ICES Journal of
Marine Science

ICES Journal of Marine Science (2016), 73(7), 1750–1763. doi:10.1093/icesjms/fsw033

Original Article

Modelling community structure and species co-occurrence using fishery observer data

Jeffrey Robert Pulver[1]*, Hui Liu[2], and Elizabeth Scott-Denton[1]

[1]*National Marine Fisheries Service, Southeast Fisheries Science Center, Galveston Laboratory, 4700 Avenue U, Galveston, TX 77551, USA*
[2]*Department of Marine Biology, Texas A&M University, Galveston, TX 77553, USA*

Corresponding author: e-mail: jeff.pulver@noaa.gov

Pulver, J. R., Liu, H., and Scott-Denton, E. Modelling community structure and species co-occurrence using fishery observer data. – ICES Journal of Marine Science, 73: 1750–1763.

Received 17 November 2015; revised 10 February 2016; accepted 14 February 2016.

In this study, we modelled fishery observer data to compare methods of identifying community structure using cluster analyses to determine stratifications and probabilistic models for examining species co-occurrence in the Gulf of Mexico deepwater reef fish fishery. Comparing cluster analysis methods, the correlation measure of dissimilarity in combination with average agglomerative linkage was the most efficient method for determining species relationships using simulated random species as a comparison tool. Cluster analysis revealed distinct species stratifications and in combination with multiscale bootstrapping generated probabilities indicating the strength of stratifications in the fishery. A more parsimonious approach with probabilistic models was also developed to quantify pairwise species co-occurrence as random, positive, or negative based on the observed vs. expected fishing sets with co-occurrence. For the most common species captured, the probabilistic models predicted positive or negative co-occurrence between 84.2% of the pairwise combinations examined. These methods provide fishery managers tools for determining multispecies quota allocations and offer insights into other bycatch species of interest.

Keywords: cluster analysis, commercial fisheries, fishery observer, species co-occurrence, species stratifications.

Introduction

The incidental captures of undersized or non-target species (bycatch) are of great concern to fishery managers due to the overexploitation of stocks not only in the Gulf of Mexico (Gulf) but worldwide (Sissenwine *et al.*, 2014). Selective fishing and its consequential bycatch have a range of unintended effects such as modifying foodwebs and ecosystem structure, altering energy flow and species interactions, and reducing system resilience and fisheries production. The commercial Gulf reef fishery targets primarily groupers (*Epinephelus* sp. and *Mycteroperca* sp.) and snappers (*Lutjanus* sp.) using two primary gear types, bottom longline and vertical line. This fishery also has incidental bycatch for a number of species. Based on observer programme coverage from 2006 through 2009, Scott-Denton *et al.* (2011) identified 183 taxa captured with bottom longline and 178 taxa with vertical line gear. While species diversity was high, only 17 species accounted for 90% of the number of captures recorded. Some of the past management options have resulted in the at-sea discarding of reef fish caught at depths that correlate with immediate mortality (Render and Wilson, 1994; Bartholomew and Bohnsack, 2005; Rudershausen *et al.*, 2007; Stephen and Harris, 2010).

Analysing fishery observer data from the Gulf deepwater reef fish fishery for community structure can provide an opportunity to examine the current quota management system that has undergone many changes in the past decade. The most recent change is a shift from a “derby” style fleet-wide quota system to an individual fishing quota (IFQ) allocation for each permit holder based on historical landings for a number of species. Branch (2009) examined how individual transferrable quotas affected various fisheries worldwide for a number of factors, including highgrading for single species and discards for multispecies fisheries. He found that highgrading and discards often declined, but may increase without effective enforcement or if the catches are not counted against the quota. Highgrading refers to selective harvesting by fishers for a species usually influenced by price differences based on fish size, i.e. increased discards of less valuable fish sizes, or due to price differentials between species in multispecies IFQ allocation categories, e.g. retaining more valuable species and discarding less valuable ones. Fishery managers can make better-informed decisions when determining multispecies IFQ allocation categories if patterns in species co-occurrence and stratifications in the fishery could be readily identified using fishery-dependent data.

Many studies have examined fish species assemblages using cluster analyses with fishery-independent and -dependent data (Rogers and Pikitch, 1992; Williams and Ralston, 2002; Farmer *et al.*, 2010; Cope and Haltuch, 2012). Heery and Cope (2014) used observer data to identify groundfish assemblages from trawls off Oregon and Washington, but encountered difficulties in identifying uncommon bycatch species on a large spatial scale using presence or absence data. Shertzer and Williams (2008) identified reef fish assemblages off the southeastern United States by analysing logbook data using hierarchical cluster analyses (HCA) aggregated by year, month, area, and depth. They found little support for using indicator species as a management tool but supported stratifying species into distinct management units as an achievable goal. One limitation of the approach used by Shertzer and Williams (2008) was that it relied on logbook data, which aggregates only the retained species from the entire fishing trip, not for each specific fishing location. During a fishing trip, a vessel may fish in many geographical areas across various habitats and environmental gradients. Thus, the spatial resolution of logbook data may not be fine enough for an accurate representation of patterns in species abundance during fishing sets. A finer geographic scale provides more accurate results in the assemblages due to the increased resolution in the species coexisting relating to similar habitat or environmental preferences. More important, the methods in Shertzer and Williams (2008) do not account for species that are discarded during the trip unless they are self-reported by vessel captains. Unlike logbook data, this study used fishery observer data that include bycatch and site-specific abundance information for a more accurate representation of community structure.

Furthermore, a more parsimonious approach with probabilistic models that only examines co-occurrence could provide insight for species of interest not available when using abundance data (Veech, 2013). This relatively recent method of examining species co-occurrence differs from cluster analysis that represents species assemblages, in that only two species are compared against each other. Probabilistic models quantify pairwise associations between species as random, positive, or negative based on the observed vs. expected site co-occurrence. Instead of focusing on the differences between each approach, both methods could be used by managers in conjunction for identifying and visualizing patterns in abundance and species co-occurrence during fishing sets using observer data. The objective of this research was to compare the utility of analytical tools necessary for quantifying species relationships and revealing stratifications, if existing, for multispecies fisheries. So far, quantitative research on the bycatch in the US Southeast Atlantic and the Gulf region, as well as elsewhere, remains insufficient. This study was initiated in an effort to address these key issues and build a baseline for a holistic perspective on a fishery beyond species composition.

Methods

Observer data and IFQ-managed species

In July 2006, the National Marine Fisheries Service (NMFS) Southeast Fisheries Science Center (SEFSC) initiated a mandatory observer programme to characterize the Gulf commercial reef fish fishery (GMFMC, 2005). Before that, the only observer coverage was a voluntary NMFS observer programme conducted from 1993 through 1995. The mandatory programme incorporates a randomized selection process to select federally permitted commercial reef fish vessels for observer coverage stratified by season, gear, and region (Scott-Denton *et al.*, 2011). To limit the scale of the study, only fishery observer data collected on vessels from 2006 through 2013 using bottom longline and vertical line gear from depths $\geq$100 m were included in the analyses. While onboard the fishing vessels, observers collected detailed information such as location, depth, gear, and capture information for each set (NMFS, 2015). Scott-Denton *et al.* (2011) and Scott-Denton and Williams (2013) provide detailed descriptions of the protocol on data collection for the reef fish observer programme. Only data that conformed to confidentiality rules mandated by the Magnuson–Stevens Fishery Conservation and Management Act were included in the analyses (NMFS, 2007). Fishing sets from vessels trolling were excluded from the analyses because these sets typically cover a large area and are not targeting bottom fish. Additionally, fishing sets with no catch were removed from the analyses.

