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Species groupings for management of the Gulf of Mexico reef fish fishery

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Abstract

The Magnuson-Stevens Reauthorization Act of 2006 requires regional fishery management councils to implement annual catch limits and accountability measures for all stocks under Federal management by 2011, to ensure overfishing does not occur. Many species are data-limited and have no formal stock assessment. One possible approach to managing these unassessed species is to assign them to assemblages that would be managed as units. The utility of this approach was evaluated using commercial and recreational fisheries data from the Gulf of Mexico. Multivariate statistical analyses revealed several consistent assemblages, and significantly positively correlated indices of abundance were identified between assessed and unassessed species in several of these assemblages. Nodal analyses provided additional guidance regarding the placement of rare species. Identified stock complexes and sub-complexes may be useful for fisheries management. Identified linkages between species also provide guidance for ecosystem-based management considerations such as the impacts of regulations upon multi-species fisheries.

Introduction

The Magnuson-Stevens Reauthorization Act (MSRA 2006) requires regional fishery management councils to implement annual catch limits (ACLs) and accountability measures (AMs) to ensure overfishing does not occur. ACLs and AMs are required for all stocks under federal management, except stocks with annual life cycles and those managed by international agreement in which the United States participates. These ACL/AM provisions must be implemented in 2010 or earlier for stocks subject to overfishing, and in 2011 or earlier for all other federally-managed stocks. The Gulf of Mexico Fisheries Management Council (Gulf Council) currently manages 42 finfish species under its Reef Fish Fishery Management Plan (FMP). Traditionally, management measures have been implemented based upon species-specific stock assessment results. However, only 14 species managed by the Gulf Council Reef Fish FMP will have been assessed by 2011 (e.g., red snapper, vermilion snapper, gray triggerfish, greater amberjack, black grouper, red grouper, goliath grouper, hogfish, yellowedge grouper, mutton snapper, yellowtail snapper, golden tilefish, blueline tilefish, and gag grouper). Establishing ACLs for many of these assessed species, as well as the remaining 28 unassessed species, will be accomplished via the Gulf Council's Generic Comprehensive ACL/AM Amendment. This amendment may also revisit and adjust ACL/AM provisions previously adopted for greater amberjack and gray triggerfish if the Council finds it is necessary in order to be consistent with policies adopted in the generic comprehensive ACL/AM amendment. Gulf Reef Fish Amendment 32 will revise ACLs/AMs for gag, red grouper, and the shallow-water grouper complex.

One possible approach for developing ACLs for unassessed species would be to assign them to assemblages that would be managed as units. National Standard 3 for fishery conservation and management (MSRA §301) states that "to the extent practicable, an individual stock of fish shall be managed as a unit throughout its range, and interrelated stocks of fish shall be managed as a unit or in close coordination." A stock complex, as defined by the recently amended National Standard 1 guidance, is "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" (74 FR 3178). Stocks may be grouped into complexes if: 1) they cannot be targeted independently of one another in a multispecies fishery; 2) there is not sufficient data to measure their status relative to established status determination criteria; or 3) when it is feasible for fishermen to distinguish individual stocks among their catch (50 CFR 600.310(b)(8) in 74 FR 3178). A management unit is defined as "a fishery or that portion of a fishery identified in a FMP as relevant to the FMP's management objectives" (50 CFR 600.320(d)). Management units may be organized based on biological, geographic, economic, technical, social, or ecological considerations (50 CFR 600.320(d)(1)).

Ideally, each assemblage would include an assessed species that would serve as a status indicator for the entire unit. Indicator species have been used in management of both terrestrial and marine systems (Simberloff 1998, Zacharias & Roff 2001). The National Standard Guidelines of U.S. Federal fishery management state that where maximum sustainable yield (MSY) cannot be specified for each stock of a mixed-stock fishery, then "MSY may be specified on the basis of one or more species as an indicator for the mixed stock as a whole or for the fishery as a whole" (50 CFR 600.310(c)(1)(iii)). In the context of the Gulf Council's Generic Comprehensive ACL/AM Amendment, regulations for the indicator species would then control the harvest of the other species in the assemblage.

An implicit assumption of the use of an indicator species for management is that population trends of the indicator species reflect those of others in the assemblage. As such, assemblages must account for interspecies similarities in the context of biological characteristics, fisheries exploitation patterns, and stock dynamics. Biological assemblages may be defined by similarities in life history, trophic behavior, and geographic distribution. For fisheries management purposes, species that are caught together should be grouped, so that regulations similarly influence all assemblage members. If trends with an indicator species truly represent those of the assemblage as a whole, the catch-per-unit-effort (CPUE) for the indicator species should exhibit synchrony with the CPUE patterns of the other members of the assemblage.

The objectives of this paper are threefold: (1) To determine whether species assemblages can be identified in the Gulf of Mexico, (2) to determine if these assemblages are consistent between commercial and recreational fisheries, and (3) to determine if stock dynamics of assessed (e.g., 'indicator') species within each assemblage are consistent with those of the assemblage as a whole. The results of these analyses should provide guidance for the Gulf Council in setting ACLs for reef fish species in the Generic Comprehensive ACL/AM Amendment.

Methods

Following Lee and Sampson (2000), multiple statistical techniques were used to identify species assemblages: (1) hierarchical cluster analyses based on life history; abundance; and presence-absence, (2) co-occurrence matrices, (3) nodal analyses, and (4) indices of abundance.

Data Overview

Commercial and headboat logbook data were used to evaluate similarities in spatial and temporal patterns of fisheries exploitation in the Gulf of Mexico. Commercial logbook records (SEFSC logbook data, accessed 17 August 2009) summarize landings on a trip level, with information for each species encountered including landings (in lbs), primary gear used, and primary area and depth of capture. Depth of capture is an important consideration when evaluating similarities in fisheries vulnerability and is only available in logbook records from 2005 onward. For the purposes of these analyses, logbook landings were summarized by species, year, month, geartype, statistical area, and depth. Only species in the Gulf Reef Fish FMP were considered. Black grouper and gag grouper landings were adjusted at a trip level for geographic differences in misidentification rates following recommendations from SEDAR-10 (2006). Year and month were defined by the date the fish were landed. Vertical line (e.g., handline and electric rig) and longline geartypes were evaluated separately. Area fished was based on the 21 Gulf of Mexico commercial logbook statistical areas. Depth of capture was aggregated into atmospheric pressure bins (e.g., 33 ft = 2 atm, 66 ft = 3 atm, etc.). Records with no reported depth or area of capture (~11%) were removed from consideration. Overall, 142,666 commercial logbook records from 2005-2008 were evaluated.

The recreational sector of the reef fish fishery was evaluated using logbook data (SEFSC headboat data, accessed 23 Jul 2009) 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 are arranged similar to commercial logbook records, and contain trip-level information on number of anglers, trip duration, date, area fished, and landings (number fish) of each species. Headboat landings were summarized by species, year, month, and area fished. Area fished was aggregated at the most common reporting level (1° latitude by 1° longitude). Records with no geographic area reported (~3%) were removed from consideration. Overall, 73,365 headboat records from 2005-2008 were evaluated.

Hierarchical Cluster Analyses

Hierarchical cluster analyses were conducted using PASW V17.0.3 (SPSS Inc., Chicago, Illinois). Hierarchical cluster analysis identifies relatively homogeneous groups of cases (or variables) based on selected characteristics. It is an agglomerative method which optimizes a route between individual entities to the entire set of entities through progressive fusion (Boesch 1977).

Life history parameters were assembled from peer-reviewed literature, Southeast Data Assessment and Review (SEDAR) reports, Stock Assessment and Fishery Evaluation (SAFE) reports, and from FishBase (Froese & Pauly 2009). Life history parameters were clustered using average linkage between groups (Sneath & Sokal 1973), with a Euclidean distance measure and a Z-score transformation by variable. In an average linkage method, the linkage function specifies the distance between two clusters as the average distance between objects from the first cluster and objects from the second cluster. Averaging is performed over all pairs (x, y) of objects, where x is an object from the first cluster and y is an object from the second cluster.

The average linkage function is expressed as follows:

$$D(X,Y) = \frac{1}{N_{X}*N_{Y}} \sum_{i=1}^{N_X} \sum_{j=1}^{N_Y} d(x_i, y_i); \quad x_i \in X, y_i \in Y \tag{1}$$

where $d(x, y)$ is the distance between objects $x \in X$ and $y \in Y$; X and Y are two sets of objects (clusters), and N_X and N_Y are the numbers of objects in clusters X and Y, respectively. Average-link clustering is less sensitive to outliers than complete-link clustering, and less likely to form long chains than single-link clustering. This method is also known as the 'unweighted pair-group method using arithmetic averages' (UPGMA), and is widely used in ecology (see Boesch 1977, McGarigal et al. 2000). This method is a space-conserving strategy that introduces little distortion to the relationships expressed in the similarity matrix (Boesch 1977).

The Euclidean distance (*ED*) measure is the square root of the sum of the squared differences between two entities (*j* and *k*) based on *P* variables:

$$ED_{jk} = \sqrt{\sum_{i=1}^{P} (x_{ij} - x_{ik})^2} \tag{2}$$

The Z-score transformation normalized the data by parameter, facilitating comparisons between species.

To compute dissimilarities between species within fisheries, each data set was formatted as a matrix, with columns representing species (*i*) and rows representing aggregation bins (*j*). For commercial fisheries, aggregation bins were year-month-area-depth combinations; for headboat fisheries, aggregation bins were year-month-area combinations. Each element of the matrix (c_{ij}) quantified the amount (in units of number fish for headboat or pounds for commercial) of a species (*i*) landed in a specific bin (*j*). Separate analyses were conducted for longline (LL) and vertical line (VL) geartypes. Landings were binned by month to maximize the variety of species landed while still capturing temporal trends in abundance. Fishermen will typically make multiple sets on a trip, sometimes in geographically distant areas, targeting different species. Binning by area and depth (commercial) reduced the probability of grouping species caught during the same time period that would likely not co-occur during any given set due to disparate geographic distributions.

Initially, species were removed if they appeared in fewer than 1% of all trips per geartype, following Shertzer and Williams (2008). Rare species may distort inferred patterns (Koch 1987, Mueter and Norcross 2000). Upon further examination, the inclusion of rare species did not impact inferred patterns in any of the cluster analyses (see Appendix); therefore, all species were included in the final analyses.

For hierarchical cluster analyses of landings data, prior to computing dissimilarities, data were transformed with a root-root transformation to moderate the influence of abundant species upon the resultant clusters:

$$c_{ij}^{*} = \sqrt[4]{c_{ij}} \tag{2}$$

This transformation is recommended for density and biomass data (Field et al. 1982). After transformation, a matrix of dissimilarities between two species (*a*, *b*) was computed using a Chi-square (χ^2) measure of distance:

$$\chi^2 = \sqrt{\frac{\sum_{i=1}^{A}\left(a_i - E(a_i)\right)^2}{E(a_i)} + \frac{\sum_{i=1}^{B}\left(b_i - E(b_i)\right)^2}{E(b_i)}}$$

The Chi-square measure is based on the chi-square test of equality for two sets of frequencies, and is the default measure in PASW for count data. The magnitude of this dissimilarity measure depends on the total frequencies of the two cases or variables whose dissimilarity is computed. Expected values (*E*) are from the model of independence of species *a* and *b*.

The resultant dissimilarity matrix was then clustered using Ward's minimum-variance linkage method, which minimizes within-group dispersion. This method agglomerates clusters when the increase in variance is less than it would be if either of the two clusters were joined with any other cluster (Sneath & Sokal 1973). Minimum-variance fusion is similar to average-linkage fusion, except that it minimizes a squared distance weighted by cluster size. Minimum-variance linkage is a space-dilating strategy because penalty by squared-distance results in tighter clusters than average-linkage.

Because sampling effort for obtaining the landings data might be considered inconsistent, reported landings data might not be quantitatively comparable between collections. Additionally, many species are heavily targeted, whereas the catch of others is incidental. Boesch (1977) suggests a binary index (e.g., 'presence-absence') may be a more appropriate measure of similarity with fisheries-dependent data. A binary index also reduces distortions caused by super-abundant (headboat and commercial) and heavier (commercial) species.

For hierarchical cluster analyses of presence-absence data, landings data matrices were converted to binary, where a '1' was assigned to positive data elements (c_{ij}) and data elements with no landings were left as '0's. Presence-absence of species in the commercial longline, commercial vertical line, and headboat fisheries were then clustered using average linkage between groups with a Sørenson measure of dissimilarity:

$$D_{ih} = \sum_{j=1}^{J} \frac{\left|c'_{ij} - c'_{hj}\right|}{\left|c'_{ij} - c'_{hj}\right|} \tag{3}$$

where D_{ih} is the distance between species i and h, and j is the number of rows (bins).

The Sørenson (e.g. 'Dice', 'Bray-Curtis', 'Czekanowski') measure is an index in which joint absences are excluded from consideration, and matches are weighted double. The Sørenson measure has been found more robust in ecological studies (Beals 1973, Field et al. 1982, Faith et al. 1987). It is commonly used in studies of fish assemblages (e.g., Mueter & Norcross 2000, Gomes et al. 2001, Williams & Ralson 2002, Shertzer & Williams 2008, Shertzer et al. 2009).

Hierarchical cluster analyses were conducted on Gulf commercial reef fish bottom longline and vertical line data as well as headboat data. Additionally, a table of Gulf reef fish vertical line landings by commercial logbook statistical area was generated and sorted by the commercial vertical line presence-absence dendrogram. This facilitated a more detailed investigation into how the distribution of the stock impacts the overall cluster output.

Nodal Analysis of Co-Occurrence

The percent co-occurrence (*PCO*) of species *i* on trips (*t*) also landing species *j* was determined for commercial longline, commercial vertical line, and headboat fisheries following:

$$PCO_{i \cap j} = \frac{\sum(t_i \cap t_j)}{\sum t_i} \tag{4}$$

The table resulting from the co-occurrence analysis was subsequently sorted by columns according to the dendrogram from the longline binary cluster output, and by rows according to the dendrogram from the vertical line binary cluster output. The cells were next conditionally formatted to facilitate visual identification of the dense cells or 'nodes' within the data matrix where groups of species and groups of collections coincide between the two fisheries clusters and also co-occur with high frequency between species (Williams and Lambert 1961, Lambert and Williams 1962). This nodal analysis was used to identify species clusters that were often caught together, and also to suggest cluster assignment for rare species by providing a visual reference for vulnerability and co-occurrence with more ubiquitous or heavily-exploited species.

Indices of Abundance

Indices of abundance were computed to investigate synchrony of dynamics between stocks. Species assemblages suggested by cluster analyses were examined to investigate the basic assumption that an indicator species could be used to infer dynamics of other species in the assemblage.

Ideally, indices of abundance would be computed from fisheries-independent data, due to inherent bias in fisheries-dependent data towards economically-important species. Unfortunately, for many species in this evaluation, fisheries-independent data is unavailable or insufficient. In this study, indices of abundance were computed from the headboat dataset similar to Shertzer & Williams (2008). The headboat fishery was chosen as the most reasonable proxy for indices of abundance because fishing effort from headboats is less targeted towards specific species than commercial fishing effort, and headboat data since 2004 has included information on discarded fish, although this data often under-represents discards. Because headboat effort is somewhat non-directed, confounding effects of density dependent catchability are somewhat minimized.

Indices of abundance were computed from catch and effort data in units of number of fish caught per angler-hour. Unlike Shertzer & Williams (2008), 'catch' incorporated discarded fish to more accurately reflect overall abundance and reduce distortions in the indices caused by selectivity due to angler preference or management regulations. Similar to Shertzer & Williams (2008), effort for a given species was based on trips that landed any species within the relevant assemblage.

To compute indices of abundance, catch and effort data were standardized using a generalized linear model (GLM). The explanatory variables were year, season, and geographic area (1 X 1 grid). Season was assigned using the official start and end dates of the four seasons, by year. The response variable was catch per unit effort. Unlike Shertzer & Williams (2008), a delta-lognormal error structure was not assumed, as the data were sufficiently aggregated to minimize distortions due to zero values (Lampert 1992).

Synchrony in dynamics between all combinations of species was measured using non-parametric Spearman's rank correlation coefficients. Three matrices of correlation coefficients were computed. The first matrix was based upon the indices of abundance, which were the annual CPUE estimates by species output from the GLM. These were standardized by dividing by the mean inter-annual CPUE estimates output from the GLM so that all species would be on a similar scale. The second matrix of correlation coefficients was computed from the first-differenced time series of log-abundances (z_t):

$$z_t = \log U_t - \log U_{t-1} = \log \frac{U_t}{U_{t-1}}; \qquad (5)$$

where U_t is the index value of a stock at time t. The third correlation coefficient matrix was computed from a binomial transformation of the first-differenced time series of log-abundances (z_t^*):

$$z_t^* = 1 \text{ if } z_t > 0, \\ z_t^* = -1 \text{ if } z_t \leq 0 \tag{6}$$

The use of first differences, as in Equation 5, puts emphasis on annual population growth rates and may reduce spurious correlation (Bjørnstad et al. 1999). The use of binomial-transformed first differences, as in Equation 6, puts emphasis on the directionality of annual population growth rates. Positive correlation of population growth rates suggests stocks have similar patterns of productivity (growth, recruitment, and mortality), and also respond similarly to inter-annual variation in fishing effort or catchability.

Results

Data Overview

In general, hierarchical cluster analysis outputs should be considered more reliable for species that are more abundant and frequently caught. Deep-water species such as yellowedge grouper, snowy grouper, blueline tilefish, silk snapper, blackfin snapper, queen snapper, and golden tilefish were landed in a much higher percentage of commercial bottom longline reef fish trips (Table 1A) as compared to commercial vertical line trips, which landed almaco jack, yellowtail snapper, and gray snapper in a much higher percentage of trips when compared to commercial longline trips (Table 1B).

Species diversity refers to the variety of living species within a geographic area. It may be measured by species richness; the number of species within a particular sample, and species evenness; the evenness in the number of each species encountered in the sample. Vertical line trips encountered a broader suite of species (e.g., higher species richness), but encountered less species on >5% of trips (e.g., lower evenness) than commercial longline trips (Table 1). Headboat trips (Table 1C) had the lowest species diversity (e.g., lowest richness and lowest evenness).

Many species had much higher landings in one fishery than the other two; for example, yellowtail snapper landings were far higher in the commercial vertical line, and sand perch landings were far higher in the headboat fishery (Table 2). Landings in the commercial bottom longline fishery were dominated by red grouper, yellowedge grouper, gag grouper, and golden tilefish (Table 2). Landings in the commercial vertical line and recreational headboat fisheries were dominated by red snapper and vermilion snapper (Table 2). In general, landings of schoolmaster snapper, mahogany snapper, wenchman, yellowmouth grouper, rock hind, cubera snapper, and dog snapper were extremely low, suggesting potential issues for clustering associated with rare species.

Table 3 provides life history parameters for managed Gulf reef fish species. Table 4 provides depth of occurrence, and color codes this depth of occurrence into shallow (yellow), shallow/mid (pink), mid/deep (pink/gray), and deep-water (gray) groups. A cursory examination of Tables 3 and 4 supports many general trends observed in fisheries. Species of the same genus often exhibit similar growth patterns. Larger organisms tend to live longer and grow more slowly (e.g., 'K-selected' species), as do organisms that live in deeper water. Many species live up to 25-30 years, and some live to be older than 50.

Hierarchical Cluster Analysis

Not surprisingly, a hierarchical cluster analysis of the life history and depth of occurrence parameters in Tables 3 and 4 showed clustering by genus and depth of occurrence, although maximum size appeared to be the dominant factor (Figure 1). This is perhaps because maximum size was captured by L_{inf} and W_{inf}, and was also probably correlated to a_{λ}, l_m, a_m, and depth of occurrence.

Cluster analyses of Gulf commercial longline landings were unable to assign many shallow-water reef species to meaningful clusters because reef fish bottom longline fishing is prohibited in <20 fathoms; therefore landings of many of these species are extremely rare (Figures 2-3, also Table 2). Major clusters were formed by shallow-water, mid-water, and deep-water complexes. The most distinctive cluster was formed by the four dominant shallow-water grouper species (e.g., red, gag, black, and scamp). The relative lack of separation between black 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 deep-water group, golden tilefish was somewhat distinct, and the deeper-water snowy grouper and yellowedge grouper were separated from the shallower-occurring blueline tilefish and speckled hind. Within the mid-water group, gray triggerfish and vermilion snapper were often caught together in high numbers.

Cluster analyses of Gulf commercial vertical line landings (Figures 4-5) provided similar results to the commercial longline, with distinct clusters of shallow-water grouper (red, gag, and black), mid-water species (silk and blackfin snapper; gray triggerfish with vermilion, red and lane snapper), and deep-water species (yellowedge and snowy grouper). Clusters for deep-water and mid-water species were less separated for the vertical line fishery as compared to the longline, perhaps due to shallower average operating depths (mean = 289 ft LL, 164 ft VL). Although the separations between them were distinct, the jack species (greater amberjack, almaco jack, banded rudderfish, and lesser amberjack) clustered nearby each other in the vertical line analysis. As with the commercial longline cluster (Figures 2-3), placement of gray snapper, red snapper, mutton snapper, and yellowtail snapper was somewhat less intuitive. In the vertical line landings analysis, a distinct cluster of gray snapper, mutton snapper, and yellowtail snapper was formed, with gray snapper slightly separated from the other two (Figure 4). Gray snapper are often caught in state waters off Florida, but are also caught near oil platforms off Louisiana (Figure 6). Red snapper have a complex management history which somewhat confounds their co-occurrence with other species, and are less frequently caught off South Florida (Figure 6). Mutton snapper and yellowtail snapper predominantly occur in the Florida Keys region, whereas many of the other species are distributed more evenly throughout the Gulf (Figure 6).

Cluster analysis of species presence-absence in Gulf reef fish headboat landings (Figure 7) provided similar results to the commercial longline and vertical line, with distinct clusters of shallow-water grouper (red and gag), mid-water species (gray triggerfish with vermilion, red and lane snapper), and deep-water species (yellowedge and snowy grouper). As with the commercial vertical line analysis, although the separations between them were distinct, several jack species (greater amberjack, almaco jack, banded rudderfish) clustered nearby each other (Figure 7). Unlike in the commercial vertical line fishery, yellowtail snapper appeared as a distinctly separated individual group in the headboat analysis (Figure 7). As with the commercial longline and vertical line presence-absence clusters, gray snapper clustered more tightly with shallow-water grouper than with other snapper stocks (Figures 3, 5, 7).

Nodal Analysis of Co-Occurrence

The nodal analysis of percent co-occurrence in commercial reef fish trips in the Gulf of Mexico (Figure 8) clearly illustrated the influence of species abundance upon even binary (e.g., presence-absence) hierarchical cluster analysis, with abundant species (e.g., warmer tones) clustering first, followed by less abundant (e.g., cooler tones) species. Similar clustering and a high-percent of co-occurrence were immediately obvious for shallow-water grouper (black, gag, red, and scamp), mid-water species (gray triggerfish with vermilion, red, and lane snapper), and deep-water grouper and tilefish (snowy and yellowedge grouper; also golden tilefish, blueline tilefish, speckled hind, and warsaw grouper). Reasonably tight grouping and co-occurrence was also observed (note solid boxes, Figure 8) for a second mid-water group (silk and blackfin snapper). Less compelling groups was also observed between several tropical species (hogfish with mutton and yellowtail snapper), some shallow-water snappers (cubera and dog) and groupers (yellowfin and yellowmouth), and among the jacks (primarily almaco jack with banded rudderfish).

Indices of Abundance

In general, the use of assessed species as indicator species was partially supported by indices of abundance computed from headboat data from 2004-2008. Many significant positive correlations between indices, log-transformed first effects, and binary log-transformed first effects were observed within complexes (all significant $p<0.05$). Within the deep-water assemblage, similar trends were observed between all species except speckled hind, which fluctuated widely through time (Figure 10). Of these trends, the unassessed warsaw grouper showed a significant positive correlation in its log-transformed first effects with the yellowedge grouper, which is scheduled for assessment in 2010. No other significant correlations were detected; however, it should be noted that the headboat fishery rarely targets deep-water species, and many species, including queen snapper and all tilefish species, had to be excluded from the analysis due to years with no landings.

