of Mexico Gray Triggerfish. SEDAR, Charleston, South Carolina.
6	SEDAR-9-SAR2. 2005. Gulf of Mexico Greater Amberjack. SEDAR, Charleston, South Carolina.
7	SEDAR-14-SAR1. 2007. Caribbean Yellowfin Grouper. SEDAR, Charleston, South Carolina.
8	SEDAR-15-AW01. 2007. Stock assessment model draft: statistical catch-at-age model. Center for Coastal Fisheries and Habitat Research, Beaufort, North Carolina.
9	SEDAR-15-SAR3. 2008. South Atlantic and Gulf of Mexico Mutton Snapper. SEDAR, Charleston, South Carolina.
10	SEDAR-17. 2008. Stock assessment report: South Atlantic Vermilion Snapper. SEDAR, Charleston, South Carolina.
11	SEDAR-10-SAR1. 2006. Gulf of Mexico Gag Grouper. SEDAR, Charleston, South Carolina.
12	SEDAR-12. 2006. Gulf of Mexico Red Grouper. SEDAR, Charleston, South Carolina.
13	SEDAR-19-SAR1. 2009. Gulf of Mexico and South Atlantic Black Grouper. SEDAR, Charleston, South Carolina.
14	Southern Demersal Working Group. 2009. Assessment of Golden Tilefish, *Lopholatilus chamaeleonticeps*, in the Middle Atlantic–southern New England region. National Marine Fisheries Service, Northeast Fisheries Science Center, 48th SAW Assessment Report, Woods Hole, Massachusetts.
15	Bortone, S. A. 1971. Studies on the biology of Sand Perch *Diplectrum formosum*. Florida Department of Natural Resources Marine Research Laboratory Technical Series 65.

TABLE A.1. Continued.

Reference	Source
16	Froese, R. and D. Pauly, editors. 2009. Species summaries of the 42 reef fish species evaluated in this study. Available: www.fishbase.org. (September 2010).
17	Harris, P. J., D. M. Wyanski, and P. T. Powers Mikell. 2004. Age, growth, and reproductive biology of Blueline Tilefish along the southeast coast of the United States, 1982–1999. Transactions of the American Fisheries Society 133:1190–1204.
18	Ross, J. L., and G. R. Huntsman. 1982. Age, growth, and mortality of Blueline Tilefish from North Carolina and South Carolina. Transactions of the American Fisheries Society 111:585–592.
19	SAFMC (South Atlantic Fishery Management Council). 2005. Stock assessment and fishery evaluation report for the snapper–grouper fishery of the South Atlantic. SAFMC, Charleston, South Carolina.
20	Sheridan, P. F. 2008. Seasonal foods, gonadal maturation, and length–weight relationships for nine fishes commonly captured by shrimp trawl on the northwest Gulf of Mexico continental shelf. Southeast Fishery Science Center, Miami.
21	SEDAR-15-SAR2. 2008. South Atlantic Greater Amberjack. SEDAR, Charleston, South Carolina.
22	SEDAR-22-DW08.2010.Yellowedge Grouper age, growth, and reproduction from the northern Gulf of Mexico. National Marine Fisheries Service, Panama City, Florida.
23	SEDAR-22-DW-01. 2010. Golden Tilefish age, growth, and reproduction from the northeastern Gulf of Mexico: 1985, 1997–2009. National Marine Fisheries Service, Panama City, Florida.
24	FFWCC (Florida Fish and Wildlife Conservation Commission). 2008. Hogfish stock assessment. Florida Fish and Wildlife Research Institute, St. Petersburg.
25	Potts, J. C., and C. S. Manooch III. 1995. Age and growth of Red Hind and Rock Hind collected from North Carolina through the Dry Tortugas, Florida. Bulletin of Marine Science 56:784–794.
26	Harris, P. J., D. M. Wyanski, D. B. White, and J. L. Moore. 2002. Age, growth, and reproduction of scamp, *Mycteroperca phenax*, in the southwestern North Atlantic, 1979–1997. Bulletin of Marine Science 70:113–132.
27	Ziskin, G. L. 2008. Age, growth and reproduction of Speckled Hind, *Epinephelus drummondhayi*, off the Atlantic coast of the Southeast United States. Doctoral dissertation. College of Charleston, Charleston, South Carolina.
28	Manooch, C. S. III, and D. L. Mason. 1987. Age and growth of the Warsaw Grouper and Black Grouper from the southeast region of the United States. Northeast Gulf Science 9:65–75.
29	Sadovy, Y., and A. Eklund. 1999. Synopsis of biological data on Nassau Grouper, *Epinephelus striatus* (Bloch, 1792) and Jewfish, *E. itaja* (Lichtenstein, 1822). NOAA Technical Report NMFS 146.
30	Ault, J., S. G. Smith, and J. A. Bohnsack. 1998. Evaluation of average length as an estimator of exploitation status for the Florida coral-reef fish community. Journal of Marine Science 62:417–423.
31	Allman, R. J., and L. A. Goetz. 2009. Regional variation in the population structure of Gray Snapper, *Lutjanus griseus*, along the West Florida Shelf. Bulletin of Marine Science 84:315–330.
32	Allman, R. J., L. R. Barbieri, and C. T. Bartels. 2005. Regional and fishery-specific patterns of age and growth of Yellowtail Snapper, *Ocyurus chrysurus*. Gulf of Mexico Science 23:211–223.
33	McBride, R. S., P. E. Thurman, and L. H. Bullock. 2008. Regional variations of Hogfish (*Lachnolaimus maximus*) life history: consequences for spawning biomass and egg production models. Journal of Northwest Atlantic Fisheries Science 41:1–12.