To exhibit how modelling community structure can provide insights for multispecies quota allocations, we first compared pre- and post-IFQ retention rates for the seven species managed under the current deepwater grouper and tilefish IFQ quota management systems. The deepwater grouper IFQ allocation is not for a single species but instead comprises four different grouper species: snowy grouper (*Epinephelus niveatus*), speckled hind (*Epinephelus drummondhayi*), warsaw grouper (*Epinephelus nigritus*), and yellowedge grouper (*Epinephelus flavolimbatus*). The tilefish IFQ allocation consists of three species: blueline tilefish (*Caulolatilus microps*), goldface tilefish (*Caulolatilus chrysops*), and golden tilefish (*Lopholatilus chamaeleonticeps*). Specifically, abundance data before and after the grouper-tilefish IFQ start date of 1 January 2010 were examined for changes in retention rates, i.e. number of fish retained out of the total number captured. Differences in retention rates between the periods were examined using Fisher's exact test. Before the implementation of the IFQ system, an open season was used to manage the tilefish and deepwater grouper quotas until they were filled. Both seasons opened on 1 January for a given year; however, the closures did not always coincide (SERO, 2015). We compared the retention rates with observer data to detect differences in discard rates between the staggered seasons. All analyses in this study were performed using R statistical software (version 3.2.1; R Core Team, 2015). (Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the NMFS, NOAA.)

Cluster analyses

The HCA were conducted on datasets with both gear types combined, each gear type, the most common species with $\geq$1000 captures, and the IFQ-managed species to investigate consistent patterns in the species assemblages. Additionally, the IFQ-managed species were separated into two groups of retained and discarded, e.g. retained and discarded blueline tilefish, to analyse patterns in retention rates for each fishing set. Only species with observations $\geq$100 during the study period were used in the HCA as rare species may distort patterns in the species assemblages (Koch, 1987). The reef fish capture data were tabulated into counts of species or species categories, e.g. spiny dogfish (genus), *Squalus*, for individual fishing sets. Count data were converted to log-transformed abundance before HCA to reduce the influence of outliers and normalize the data. Since HCA requires no *a priori* assumptions, it is necessary to validate the final results using additional approaches (Borcard *et al.*, 2011). For this study, the correlation and Bray–Curtis dissimilarity measures were compared for each grouping of the analysis. For each measure of dissimilarity, the distance was calculated with both the average agglomerative linkage and Ward's linkage to compare the two for consistent groupings. The HCA was done using the package "pvclust" in R with 1000 multiscale bootstraps to create probabilities to evaluate the statistical significance in each cluster or stratification (Suzuki and Shimodaira, 2011). The approximately unbiased (AU) probabilities, instead of the bootstrapped probabilities, were used because they provide a more accurate approximation of the strength of the relationships in the dendrogram (Liu *et al.*, 2012).

In addition to the HCA with multiscale bootstrapping, simulated random data were included with the actual catch data to verify species stratifications and compare methods of dissimilarity and linkage. Cope and Haltuch (2012) used a technique of incorporating simulated random species into the analyses with a 0.5 probability of occurrence to identify the significance of the clusters formed by HCA. The idea behind this method is that any species included in an assemblage with a higher dissimilarity than that of the simulated random species should not be considered valid in the assemblage. The Bray–Curtis measure and average agglomerative linkage were the only methods used by Cope and Haltuch (2012) to detect patterns in species assemblages. However, in this study, we compared multiple combinations of dissimilarity measure and linkage. The optimal method for dissimilarity measure and linkage in our study was chosen when the simulated random species had the highest dissimilarity consistently for all subsets of the data in the resulting dendrograms. The simulated random data used for comparisons in this study were five species with a 0.5 probability of occurrence during the fishing sets with abundance equal to the mean positive abundance for that dataset.

Once the optimal dissimilarity measure and linkage were determined with simulated random data, we compared stratifications in the dendrograms using significant clusters for species stratifications with an AU probability $\geq$0.95. The significant stratifications were used to reveal patterns in covariance between the IFQ-managed species managed with multispecies deepwater quotas. By comparing these patterns in covariance with the retention rates observed, insights can be derived into fisher behaviour during fishing sets. Finally, for the optimal HCA methodology, the probability of occurrence for simulated random species was increased 0.05 increments for each dataset until they significantly clustered with actual observed species to further evaluate the strength of species stratifications.

Probabilistic models

The probabilistic models to analyse species relationships use a simplistic pairwise approach comparing species co-occurrence on observed sites (fishing sets) to the distribution expected if the species were distributed independently from each other (Veech, 2013). These models quantify pairwise associations between species as random or significantly non-random plus whether the significant association is higher or lower than the expected value. These models only test co-occurrence between two species without taking into account that additional species may be dependent of their occurrence, thus differs significantly from HCA that progressively merges elements in the distance matrix. To generate the models, the same tabulated catch data used in the cluster analyses with $\geq$100 captures, $\geq$1000 captures, and the IFQ-managed species were converted to presence–absence during fishing sets. The probabilistic models were generated with the package "cooccur" in R (Griffith *et al.*, 2014). The simulated random data with a random 0.5 probability of species occurrence were included in the analysis with $\geq$100 captures observed to serve as a null model. Heat maps were generated from the models to visualize the species pairwise associations as negative, random, or positive. In addition to the pairwise associations, the groupings were compared with any stratification present in the cluster analysis results for consistent patterns in covariance.

Results

From 2006 through 2013, in depths $\geq$100 m, observers recorded a total of 117 702 reef fish captures. Of these captures, 99 510 fish were recorded from vessels using bottom longline gear, and 18 192 from vertical line gear. A total of 200 species groupings were recorded for both gear types combined, of which 173 groupings were unique to vessels using bottom longline gear and 106 groupings unique for vertical line gear. For both gear types, 51 species groupings were included in the analyses when captures with $n < 100$ observations were removed (Table 1). Yellowedge grouper, golden tilefish, and blueline tilefish were the three most abundant species observed and were primarily captured using bottom longline gear. Vermilion snapper (*Rhomboplites aurorubens*) was the most common species recorded for vertical line gear with 7150 captures. A total of 3194 fishing sets with captures recorded were observed for both gear types, of which 1978 were bottom longline sets, and 1216 were vertical line sets. A small number of species groupings dominated the catch with the ten most abundant species accounting for >78% of the number of captures, and the three most abundant comprising >50% (Table 1).

Significant differences were found in the retention rates for five of the seven IFQ-managed species in the deepwater reef complex (Table 2). All tilefish species had lower retention rates compared with the IFQ grouper species; however, only 43 captures were goldface tilefish indicative of a rarely encountered species. The species with the greatest difference relative to the number of fish discarded after the implementation of the IFQ system was golden tilefish with a post-IFQ retention rate of 80.3%, compared with 97.1% before the IFQ implementation. Blueline tilefish had the highest percentage (>44%) of discards under IFQ management but were less commonly captured than golden tilefish, thus representing a smaller overall number of discards observed. Yellowedge, snowy, and warsaw grouper species all had retention rates >96% under IFQ management indicating little evidence of highgrading among these species managed under the IFQ allocation category. Before the IFQ system when fishery observer data were available, there is evidence that most tilefish (>96%) were retained under the derby system when the season was open (Table 3).

For examining community structure with HCA, the most consistent method for filtering out the simulated random species across all subsets of the data was the correlation measure of dissimilarity with average agglomerative linkage (Figure 1). For all subsets of data with this combination, the simulated random species never had a dissimilarity measure <0.9 and resulted in the simulated random species being absent from all significant clusters (AU $\geq$ 95). The correlation measure of dissimilarity did not perform as well with Ward's linkage due to the simulated random species consistently significantly clustering with actual observed species for all subsets of the data. Using the Bray–Curtis measure of dissimilarity with both average and Ward's linkage resulted in the simulated

Table 1. The number of captures observed at depth ($\geq$100 m) with observations ($n \geq 100$) by gear type recorded by the observer programme from 2006 through 2013 in the commercial Gulf reef fish fishery.