Within the jacks assemblage, similar trends were observed between greater amberjack and almaco jack, and between banded rudderfish and lesser amberjack; however, none of these positive correlations were significant (Figure 11). Significant negative correlations were detected between almaco jack and banded rudderfish, and between greater amberjack and lesser amberjack. Overall, no significant positive correlations were observed between indices of abundance for assessed and unassessed species in this assemblage.

Within the mid-water assemblage, many positive and significant correlations were observed (Figure 12). Significant positive correlations were detected between blackfin snapper and red snapper, lane snapper and vermilion snapper, lane snapper and silk snapper, and between gray triggerfish and silk snapper. Overall, indices of abundance for each of the 3 unassessed species in the assemblage were significantly positively correlated with at least 1 assessed species.

Within the shallow-water grouper assemblage, many significant correlations were detected (Figure 13). Significant positive correlations were observed between black grouper and scamp, gag and red hind, gag and red grouper, red grouper and rock hind, sand perch and yellowfin grouper, and yellowfin and yellowmouth grouper. A significant negative correlation was observed between rock hind and yellowfin grouper. Overall, indices of abundance for 3 of the 6 unassessed species in the shallow-water grouper assemblage were significantly positively correlated with at least 1 assessed species.

Within the shallow-water snapper assemblage, many significant correlations were detected (Figure 14). Significant positive correlations were observed between gray snapper and yellowtail snapper. Significant negative correlations were observed between cubera snapper and gray snapper, mutton snapper and hogfish, and between dog snapper and yellowtail snapper. A positive, but non-significant trend was observed between mutton snapper and yellowtail snapper.

Discussion

The MSRA requires fishery management plans to “establish a mechanism for specifying annual catch limits…at a level such that overfishing does not occur in the fishery” (MSRA §303(a)(15)). Traditionally, a formal stock assessment, such as those conducted by the SEDAR process, will specify an overfishing limit (OFL) corresponding with yield at the maximum fishing mortality threshold (MFMT) or the fishing mortality rate that will allow the stock to rebuild by a target year ($F_{rebuild}$). Next, the Council’s Scientific and Statistical Committee (SSC) sets an acceptable biological catch level (ABC) that cannot be set higher than OFL, as it accounts for scientific uncertainty in the estimate of OFL. Finally, an ACL is set by the Council. The ACL is the level of annual catch of the stock or stock complex that serves as the basis for invoking AMs. The ACL cannot be set higher than ABC, as it accounts for management uncertainty in ABC.

The Gulf Council currently has ACLs specified for red and gag grouper, the commercial shallow-water grouper complex, gray triggerfish, and greater amberjack. Additional ACLs may be specified for black grouper, yellowedge grouper, golden tilefish, and possibly blueline tilefish following SEDAR assessments in 2010. By 2011, the Gulf Council will need to establish ACLs for numerous unassessed reef fish stocks. Setting stock-specific ACLs for many of these stocks may be unrealistic due to inadequate data to determine stock status relative to established status determination criteria (SDC). Many of these stocks suffer from issues with species identification (i.e., jacks, anchor; blackline; and goldface tilefish) and/or extreme fluctuations in relative landings through time due to rarity or lack of targeted fishing effort (i.e., schoolmaster and mahogany snapper). Thus, specifying a single-species ACL based on average catch for these stocks might result in periodic overages that would require AM implementation, creating additional burdens on science and enforcement. Grouping unassessed stocks into complexes may help avoid implementing AMs for species whose landings fluctuate due to rarity or species identification issues.

The primary goal of a stock complex in the context of the Gulf Comprehensive ACL/AM Amendment is to determine how to best aggregate unassessed stocks in order to establish an ACL. Unfortunately, unassessed stocks are often rarely caught, and are difficult to cluster. Additionally, using assessed stocks as indicators may be the only practical way to set an ACL, but assessed stocks may not be the most vulnerable stocks in the complex. In fact, examination of Table 6 suggests that only the shallow-water grouper complex has an indicator stock (gag) that is the most vulnerable member of the complex per PSA scores. Using an assessed stock as an indicator may not prevent overfishing of the more vulnerable stocks, although no SDC exists to determine this.

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. In a resource-limited environment, niche theory (May & MacArthur 1972, Landres et al. 1988, Leibold 1995) predicts that coexisting species would differ in their life history (e.g., reproductive dynamics, foraging behavior, habitat requirements) and population dynamics (e.g., responses to competition, predation, disease, and environmental variation). If these differences are substantial enough, population trends for one stock may not readily extrapolate to others in the complex (e.g, Niemi et al. 1997, Shaul et al. 2007, Shertzer & Williams 2008). The use of indicator species is not recommended unless supported by strong evidence from the system in question (Landres et al. 1988, Niemi et al. 1997).

Fishery-independent data is preferable for inferring patterns of biodiversity (e.g., Jay 1996, Collie et al. 2008), but is extremely limited for the majority of the stocks managed by the Gulf Council. Use of fishery-dependent headboat data as a proxy for trends in population abundance introduced several layers of bias (e.g. gear, spatial, temporal, depth) into our evaluation of indices of abundance. A more balanced approach might be to also evaluate fishery-dependent commercial logbook data and reef fish observer data for trends in population abundance. Future studies should attempt to integrate these multiple approaches to evaluating indices of abundance in the absence of fishery-independent data.

Using headboat logbook data, we identified several significant positive correlations in indices of abundance for assessed and unassessed stocks within proposed complexes. However, several unassessed stocks within each complex showed no significant positive correlations with any assessed stocks. This could be attributed to a variety of factors, including: (1) restricting the analysis to 5 years (2004-2008) limited statistical power; requiring a near-perfect correspondence to achieve significance, (2) using headboat data limited the analysis in terms of identifying trends for less targeted complexes such as the deep-water complex, (3) data for several unassessed stocks was too limited to perform an analysis, and (4) assessed stocks simply might not be good indicators for some unassessed stocks. Several significant negative correlations were observed between some assessed and unassessed stocks in the 'Jacks' complex and the 'Shallow-water Snapper' complex; these complexes were poorly supported by our cluster analyses.

Not surprisingly, the stock groupings formed by our cluster analyses were controlled by the input variables of sector, gear, area, and depth. Of these, depth appeared the most important, with distinct shallow-water, mid-water, and deep-water assemblages frequently appearing in the output. The strength and composition of observed assemblages varied by sector and gear. Headboat was less likely to catch deep-water stocks because deep-water stocks are farther offshore and not often targeted by limited duration headboat trips. Commercial bottom longline was less likely to catch shallow-water stocks because commercial bottom longline is prohibited within 20 fathoms in the eastern Gulf of Mexico and within 50 fathoms in the western Gulf of Mexico (e.g., west of Cape San Blas, Florida). Subtle spatial trends were also observed in assemblages. For example, in the commercial vertical line sector, 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 distinctly separated. This is possibly due to differences in vulnerability to gears and fishing methods as well as differences in geographic and depth distributions. Caution should be taken when interpreting our results, as years of overexploitation may have altered community structure and species composition (Hughes 1994).

There are three approaches towards applying stock complexes to ACL/AM management: (1) set species-specific ACLs, (2) set ACLs for stock complexes and ACLs for indicator stocks within those complexes, and (3) set ACLs for stock complexes without using indicator stocks. These approaches are not mutually exclusive. For example, a broad complex might be formed with an overall ACL, which, if exceeded, would trigger AMs. Within this broader complex, one or several sub-complexes might be designated. Each sub-complex could have an ACL either based on all species in the complex or on one or more indicator species. If this sub-complex ACL were exceeded, AMs might be implemented that impact all or some of the members of the sub-complex. Finally, some sub-complexes might contain only one species, and would require a species-specific ACL.

Our analyses supported existing stock complexes for deep-water grouper and tilefishes and suggested a possible merger of these complexes, with some sub-complexes and additions (Figure 15). Each sub-complex in Figure 16 contains an indicator species that should have a completed assessment by 2011. One potential sub-complex would be yellowedge, warsaw, and snowy grouper. Yellowedge and snowy grouper occur at similar depths and always cluster next to one another. Yellowedge and warsaw grouper are positively significantly correlated in their indices of abundance. Golden tilefish occurs at similar depths but is less structure-affiliated. It often clusters near yellowedge, but with some separation. As anchor, blackline, and goldface tilefish occur at similar depths as golden tilefish and are not currently reported to species, it may be necessary to cluster these species with golden tilefish for ACL management. Finally, blueline tilefish and speckled hind often clustered strongly together, near the rest of the deep-water complex, but usually on their own branch. These species occur in shallower waters than the rest of the tilefish and deep-water grouper, and are structure-oriented.

Placement of queen snapper, misty grouper, and wenchman was challenging; these species occur at similar depths but in different geographic areas, with wenchman only reported off Louisiana. A major goal of the nodal analysis was to integrate multiple perspectives for the assignment of rare species to aggregate groups (note dashed boxes in Figure 8). When making these more subjective decisions, it seemed prudent to discount the four dominant shallow-water grouper species; they were so hyper-abundant in the landings that everything co-occurred with them to some extent. Based upon percent co-occurrence and cluster analysis output, it appeared reasonable to include queen snapper and misty grouper with the deep-water grouper and tilefish complex, especially upon examination of their depth of occurrence (Table 4). Wenchman occur in mid-to-deep-water, and were often caught with yellowedge grouper, blueline tilefish, and queen snapper; therefore it seemed reasonable to include them with the deep-water complex.

Our analyses provided little support for the establishment of a 'Jacks' complex (Figure 16). Jacks clustered near one another in the vertical line and headboat fisheries, but on distinct branches. Indices of abundance for almaco jack and banded rudderfish were significantly negatively correlated. The index of abundance for the only assessed species, greater amberjack, was significantly negatively correlated with the second most abundantly-landed species, lesser amberjack. SEDAR 15 (2009) concluded that lesser amberjack and almaco jack were correctly identified in most instances, but smaller greater amberjack and banded rudderfish were often misidentified. The overall impacts of misidentification on the outcomes of the cluster analyses may be negligible, since they are misidentified with other members of the same sub-complex, but the impacts on the indices of abundance could be substantial. Issues with misidentification would also lead to problems in setting single-species ACLs for these species unless the rate of misidentification has been (and remains) constant through time.

Our analyses provided strong support for the creation of a 'Mid-water' complex (Figure 17). Gray triggerfish, vermilion, red, and lane snapper consistently clustered together. Indices of abundance were significantly positively correlated between vermilion and lane snapper. In the commercial clusters, vermilion clustered closest to gray triggerfish; whereas in the headboat cluster, it clustered closest to red snapper. Silk and blackfin snapper consistently clustered together, but were always separate from the other (more abundant) mid-water species. Although these groups were consistently separated in clusters, there were positive significant correlations in indices of abundance between them (e.g. between silk and lane snapper, and between blackfin and red snapper). This could be an argument for merging the two groups into a single mid-water complex such as depicted in Figure 17. It may be desirable to manage gray triggerfish (along with generic triggerfishes) separately due to differences in life history.

Our analyses supported the current shallow-water grouper complex of red; black; yellowmouth; and yellowfin grouper, red and rock hind, scamp, and gag (Figure 18). Red grouper and gag always clustered together, and were often clustered with scamp and black grouper. Black grouper always clustered with gag in the commercial fishery, but this is likely an artifact of the misidentification adjustment applied, which ensures that some percentage of black grouper will be caught on every trip landing gag and vice versa. These species were separated in the headboat cluster. Although these species overlap in their distributions and are vulnerable to the same gears and fishing techniques, the core of the black grouper distribution is focused in the Florida Keys, whereas the gag is more ubiquitously distributed across the eastern Gulf. Scamp clustered with mid-water species in the commercial vertical line landings cluster and with jacks in the headboat binary cluster, but clustered with shallow-water grouper in all other clusters, including the commercial vertical line binary cluster. Scamp is often caught with mid-water species in the western Gulf, where there are less targeted trips for shallow-water grouper, and is caught primarily with shallow-water grouper species in the eastern Gulf. There are five sets of significant positive correlations between species in this complex, including 3 between an unassessed species and an assessed species. Additionally, an assessed species (gag) is the most vulnerable species in the complex per PSA score (see Table 6). Currently, dwarf sand perch and sand perch are designated as 'Research Only' species in the Gulf Reef Fish FMP. These species could be designated as Ecosystem Component species, in which case no ACL would need to be specified. If they remain 'in the fishery', they could arguably be integrated into the shallow-water grouper complex, as sand perch and yellowfin grouper have significantly positively correlated indices of abundance.

Our analyses provided limited support for a shallow-water snapper complex (Figure 19). Placing these species was challenging because while gray, mutton, and yellowtail snapper are abundant, landings of the other shallow-water snapper species are rare. Clustering the rare snapper species was driven primarily through an examination of the nodal analysis output (Figure 8). Every trip that landed a schoolmaster snapper also landed a mutton snapper; therefore, it appeared reasonable to include schoolmaster with a shallow-water snapper aggregate; although schoolmaster snapper total landings were extremely low (Table 2). Every trip landing a mahogany snapper also landed a gray snapper. Landings of mahogany and schoolmaster snapper were too rare to perform any indices of abundance analyses. Dog snapper and mutton snapper were often landed together. Mutton snapper and cubera snapper have similar life histories.

Although gray and yellowtail snapper had significantly positively correlated indices of abundance, many other species had significant negative correlations. The gray snapper has a substantial fishery in Florida state waters, especially the Florida Keys, where it co-occurs to some extent with yellowtail snapper; however, it also has a sizeable fishery on the offshore reefs and oil rigs in the western Gulf of Mexico. This perhaps explains why gray snapper sometimes clusters with tropical species such as yellowtail snapper and hogfish, and other times clusters with shallow-water grouper (e.g., scamp) and mid-water snapper species (e.g., red snapper). The hogfish, mutton snapper, and yellowtail snapper have tropical fisheries predominantly concentrated in the Florida Keys, and may need either a different complex or a separate complex for each. Successful stock assessments have been completed for both yellowtail and mutton snapper, possibly allowing ACLs to be set on a species-specific basis. Because yellowtail snapper are often caught while surface fishing it may not be useful to include this species in complex. Similarly, hogfish is a wrasse, not a snapper, and rarely takes a hook. It is primarily targeted by spearfishers, making it a good candidate for a species-specific ACL. The unique dynamics of these shallow-water snapper fisheries, the challenges of clustering rare species, and the lack of significantly positively-correlated indices of abundance are major reasons why multiple single-species sub-complexes may be needed for these tropical and shallow-water snapper species (Figure 19).

In conclusion, our study results indicate that in some instances stock complexes may be appropriate for managing reef fish species and setting ACLs. Although ACLs set on a species-specific basis may be desirable for many species, stock complexes may provide a temporary solution for setting ACLs for species lacking stock assessments. In establishing stock complexes, managers should consider the geographic and depth distribution of species, life history characteristics, exploitation patterns, and vulnerabilities. Managers should then adapt their management strategies as new information and understanding of species linkages and complexes arises. 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 be targeted at gaining a high-resolution map of the biogeographic distribution of fish stocks, the spatial distribution of fishing effort, 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), invasive species (Albins & Hixon 2008), habitat degradation (Hoss & Engel 1996, Anderson et al. 2008), and climate change (Holbrook et al. 1997, Attrill & Power 2002, Genner et al. 2004, Perry et al. 2005, Collie et al. 2008).

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Table 1. Percent of A) commercial bottom longline, B) commercial vertical line, and C) headboat trips (2005-2008) in Gulf of Mexico with landings of listed species.

A. COM. BOTTOM LONGLINE			B. COM. VERTICAL LINE			C. HEADBOAT		
COMMON NAME	**TRIPS**	**PCT**	**COMMON NAME**	**TRIPS**	**PCT**	**COMMON NAME**	**TRIPS**	**PCT**
red grouper	4368	75%	black grouper	16949	53%	red snapper	7611	34%
black grouper	4282	73%	gag	16948	53%	gray triggerfish	7230	33%
gag	4282	73%	red grouper	16172	51%	vermilion snapper	6434	29%
scamp	3157	54%	red snapper	13376	42%	gag	6241	28%
gray snapper	1780	30%	vermilion snapper	10730	34%	red grouper	6059	27%
yellowedge grouper	1575	27%	gray snapper	10164	31%	lane snapper	5701	26%
greater amberjack	1363	23%	scamp	8862	28%	gray snapper	4106	19%
snowy grouper	1279	22%	gray triggerfish	7991	25%	sand perch	3728	17%
mutton snapper	1162	20%	lane snapper	5172	16%	scamp	2588	12%
golden tilefish	889	15%	greater amberjack	3914	12%	greater amberjack	2205	10%
red snapper	855	15%	yellowtail snapper	3596	11%	almaco jack	1258	6%
speckled hind	716	12%	almaco jack	1792	6%	banded rudderfish	923	4%
gray triggerfish	685	12%	mutton snapper	1484	5%	yellowtail snapper	754	3%
blueline tilefish	634	11%	warsaw grouper	1468	5%	rock hind	707	3%
lane snapper	537	9%	yellowedge grouper	1050	3%	warsaw grouper	571	3%
vermilion snapper	504	9%	snowy grouper	999	3%	blue runner	391	2%
warsaw grouper	497	9%	blueline tilefish	817	3%	black grouper	318	1%
silk snapper	432	7%	lesser amberjack	773	2%	crevalle jack	261	1%
blackfin snapper	323	6%	banded rudderfish	550	2%	hogfish	230	1%
lesser amberjack	183	3%	silk snapper	530	2%	mutton snapper	114	1%
queen snapper	162	3%	speckled hind	454	1%	snowy grouper	109	>0%
yellowtail snapper	130	2%	red hind	450	1%	speckled hind	105	>0%
misty grouper	106	2%	queen snapper	357	1%	red hind	63	>0%
red hind	83	1%	blackfin snapper	342	1%	lesser amberjack	52	>0%
almaco jack	56	1%	hogfish	292	1%	yellowedge grpr.	49	>0%
dog snapper	44	1%	golden tilefish	246	1%	cubera snapper	43	>0%
banded rudderfish	36	1%	yellowfin grouper	90	1%	yellowmouth grpr.	39	>0%
cubera snapper	34	1%	misty grouper	85	>0%	blackfin snapper	29	>0%
unc snappers	27	>0%	unc snappers	26	>0%	blueline tilefish	17	>0%
yellowfin grouper	25	>0%	unc amberjack	20	>0%	silk snapper	16	>0%
unc groupers	14	>0%	cubera snapper	16	>0%	yellowfin grouper	13	>0%
hogfish	10	>0%	unc groupers	16	>0%	dog snapper	12	>0%
schoolmaster snapper	8	>0%	dog snapper	15	>0%	marbled grouper	8	>0%
wenchman	1	>0%	unc jacks	13	>0%	jewfish	5	>0%
unc jacks	1	>0%	yellowmouth grper.	12	>0%	queen snapper	2	>0%
unc tilefish	1	>0%	wenchman	11	>0%	coney	1	>0%
unc triggerfish	1	>0%	unc triggerfish	7	>0%			
			unc tilefish	6	>0%			
			mahogany snapper	2	>0%			
			nassau grouper	1	>0%			
			schoolmaster snapper	1	>0%			
			schoolmaster snapper	1	>0%			

Source: SEFSC Commercial and Headboat Logbooks (August 2009).

Table 2. Total landings (thousands of lbs, whole weight) by commercial bottom longline (LL), commercial vertical line (VL), and headboat fisheries in the Gulf of Mexico (2005-2008). Species-fishery combinations with < 10 TP landings highlighted as potential issues in clustering due to low abundance.

COMMON	Com. LL	Com. VL	Headboat	Grand Total
schoolmaster	0.0	0.0	0.0	0.0
mahogany snapper	0.0	0.1	0.0	0.1
wenchman	0.0	1.2	0.0	1.2
yellowmouth grouper	0.0	1.4	1.5	2.9
rock hind	0.0	0.0	3.4	3.4
cubera snapper	1.9	1.0	2.0	4.9
dog snapper	1.7	6.3	0.2	8.2
hogfish	0.2	13.9	0.7	14.8
red hind	16.2	6.6	0.2	23.0
sand perch	0.0	0.0	33.1	33.1
blackfin snapper	25.8	21.9	1.3	49.0
yellowfin grouper	41.9	13.2	0.5	55.6
banded rudderfish	1.7	30.6	42.2	74.5
queen snapper	17.5	70.0	0.0	87.5
misty grouper	61.2	31.9	0.0	93.1
lesser amberjack	20.3	74.4	2.5	97.2
almaco jack	3.9	136.5	16.4	156.8
silk snapper	47.4	121.2	1.7	170.3
speckled hind	209.9	39.0	1.1	250.0
lane snapper	5.5	273.1	113.6	392.2
warsaw grouper	147.3	275.1	20.8	443.2
blueline tilefish	456.1	52.7	0.1	508.9
mutton snapper	484.3	75.3	14.1	573.7
black grouper	387.0	255.0	5.9	647.9
gray triggerfish	41.6	380.9	253.6	676.1
snowy grouper	544.9	212.1	1.2	758.2
gray snapper	49.0	634.1	164.2	847.3
scamp	581.3	693.4	35.0	1,309.7
yellowtail snapper	1.8	1,374.8	13.1	1,389.7
golden tilefish	1,623.9	16.4	0.0	1,640.3
greater amberjack	276.1	1,777.3	255.2	2,308.6
yellowedge grouper	3,390.0	166.8	0.8	3,557.6
gag	2,302.0	4,438.3	310.7	7,051.0
vermilion snapper	35.2	8,551.8	928.5	9,515.5
red snapper	864.1	13,389.4	1,997.5	16,251.0
red grouper	12,741.1	7,231.3	170.6	20,143.0
Grand Total	**24,380.8**	**40,367.0**	**4,391.6**	**69,139.4**

Source: SEFSC Commercial Logbook (Aug 2009), SEFSC Recreational ACL Landings Dataset (Nov 2009).

Table 3. Life history parameters for managed reef fish species in Gulf of Mexico (see Appendix for references).

