

Abstract—For many fish stocks, resource management cannot be based on stock assessment because data are insufficient—a situation that requires alternative approaches to management. One possible approach is to manage data-limited stocks as part of an assemblage and to determine the status of the entire unit by a data-rich indicator species. The utility of this approach was evaluated in analyses of 15 years of commercial and 34 years of recreational logbook data from reef fisheries off the southeastern United States coast. Multivariate statistical analyses successfully revealed three primary assemblages. Within assemblages, however, there was little evidence of synchrony in population dynamics of member species, and thus, no support for the use of indicator species. Nonetheless, assemblages could prove useful as management units. Their identification offers opportunities for implementing management to address such ecological considerations as bycatch and species interrelations.

Fish assemblages and indicator species: reef fishes off the southeastern United States

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Most approaches to fishery management rely on results from stock assessment. Data-limited situations, however, may not conform to conventional assessment methods, necessitating other approaches to management (Kruse et al., 2005). One possible approach with data-limited stocks is to assign them to assemblages that are managed as units. Ideally, each assemblage would include at least one data-rich species that could be assessed and serve as a status indicator of the entire unit. Managing assemblages by means of indicator species is arguably a small but practical step in the direction of ecosystem-based management (Hall and Mainprize, 2004).

Assemblages may be defined by similarities in such biological characteristics as life history, trophic behavior, or home range. For the purpose of fishery management, however, an assemblage should consist of species caught together, if regulations on fishing are to benefit assemblage members. This is particularly true if regulations are focused on an indicator species but the intent is also to control the harvest of other species in the assemblage.

Indicator species have been used in management of both terrestrial and marine systems (Simberloff, 1998; Zacharias and Roff, 2001). The term “indicator species” has no single definition (Landres et al., 1988); it is used here as suggested by the National Standard Guidelines of U.S. federal fishery management, which states 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.” (Federal Register, 1998) According to this usage, the stock status of the indicator is extrapolated to represent that of other species in the assemblage, or analogously, other stocks of the same species. Such an approach requires the assumption that population trends of an indicator species reflect those of others in the assemblage.

The approach of managing multi-species assemblages by means of indicator species raises two fundamental questions. First, can assemblages be identified? As mentioned, species of an assemblage would need to be caught together if regulations are to affect the entire unit. Second, if an assemblage can be identified, do its members have similar stock dynamics? If not, focusing management on the indicator species may not provide the intended benefits to other stocks.

We address both questions, using as a case study the snapper-grouper complex off the southeastern United States. As defined for management, the complex contains 73 species (Appendix), the majority of which cannot be assessed with currently available data. The objectives of this study are 1) to identify assemblages of finfish species within the snapper-grouper complex and 2) to examine synchrony of stock dynamics within assemblages. To accomplish the first objective, multivariate statistical techniques

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were applied to data from recreational and commercial fisheries, and to accomplish the second, indices of abundance were computed and tested for correlation.

Materials and methods

Data used in multivariate analyses

To identify assemblages of species within fishery landings, statistical grouping techniques were applied to two fishery data sets, one recreational (headboat) and one commercial. Both data sets encompassed areas from Cape Hatteras, North Carolina to Key West, Florida. These data were chosen because of their importance for stock assessment of species in the snapper-grouper complex.

The recreational sector was represented by logbook data reported by headboat operators and verified by port samplers. Headboats are large, for-hire vessels that typically accommodate 20–60 anglers on half- or full-day trips. Data collection began in 1972 with a focus on coastal waters off North and South Carolina. The area of collection was extended in 1976 to include the coastal waters of Georgia and northern Florida, and again in 1978 to include those of southern Florida. We used 1972–2005 headboat data. Records from each trip contained information on number of anglers, trip duration, date, geographic area, and landings (number fish) of each species.

The commercial sector was represented by logbook data reported by commercial anglers with snapper-grouper permits. We used 1992–2006 commercial data; however, 2006 was a partial year (data through September). Records contained information similar to those in the headboat data set, but landings were reported in weight (pounds). Excluded were nonsensical records suspected to be misreported or misrecorded. Analyses of commercial data were restricted to trips with handline gear (~87% of records) to avoid the possibility of confounding estimated assemblages with effects of gear. Furthermore, these analyses included only trips of one-day duration (~50% of records) to minimize the possibility that catch in a trip was taken from widely separated geographic areas with potentially different assemblages.