Common name	Scientific name	Number of captures observed	% on bottom longline gear	% on vertical line gear
Yellowedge grouper	*Epinephelus flavolimbatus*	26 047	98.9	1.1
Golden tilefish	*Lopholatilus chamaeleonticeps*	22 841	99.6	0.4
Blueline tilefish	*Caulolatilus microps*	10 545	97.9	2.1
Vermillion snapper	*Rhomboplites aurorubens*	7200	0.7	99.3
King snake eel	*Ophichthus rex*	6193	99.8	0.2
Snowy grouper	*Epinephelus niveatus*	4840	88.3	11.7
Cuban dogfish	*Squalus cubensis*	4286	99.8	0.2
Red porgy	*Pagrus pagrus*	4029	21.2	78.8
Smooth dogfish	*Mustelus canis*	3989	99.0	1.0
Red snapper	*Lutjanus campechanus*	2467	46.1	53.9
Atlantic sharpnose shark	*Rhizoprionodon terraenovae*	1899	99.1	0.9
Scamp grouper	*Mycteroperca phenax*	1761	60.0	40.0
Greater amberjack	*Seriola dumerili*	1652	65.0	35.0
Southern hake	*Urophycis floridana*	1291	99.6	0.4
Spiny dogfish (genus)	*Squalus* sp.	1158	99.5	0.5
Spotted hake	*Urophycis regia*	1135	99.6	0.4
Gag grouper	*Mycteroperca microlepis*	1110	31.1	68.9
Speckled hind	*Epinephelus drummondhayi*	1074	72.3	27.7
Blacktail moray	*Gymnothorax kolpos*	1006	99.3	0.7
Hake (genus)	*Urophycis* sp.	992	99.4	0.6
Grouped sharks	*General sharks*	944	90.5	9.5
Chub mackerel	*Scomber japonicus*	914	0.1	99.9
Spinycheek scorpionfish	*Neomerinthe hemingwayi*	779	98.3	1.7
Silk snapper	*Lutjanus vivanus*	774	32.7	67.3
Dogfish (genus)	*Mustelus* sp.	560	99.3	0.7
Pale spotted eel	*Ophichthus puncticeps*	523	100.0	0.0
Red grouper	*Epinephelus morio*	511	97.7	2.3
Bearded brotula	*Brotula barbata*	484	98.6	1.4
Almaco jack	*Seriola rivoliana*	411	41.4	58.6
Blackedge moray	*Gymnothorax nigromarginatus*	353	98.6	1.4
Purplemouth moray	*Gymnothorax vicinus*	305	91.8	8.2
Gulf hake	*Urophycis cirrata*	287	98.3	1.7
Queen snapper	*Etelis oculatus*	260	69.6	30.4
Blackfin tuna	*Thunnus atlanticus*	255	95.7	4.3
Blackfin snapper	*Lutjanus buccanella*	236	19.1	80.9
Warsaw grouper	*Epinephelus nigritus*	226	62.8	37.2
Scalloped hammerhead	*Sphyrna lewini*	222	99.5	0.5
Sandbar shark	*Carcharhinus plumbeus*	212	100.0	0.0
Moray eel (genus)	*Gymnothorax* sp.	208	95.7	4.3
Blacktip shark	*Carcharhinus limbatus*	203	94.6	5.4
Silky shark	*Carcharhinus falciformis*	175	48.0	52.0
Bigeye sixgill shark	*Hexanchus nakamurai*	164	100.0	0.0
Dolphin fish	*Coryphaena hippurus*	160	90.6	9.4
Night shark	*Carcharhinus signatus*	159	100.0	0.0
Wenchman	*Pristipomoides aquilonaris*	140	55.0	45.0
Little tunny	*Euthynnus alletteratus*	131	87.8	12.2
Shortspine dogfish	*Squalus mitsukurii*	128	100.0	0.0
Tiger shark	*Galeocerdo cuvier*	126	99.2	0.8
Blackbelly rosefish	*Helicolenus dactylopterus*	110	76.4	23.6
Sharpnose sevengill shark	*Heptranchias perlo*	103	100.0	0.0
Sixgill shark (genus)	*Hexanchus* sp.	101	99.0	1.0

random species being included in significant stratifications and with smaller dissimilarities than observed species for all subsets of the data (Figures 2 and 3). When validating the optimal combination by increasing the probability of simulated random occurrence in 0.05 increments, the simulated random species did not significantly cluster with actual observed species until the probability of occurrence was increased to 0.8 for the full dataset. For subsets of the data with bottom longline and vertical line gears, the simulated random species had smaller dissimilarity values than some of the rarely caught species, but were never placed in any significant stratification. In the analysis for species with observations $\geq$1000 (Figure 4), the simulated random species did not cluster significantly with any observed species until the probability of random occurrence was increased above 0.95 in the species matrix.

Distinct stratifications were evident in the fishery using the optimal HCA method examined of the correlation measure of dissimilarity with average linkage. The IFQ-managed species of blueline tilefish, yellowedge grouper, and snowy grouper consistently

Table 2. Retention rates for the IFQ-managed deepwater reef fish species using fishery observer data from 2006 through 2013.

Species	Number retained Pre-IFQ	Number retained Post-IFQ	Number discarded Pre-IFQ	Number discarded Post-IFQ	Retention rate Pre-IFQ	Retention rate Post-IFQ	Fisher's exact test *p*-value
Golden tilefish	2169	16 464	65	4042	97.1%	80.3%	<0.001
Blueline tilefish	1723	3863	1761	3062	49.5%	55.8%	<0.001
Goldface tilefish	4	12	3	24	57.1%	33.3%	0.39
Yellowedge grouper	6834	18 925	41	233	99.4%	98.8%	<0.001
Snowy grouper	105	3968	13	75	89.0%	98.1%	<0.001
Speckled hind	392	583	6	93	98.5%	86.2%	<0.001
Warsaw grouper	98	115	8	4	92.5%	96.6%	0.24

Table 3. Retention rates for most common tilefish species pre-IFQ for periods before and after aggregated deepwater grouper closure.

Fishing season	2007 Open, 1 January – 18 April	2007 Closed, 19 April – 2 June	2008[a] Open, 1 January – 10 May	2009 Open, 1 January – 15 May	2009 Closed, 16 May – 27 June
Golden tilefish					
Number kept	44	0	211	1913	1
Number discarded	0	5	8	22	30
Retention rate	100.0%	0.0%	96.3%	98.9%	3.2%
Blueline tilefish					
Number kept	3	9	155	1555	1
Number discarded	0	589	0	57	1115
Retention rate	100.0%	1.5%	100.0%	96.5%	0.1%

[a] In 2008, the deepwater grouper closure coincided with the tilefish closure.

clustered significantly together for all subsets of the data (Figures 1 and 4). Golden tilefish clustered significantly separate from the other IFQ species for all subsets of the data examined (Figures 1, 4, and 5). When the most common species were examined, golden tilefish were still significantly separate from blueline tilefish and yellowedge grouper with substratification AU values of 96 and 97 (Figure 4). Additionally, consistent relationships for other species were present for all subsets of the data such as golden tilefish with cuban dogfish (*Squalus cubensis*) and red porgy (*Pagrus pagrus*) with scamp grouper (*Mycteroperca phenax*). When the IFQ-managed species disposition was added for cluster analysis, previous stratifications were evident such as retained and discarded golden tilefish clustering significantly together, but not with any other IFQ-managed species (Figure 5). Blueline tilefish being kept and discarded clustered significantly with yellowedge grouper, snowy grouper, and speckled hind that were retained. Discarded yellowedge, snowy, and speckled hind grouper significantly clustered together indicating that they are not being retained during the same fishing sets.

The probabilistic models detected non-random pairwise co-occurrence between 47.6% of the 1540 species pair analysed (Table 4). Due to an expected pair co-occurrence of <1, 84 species pair combinations were filtered from the analysis. The simulated random species were recognized as random on $>90\%$ of the possible combinations, with at most 9 and as few as 2 non-random pairwise associations predicted out of the 56 possible combinations for a simulated random species (Figure 6). Generally, a greater percentage of non-random pairwise co-occurrence was predicted for species that were captured on more fishing sets with few insights derived for less commonly captured species. Similar patterns in species abundance covariance revealed by the cluster analyses were present, but any stratification was difficult to discern due to a large number of species included in the heat map.