Common Name	Species Name	a_λ (yr)	K	L_{inf} (cm)	$a_\circ$ (yr)	W_{inf} (kg)	L_m (mm)	a_m (mo)	Ref
Red Grouper	*Epinephelus morio*	29.0	0.16	85.4	-0.19	23	572	25	12,19
Gag	*Mycteroperca microlepis*	31.0	0.14	130.0	-0.39	37	656	36	11,19
Rock Hind	*Epinephelus adscensionis*	12.0	0.16	60.1	-2.50	4	280	28	19
Red Hind	*Epinephelus guttatus*	19.5	0.20	76.0	0.00	3	215	25	19
Black Grouper	*Mycteroperca bonaci*	33.0	0.14	133.4	-0.90	41	826	62	13
Scamp	*Mycteroperca phenax*	30.0	0.09	108.0	0.00	14	353	14	19
Yellowfin Grouper	*Mycteroperca venenosa*	15.0	0.10	89.5	0.00	19	540	43	7,19
Yellowmouth Grouper	*Mycteroperca interstitalis*	28.0	0.06	85.4	-4.60	10	840	36	19
Mutton Hamlet	*Epinephelus afer*	24.0	0.12	93.7	0.00	10	493	62	20
Coney Grouper	*Epinephelus fulva*	11.0	0.14	41.0	-5.30	5	186	13	2,19
Marbled Grouper	*Epinephelus inermis*	24.0	0.12	93.7	-1.05	10	937	62	19
Yellowedge Grouper	*Epinephelus flavolimbatus*	85.0	0.10	98.4	-0.06	19	1150	60	19
Snowy Grouper	*Epinephelus niveatus*	28.0	0.09	132.0	-1.01	30	670	60	19
Speckled Hind	*Epinephelus drummondhayi*	15.0	0.13	97.0	-1.01	30	508	55	19
Warsaw Grouper	*Epinephelus nigritus*	41.0	0.14	163.0	-0.77	263	810	49	3,19
Misty Grouper	*Epinephelus mystacinus*	41.0	0.07	163.3	-1.58	107	811	98	16,15
Nassau Grouper	*Epinephelus striatus*	29.0	0.09	90.0	-1.43	27	500	84	16,20
Goliath Grouper	*Epinephelus itajara*	37.0	0.13	201.0	-0.78	455	1100	48	8
Sand Perch	*Diplectrum formosum*	2.0	0.29	27.7	0.11	1	165	72	10,19
Dwarf Sand Perch	*Diplectrum bivittatum*	7.0	0.41	26.3	-0.42	1	157	20	4,19
Red Snapper	*Lutjanus campechanus*	53.0	0.35	100.0	-0.50	22.8	230	43	19
Vermilion Snapper	*Rhomboplites aurorubens*	26.0	0.12	50.6	-3.09	3.2	320	24	19
Yellowtail Snapper	*Ocyurus chrysurus*	17.0	0.17	60.0	-0.53	4	224	75	19
Gray Snapper	*Lutjanus griseus*	24.0	0.23	58.1	-0.61	20	230	24	9
Silk Snapper	*Lutjnaus vivanus*	29.0	0.10	81.2	-1.32	8	434	63	16
Lane Snapper	*Lutjanus syngaris*	19.0	0.20	51.0	-0.73	8	147	12	19
Mutton Snapper	*Lutjanus analis*	14.5	0.16	86.9	-0.94	9	330	37	19
Wenchman	*Pristipomoides aquilonaris*	11.0	0.27	58.1	-0.52	5	321	29	19
Queen Snapper	*Etelis oculatus*	30	0.61	103.0	-0.19	53	536	12	19
Schoolmaster	*Lutjanus apodus*	8.1	0.35	36.6	-0.45	11	250	24	19
Blackfin Snapper	*Lutjanus buccanella*	8.2	0.35	62.0	-0.39	14	250	21	19
Cubera Snapper	*Lutjanus cyanopterus*	22.1	0.13	105.0	-0.94	57	546	55	19
Dog Snapper	*Lutjanus jocu*	29.0	0.10	90.2	-1.28	29	430	74	5,19
Mahogany Snapper	*Lutjanus mahogoni*	28.5	0.10	49.9	-1.51	13	130	55	6,19,21
Black Snapper	*Apsilus dentatus*	4.4	0.65	63.8	-0.20	3	349	12	19
Gray Triggerfish	*Balistes capriscus*	12.0	0.38	46.6	-0.33	6	142	12	19
Queen Triggerfish	*Balistes vetula*	12.5	0.30	52.5	-0.48	5	293	26	19
Ocean Triggerfish	*Canthidermis sufflamen*	14.3	0.20	67.3	-0.68	6	366	38	16
Scrawled Filefish	*Aluterus scriptus*	36.0	0.08	113.0	-1.52	3	583	89	17,18
Unicorn Filefish	*Aluterus monocerus*	26.1	0.11	78.7	-1.21	8	421	67	17,18
Orange Filefish	*Aluterus schoepfi*	20.4	0.14	63.2	-1.00	17	346	55	1,14
Greater Amberjack	*Seriola dumerilli*	17.0	0.23	111.0	-0.79	81	788	27	1,14
Crevalle Jack	*Caranx hippos*	19.0	0.17	127.1	-0.67	9	648	48	19
Blue Runner	*Caranx crysos*	11.0	0.38	40.4	-0.40	5	231	22	12,19
Banded Rudderfish	*Seriola zonata*	10.3	0.28	77.5	-0.46	5	415	27	11,19
Almaco Jack	*Seriola rivoliana*	22.2	0.13	163.3	-0.83	6	811	53	19
Lesser Amberjack	*Seriola fasciata*	10.2	0.28	69.9	-0.47	5	379	27	19
Blueline Tilefish (fem.)	*Caulolatilus microps*	32.0	0.15	86.7	-2.09	6	338	36	13
Blueline Tilefish (male)	*Caulolatilus microps*	32.0	0.09	122.2	-1.84	17	363	36	19
Golden Tilefish (fem.)	*Lopholatilus chamaeleonticeps*	50.0	0.10	112.0	-0.55	23	443	60	7,19
Golden Tilefish (male)	*Lopholatilus chamaeleonticeps*	50.0	0.08	141.5	-0.09	50	574	66	19
Hogfish	*Lachnolaimus maximus*	23.0	0.08	91.2	-1.78	10	165	84	20

Note: a_λ denotes maximum age in years, K denotes Brody growth coefficient, L_{inf} denotes asymptotic length coefficient for von Bertalanffy growth equation, $a_\circ$ denotes theoretical age at length zero scaling parameter for von Bertlanffy growth equation, W_{inf} denotes theoretical maximum weight in kilograms, L_m denotes length (in mm) at maturity, a_m denotes age (in months) at maturity.

Table 4. Depth of occurrence for managed reef fish species in Gulf of Mexico (Source: Fishbase).

Depth (m)	0	30	60	90	120	150	180	210	240	270	300	330	360	390	420+
hogfish	■	■													
black grouper	■	■													
dog snapper	■	■													
schoolmaster	■	■	■												
cubera snapper		■													
sand perch	■	■	■												
Nassau grouper	■	■	■	■											
mahogany snapper	■	■	■	■											
goliath grouper	■	■	■	■											
dwarf sand perch	■	■	■	■											
red hind	■	■	■	■											
mutton snapper		■	■	■											
scamp		■	■	■											
rock hind	■	■	■	■	■										
yellowfin grouper	■	■	■	■	■										
yellowmouth grouper	■	■	■	■	■	■									
banded rudderfish		■	■	■	■										
almaco jack	■	■	■	■	■	■									
yellowtail snapper	■	■	■	■	■	■	■								
gray snapper	■	■	■	■	■	■	■								
lesser amberjack			■	■	■										
gag		■	■	■	■	■									
red snapper	■	■	■	■	■	■	■								
speckled hind		■	■	■	■	■	■								
blackfin snapper		■	■	■	■	■	■								
blueline tilefish		■	■	■	■	■	■	■							
silk snapper				■	■	■	■	■	■						
red grouper	■	■	■	■	■	■	■	■	■	■	■	■			
yellowedge grouper			■	■	■	■	■	■	■	■					
vermilion snapper		■	■	■	■	■	■	■	■	■	■				
gray triggerfish	■	■	■	■	■	■	■	■	■	■	■	■	■		
greater amberjack	■	■	■	■	■	■	■	■	■	■	■	■	■		
wenchman		■	■	■	■	■	■	■	■	■	■	■	■		
black snapper				■	■	■	■	■	■	■	■				
lane snapper	■	■	■	■	■	■	■	■	■	■	■	■	■	■	
misty grouper					■	■	■	■	■	■	■	■	■	■	
queen snapper				■	■	■	■	■	■	■	■	■	■	■	■
snowy grouper		■	■	■	■	■	■	■	■	■	■	■	■	■	■
warsaw grouper			■	■	■	■	■	■	■	■	■	■	■	■	■
anchor, blackline, goldface tilefish				■	■	■	■	■	■	■	■	■	■	■	■
golden tilefish				■	■	■	■	■	■	■	■	■	■	■	■

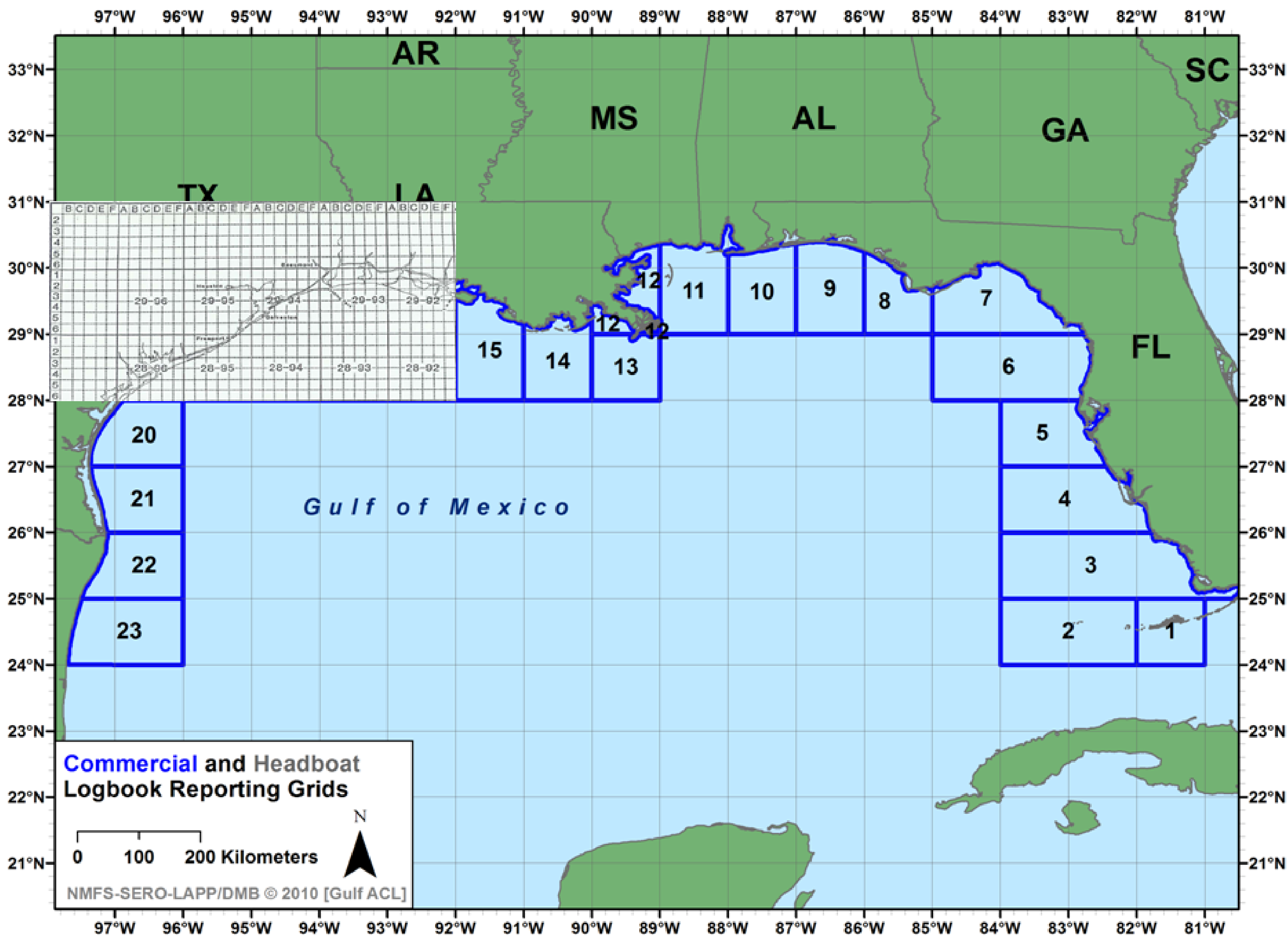


Figure 1. Gulf commercial and headboat logbook statistical reporting areas. Note headboat operators often report at a subgrid scale denoted by the minor ticks on the image border. Numeric labels correspond to commercial reporting areas.

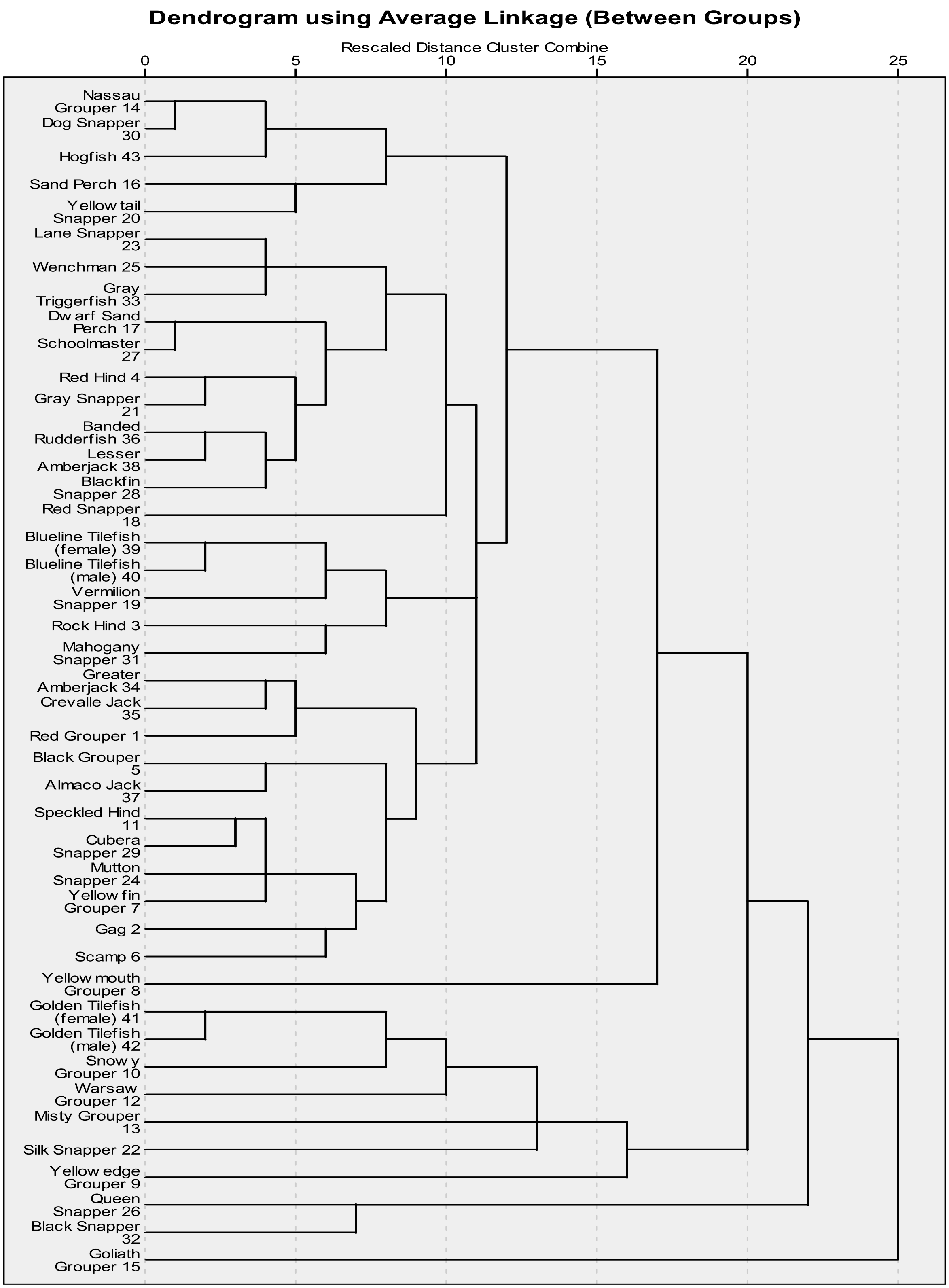


Figure 1. Hierarchical cluster analysis of life history parameters for managed Gulf reef fish species (Linkage Method: Between (Average), Dissimilarity Measure: Euclidean Distance, Transformation: Z-Score by Variable).

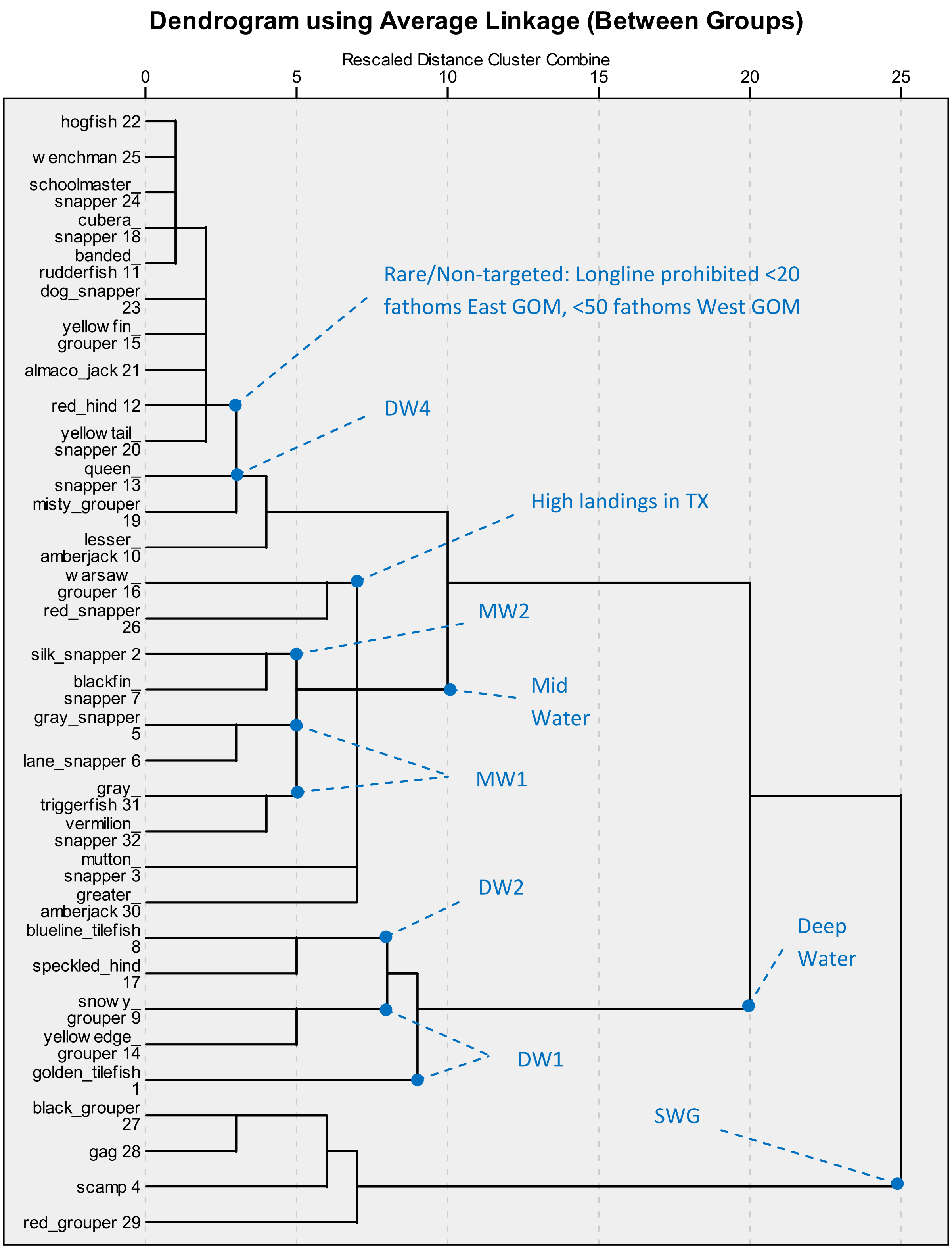


Figure 2. Hierarchical cluster analysis of Gulf reef fish commercial longline landings aggregated by year, month, area, and depth (Linkage Method: Ward's, Dissimilarity Measure: Chi-Square (count), Transformation: Root-Root).

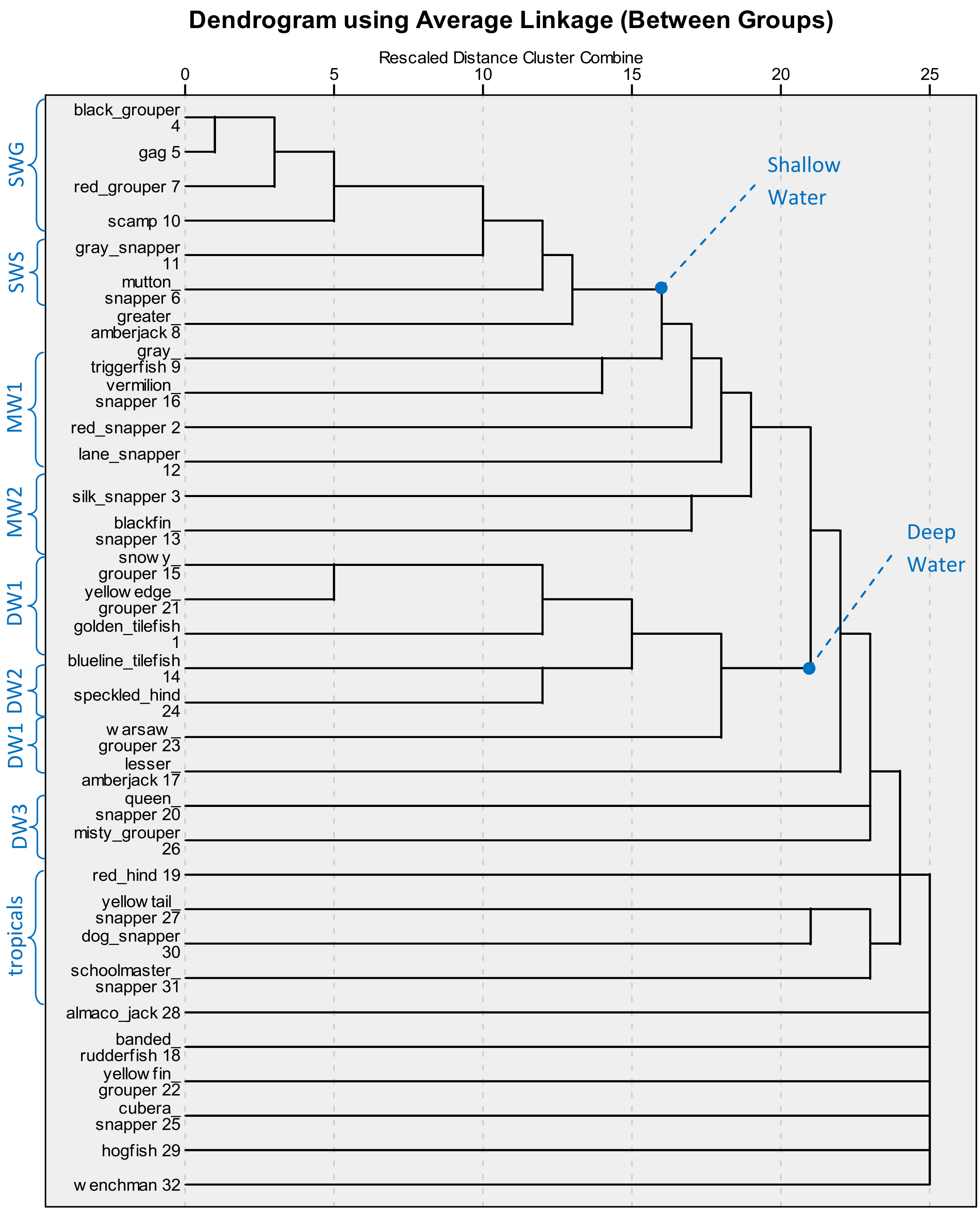


Figure 3. Hierarchical cluster analysis of species presence-absence in Gulf reef fish commercial longline landings aggregated by year, month, area, and depth (Linkage Method: Between (Average), Dissimilarity Measure: Sørenson (Binary)).