Species assemblages

Following Lee and Sampson (2000), we used more than one statistical technique to identify species assemblages. We applied three techniques: ordination and two types of cluster analysis. For all three techniques, the Sørensen (also called Bray-Curtis) measure of dissimilarity (distance) between species was used (McCune and Grace, 2002). In comparison to other measures, Sørensen distance has been found more robust in ecological studies (Field et al., 1982; Faith et al., 1987) and provides more ecologically interpretable results (Beals, 1973). Perhaps for these reasons, it has been considered appropriate in

studies of fish assemblages (e.g., Mueter and Norcross, 2000; Gomes et al., 2001; Williams and Ralston, 2002).

To compute dissimilarities, we formatted each data set as a matrix, with rows representing species and columns representing vessel-months. That is, each element (c_{ij}) of the matrix quantified the amount (in units of number fish for headboat or pounds for commercial) of a species (i) landed by each vessel pooled over one month (vessel-month j). The duration of a month was chosen as a reasonable compromise between maximizing the variety of species landed (longer duration) and minimizing the number of different locations fished (shorter duration). Locations fished per vessel were generally consistent within a month, but could have changed on the time scale of seasons (perhaps following fish migrations, for example). Species were removed if they appeared in fewer than 1% of all trips because rare species may distort inferred patterns (Koch, 1987; Mueter and Norcross, 2000). This restriction left 25,293 records of vessel-month-species in the headboat data set and 143,426 in the commercial data set.

Before computing dissimilarities, data were transformed with the root-root transformation to moderate the influence of abundant species:

$$c'_{ij} = \sqrt{\sqrt{c_{ij}}} = \sqrt[4]{c_{ij}} \quad (1)$$

This transformation has been preferred for density and biomass data, particularly when used in connection with the Sørensen measure of distance (Field et al., 1982). After transformation, a matrix of dissimilarities between species was computed with the Sørensen measure of distance:

$$D_{ih} = \sum_{j=1}^J \frac{|c'_{ij} - c'_{hj}|}{(c'_{ij} + c'_{hj})}, \quad (2)$$

where D_{ih} = the distance between species i and h ; and J = the number of columns (vessel-months).

To identify species assemblages, the ordination method of nonmetric multidimensional scaling (NMDS) was applied to the matrix of dissimilarities (Kruskal, 1964). As stated by McCune and Grace (2002), "Nonmetric multidimensional scaling is the most generally effective ordination method for ecological community data and should be the method of choice, unless a specific analytical goal demands another method." NMDS searches for positions of n objects (here, n species) in d dimensions such that dissimilarities in ordination space are close to those of the original space. We extracted the first two dimensions of ordination space ($d=2$) for graphical presentation.

In addition to ordination, we applied nonhierarchical and agglomerative hierarchical cluster analyses. The nonhierarchical cluster analysis was used to partition species into groups, based on the method of k -medoids, a more robust version of the classical method of k -means (Kaufman and Rousseeuw, 1990). The k -medoids approach attempts to identify k objects from the data set

that best represent all objects. Clusters are created by assigning each object in the data set to its nearest representative (i.e., medoid).

As with any nonhierarchical method, the number of clusters k must be specified *a priori*. We applied a range of values and selected the k most concordant with the data, as quantified by highest average silhouette width. The silhouette width of each species measures its goodness of clustering. For any given k , silhouette widths averaged over species within clusters indicate relative strength of assemblages; across k , the highest average width computed from all species corresponds to the optimal number of clusters (Rousseeuw, 1987). To examine uncertainty in the optimal number, a bootstrap procedure was applied in which columns (vessel-months) of the original data matrices were resampled with replacement to produce $n=1000$ bootstrapped matrices of the original dimension, and then $n=1000$ average silhouette widths were recomputed for each k .

The hierarchical cluster analysis was included to provide a comparison with clusters computed by k -medoids and to quantify associations among species, as represented by dendrograms. The hierarchical analysis was based on the linkage method of McQuitty (McCune and Grace, 2002).

Indices of abundance

Indices of abundance were computed to examine synchrony of dynamics among stocks and thus, to investigate the basic assumption that an indicator species could be used to infer dynamics of other species in the assemblage. This investigation focused on the three strongest assemblages (i.e., strongest coherence among members), as measured by average silhouette widths from the cluster analysis. Because the strongest assemblages were examined, this investigation is a best-case scenario. If strongly associated populations do not exhibit synchronous dynamics, one should not assume that weakly associated populations do otherwise.

Ideally, indices of abundance should be computed from fishery independent data; however, for many species here, such data were unavailable or insufficient. In this study, indices were computed from the headboat data set. Fishing effort from headboats is applied generally toward many species, rather than toward specific targets. Because effort is nondirected, any confounding effects of density-dependent catchability are likely to be minimized, and in this regard, headboat data are similar to fishery-independent data.