Stratifications were easier to distinguish when the more common species were examined with the model predicting non-random co-occurrence between 84.2% of the 171 pairwise combinations (Figure 7). The model predicted the same positive co-occurrence relationship between the IFQ-managed species of blueline tilefish, yellowedge grouper, and snowy grouper as well as negative co-occurrence between golden and blueline tilefish. A similar stratification consisting primarily of vermilion snapper, red snapper (*Lutjanus campechanus*), and red porgy was also evident in both modelling approaches. The probabilistic model differed from HCA in that it predicted a significant positive relationship between golden tilefish and yellowedge grouper indicating that the two species do co-occur more than expected on some fishing sets. Greater amberjack (*Seriola dumerili*) and snowy grouper had the greatest number of random associations, 7 and 6, respectively, suggesting weak associations with other commonly captured species in the deepwater fishery. Yellowedge grouper and cuban dogfish had no random pairwise associations in the fishery possibly due to these species having widespread distributions in the community structure of the fishery. For fishing sets that only captured the IFQ-managed species, the model was more robust predicting non-random co-occurrence between all associations except between warsaw grouper and speckled hind (Figure 8). Similar to previous patterns, warsaw grouper had only negative and random pairwise co-occurrence predicted with the other IFQ-managed species, providing little support for using a more commonly encountered species as an indicator for the presence of warsaw grouper co-occurrence using this approach.

Discussion

This research is of primary interest to fisheries scientists and managers interested in deriving insights from stratifications or species co-

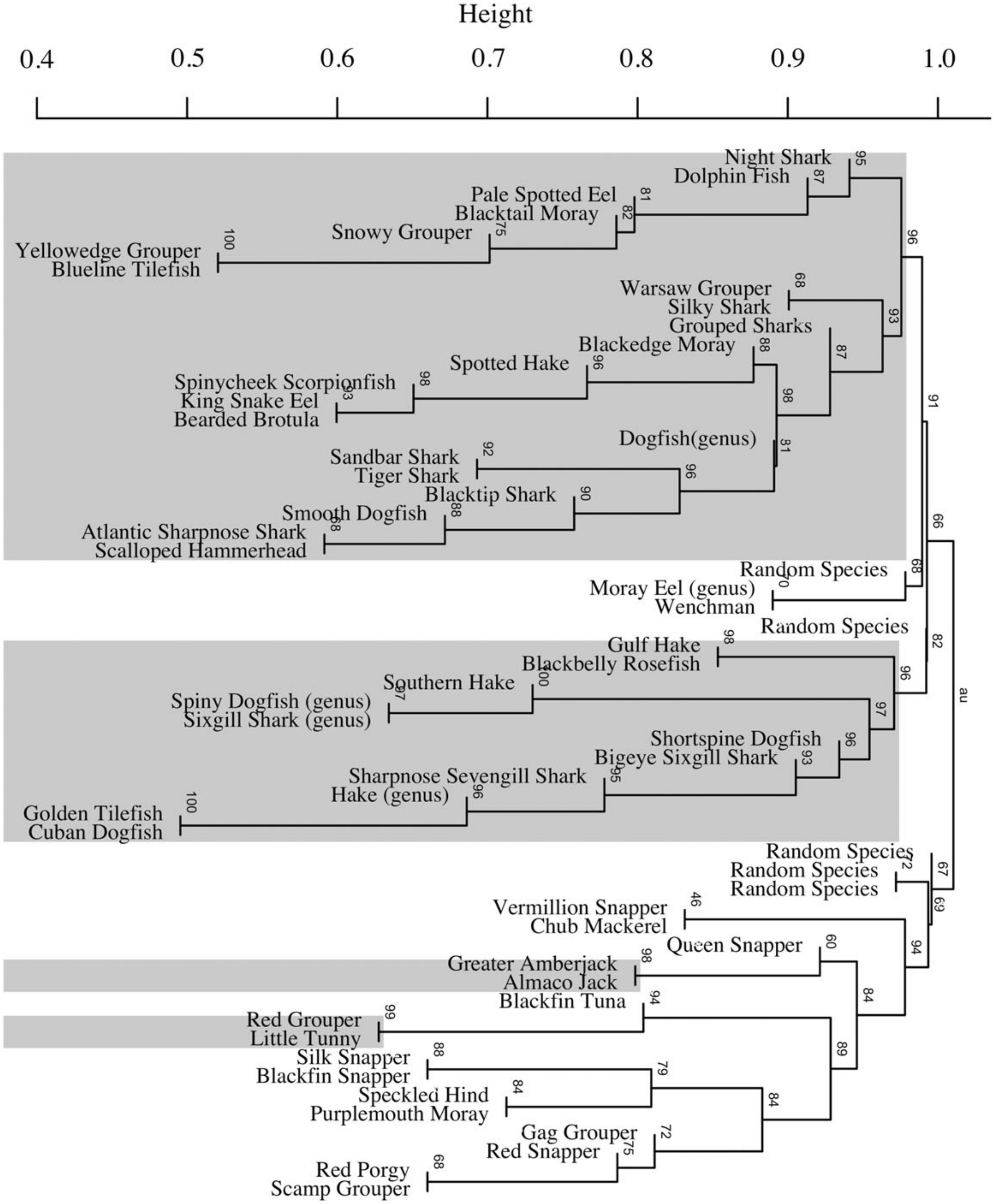

Figure 1. Dendrogram of species clusters for gear types combined using the correlation measure of dissimilarity with average agglomerative linkage. Significant clusters (AU $\geq$ 95) are shaded in all dendrograms.

occurrence using fishery observer data. The techniques presented are useful for determining if multispecies quota allocations could be divided into more or less distinct management units based on their stratification and co-occurrence. Using the multispecies IFQ-managed tilefish as an example, a refinement of the current allocation category into more distinct units (i.e. golden tilefish separately) may be warranted since evidence exists that this species has minimal co-occurrence with other IFQ-managed tilefish and grouper species