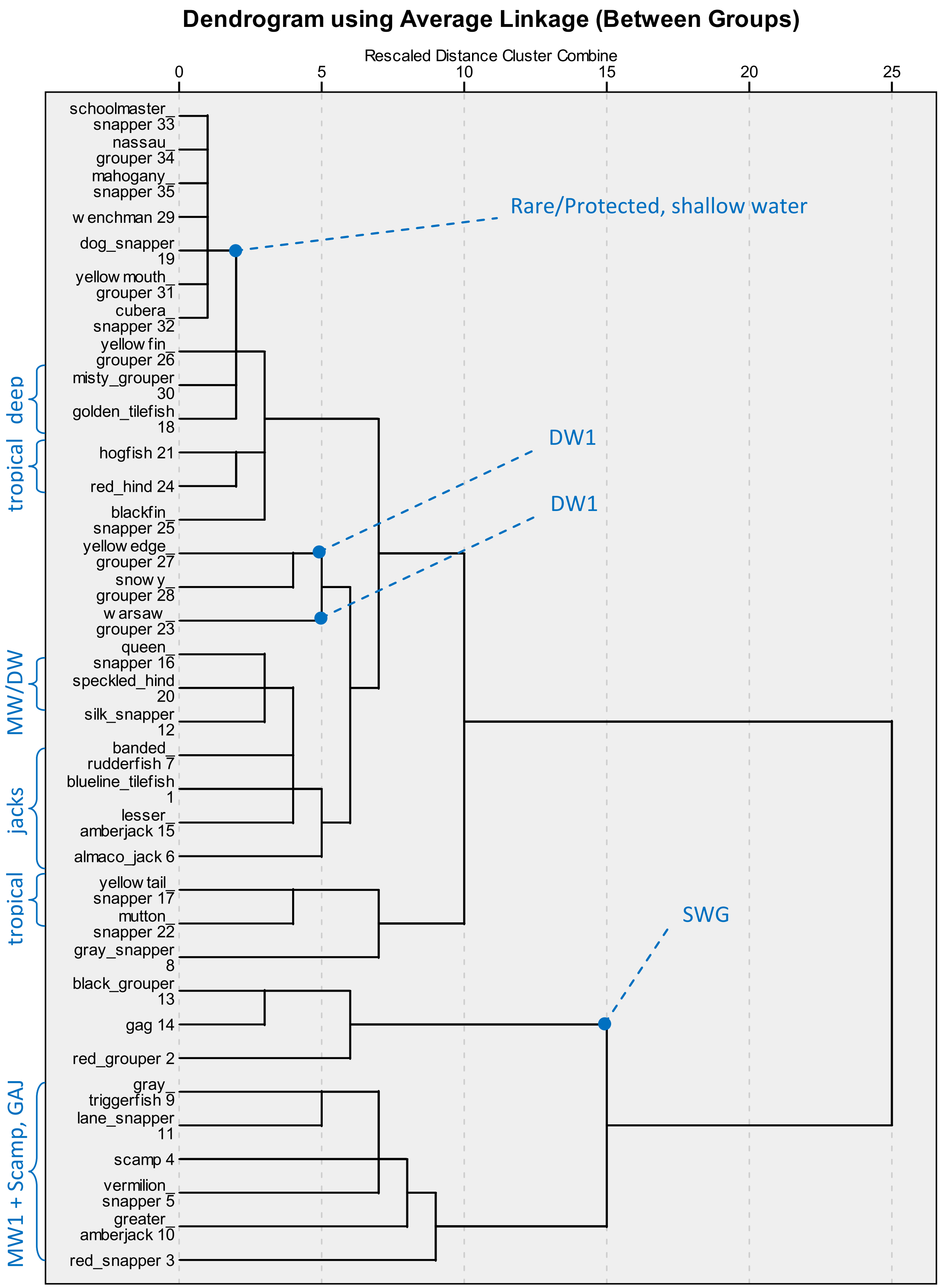


Figure 4. Hierarchical cluster analysis of Gulf reef fish commercial vertical line landings aggregated by year, month, area, and depth (Linkage Method: Ward's, Dissimilarity Measure: Chi-Square (count), Transformation: Root-Root).

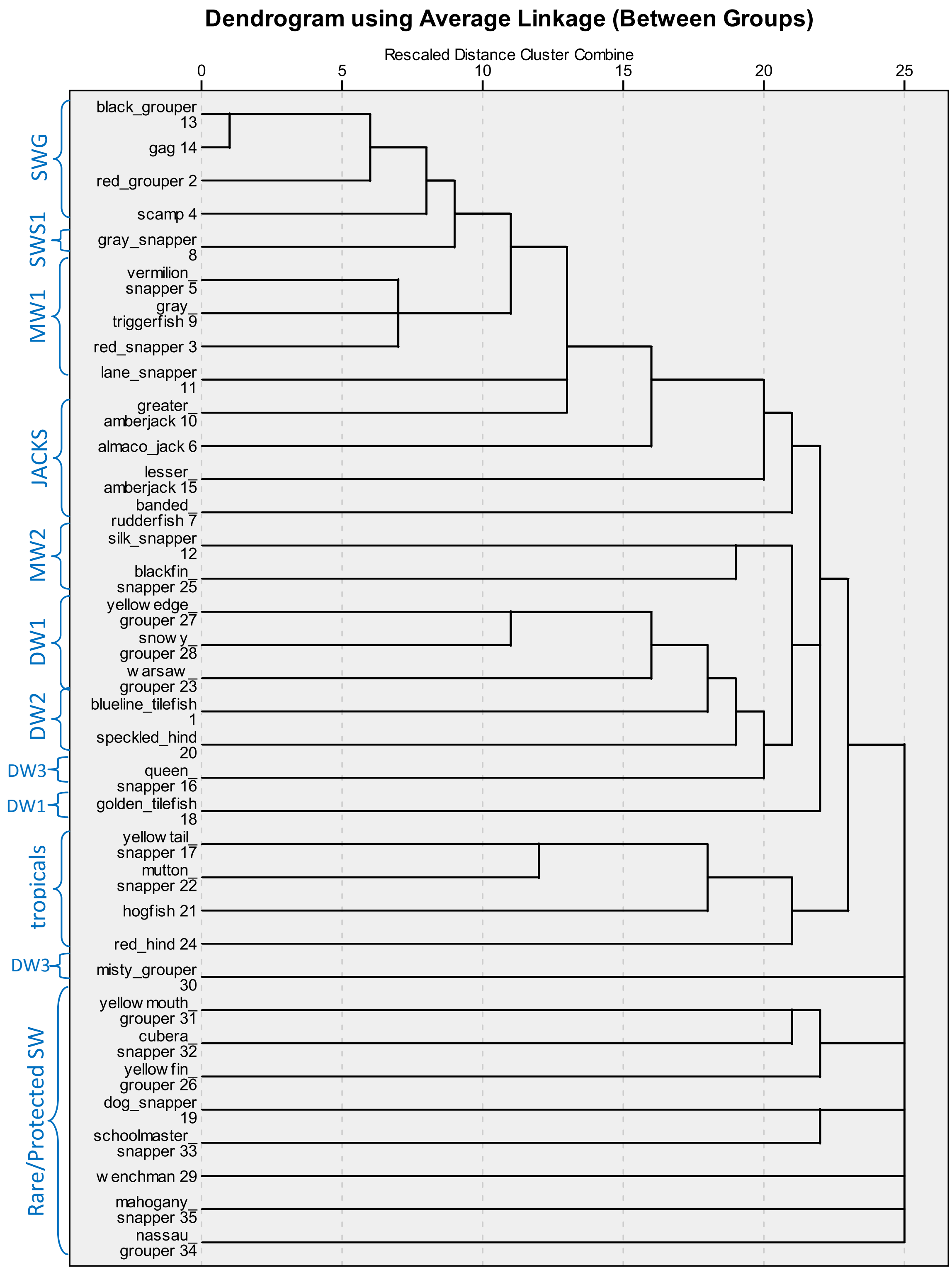


Figure 5. Hierarchical cluster analysis of species presence-absence in Gulf reef fish commercial vertical line landings aggregated by year, month, area, and depth (Linkage Method: Between (Average), Dissimilarity Measure: Sørenson (Binary)).

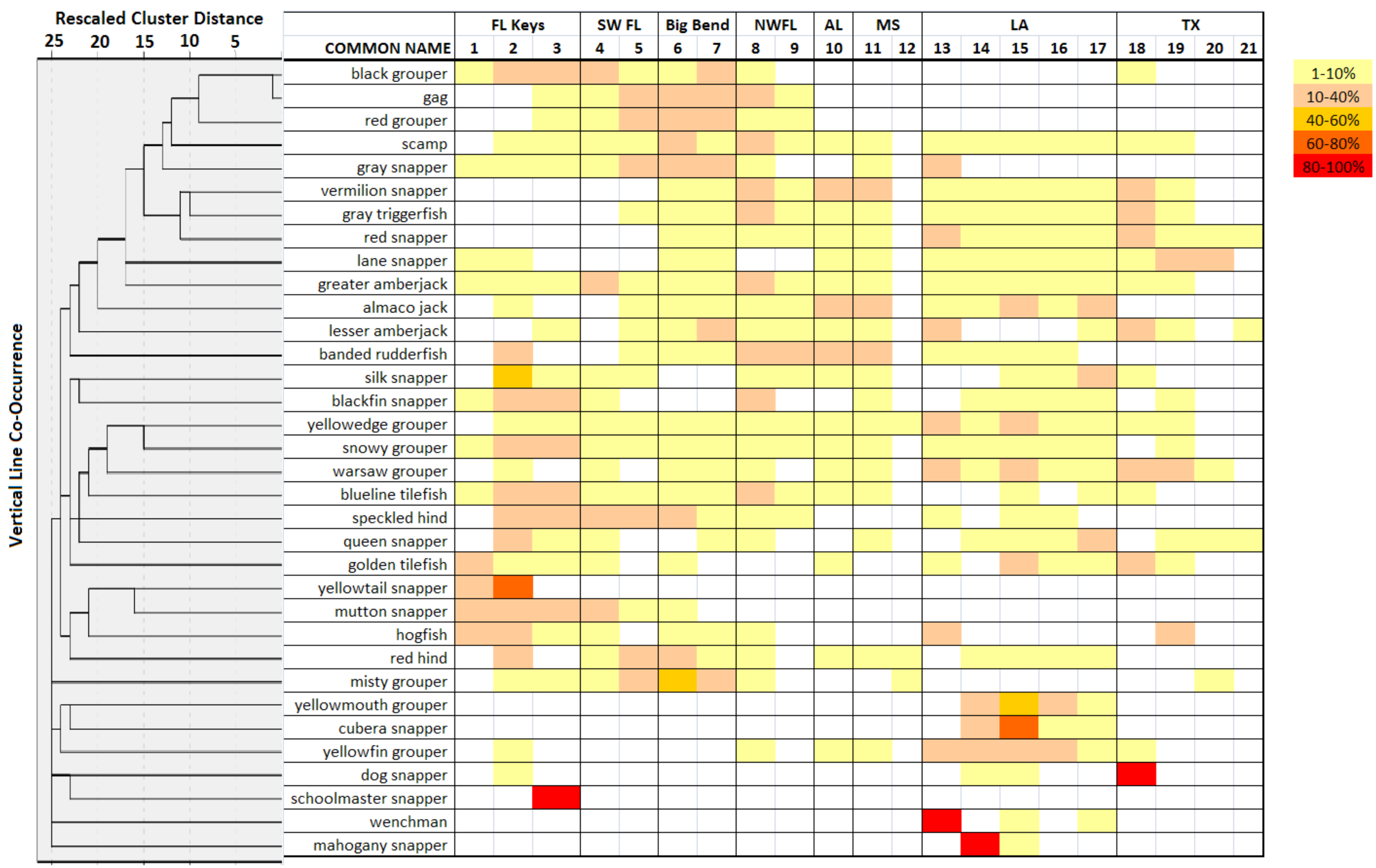


Figure 6. Plot of species presence-absence in Gulf reef fish commercial vertical line landings aggregated by year, month, area, and depth (Linkage Method: Ward's, Dissimilarity Measure: Jaccard (binary)) relative to percent of landings (2005-2008) originating from commercial logbook statistical areas 1-21, illustrating impacts of spatial distribution of exploited stock on resultant clusters.

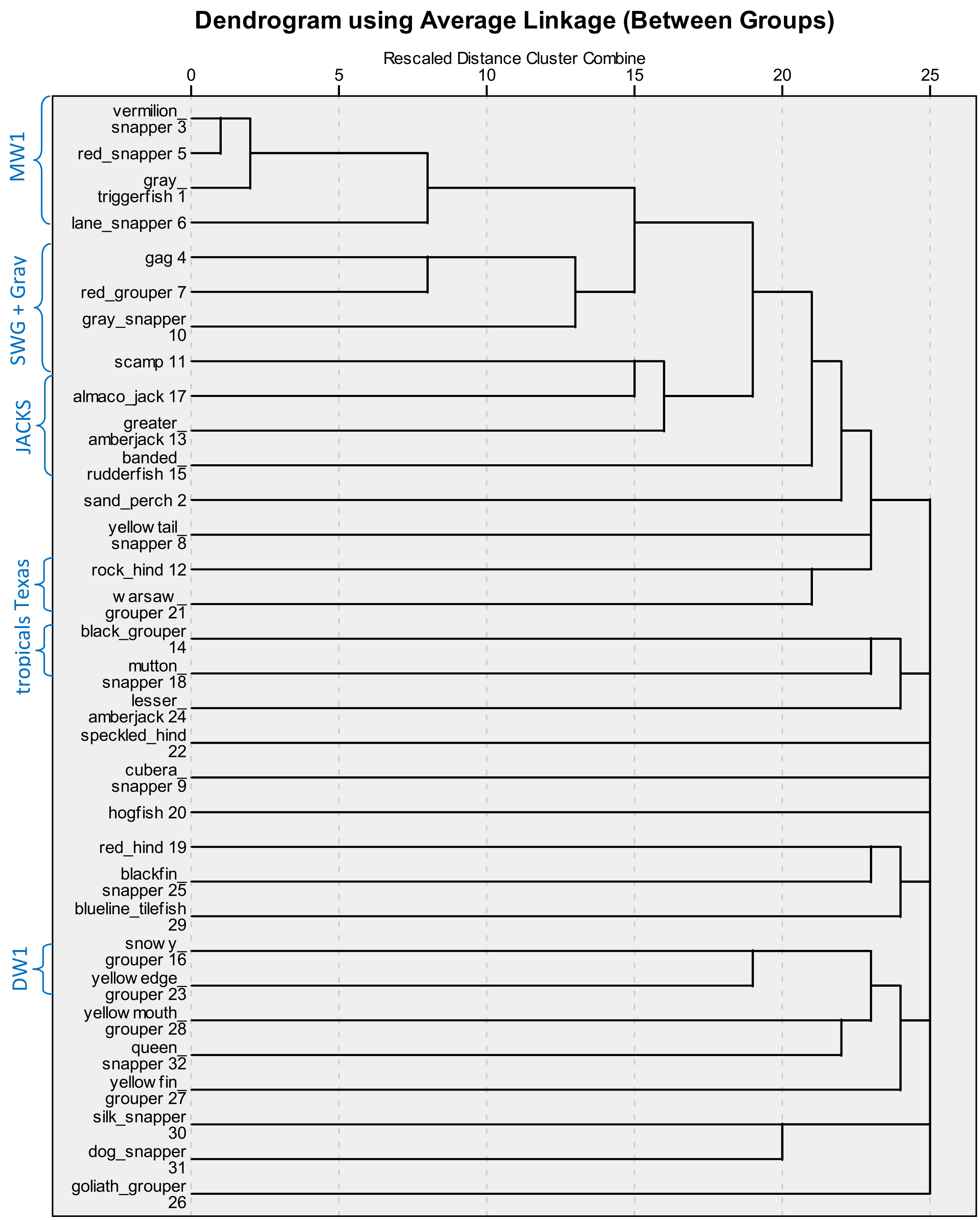


Figure 7. Hierarchical cluster analysis of species presence-absence in Gulf reef fish headboat landings aggregated by trip and area fished (Linkage Method: Farthest (Complete), Dissimilarity Measure: Sørenson (Binary)).

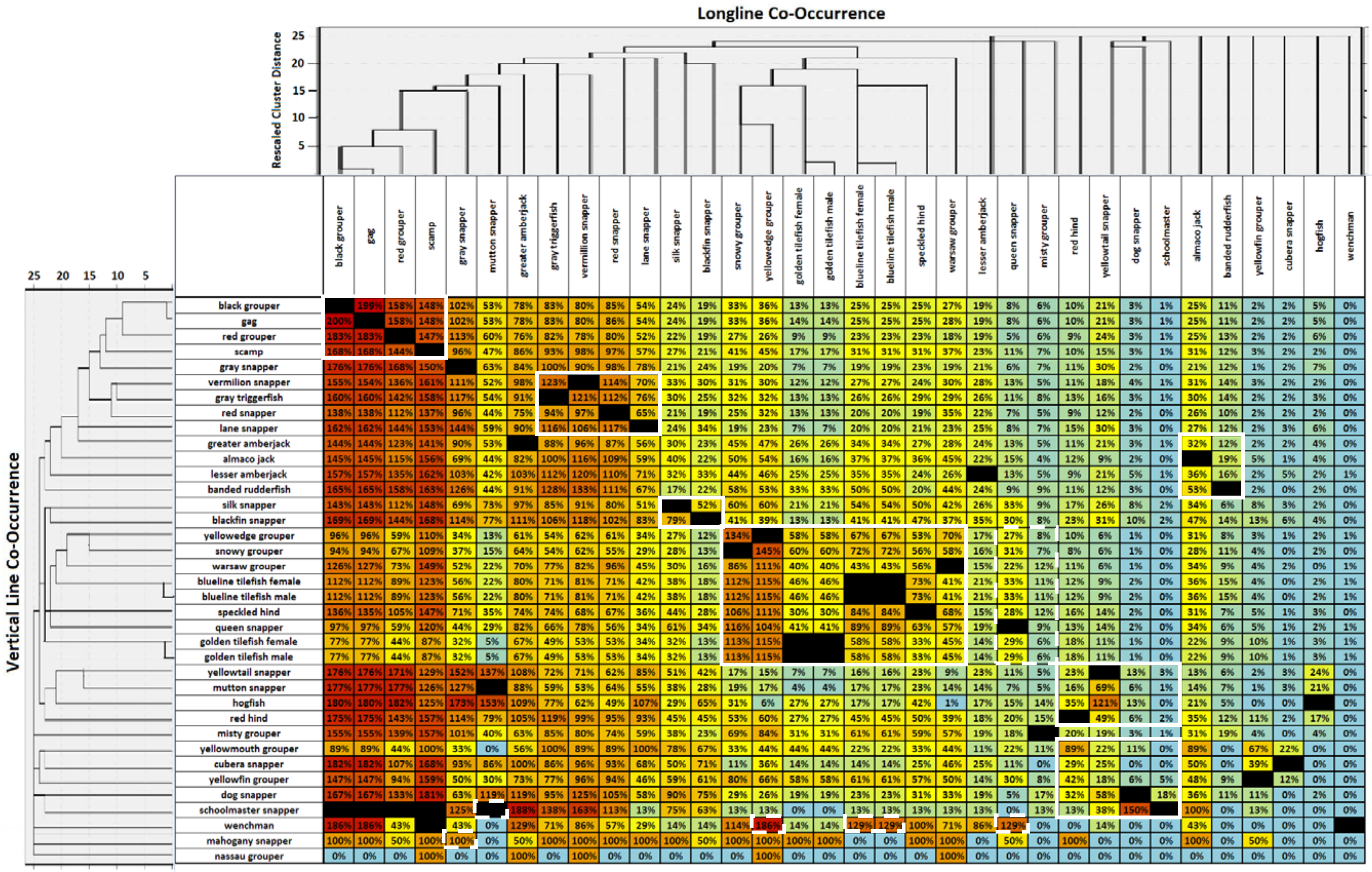


Figure 8. Nodal analysis of species presence-absence in Gulf reef fish commercial longline and vertical line landings aggregated by year, month, area, and depth (Linkage Method: Ward's, Dissimilarity Measure: Sørenson (binary)). Values in table represent summed percent co-occurrence of species in column when species in row is landed. Solid white boxes represent consistent species groups, dashed white indicate potential groups for rare species.

Table 6. Possible species groupings for Gulf Council's generic comprehensive ACL/AM amendment. Note potential indicator species with completed or pending assessments and overfishing limit (OFL) estimates. Productivity-Susceptibility Analysis (PSA) scores of overall risk from MRAG Americas Gulf of Mexico Final Report when available (MRAG 2009a,b). Most vulnerable species within each complex denoted by red box on PSA score.

GROUP	COMMON NAME	SPECIES NAME	ASSESSED	OFL	PSA
DW1	**yellowedge grouper**	***Epinephelus flavolimbatus***	**2010**	**?**	**3.64**
DW1	**anchor tilefish**	***Caulolatilus intermedius***	**2010?**	**N**	**-**
DW1	**blackline tilefish**	***Caulolatilus cyanops***	**2010?**	**N**	**-**
DW1	**golden tilefish (tilefish)**	***Lopholatilus chamaeleonticeps***	**2010**	**?**	**3.33**
DW1	**goldface tilefish**	***Caulolatilus crysops***	**2010?**	**N**	**-**
DW1	snowy grouper	*Epinephelus niveatus*		N	3.54
DW1	warsaw grouper	*Epinephelus nigritus*		N	$\boxed{3.89}$
DW2	blueline tilefish	*Caulolatilus microps*	**2010**	**?**	3.4*
DW2	speckled hind	*Epinephelus drummondhayi*			3.42*
DW3	misty grouper	*Epinephelus mystacinus*			3.66
DW3	queen snapper	*Etelis oculatus*			3.08*
DW3	wenchman	*Pristipomoides aquilonaris*			-
JACKS	**greater amberjack**	***Seriola dumerili***	**2006**	**Y**	**3.23**
JACKS	almaco jack	*Seriola rivoliana*			3.35*
JACKS	banded rudderfish	*Seriola zonata*			3.26*
JACKS	lesser amberjack	*Seriola fasciata*			$\boxed{3.64}$
MW1	**gray triggerfish**	***Balistes capriscus***	**2006**	**Y**	**2.46***
MW1	**red snapper**	***Lutjanus campechanus***	**2010**	**Y**	**3.37**
MW1	**vermilion snapper**	***Rhomboplites aurorubens***	**2006**	**N**	**3.07**
MW1	lane snapper	*Lutjanus synagris*			2.99
MW2	blackfin snapper	*Lutjanus buccanella*			3.36*
MW2	silk snapper	*Lutjanus vivanus*			3.52
SWG1	**black grouper**	***Mycteroperca bonaci***	**2010**	**?**	**3.48**
SWG1	**gag**	***Mycteroperca microlepis***	**2006**	**Y**	$\boxed{\mathbf{3.52}}$
SWG1	**red grouper**	***Epinephelus morio***	**2007**	**Y**	**3.28**
SWG1	scamp	*Mycteroperca phenax*			3.25
SWG2	dwarf sand perch	*Diplectrum formosum*			-
SWG2	red hind	*Epinephelus guttatus*			3.05
SWG2	rock hind	*Epinephelus adscensionis*			3.23*
SWG2	sand perch	*Diplectrum bivattatum*			-
SWG2	yellowfin grouper	*Mycteroperca venenosa*			3.39*
SWG2	yellowmouth grouper	*Mycteroperca interstitialis*			3.2*
SWG3	**goliath grouper**	***Epinephelus itajara***	**2004**	**Protected**	**3.42**
SWG4	Nassau grouper	*Epinephelus striatus*		Protected	3.3
SWS1	gray (mangrove) snapper	*Lutjanus griseus*			3.17
SWS2	**yellowtail snapper**	***Ocyurus chrysurus***	**2003**		**2.84**
SWS2	**hogfish**	***Lachnolaimus maximus***	**2004**		**3.05**
SWS3	**mutton snapper**	***Lutjanus analis***	**2008**		**3.27**
SWS3	cubera snapper	*Lutjanus cyanopterus*			$\boxed{3.92^*}$
SWS3	dog snapper	*Lutjanus jocu*			3.29*
SWS3	mahogany snapper	*Lutjanus mahogoni*			3.55*
SWS3	schoolmaster	*Lutjanus apodus*			3.49*

DW = deep-water, MW = mid-water, SWG = shallow-water grouper, SWS = shallow-water snapper. (*) = from MRAG South Atlantic Final Report.