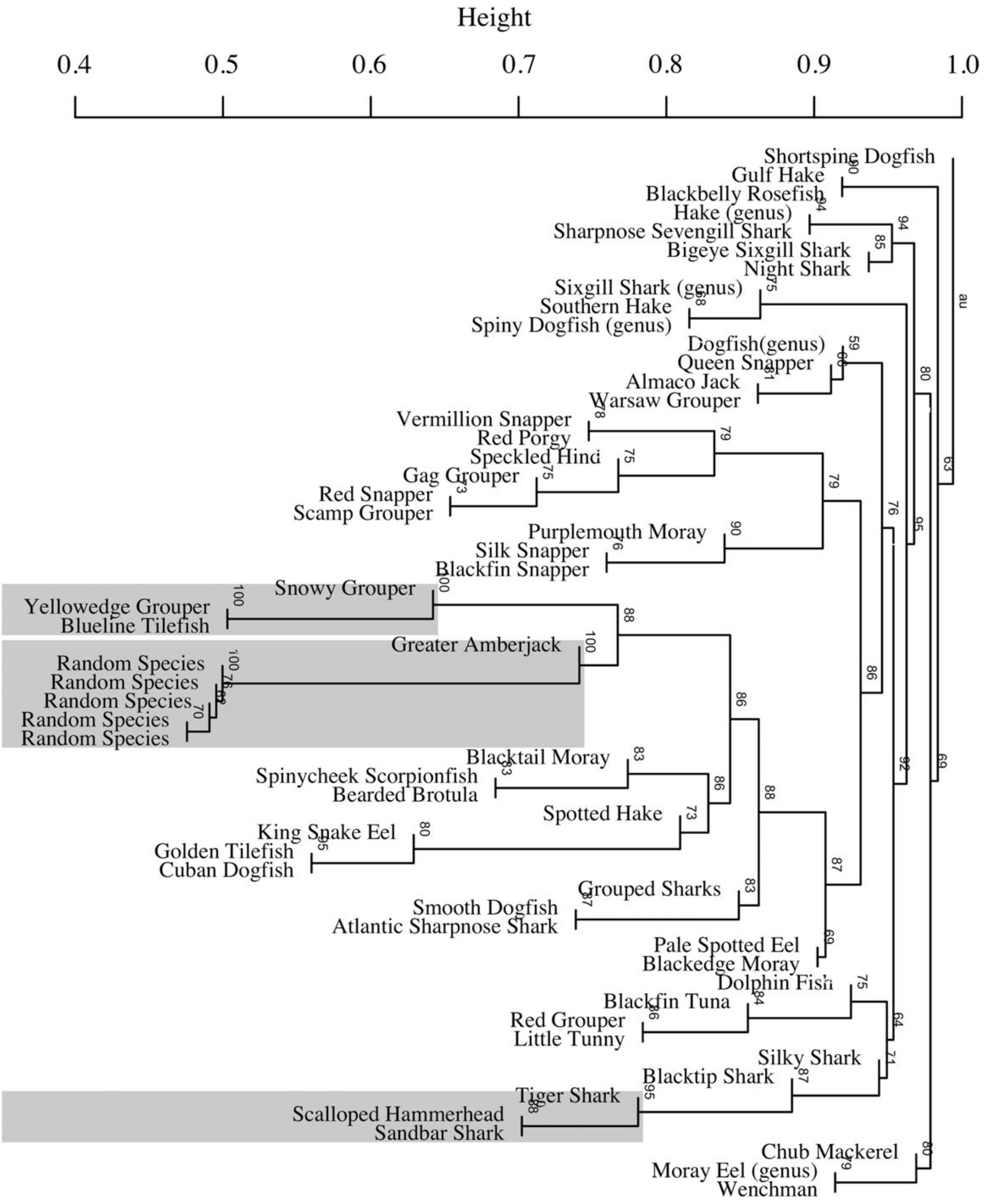

Figure 2. Dendrogram of species clusters for gear types combined using the Bray–Curtis dissimilarity measure and average agglomerative linkage.

only occurring with yellowedge grouper on some fishing sets. Figure 5 suggests the intention of fishers to selectively target golden tilefish separately from the other IFQ-managed species on fishing sets. Conversely, a less distinct management unit may be warranted for blueline tilefish since it appears consistently in significant stratifications with the other common IFQ-managed deepwater grouper species, mostly yellowedge and snowy grouper, for all subsets of the HCA. Figure 5 illustrates this with yellowedge, snowy, and speckled hind grouper being retained significantly clustered with blueline tilefish retained and discarded, which implies that

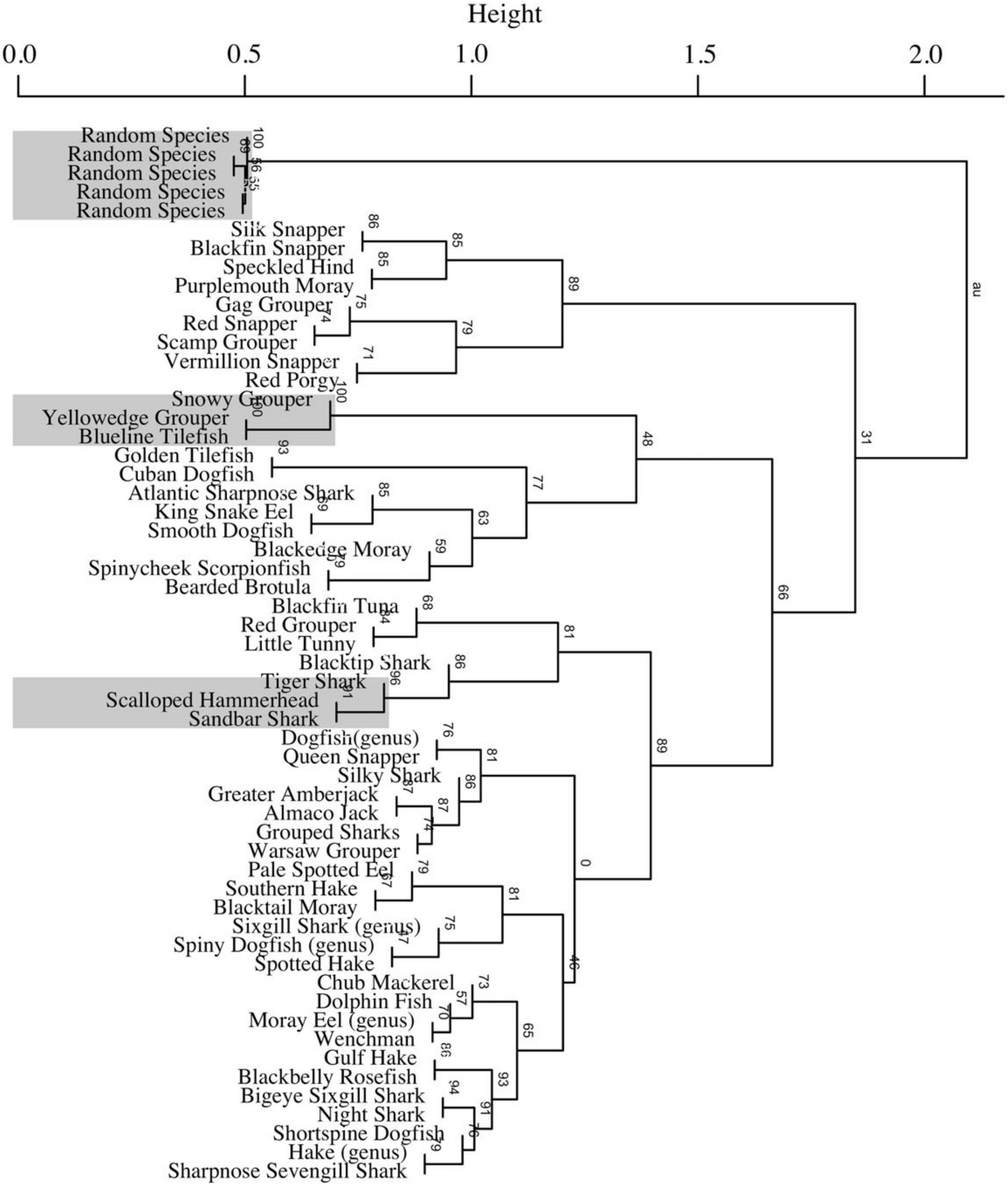

Figure 3. Dendrogram of species clusters for gear types combined using the Bray–Curtis measure of dissimilarity with Ward's linkage.

blueline tilefish cannot be selectively targeted, but instead are consistently captured with the most common deepwater grouper species.

The modelling results are consistent with evidence that before IFQ management vessels selectively targeted golden tilefish, but that blueline tilefish were captured when targeting deepwater grouper species. This is based on the number of discards observed from 2007 through 2009 in which large numbers of discarded blueline tilefish only occurred when the closures did not coincide. This provides evidence that fishers can selectively harvest golden tilefish, but when targeting deepwater grouper, blueline tilefish are incidental bycatch. The current differences in retention rates among the species may be due to price differentials. For example, in 2012, blueline tilefish ex-vessel price was \$1.32 lb^{-1}, while golden tilefish was higher at \$2.50 lb^{-1}, possibly explaining

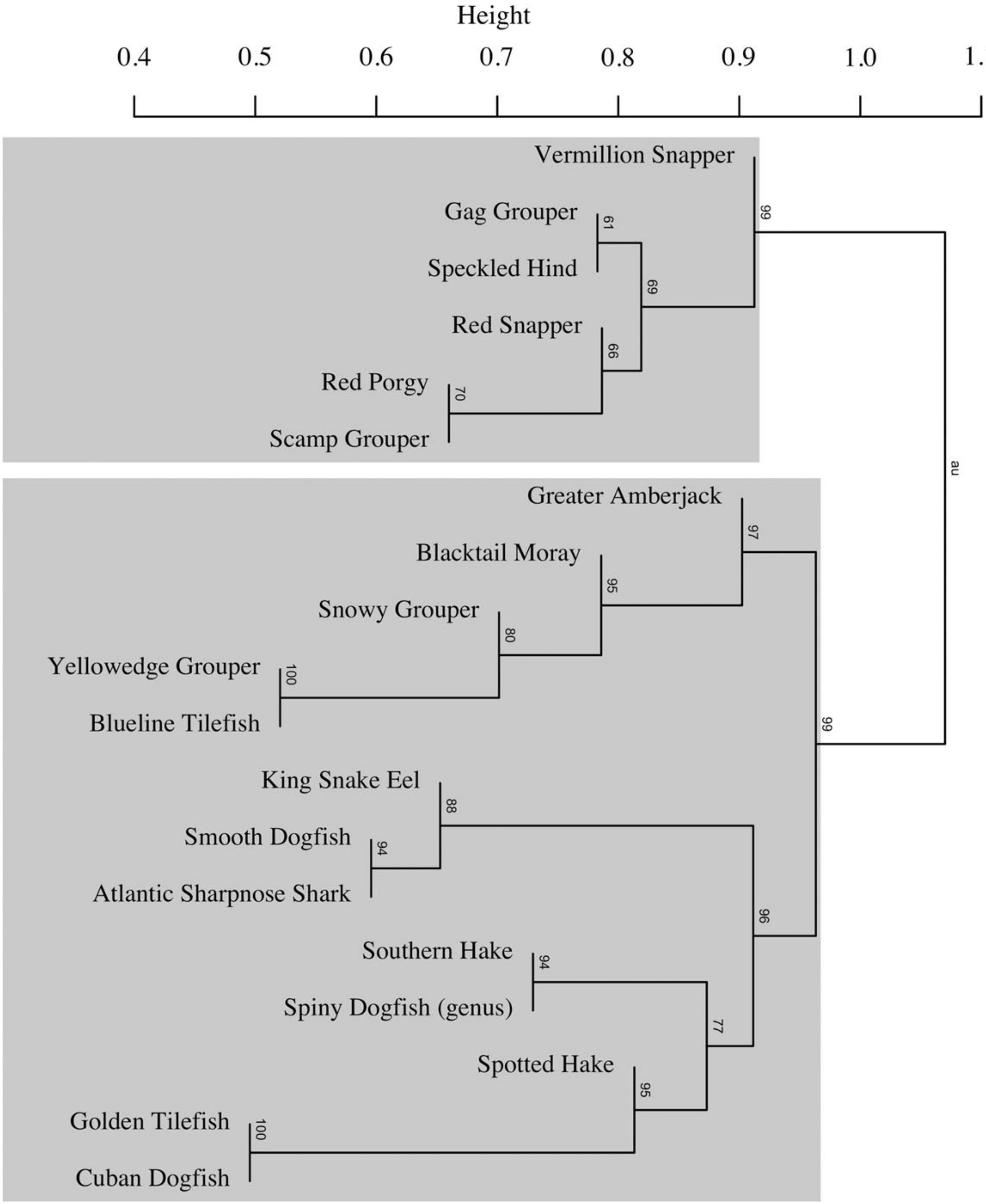

Figure 4. Dendrogram of species clusters with ≥1000 captures recorded using the correlation dissimilarity measure and average agglomerative linkage.

the higher retention rate for that species (SERO, 2013). Another possible reason for the difference in retention rates is that vessels may have insufficient tilefish IFQ allocation available to retain all the blueline tilefish captured when targeting grouper species. The blueline tilefish retention rate of 55.8% under the current IFQ management scheme through 2013 indicates a high amount of discarding and represents an inefficient use of this fishery resource.

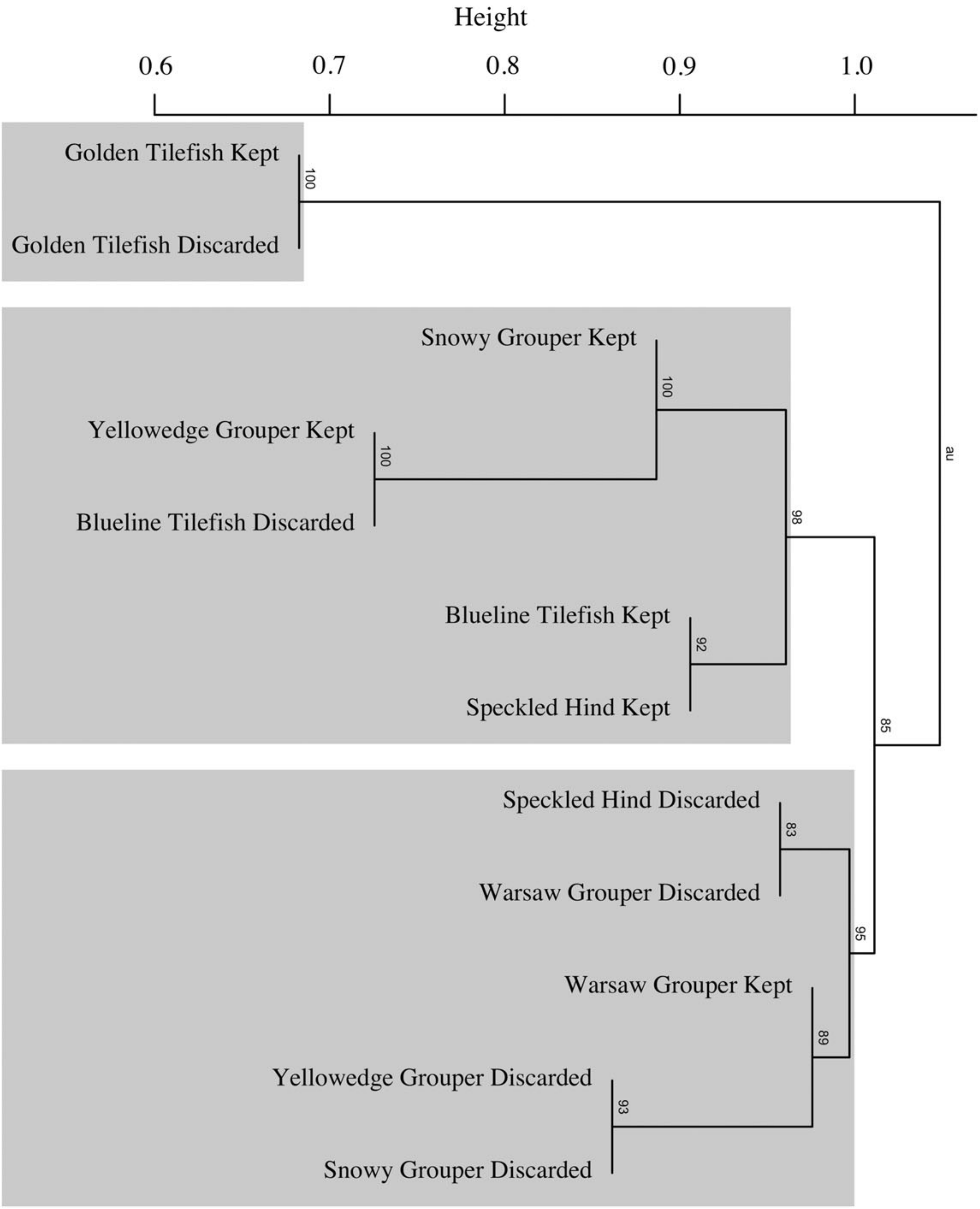

Figure 5. Dendrogram of clusters for IFQ species kept or discarded using the correlation dissimilarity measure and average agglomerative linkage.

Methodologically, Bray–Curtis may be a robust measure of composition for species assemblages in other ecological contexts, but for fishery data on a large spatial scale, our study showed that the correlation measure was superior to Bray–Curtis using HCA. Singh *et al.* (2011) using HCA to study Icelandic groundfish assemblages found similar results with Bray–Curtis only performing better when the data were highly aggregated, most likely due to the minimization of the number of sites. Simulated random species have often been used as a null model for evaluating the significance of species relationships since first being introduced by Strauss (1982). However,

Table 4. Summary of the probabilistic model results for positive, negative, and random pairwise species co-occurrence for the three datasets examined.

Datasets	≥100 captures	≥1000 captures	IFQ-managed
Number of species	56	19	6
Number of fishing sets	3194	3194	2480
Total combinations	1540[a]	171	15
Positive co-occurrence	429	72	5
Negative co-occurrence	264	72	9
Random co-occurrence	763	27	1
% Non-random	47.6	84.2	93.3

[a] Eighty-four species pair combinations were removed due to an expected co-occurrence of <1.0.