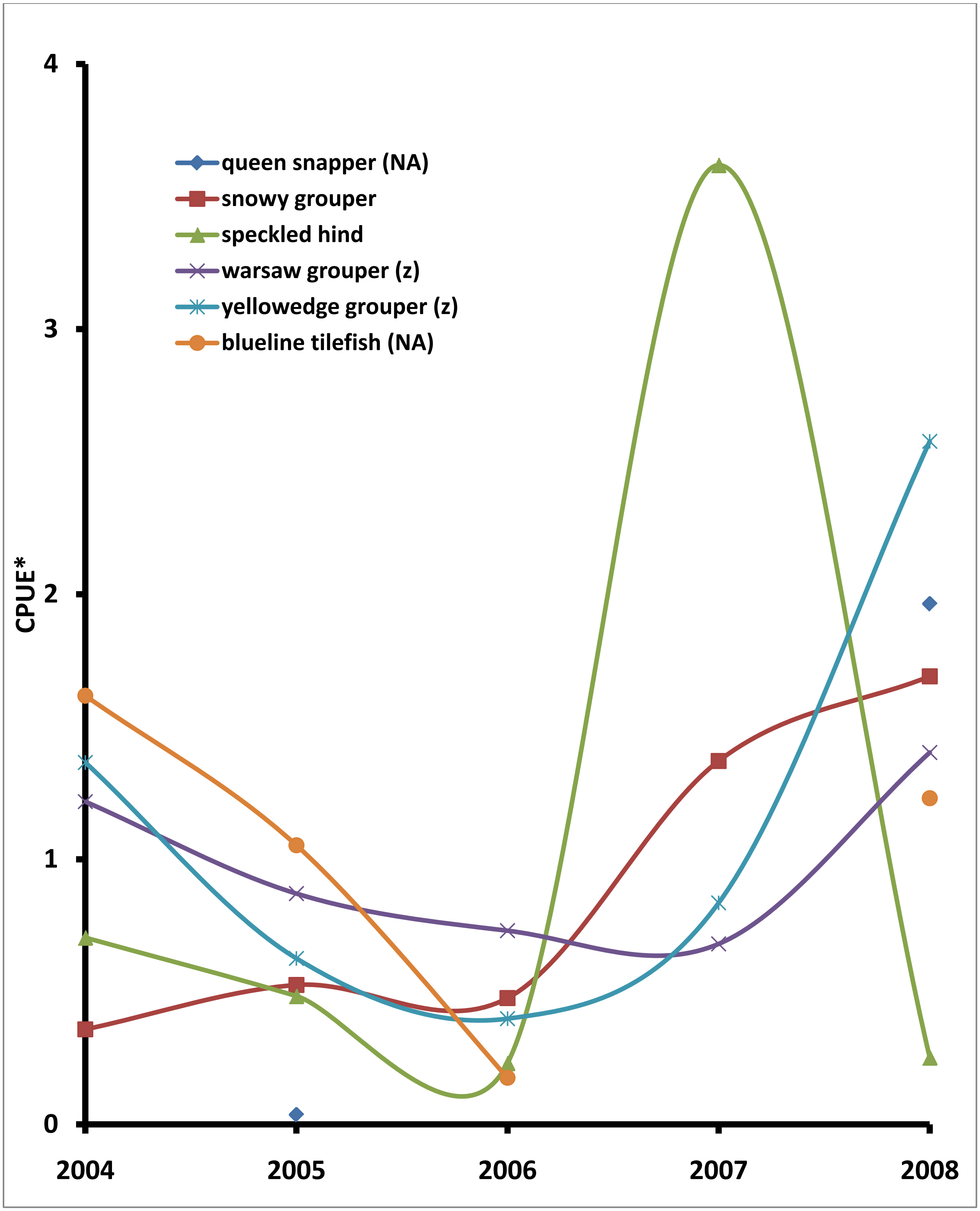


Figure 10. Standardized, scaled catch per unit effort from headboat fishery shown as index of abundance for deep-water group. Letters denote significantly correlated indices of abundance (1-2), log-transformed first effects (u-z), and binomial log-transformed first effects (q-s).

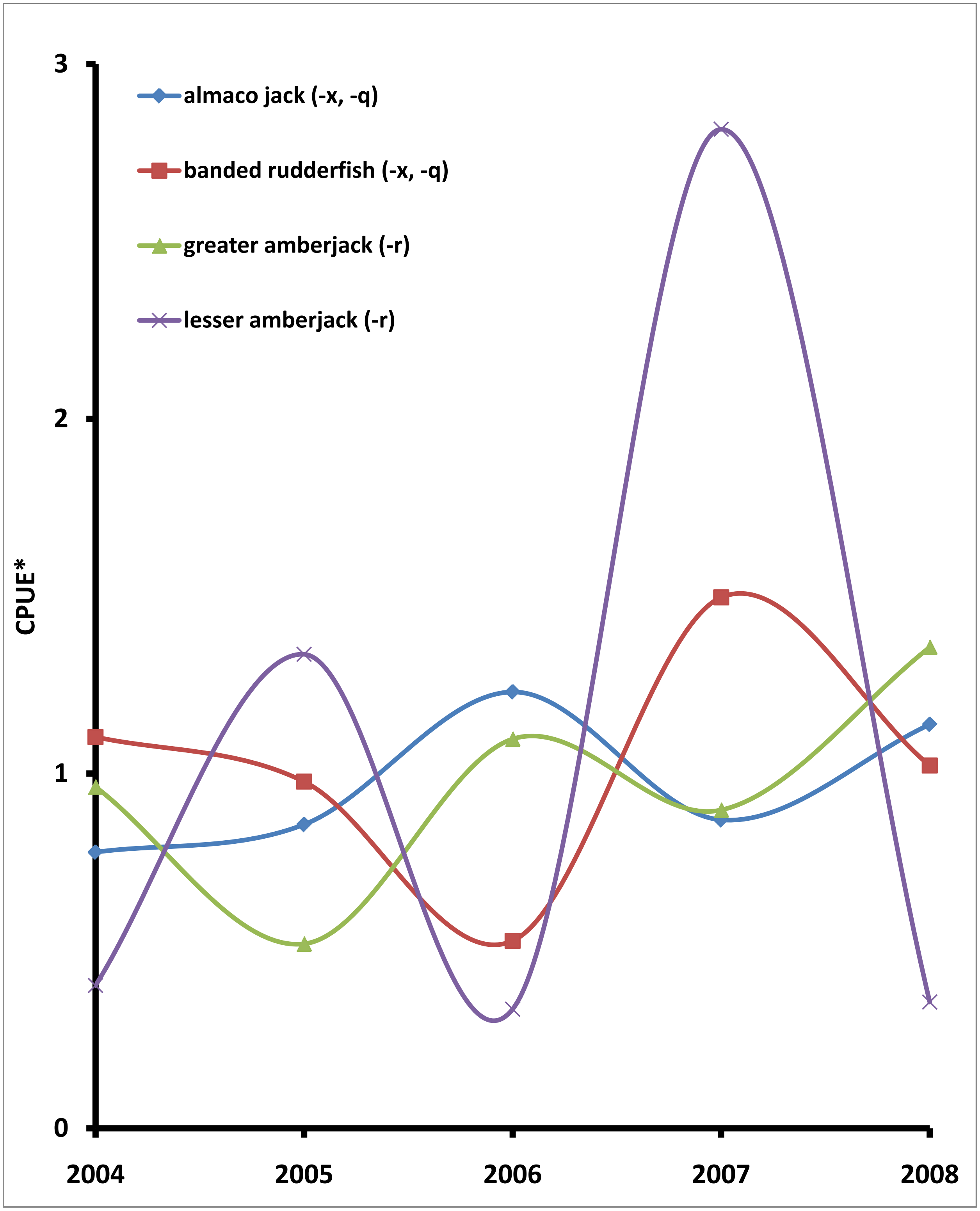


Figure 11. Standardized, scaled catch per unit effort from headboat fishery shown as index of abundance for jacks group. Letters denote significantly correlated indices of abundance (1-2), log-transformed first effects (u-z), and binomial log-transformed first effects (q-s).

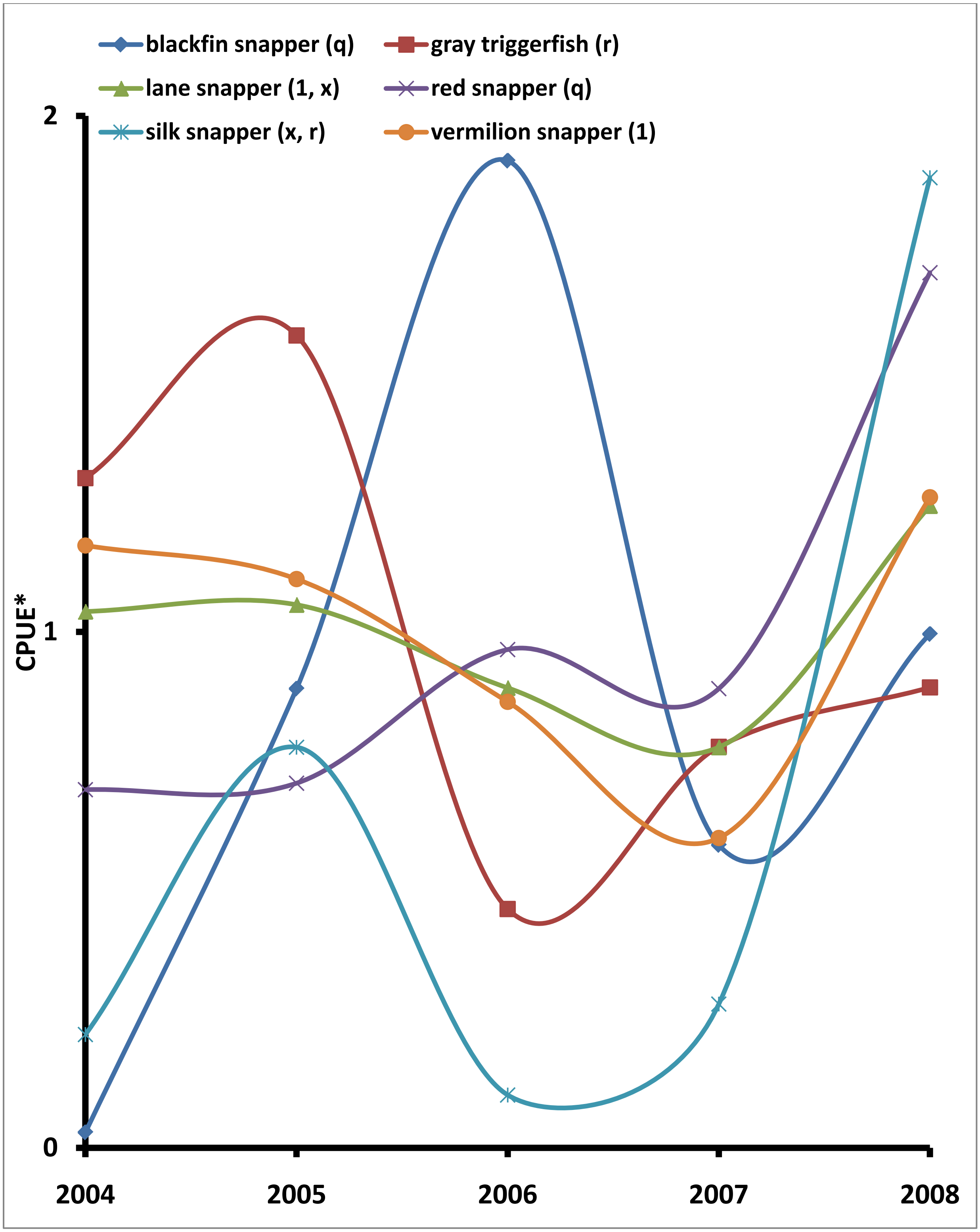


Figure 12. Standardized, scaled catch per unit effort from headboat fishery shown as index of abundance for mid-water group. Letters denote significantly correlated indices of abundance (1-2), log-transformed first effects (u-z), and binomial log-transformed first effects (q-s).

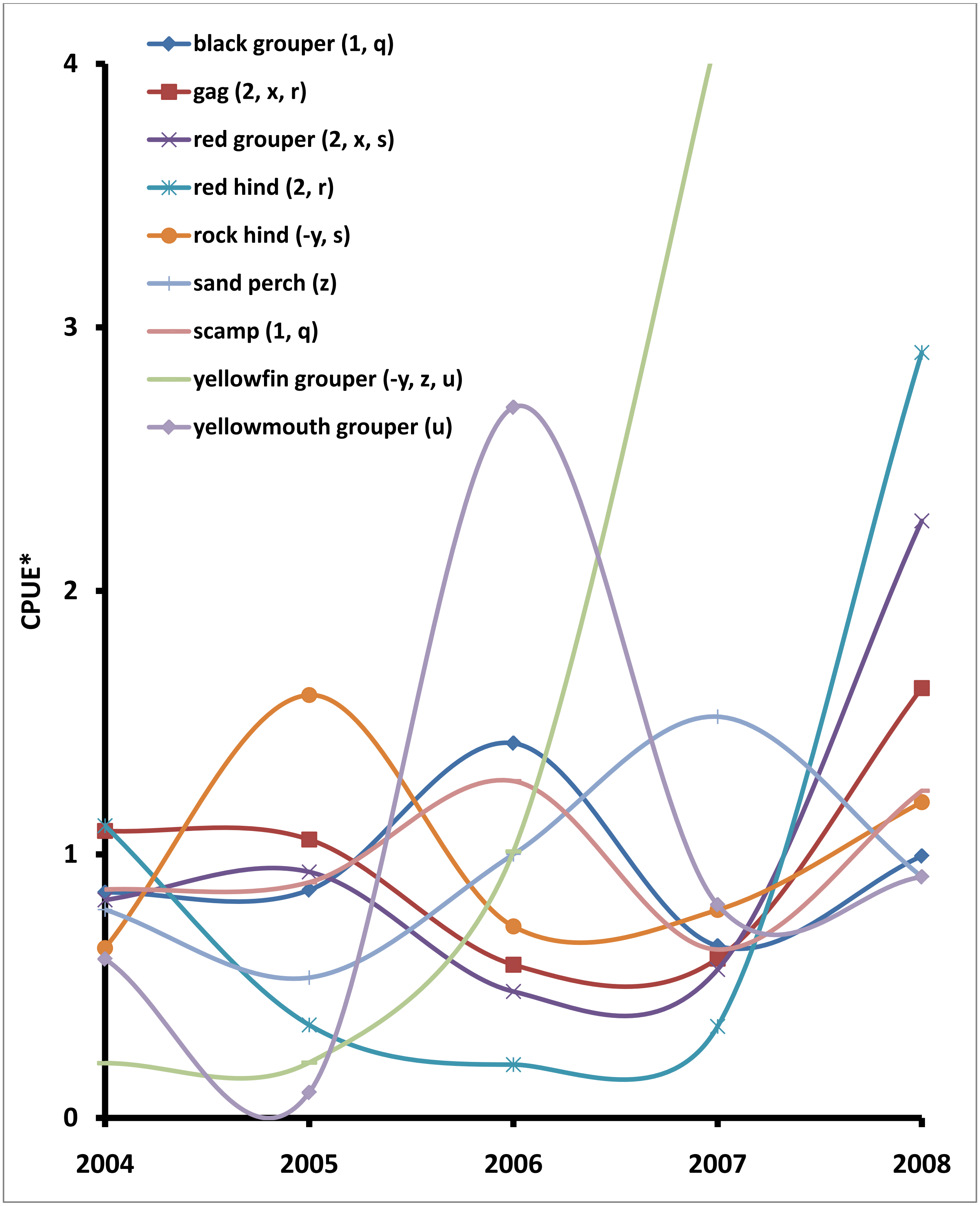


Figure 13. Standardized, scaled catch per unit effort from headboat fishery shown as index of abundance for shallow-water grouper. Letters denote significantly correlated indices of abundance (1-2), log-transformed first effects (u-z), and binomial log-transformed first effects (q-s).

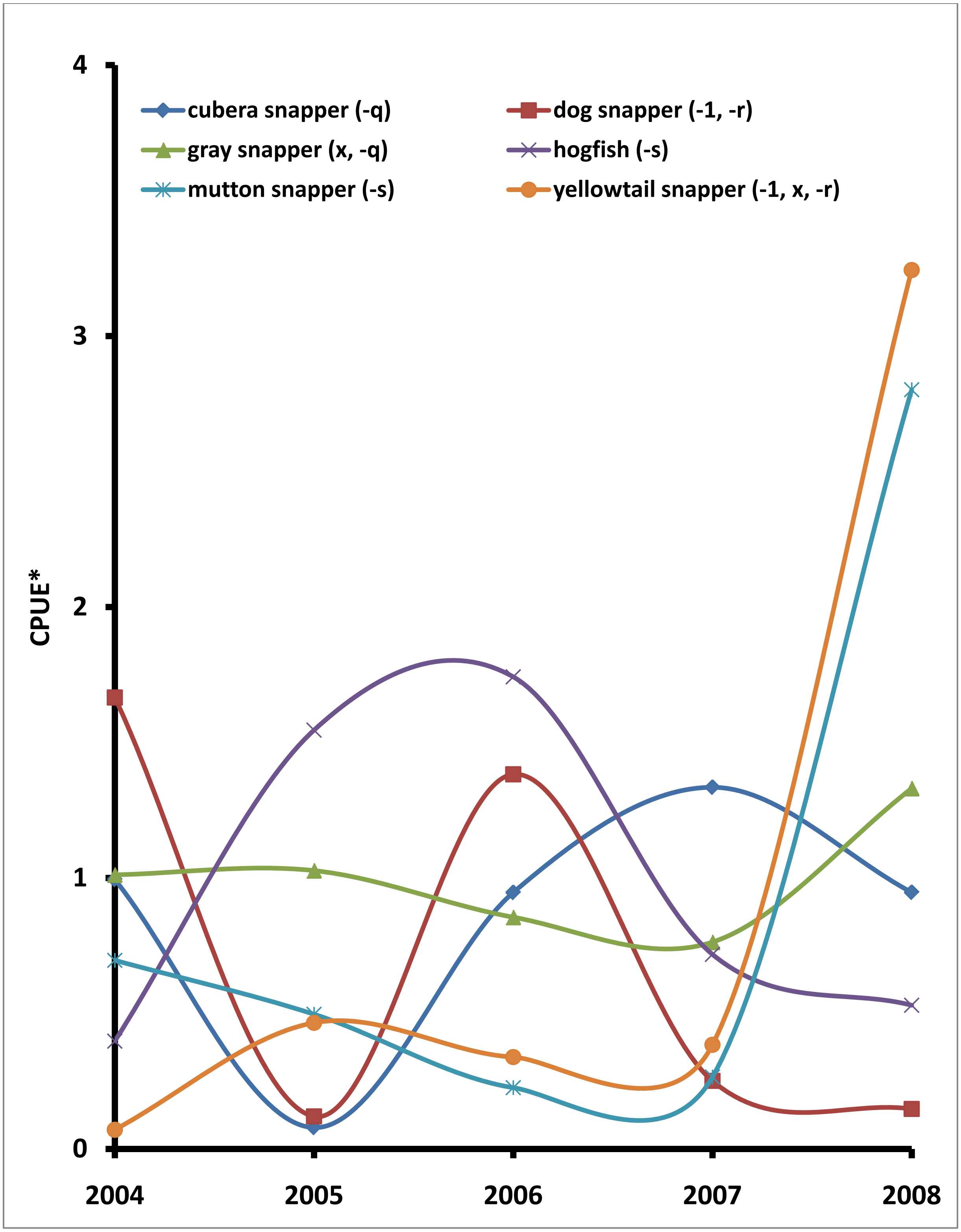


Figure 14. Standardized, scaled catch per unit effort from headboat fishery shown as index of abundance for shallow-water snapper. Letters denote significantly correlated indices of abundance (1-2), log-transformed first effects (u-z), and binomial log-transformed first effects (q-s).

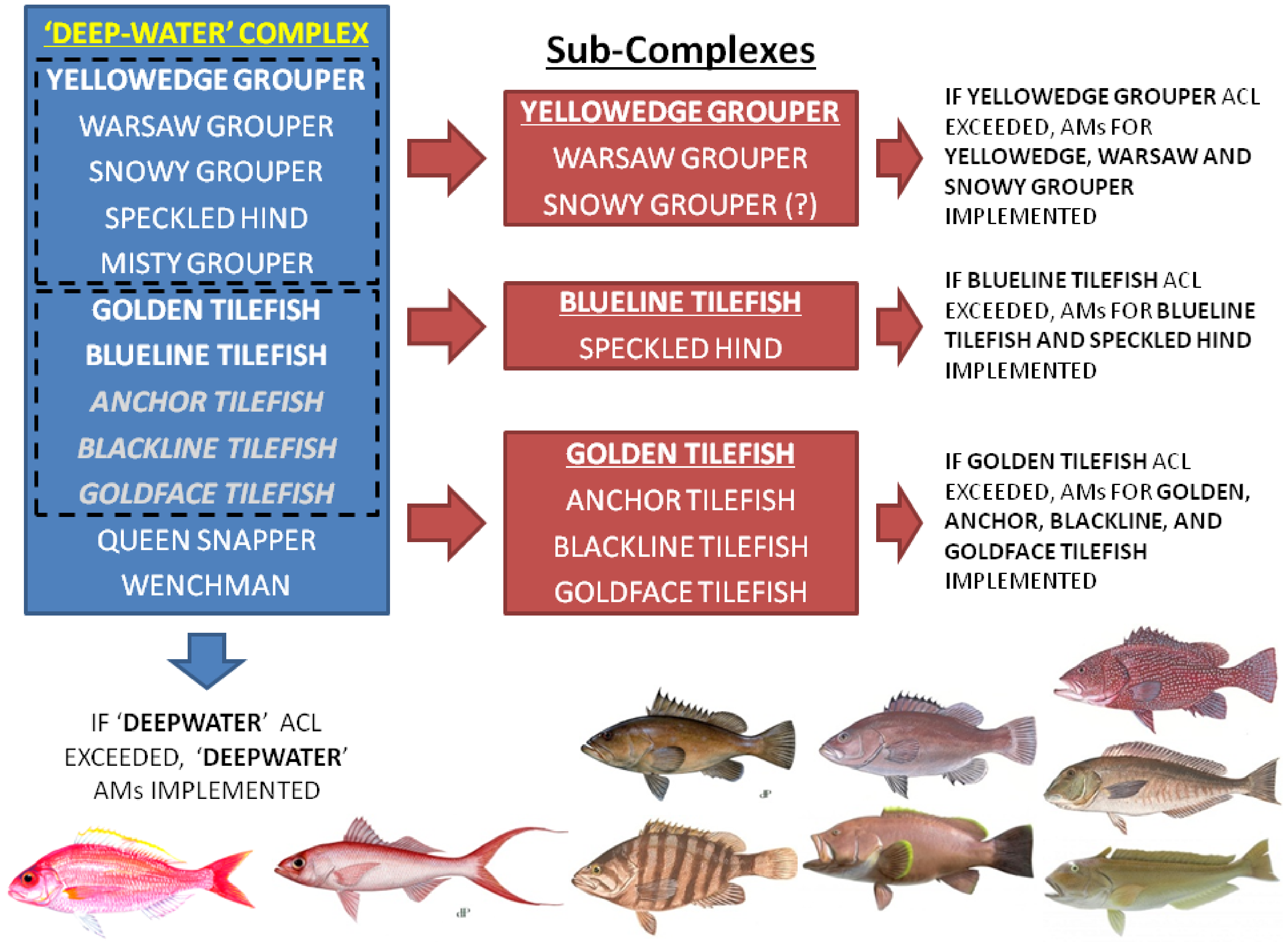


Figure 15. ACL/AM flowchart for 'deepwater' stock complex (blue) , with sub-complexes (red) allowing more targeted AMs via indicator species (bold). Current complexes indicated in dashed black boxes.

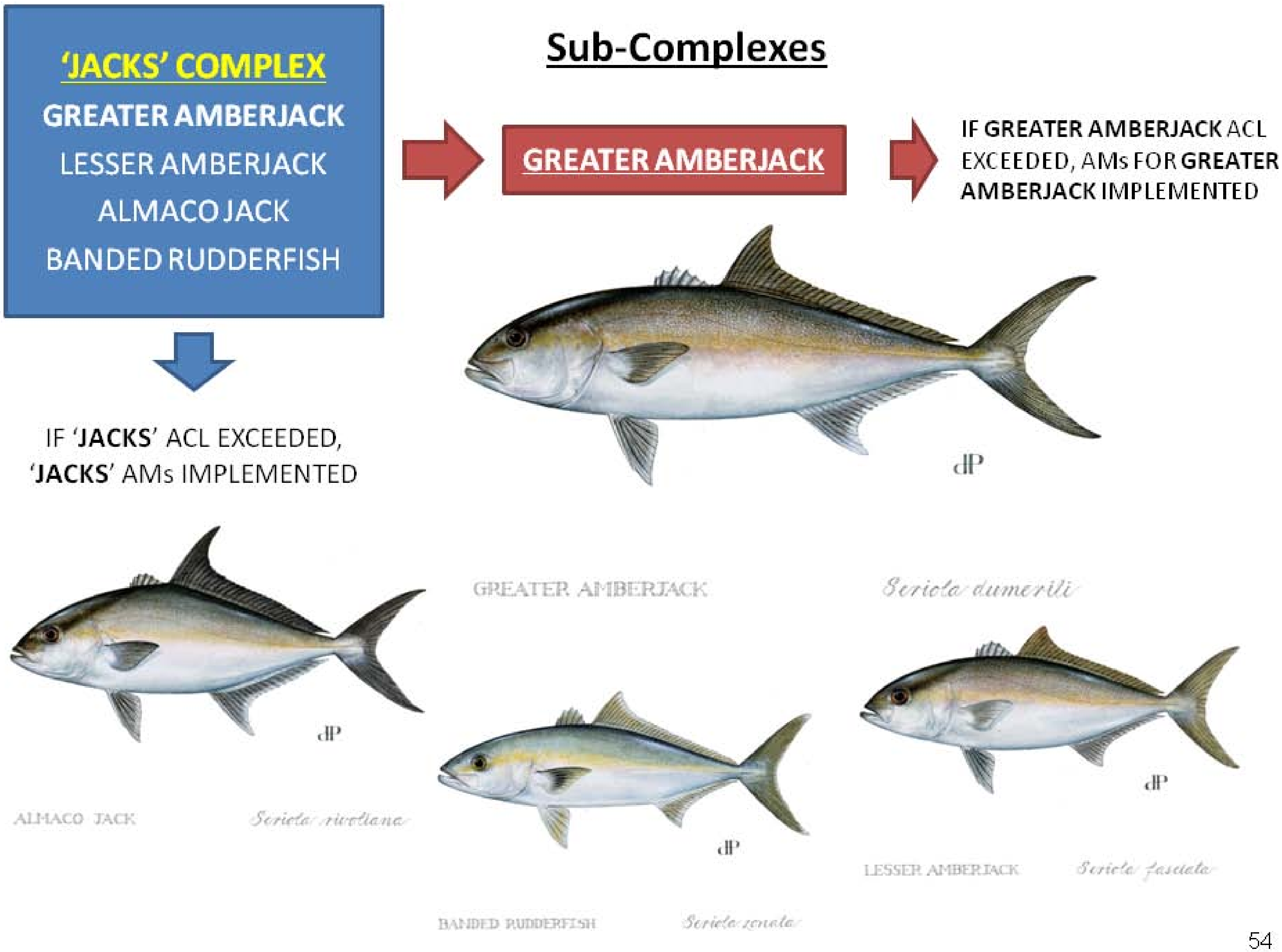


Figure 16. ACL/AM flowchart for 'jacks' stock complex (blue), with single-species control for greater amberjack (red), which is assessed but does not work well as indicator for other jacks.