Figure 6. Heat map of pairwise species co-occurrence from the probabilistic model with ≥100 captures recorded.

only a limited number of ecological studies have applied the techniques as a comparison tool between the measures of dissimilarity and linkage choices combined with a bootstrap approach. Our findings indicated that the correlation method of dissimilarity outperformed the Bray–Curtis measure substantially by filtering out the simulated random species for all subsets of the data. The correlation measure in combination with average linkage was even more robust when less likely encountered species were removed, which is indicated by

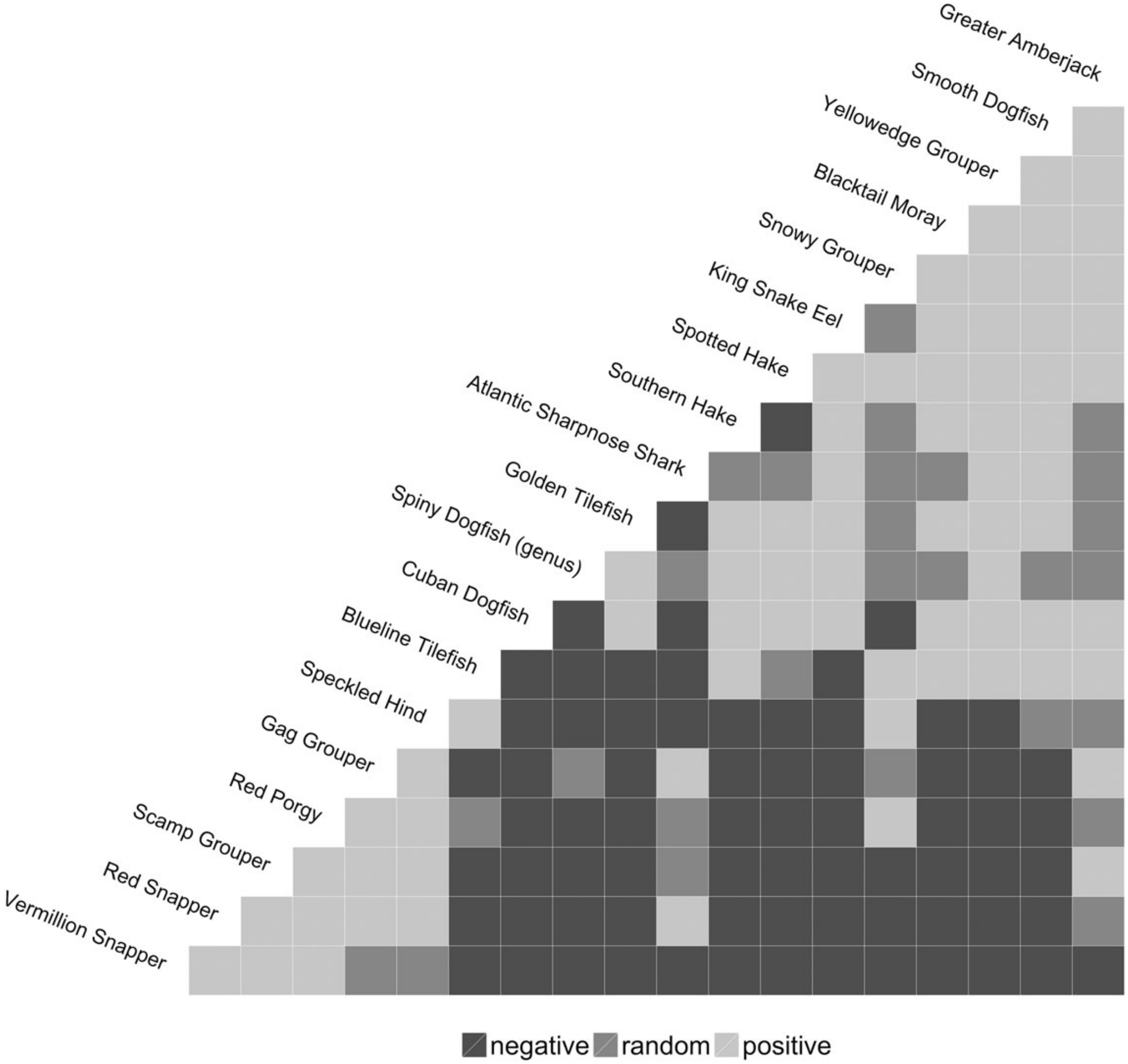

Figure 7. Heat map of pairwise species co-occurrence from the probabilistic model with ≥1000 captures recorded.

the high probability of co-occurrence needed for the simulated random species to be significantly clustered with observed species. The Bray–Curtis measure of dissimilarity with both average and Ward's linkage may be inefficient at determining species relationships on a large spatial scale with this type of dataset because the simulated random species consistently exhibited a lower dissimilarity than observed species and were present in significant clusters. While a number of different probabilities of occurrence for the simulated random data were examined in this study, future studies could compare the results from simulating different levels of abundance using similar methodologies.

Applying the Bray–Curtis measure with the simulated random species as a null model, only one defined cluster or stratification would be considered valid in this study: blueline tilefish, yellowedge grouper, and snowy grouper (Figure 2). However, under the assumption that the correlation measure of dissimilarity is a more robust choice for determining stratifications with HCA in species assemblages, three distinct groups were present. These represent a shallow-water component consisting of snapper species, a mid-depth component including yellowedge and snowy grouper with blueline tilefish, and a deeper depth component of golden tilefish, cuban dogfish, and king snake eel. Additionally, the stratification of the fishery into smaller subunits may allow more accurate determinations of bycatch levels or provide insights into other species of concern. For instance, in the mid-depth cluster, many of the large shark species were clustered together indicating that these species may be captured on fishing sets with extended soak times, certain bait types, or other unknown factors that are influencing capture. In addition, the four most commonly discarded IFQ-managed grouper species were significantly clustered separately from those being retained possibly due to insufficient IFQ allocations.

For future studies, average linkage is recommended over Ward's linkage due to its efficiency in recognizing simulated random data. Other studies using metrics such as the cophenetic correlation

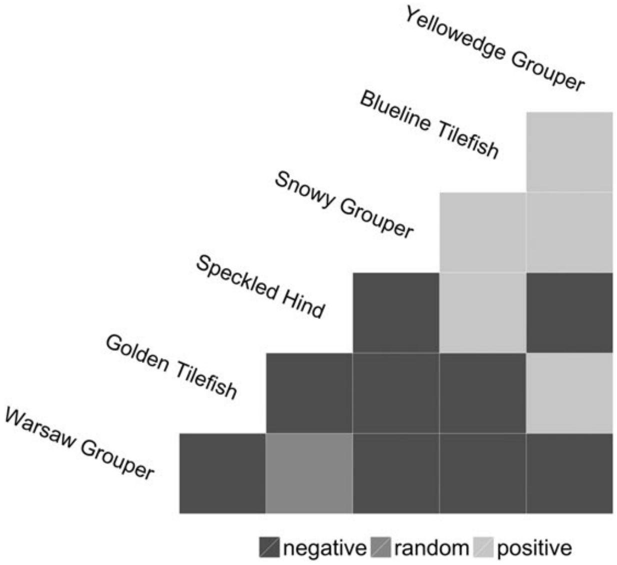

Figure 8. Heat map of pairwise species co-occurrence from the probabilistic model for the deepwater IFQ-managed species.

coefficient or agglomerative coefficient for evaluating cluster validity have recommended Ward's linkage, but none of these studies have used simulated random data for a null model as this study. Jackson *et al.* (2010) examined cluster analysis and ordination commonly used by community ecologists and stated the field has been slow to adopt recent advances such as the bootstrap or Bayesian methods. The authors advocated using the bootstrap approach with the caveat that since the independence of the fish species at sites cannot be assumed; the probabilities should represent the degree of association between species instead of a test of statistical significance related to a null hypothesis. This precaution was given because interspecific dynamics may violate the assumption of independence between different sampling sites. While the lack of a significant association between species does not mean that none exists, significant relationships suggest a possible direction for future ecological research.

Our research revealed that the optimal HCA complemented the probabilistic models for species co-occurrence for most species stratifications. For the species with ≥100 captures observed, the model was able to recognize the simulated random species as random for >90% of the pairwise associations. More insights were derived for the more commonly captured species, but aggregating some of the more indistinct species groupings together could alleviate this by reducing the overall number of pairwise species combinations included in the analysis. For instance, some of the grouping representing either genus or family due to questionable species identification could be eliminated from future analyses to reduce the overall number of possible combinations and thus increase the detection power. Also, researchers could limit the fishing sets by geographic subregion or by a certain species of interest when certain species co-occurrences are of interest. Overall, this parsimonious approach for examining community structure is not without controversy because modelling only pairwise associations between species ignores many of the patterns that can be derived from abundance data such as diversity indices, species abundance covariance, and links to environmental variables (Soberón, 2015). Veech (2014) argues some of the proposed limitations of this simplistic approach, but regardless it represents a viable tool for managers that can be easily implemented when co-occurrence is the primary goal of the research.

Specific determinations of stock status are one of the driving forces of current fishery management schemes and managers often have to rely on limited data sources. A recent report on the status of the Gulf of Mexico ecosystem found that abundance indices for tilefish and some of the grouper species in our research have been in decline since the 1980s, while some of the primary species of commercial and recreational importance such as red snapper and red grouper (*Epinephelus morio*) in the Gulf region have increased in abundance (Karnauskas *et al.*, 2013). The authors suggest these fluctuations in abundance may be due to the greater attention applied to the species of higher importance, and that fishers may be targeting secondary species to compensate for increased regulation on higher-profile species. As an initial quantitative study on Gulf of Mexico bycatch issues, this research is an important step in advancing ecosystem-based fisheries management through our increased understanding of the complex marine environment. The statistical techniques presented in this study can be applied for analysing fishery observer or independent data to reveal underlying stratifications and co-occurrence in other regions. These approaches provide fishery managers useful tools for visualizing community structure when proposing actions that can affect multiple species and will be highly valuable in assessing the potential impacts of regulatory mandates.

References

Bartholomew, A., and Bohnsack, J. A. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Reviews in Fish Biology and Fisheries, 15: 129–154.

Borcard, D., Gillet, F., and Legendre, P. 2011. Numerical Ecology with R. Springer Science, New York.

Branch, T. A. 2009. How do individual transferable quotas affect marine ecosystems? Fish and Fisheries, 10: 39–57.

Cope, J. M., and Haltuch, M. A. 2012. Temporal and spatial summer groundfish assemblages in trawlable habitat off the west coast of the USA, 1977 to 2009. Marine Ecology and Progress Series, 451: 187–200.

Farmer, N. A., Malinowski, R. P., and McGovern, M. K. 2010. Species groupings for management of the Gulf of Mexico reef fish fishery. NOAA, NMFS, SERO-LAPP-2010-03 Report. 90 pp.

GMFMC. 2005. Reef Fish Amendment 22. Gulf of Mexico Fishery Management Council, Tampa, FL. http://gulfcouncil.org/Beta/GMFMCWeb/downloads/Amend%2022%20Final%2070204.pdf.

Griffith, D., Veech, J., and Marsh, C. 2014. cooccur: Probabilistic species co-occurrence in R. R package version 1.0. http://CRAN.R project.org/package=cooccur.

Heery, E., and Cope, J. M. 2014. Co-occurrence of bycatch and target species in the groundfish demersal trawl fishery of the U.S. west coast; with special consideration of rebuilding stocks. Fishery Bulletin, 112: 36–48.

Jackson, D. A., Walker, S. C., and Poos, M. S. 2010. Cluster analysis of fish community data: "new" tools for determining meaningful groupings of sites and species assemblages. American Fisheries Society Symposium Series, 73: 503–527.

Karnauskas, M., Schirripa, M. J., Kelble, C. R., Cook, G. S., and Craig, J. K. (Eds) 2013. Ecosystem status report for the Gulf of Mexico. NOAA Technical Memorandum. NMFS-SEFSC-653. 52 pp.

Koch, C. F. 1987. Prediction of sample size effects on the measured temporal and geographic distribution patterns of species. Paleobiology, 13: 100–107.

Liu, H., Fogarty, M. J., Glaser, S. M., Altman, I., Hsieh, C., Kaufman, L., Rosenberg, A. A., *et al.* 2012. Nonlinear dynamic features and co-predictability of the Georges Bank fish community. Marine Ecology and Progress Series, 464: 195–207.

NMFS. 2007. Magnuson–Stevens Fishery Conservation and Management Act. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Washington, DC.

NMFS. 2015. Characterization of the U.S. Gulf of Mexico and southeastern Atlantic otter trawl and bottom reef fish fisheries. Observer Training Manual. NMFS, Southeast Fisheries Science Center, Galveston Laboratory, Galveston, TX. http://www.galvestonlab.sefsc.noaa.gov/forms/observer/obs_training_manual_6_2015.pdf.

R Core Team. 2015. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Render, J. H., and Wilson, C. A. 1994. Hook-and -line mortality of caught and released red snapper around oil and gas platform structural habitat. Bulletin of Marine Science, 55: 1106–1111.

Rogers, J. B., and Pikitch, E. K. 1992. Numerical definition of groundfish assemblages caught off the coasts of Orgeon and Washington using commercial fishing strategies. Canadian Journal of Fisheries and Aquatic Sciences, 49: 2648–2656.

Rudershausen, P. J., Buckel, J. A., and Williams, E. H. 2007. Discard composition and release fate in the snapper and grouper commercial hook-and-line fishery in North Carolina, USA. Fisheries Management and Ecology, 14: 103–113.

Scott-Denton, E., Cryer, P. F., Gocke, J. P., Harrelson, M. R., Kinsella, D. J., Pulver, J. R., Smith, R. C. *et al.* 2011. Descriptions of the U.S. Gulf of Mexico reef fish bottom longline and vertical line fisheries based on observer data. Marine Fisheries Review, 73: 1–26.

Scott-Denton, E., and Williams, J. A. 2013. Observer Coverage of the 2010–2011 Gulf of Mexico Reef Fish. NOAA Technical Memorandum. NMFS-SEFSC-646. 65 pp.

SERO. 2013. Gulf of Mexico 2012 grouper-tilefish individual fishing quota annual report. National Marine Fisheries Service, Southeast Regional Office, St Petersburg, FL. http://sero.nmfs.noaa.gov/sustainable_fisheries/lapp_dm/documents/pdfs/2013/2012_gt_annualreport.pdf.

SERO. 2015. Historical Gulf of Mexico reef fish commercial landings. National Marine Fisheries Service, Southeast Regional Office, St Petersburg, FL. http://sero.nmfs.noaa.gov/sustainable_fisheries/acl_monitoring/commercial_gulf/reef_fish_historical/index.html.

Shertzer, K. W., and Williams, E. H. 2008. Fish assemblages and indicator species: reef fishes off the southeastern United States. Fishery Bulletin, 106: 257–269.

Singh, W., Hjorleifsson, E., and Stefansson, G. 2011. Robustness of fish assemblages derived from three hierarchical agglomerative clustering algorithms performed on Icelandic groundfish survey data. ICES Journal of Marine Science, 68: 189–200.

Sissenwine, M. M., Mace, P. M., and Lassen, H. J. 2014. Preventing overfishing: evolving approaches and emerging challenges. ICES Journal of Marine Science, 71: 153–156.

Soberón, J. 2015. Pairwise versus presence–absence approaches for analyzing biodiversity patterns. Journal of Biogeography, 42: 807–808.

Stephen, J. A., and Harris, P. J. 2010. Commercial catch composition with discard and immediate release mortality proportions off the southeastern coast of the United States. Fisheries Research, 103: 18–24.

Strauss, R. E. 1982. Statistical significance of species clustered in association analysis. Ecology, 63: 634–639.

Suzuki, R., and Shimodaira, H. 2011. pvclust: Hierarchical clustering with p-values via multiscale bootstrap resampling. R package version 1.2-2. http://CRAN.Rproject.org/package=pvclust.

Veech, J. A. 2013. A probabilistic model for analyzing species co-occurrence. Global Ecology and Biogeography, 22: 252–260.

Veech, J. A. 2014. The pairwise approach to analyzing species co-occurrence. Journal of Biogeography, 41: 1029–1035.

Williams, E. H., and Ralston, S. 2002. Distribution and co-occurrence of rockfishes (family: Sebastidae) over trawlable shelf and slope habitats of California and southern Oregon. Fishery Bulletin, 100: 836.

Handling editor: Ernesto Jardim