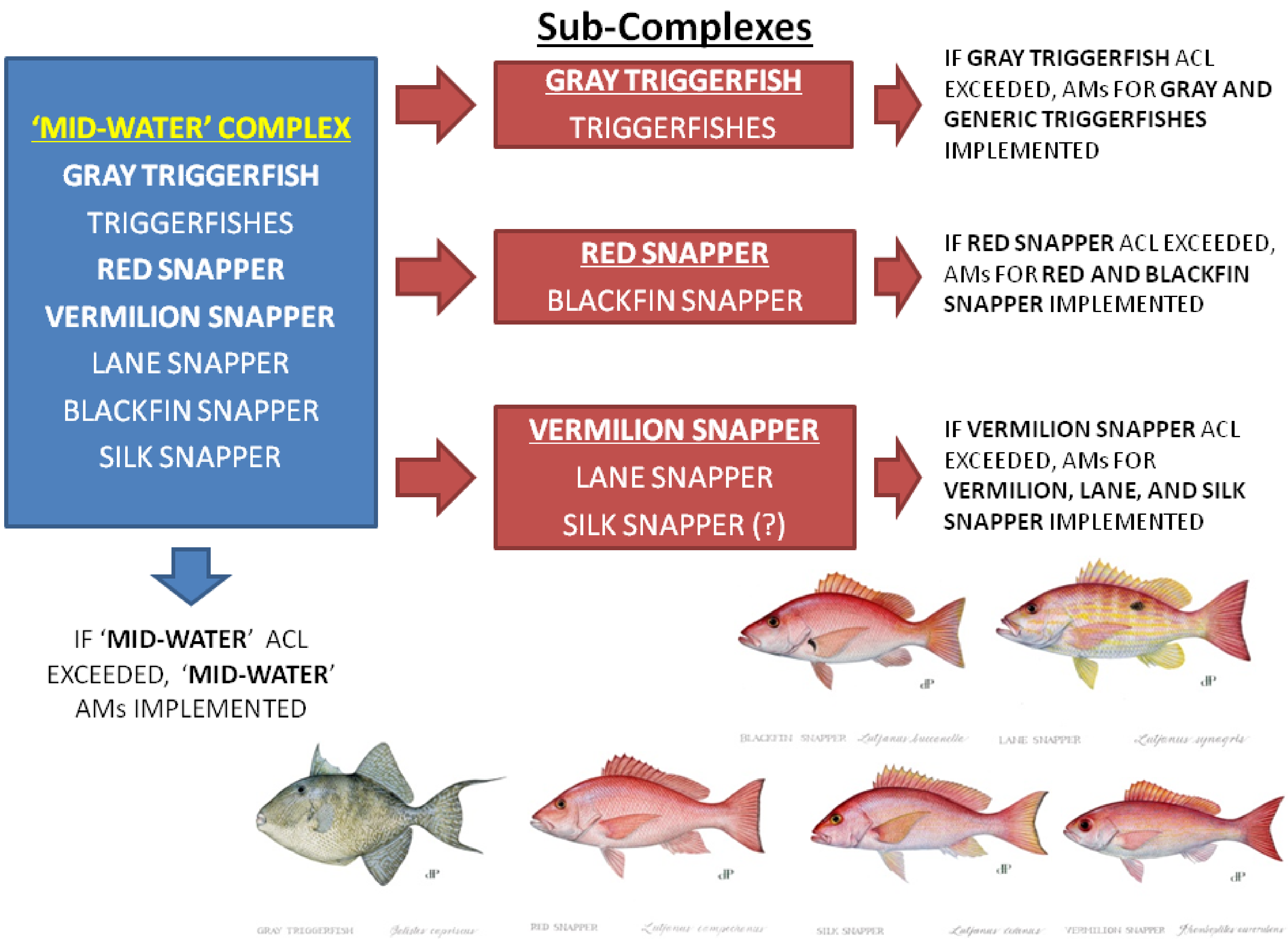


Figure 17. ACL/AM flowchart for 'midwater' stock complex (blue), with sub-complexes (red) allowing more targeted AMs via indicator species (bold).

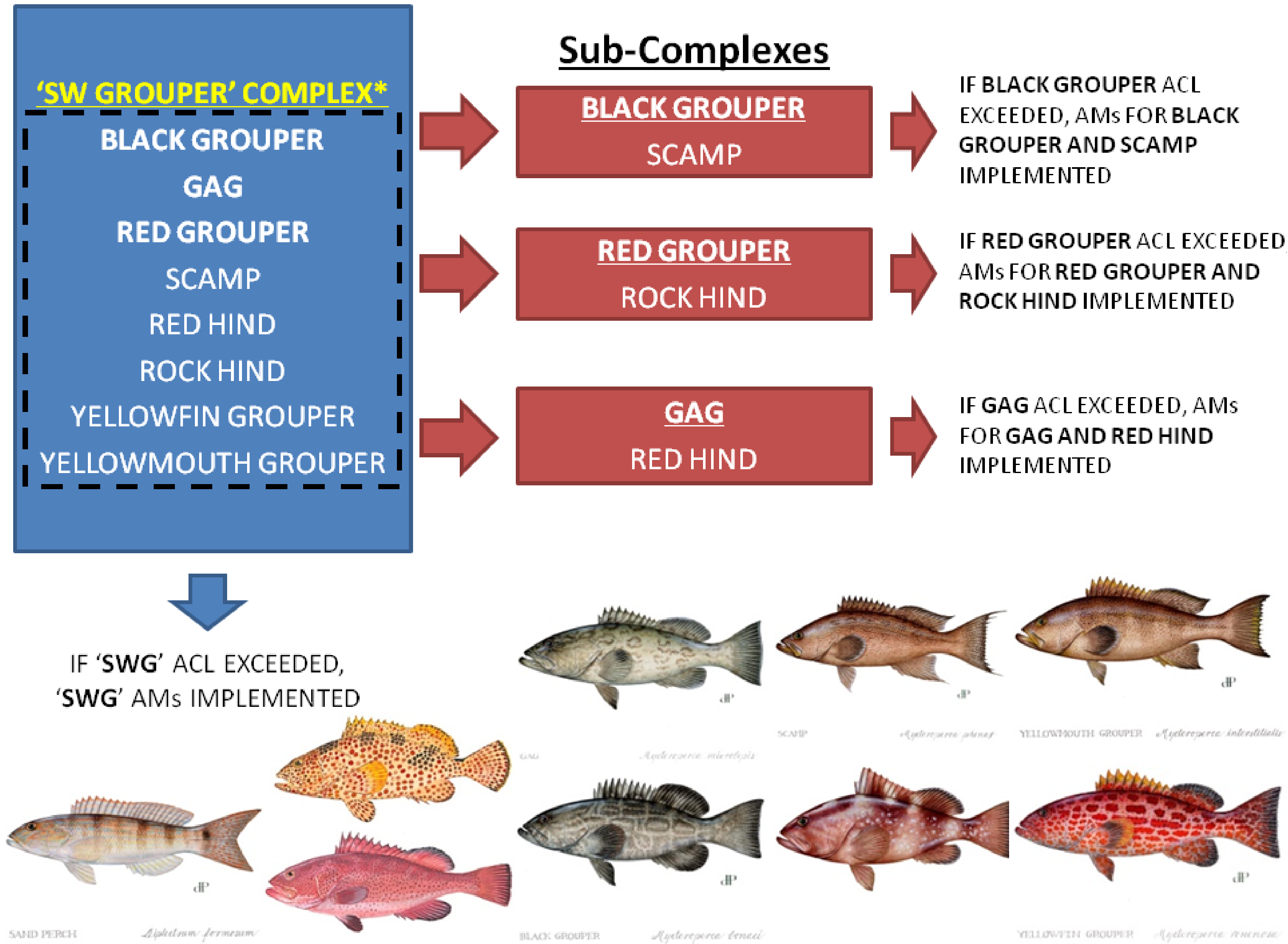


Figure 18. ACL/AM flowchart for 'shallow-water grouper' stock complex (blue), with sub-complexes (red) allowing targeted AMs via indicator species (bold). Current complex denoted by dashed black box.

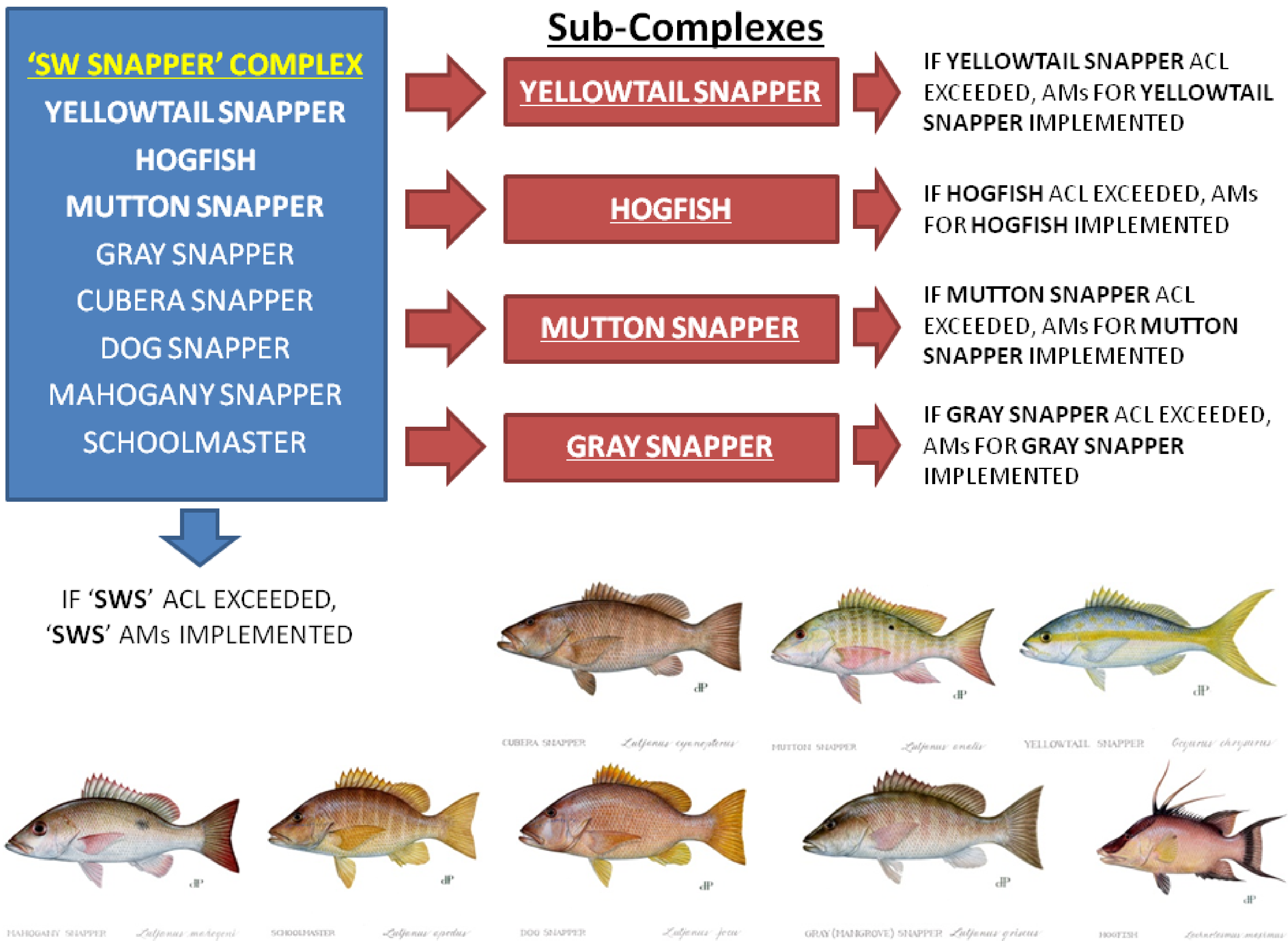


Figure 19. ACL/AM flowchart for 'shallow-water snapper' stock complex (blue), with sub-complexes (red) allowing targeted AMs via indicator species (bold).

Table A1. References for life history parameters (see Table 3).

Ref#	Source
1	NEFSC. 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. (http://www.sefsc.noaa.gov/sedar/). 594 p.
3	SEDAR6-SAR1. 2004. Goliath grouper. SEDAR Charleston, South Carolina. (http://www.sefsc.noaa.gov/sedar/). 114 p.
4	SEDAR 8-SAR1. 2005. Caribbean yellowtail snapper. SEDAR Charleston, South Carolina. (http://www.sefsc.noaa.gov/sedar/). 179 p.
5	SEDAR 9-SAR1. 2005. Gulf of Mexico gray triggerfish. SEDAR Charleston, SC (http://www.sefsc.noaa.gov/sedar/). 195 p.
6	SEDAR 9-SAR2. 2005. Gulf of Mexico greater amberjack. SEDAR Charleston, SC (http://www.sefsc.noaa.gov/sedar/). 178 p.
7	SEDAR 14-SAR1. 2007. Caribbean yellowfin grouper. SEDAR Charleston, SC (http://www.sefsc.noaa.gov/sedar/). 163 p.
8	SEDAR 15-AW01. October 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. (http://www.sefsc.noaa.gov/sedar/). 52 p.
10	SEDAR 17. 2008. Stock Assessment report South Atlantic vermillion Snapper. SEDAR Charleston, South Carolina. (http://www.sefsc.noaa.gov/sedar/). 450 p.
11	SEDAR 10-SAR1. 2006. Gulf of Mexico gag grouper. SEDAR Charleston, South Carolina. (http://www.sefsc.noaa.gov/sedar/). 250 p.
12	SEDAR 12. 2006. Gulf of Mexico red grouper. SEDAR Charleston, South Carolina. (http://www.sefsc.noaa.gov/sedar/). 358 p.
13	SEDAR 19-SAR1. 2009. Gulf of Mexico and South Atlantic black grouper. SEDAR Charleston, South Carolina. (http://www.sefsc.noaa.gov/sedar/). 209 p.
14	Southern Demersal Working Group. 2009. Assessment of Golden tilefish, Lopholatilus chamaeleonticeps, in the Middle Atlantic-Southern New England region. 48th SAW Assessment Report. 170 p.
15	Bortone, S.A. 1971. Studies on the biology of sand perch Diplectrum formosum. State of Florida Marine Research Laboratory, Technical Series No. 65. 30 p.
16	Froese, R. and D. Pauly. Editors. 2009. FishBase. World Wide Web electronic publication. www.fishbase.org.version (10/2009).
17	Harris, P.J., D.M. Wyanski and P.T. Powers Mikell, 2004. Age, Growth and Reproduction of Tilefish, Lopholatilus Chamaeleonticeps, along the Southeast Atlantic Coast of the United States, 1982-1999. Trans. Am. Fish. Soc. 133(5): 1190-1204.
18	Ross, J.L. and G.R. Huntsman, 1982. Age, growth, and mortality of blueline tilefish from North Carolina and South Carolina. Trans. Am.Fish.Soc. 111(5): 585-592.
19	South Atlantic Fishery Management Council. 2005. Stock Assessment and Fishery Evaluation Report for the Snapper Grouper Fishery of the South Atlantic. SAFMC Charleston, SC. 130 p.
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. SEFSC Miami, Florida. 40 p.
21	SEDAR 15-SAR2. 2008. South Atlantic greater amberjack. SEDAR Charleston, South Carolina. (http://www.sefsc.noaa.gov/sedar/). 379 p.

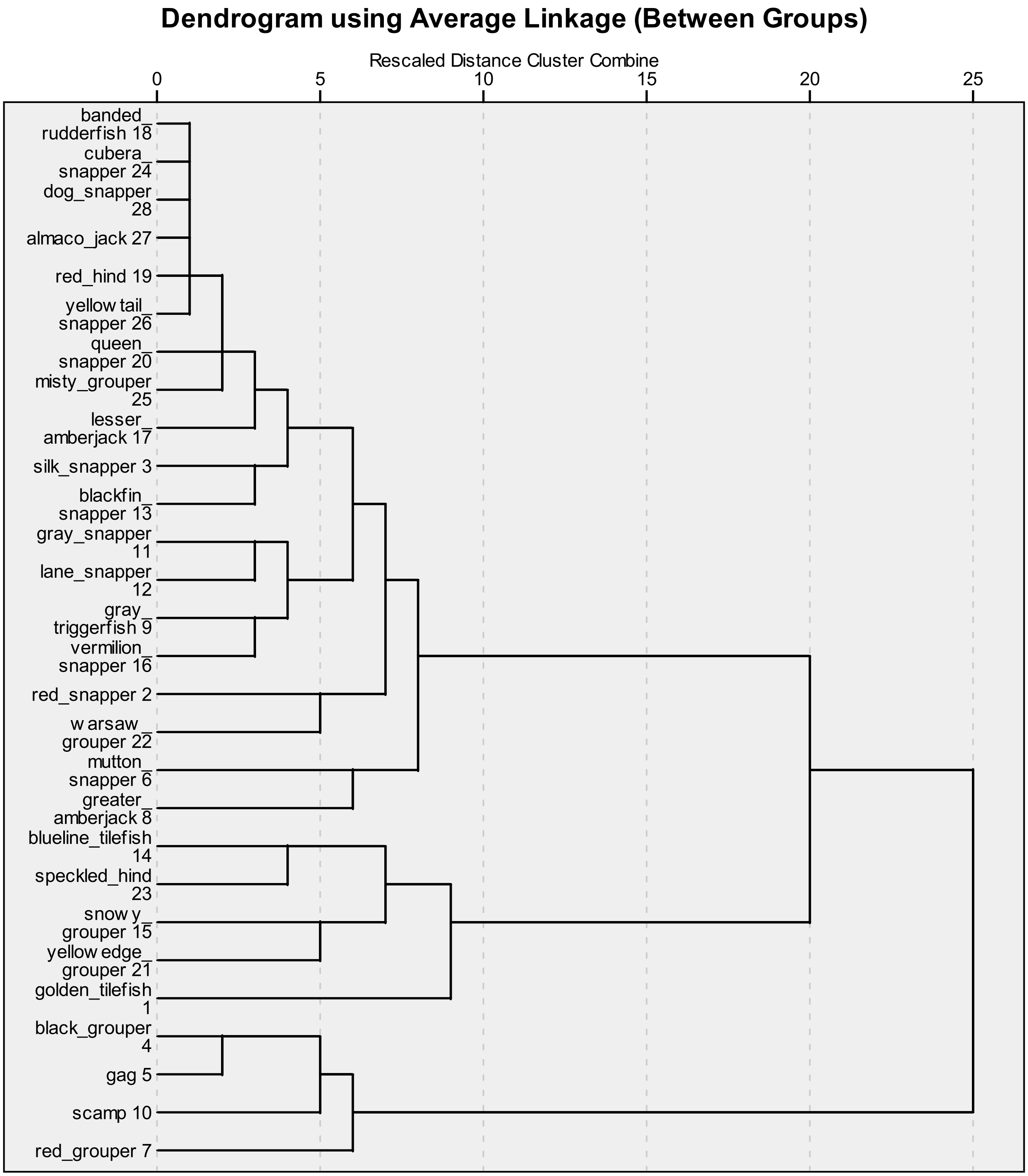


Figure A1. Hierarchical cluster analysis of Gulf reef fish commercial longline landings aggregated by year, month, area, and depth for species landed on >1% of trips (Linkage Method: Ward's, Dissimilarity Measure: Chi-square (count), Transformation: Root-Root on landings).

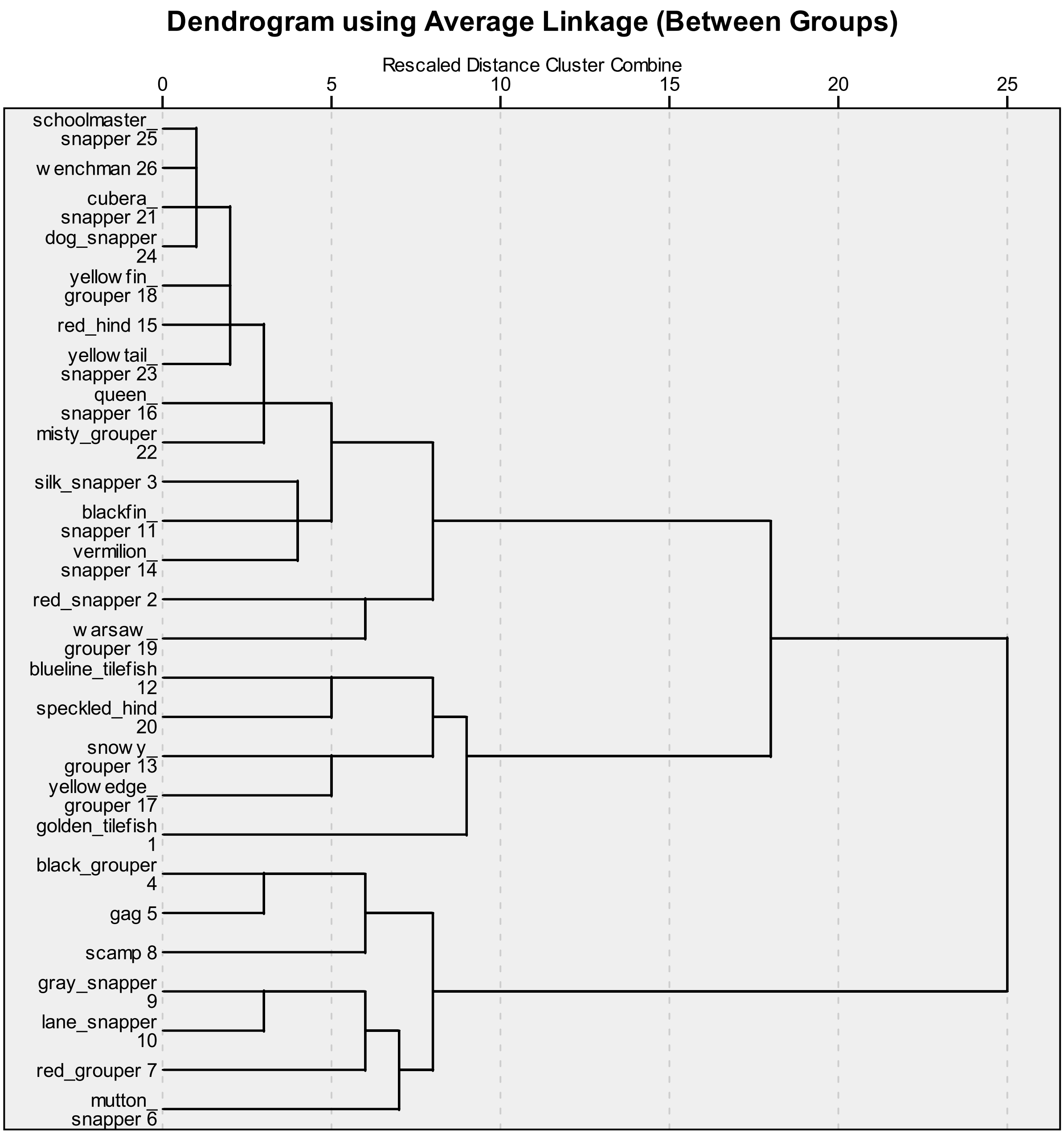


Figure A2. Hierarchical cluster analysis of Gulf grouper-snapper-tilefish commercial longline landings aggregated by year, month, area, and depth (Linkage Method: Ward's, Dissimilarity Measure: Chi-square (count), Transformation: Root-Root on landings).

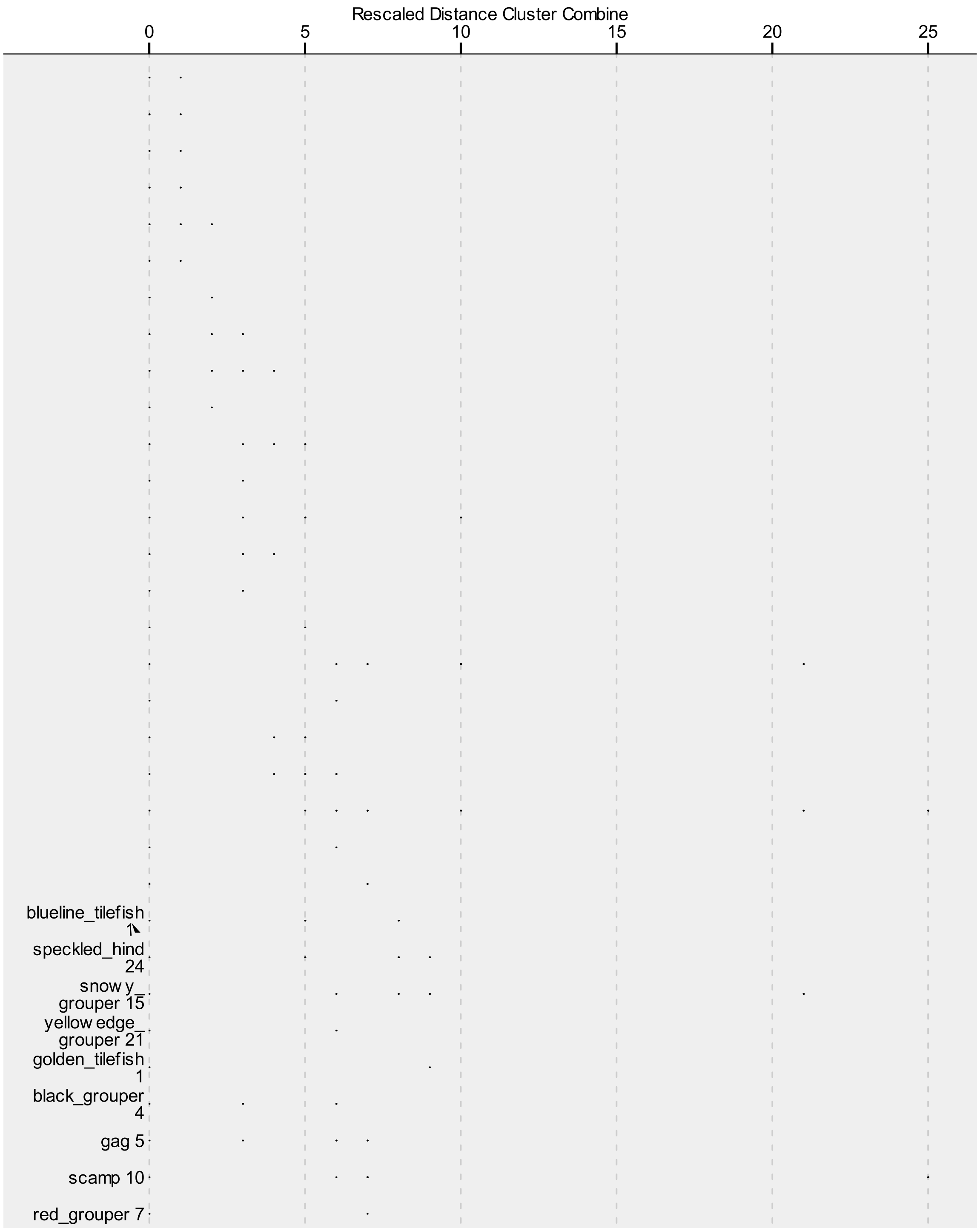


Figure A3. Hierarchical cluster analysis of Gulf reef fish commercial longline landings in numbers, computed by dividing landings by average weight from the Reef Fish Observer Program, aggregated by year, month, area, and depth (Linkage Method: Ward's, Dissimilarity Measure: Chi-square (count), Transformation: Root-Root on landings in numbers, Range 0-1 by Case).

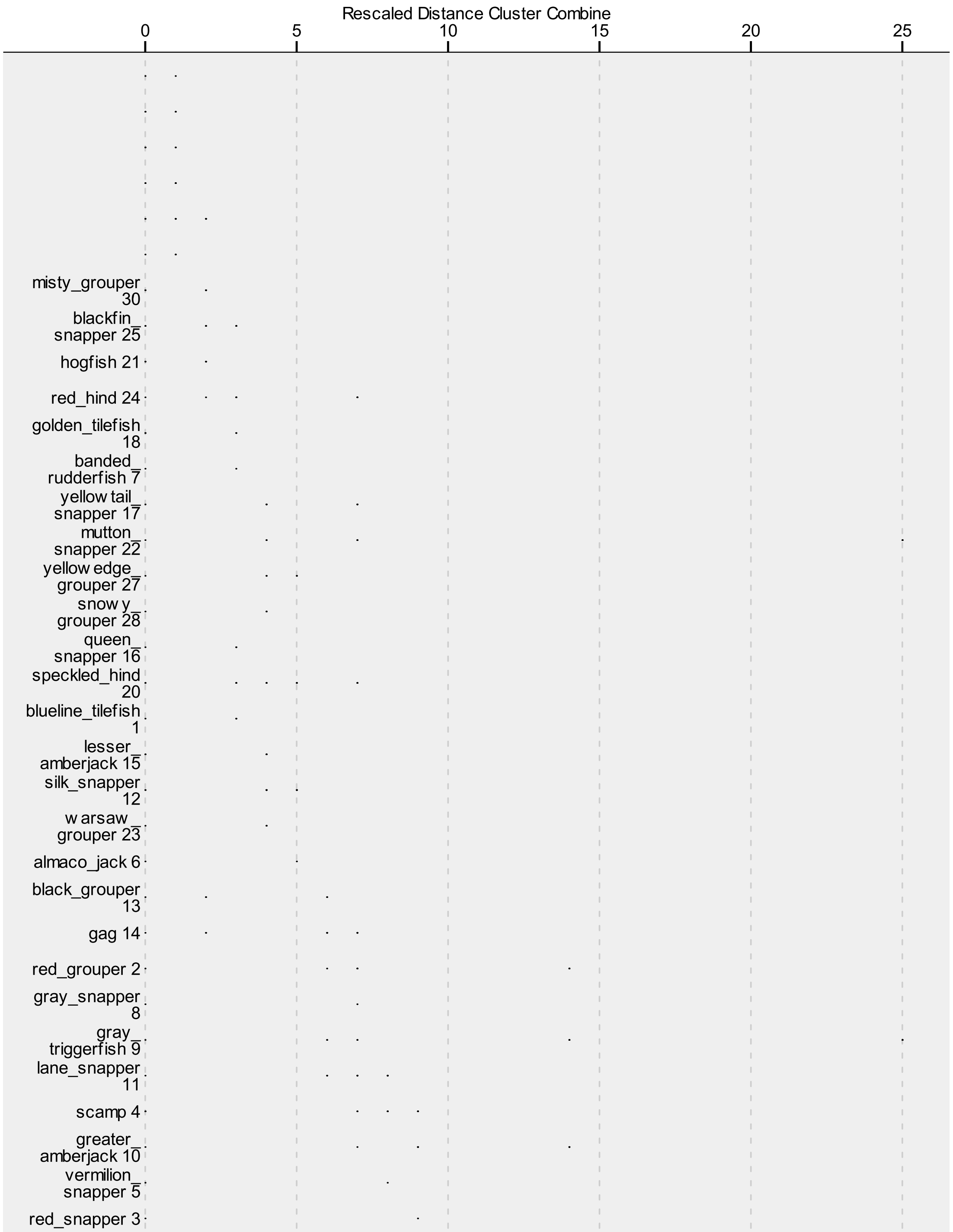


Figure A4. Hierarchical cluster analysis of Gulf reef fish commercial vertical line landings in numbers, computed by dividing landings by average weight from the Reef Fish Observer Program, aggregated by year, month, area, and depth (Linkage Method: Ward's, Dissimilarity Measure: Chi-square (count), Transformation: Root-Root on landings in numbers, Range 0-1 by Case).

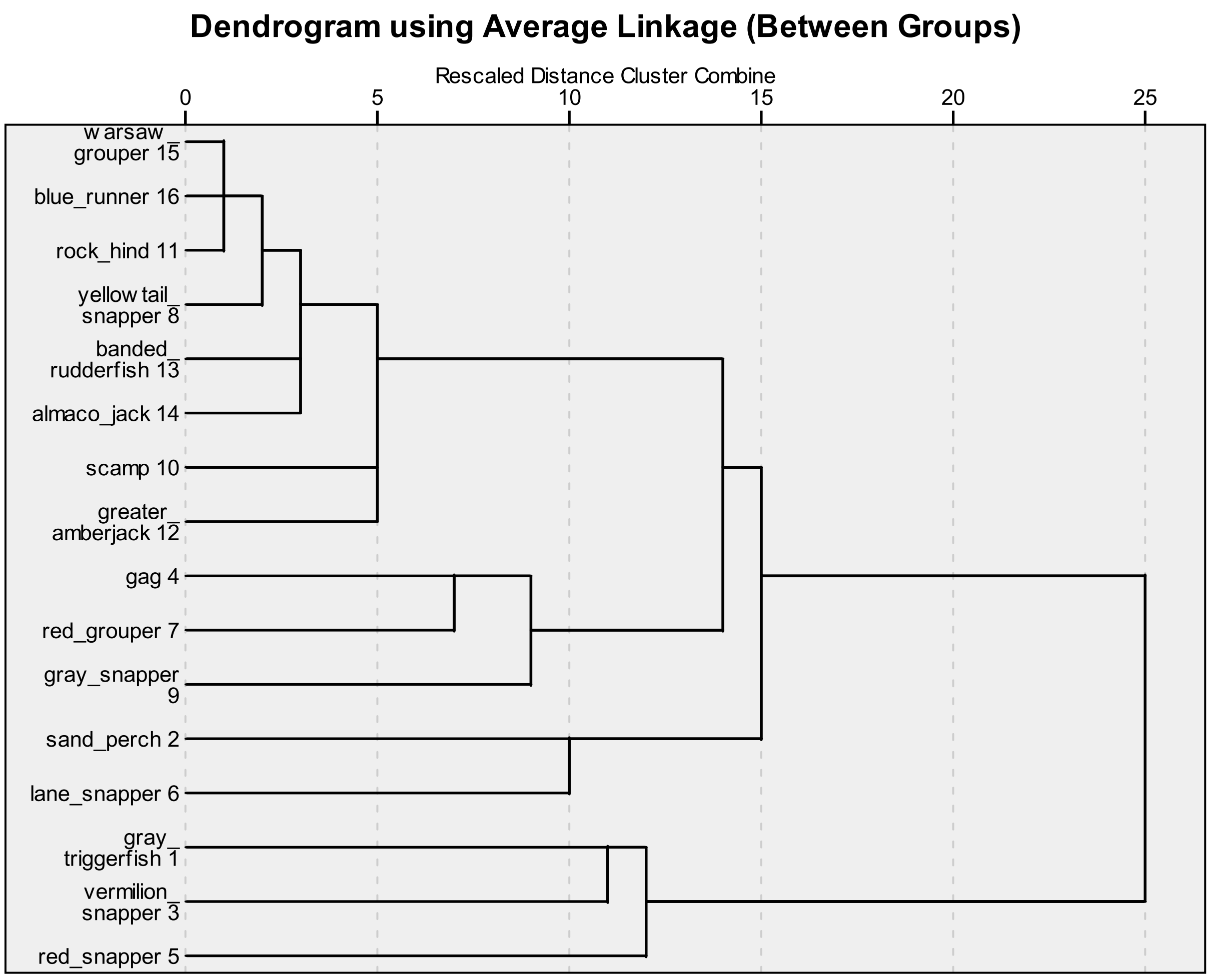


Figure A5. Hierarchical cluster analysis of Gulf reef fish headboat landings aggregated by trip and area fished for species landed on >1% of trips (Linkage Method: Ward's, Dissimilarity Measure: Chi-square (count), Transformation: Root-Root on landings in numbers).

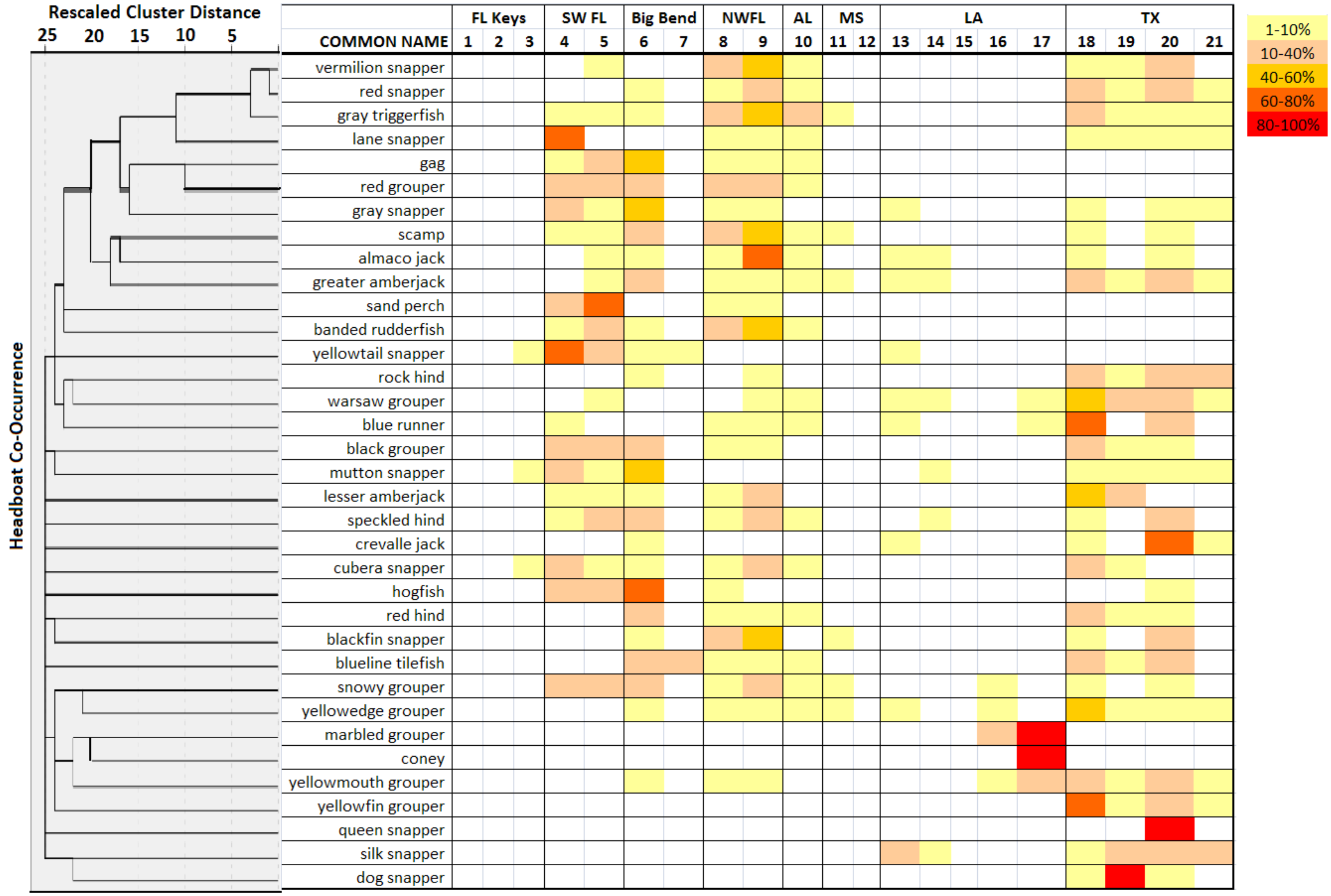
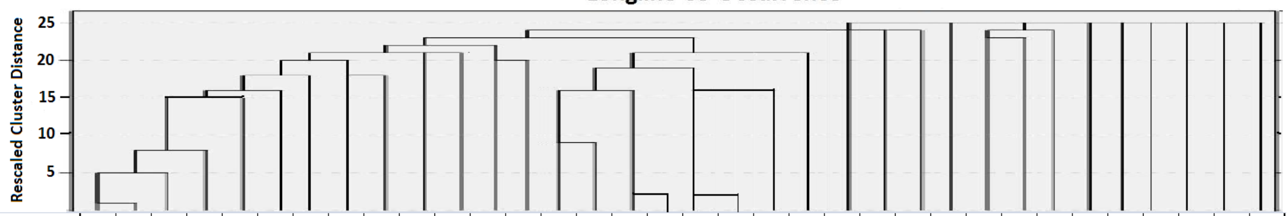
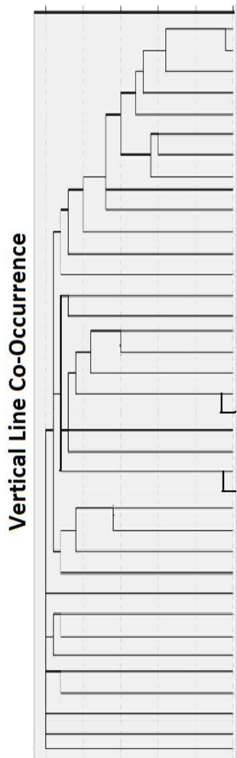


Figure A6. Plot of species presence-absence in Gulf reef fish headboat landings aggregated by trip, year, month, and area (Linkage Method: Ward's, Dissimilarity Measure: Jaccard (binary)) relative to percent of landings (2005-2008) originating from commercial logbook statistical areas 1-21, illustrating impacts of spatial distribution of exploited stock on resultant clusters. Note no headboat info was collected in areas 13-16 in 2005-2006.

Longline Co-Occurrence





	Black Grouper	Gag	Red Grouper	Scamp	Gray Snapper	Mutton Snapper	Greater Amberjack	Gray Triggerfish	Vermillion Snapper	Red Snapper	Lane Snapper	Silk Snapper	Blackfin Snapper	Snowy Grouper	Yellowedge Grouper	Golden Tilefish female	Golden Tilefish male	Blueline Tilefish Female	Blueline Tilefish Male	Speckled Hind	Warsaw Grouper	Lesser Amberjack	Queen Snapper	Misty Grouper	Red Hind	Yellowtail Snapper	Dog Snapper	Schoolmaster	Almaco Jack	Banded Rudderfish	Yellowfin Grouper	Cubera Snapper	Hogfish	Wenchman
Black Grouper		3.9	9.9	10.4	13.8	8.5	9.3	27.3	21.8	12.1	23.5	13.4	18.5	12.0	20.6	20.7	19.9	10.6	8.3	5.2	22.3	14.5	35.9	21.4	12.9	11.7	4.2	19.4	2.2	11.7	6.2	2.5	10.4	18.4
Gag	3.9		4.4	3.3	8.3	4.8	5.8	17.9	16.3	8.8	13.8	7.8	11.1	8.1	19.2	11.9	12.1	6.8	4.5	3.6	16.8	7.0	21.6	19.5	7.7	11.6	7.7	15.0	3.6	6.0	4.2	3.0	14.1	10.3
Red Grouper	9.9	4.4		4.6	3.8	5.6	3.0	8.1	13.4	8.0	4.9	12.3	6.8	7.4	24.4	12.8	15.1	6.6	6.4	5.0	20.5	7.3	21.3	31.0	4.9	9.1	10.6	10.2	8.5	5.2	3.4	6.7	17.1	4.1
Scamp	10.4	3.3	4.6		4.6	3.8	10.2	13.2	16.1	9.0	9.0	11.9	8.1	15.4	28.9	17.5	19.8	7.7	6.1	6.5	27.7	5.9	26.0	34.5	3.1	11.8	10.5	10.5	10.1	5.0	4.2	5.9	15.6	9.0
Gray Snapper	13.8	8.3	3.8	4.6		2.5	8.8	4.0	10.2	6.3	2.8	12.8	2.2	16.3	36.9	20.2	25.6	5.1	7.2	5.6	32.5	4.0	23.5	41.1	1.1	5.7	8.8	2.8	14.6	2.5	4.6	6.6	12.0	3.0
Vermilion Snapper	21.8	16.3	13.4	16.1	10.2	9.6	15.7	16.3		18.1	9.4	10.3	14.2	16.6	40.8	19.9	27.9	2.9	6.1	10.6	34.2	12.7	31.3	33.8	16.0	16.0	14.8	16.9	22.0	12.9	17.3	14.0	15.5	10.8
Gray Triggerfish	27.3	17.9	8.1	13.2	4.0	9.7	12.0		16.3	12.5	2.4	22.4	2.1	22.0	52.5	26.9	33.4	12.7	16.3	13.5	40.1	7.4	18.8	54.5	6.2	12.3	21.6	4.6	25.0	6.0	12.3	17.6	24.7	2.4
Red Snapper	12.1	8.8	8.0	9.0	6.3	9.4	13.5	12.5	18.1		11.8	14.7	10.5	16.2	24.3	15.1	18.4	8.1	9.0	10.7	27.2	11.6	20.4	32.9	7.8	10.5	10.3	12.6	14.7	9.9	11.5	9.8	14.5	11.1
Lane Snapper	23.5	13.8	4.9	9.0	2.8	7.2	10.0	2.4	9.4	11.8		15.7	4.2	15.3	43.9	18.7	25.1	7.2	9.7	9.9	33.0	7.4	22.5	44.8	5.5	10.5	17.2	7.5	21.1	6.4	9.6	14.1	19.8	1.9
Greater Amberjack	9.3	5.8	3.0	10.2	8.8	8.5		12.0	15.7	13.5	10.0	16.0	9.5	6.7	30.0	17.5	18.3	9.3	8.4	5.8	15.1	10.2	20.7	28.1	10.5	13.7	13.4	14.0	6.5	7.4	6.2	7.6	20.7	6.9
Almaco Jack	2.2	3.6	8.5	10.1	14.6	8.7	6.5	25.0	22.0	14.7	21.1	14.5	17.5	7.9	25.9	19.1	17.7	11.0	7.3	5.0	20.6	14.3	33.2	21.3	13.2	13.4	7.8	21.0		11.2	6.0	4.4	13.5	16.0
Lesser Amberjack	14.5	7.0	7.3	5.9	4.0	2.5	10.2	7.4	12.7	11.6	7.4	8.6	2.1	17.3	38.1	20.1	24.4	7.6	9.4	5.1	32.4		16.2	34.5	4.2	8.9	12.0	4.2	14.3	0.7	6.1	6.9	15.6	3.6
Banded Rudderfish	11.7	6.0	5.2	5.0	2.5	1.6	7.4	6.0	12.9	9.9	6.4	10.8	1.3	15.8	38.0	21.4	25.3	7.0	8.3	3.9	31.6	0.7	18.5	36.4	2.4	7.2	9.9	2.8	11.2		3.8	5.3	13.8	3.0
Silk Snapper	13.4	7.8	12.3	11.9	12.8	7.8	16.0	22.4	10.3	14.7	15.7		15.4	9.8	23.6	7.3	10.7	6.0	6.5	5.7	23.3	8.6	24.0	12.8	15.1	10.7	9.6	20.0	14.5	10.8	11.9	8.0	11.7	11.5
Blackfin Snapper	18.5	11.1	6.8	8.1	2.2	4.1	9.5	2.1	14.2	10.5	4.2	15.4		19.6	46.4	24.8	30.0	9.3	11.9	7.5	36.1	2.1	17.5	44.9	2.9	8.4	14.4	1.6	17.5	1.3	7.1	9.9	17.5	1.9
Yellowedge Grouper	20.6	19.2	24.4	28.9	36.9	36.0	30.0	52.5	40.8	24.3	43.9	23.6	46.4	22.8		16.3	14.9	29.2	27.6	29.7	26.1	38.1	40.2	22.4	39.4	38.3	29.3	51.3	25.9	38.0	31.3	27.5	41.6	40.0
Snowy Grouper	12.0	8.1	7.4	15.4	16.3	13.5	6.7	22.0	16.6	16.2	15.3	9.8	19.6		22.8	5.8	5.8	9.6	7.3	7.3	11.6	17.3	26.4	12.8	18.7	14.2	13.7	27.3	7.9	15.8	11.4	11.1	18.5	11.8
Warsaw Grouper	22.3	16.8	20.5	27.7	32.5	30.1	15.1	40.1	34.2	27.2	33.0	23.3	36.1	11.6	26.1	14.4	10.8	25.1	20.5	22.1		32.4	28.8	13.5	36.1	35.0	30.0	46.1	20.6	31.6	27.5	22.9	38.8	29.3
Blueline Tilefish Female	10.6	6.8	6.6	7.7	5.1	3.8	9.3	12.7	2.9	8.1	7.2	6.0	9.3	9.6	29.2	12.7	17.9		1.1	4.1	25.1	7.6	25.2	25.0	8.3	8.6	6.6	12.0	11.0	7.0	8.6	5.7	8.4	7.1
Blueline Tilefish Male	8.3	4.5	6.4	6.1	7.2	4.3	8.4	16.3	6.1	9.0	9.7	6.5	11.9	7.3	27.6	11.3	14.5	1.1		3.8	20.5	9.4	27.2	21.0	9.0	10.3	6.6	15.9	7.3	8.3	7.8	4.8	8.8	9.5
Speckled Hind	5.2	3.6	5.0	6.5	5.6	1.7	5.8	13.5	10.6	10.7	9.9	5.7	7.5	7.3	29.7	14.3	16.5	4.1	3.8		22.1	5.1	27.0	21.4	5.9	4.0	3.2	9.8	5.0	3.9	2.3	1.2	6.2	6.0
Queen Snapper	35.9	21.6	21.3	26.0	23.5	26.3	20.7	18.8	31.3	20.4	22.5	24.0	17.5	26.4	40.2	22.2	24.7	25.2	27.2	27.0	28.8	16.2		38.1	27.3	35.3	40.7	26.4	33.2	18.5	31.3	30.9	48.6	16.9
Golden Tilefish female	20.7	11.9	12.8	17.5	20.2	19.1	17.5	26.9	19.9	15.1	18.7	7.3	24.8	5.8	16.3		1.3	12.7	11.3	14.3	14.4	20.1	22.2	11.2	23.5	19.6	20.2	33.8	19.1	21.4	19.6	18.1	24.8	16.5
Golden Tilefish male	19.9	12.1	15.1	19.8	25.6	23.0	18.3	33.4	27.9	18.4	25.1	10.7	30.0	5.8	14.9	1.3		17.9	14.5	16.5	10.8	24.4	24.7	8.5	27.6	23.7	22.8	40.0	17.7	25.3	21.3	19.5	28.8	21.5
Yellowtail Snapper	11.7	11.6	9.1	11.8	5.7	4.7	13.7	12.3	16.0	10.5	10.5	10.7	8.4	14.2	38.3	19.6	23.7	8.6	10.3	4.0	35.0	8.9	35.3	32.8	5.9		3.8	8.4	13.4	7.2	4.9	5.5	4.4	7.2
Mutton Snapper	8.5	4.8	5.6	3.8	2.5		8.5	9.7	9.6	9.4	7.2	7.8	4.1	13.5	36.0	19.1	23.0	3.8	4.3	1.7	30.1	2.5	26.3	31.3	2.4	4.7	4.8	5.1	8.7	1.6	2.6	2.3	7.0	5.0
Hogfish	10.4	14.1	17.1	15.6	12.0	7.0	20.7	24.7	15.5	14.5	19.8	11.7	17.5	18.5	41.6	24.8	28.8	8.4	8.8	6.2	38.8	15.6	48.6	30.0	12.1	4.4	1.8	16.5	13.5	13.8	10.1	5.6		17.3
Red Hind	12.9	7.7	4.9	3.1	1.1	2.4	10.5	6.2	16.0	7.8	5.5	15.1	2.9	18.7	39.4	23.5	27.6	8.3	9.0	5.9	36.1	4.2	27.3	44.0		5.9	8.9	3.2	13.2	2.4	3.1	6.2	12.1	5.0
Misty Grouper	21.4	19.5	31.0	34.5	41.1	31.3	28.1	54.5	33.8	32.9	44.8	12.8	44.9	12.8	22.4	11.2	8.5	25.0	21.0	21.4	13.5	34.5	38.1		44.0	32.8	25.6	54.5	21.3	36.4	32.3	23.0	30.0	36.7
Yellowmouth Grouper	20.9	25.4	27.1	31.6	27.5	22.2	23.2	40.5	10.5	33.8	31.6	25.0	34.4	25.9	46.1	38.8	44.7	13.0	14.8	19.8	42.7	31.1	56.9	39.2	33.5	30.6	19.6	34.7	22.4	28.6	28.1	20.1	21.9	31.2
Cubera Snapper	2.5	3.0	6.7	5.9	6.6	2.3	7.6	17.6	14.0	9.8	14.1	8.0	9.9	11.1	27.5	18.1	19.5	5.7	4.8	1.2	22.9	6.9	30.9	23.0	6.2	5.5	1.9	10.7	4.4	5.3	2.6		5.6	10.3
Yellowfin Grouper	6.2	4.2	3.4	4.2	4.6	2.6	6.2	12.3	17.3	11.5	9.6	11.9	7.1	11.4	31.3	19.6	21.3	8.6	7.8	2.3	27.5	6.1	31.3	32.3	3.1	4.9	5.4	8.0	6.0	3.8		2.6	10.1	6.7
Dog Snapper	4.2	7.7	10.6	10.5	8.8	4.8	13.4	21.6	14.8	10.3	17.2	9.6	14.4	13.7	29.3	20.2	22.8	6.6	6.6	3.2	30.0	12.0	40.7	25.6	8.9	3.8		13.6	7.8	9.9	5.4	1.9	1.8	14.0
Schoolmaster	19.4	15.0	10.2	10.5	2.8	5.1	14.0	4.6	16.9	12.6	7.5	20.0	1.6	27.3	51.3	33.8	40.0	12.0	15.9	9.8	46.1	4.2	26.4	54.5	3.2	8.4	13.6		21.0	2.8	8.0	10.7	16.5	5.5
Wenchman	18.4	10.3	4.1	9.0	3.0	5.0	6.9	2.4	10.8	11.1	1.9	11.5	1.9	11.8	40.0	16.5	21.5	7.1	9.5	6.0	29.3	3.6	16.9	36.7	5.0	7.2	14.0	5.5	16.0	3.0	6.7	10.3	17.3	
Mahogany Snapper	12.9	12.4	10.3	10.0	4.5	4.2	16.3	14.0	8.9	9.8	9.5	10.9	10.2	18.0	38.3	21.9	28.1	4.6	6.8	5.6	37.9	10.3	39.9	36.9	6.1	3.3	3.4	8.9	16.3	8.7	7.4	5.9	3.3	9.8
Nassau Grouper	4.6	9.2	11.8	13.8	11.4	6.9	13.9	24.3	15.7	12.3	19.4	9.7	17.2	12.2	28.3	19.3	21.6	7.6	7.6	3.8	29.0	14.6	42.8	22.8	12.0	4.3	0.4	16.9	7.9	12.3	6.9	2.9	2.2	15.5

Figure A7. Nodal analysis of species presence-absence in Gulf reef fish commercial vertical line and longline landings aggregated by year, month, area, and depth (Linkage Method: Ward's, Dissimilarity Measure: Sørenson (binary)). Values in table represent life history dissimilarity coefficients (Euclidean distance).

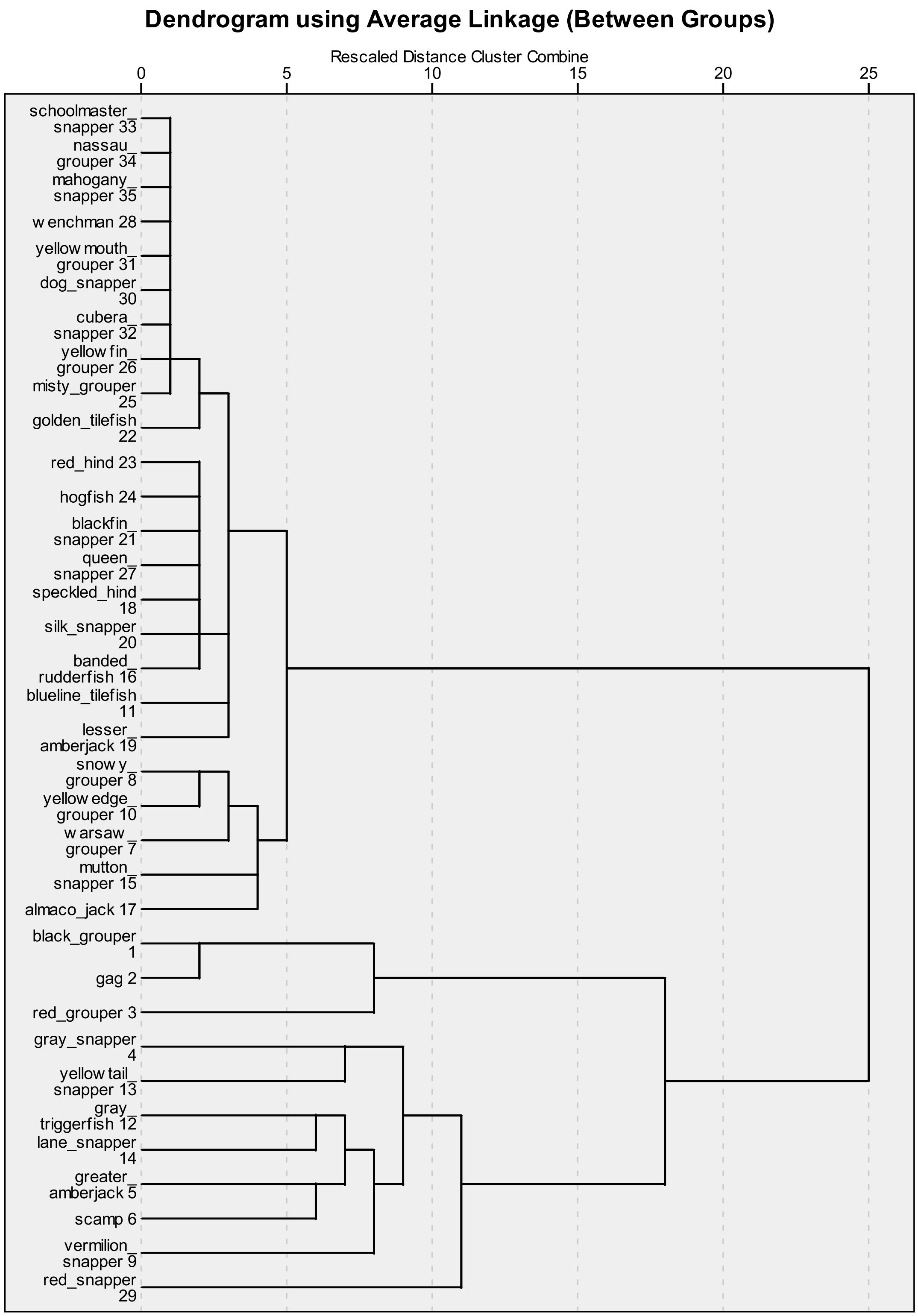


Figure A8. Hierarchical cluster analysis of Gulf reef fish commercial vertical line landings, aggregated by year, month, area, depth and trip (Linkage Method: Ward's, Dissimilarity Measure: Chi-square (count), Transformation: Root-Root on landings in numbers).

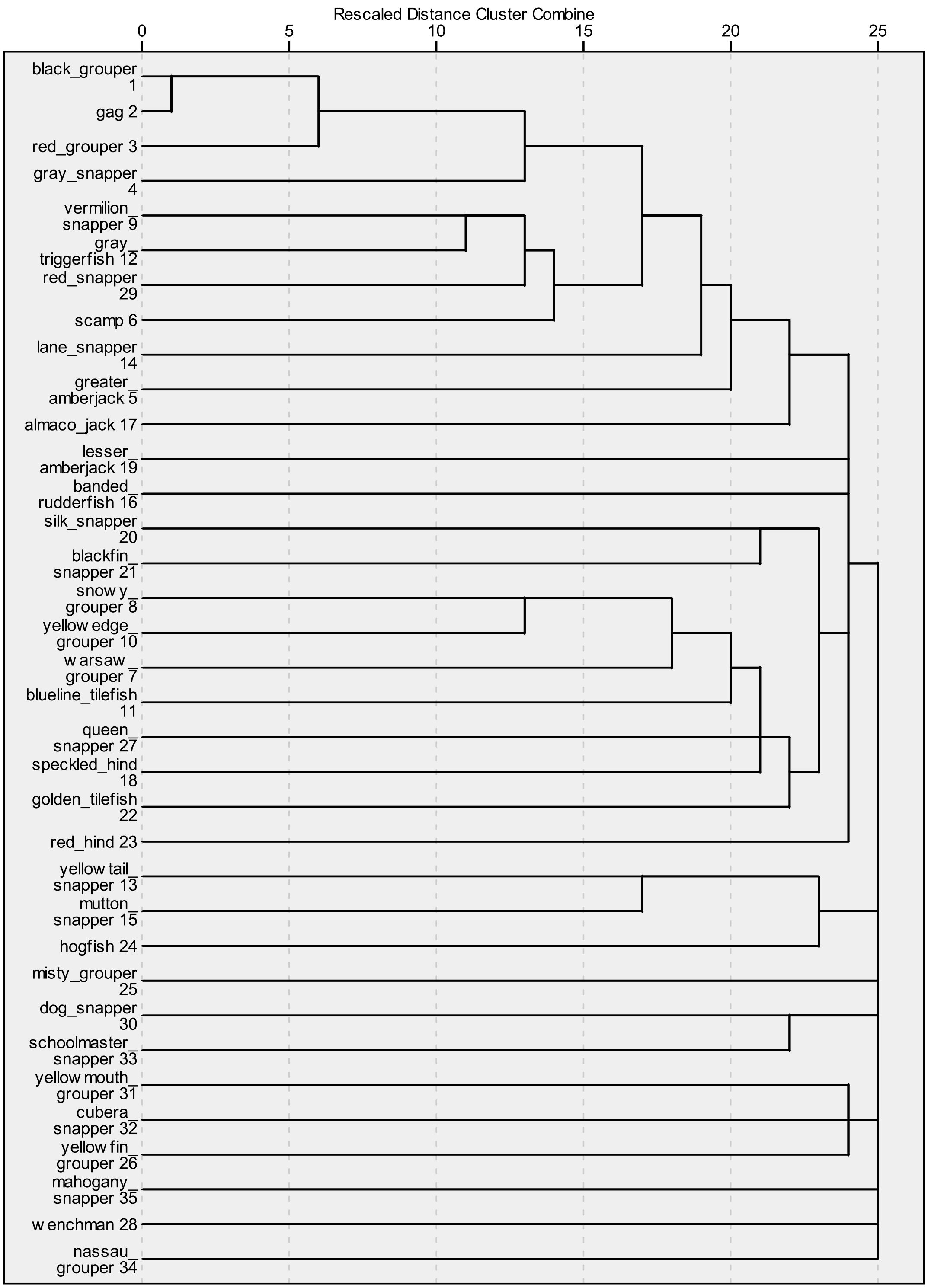


Figure A9. Hierarchical cluster analysis of species presence-absence in Gulf reef fish commercial vertical line landings aggregated by year, month, area, depth and trip (Linkage Method: Between (Average), Dissimilarity Measure: Sørenson (Binary)).

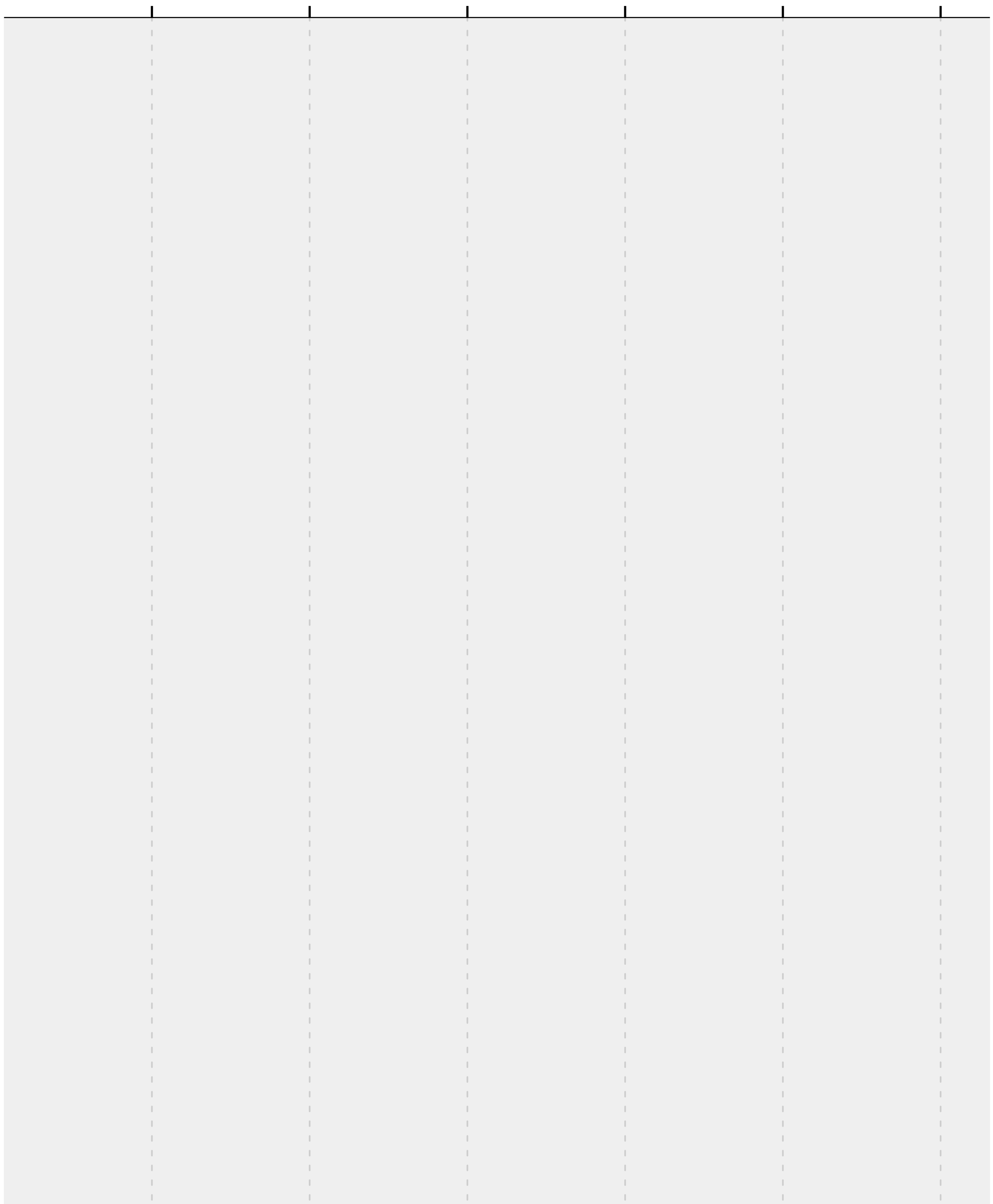


Figure A10. Hierarchical cluster analysis of Gulf reef fish commercial longline landings, aggregated by year, month, area, depth and trip (Linkage Method: Ward's, Dissimilarity Measure: Chi-square (count), Transformation: Root-Root on landings in numbers).

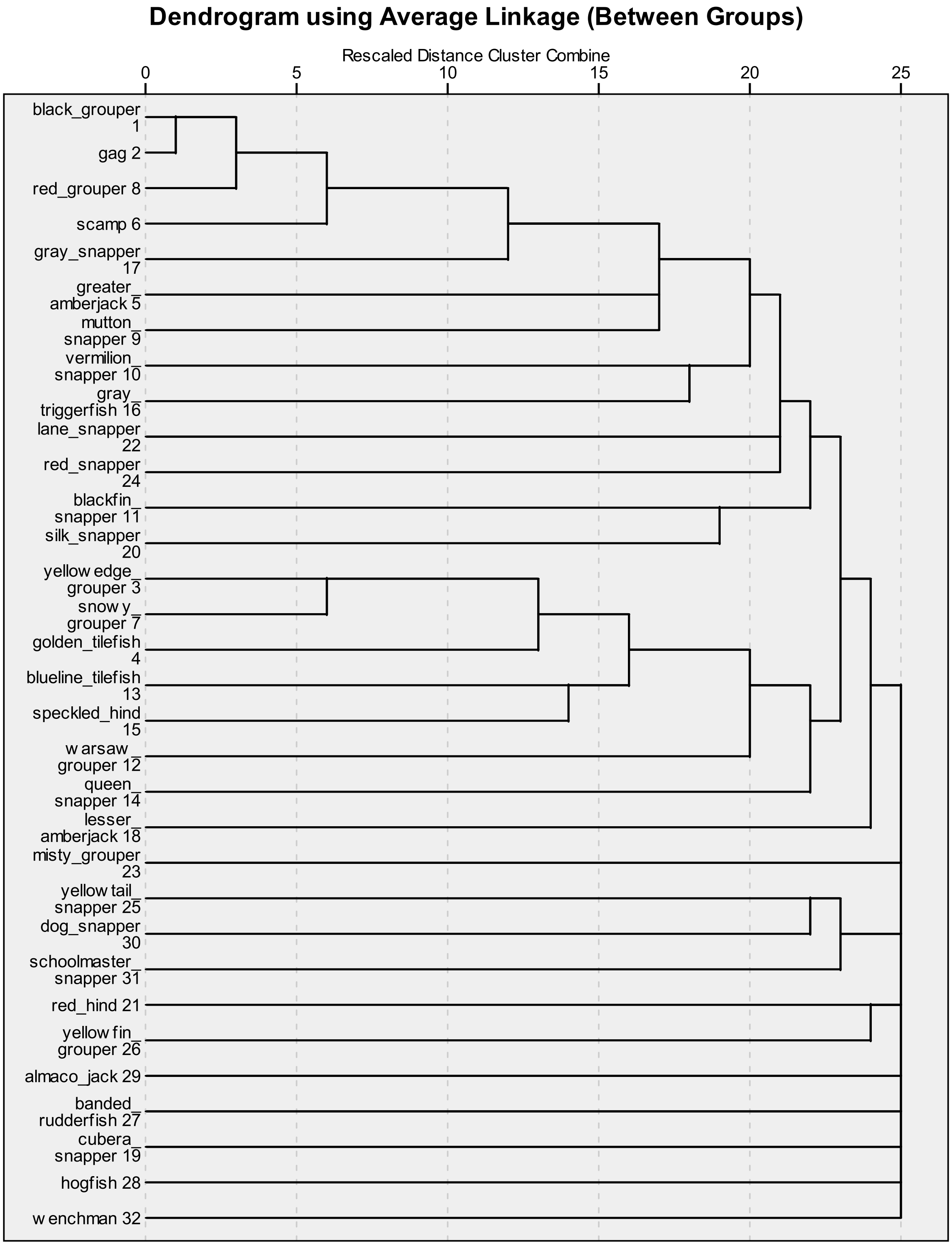


Figure A11. Hierarchical cluster analysis of Gulf reef fish commercial longline landings, aggregated by year, month, area, depth and trip (Linkage Method: Between (Average), Dissimilarity Measure: Sørenson (Binary)).