Indices of abundance were computed from catch and effort data in units of number of fish landed per angler-hour. Data were considered from 1978, the first year of full area coverage, to 2005. For each species, a trip was included only if a species from the relevant assemblage was landed. Thus, many trips were excluded, and some trips were included that had effort but zero catch. This approach represents effective effort more accurately than if all trips were included (a situation that would inflate the assumed effort) or if trips were restricted to

those that landed the species in question (a situation that would deflate the assumed effort).

To compute indices of abundance, catch and effort data were standardized using a generalized linear model (Hardin and Hilbe, 2001). The explanatory variables for the model were year, month, and geographic area. To ensure adequate sample sizes by geographic area, sampling areas were aggregated into four regions: North Carolina, South Carolina, Georgia-northern Florida, and southern Florida (south of Cape Canaveral). The response variable was catch per effort, assumed to be distributed with delta-lognormal error structure (Lo et al., 1992; Stefánsson, 1996; Maunder and Punt, 2004). In this structure, the proportion of positive values is modeled with binomial error, and positive values themselves are modeled with lognormal error. Indices were not computed for species that were caught in fewer than 20% of trips on the relevant assemblage, to avoid estimation error associated with inflation of zero values (Lampert, 1992). Because this criterion excludes rarely caught species, evidence of synchrony in our results should be viewed as a necessary but not sufficient condition for the use of indicator species.

Synchrony in dynamics between any two stocks was measured by the Spearman's rank correlation coefficient, computed both from 1) the indices of abundance and 2) the first-differenced time series of log-abundances (z_t):

$$z_t = \log U_t - \log U_{t-1} = \log \frac{U_t}{U_{t-1}}, \quad (3)$$

where U_t = the index value of a stock at time t . Positive correlation of the indices themselves would indicate similar trends in abundance over time. The use of first differences, as in Equation 3, rather than raw or relative abundance, puts emphasis on annual population growth rates and may reduce spurious correlation (Bjørnstad et al., 1999). Positive correlation of growth rates would indicate that stocks not only have similar patterns of productivity (growth, recruitment, and mortality), but that they also respond similarly to interannual variation in fishing effort or catchability.

Significance levels of correlation coefficients were obtained nonparametrically with $n=10,000$ randomizations of z_t (Prager and Hoenig, 1989; Edgington, 1995; Bjørnstad et al., 1999). A coefficient that ranks sufficiently high in relation to the randomizations could be considered significantly positive, and a coefficient that ranks low, significantly negative. Significance was determined with a two-tailed test at the $\alpha=0.1$ level with Bonferroni correction.

Results

Species assemblages

Multidimensional scaling did not reveal strongly isolated groups of species in ordination space (Fig. 1). It did, however, reveal consistency of ordination in the sense

that many species had similar neighbors across headboat and commercial data sets. For example, in both data sets, lane snapper was near blue runner, gray snapper,

mutton snapper, and yellowtail snapper (see Appendix for scientific names). This repeatability of results provides evidence of species assemblages.

The *k*-medoid cluster analyses identified *k*=14 clusters as most compatible with the headboat data and *k*=7 clusters as most compatible with the commercial data (Fig. 2). These optimal numbers of clusters were not cleanly defined because peaks in average silhouette widths lacked distinction (Fig. 2). In general, assemblages were similar across data sets, at least for species that were present in both data sets (Table 1).

Hierarchical cluster analyses provided associations among species that were consistent with the assemblages of *k*-medoid analyses. In hierarchical analysis of the headboat data (Fig. 3), three assemblages had the strongest similarities among member species, labeled here as the deepwater assemblage (blueline tilefish, snowy grouper, speckled hind, and yellowedge grouper), southern assemblage (blue runner, gray snapper, lane snapper, mutton snapper, and yellowtail snapper), and northern assemblage (bank sea bass, black sea bass, knobbed porgy, gag, gray triggerfish, greater amberjack, red porgy, red snapper, scamp, tomtate, vermilion snapper, white grunt, and whitebone porgy). In hierarchical analysis of the commercial data, the same three assemblages were identified with few differences in constituent species (Fig. 4). In both data sets, these assemblages had the strongest coherence among member species, as measured by each cluster's average silhouette width (Table 1). Thus, the deepwater, southern, and northern assemblages were examined further for synchrony in indices of abundance.

Indices of abundance

Although data through 2005 were considered, indices of the deepwater assemblage were derived through 1993, because 1994 began regulations that would have invalidated catch per effort as an index of abundance (i.e., one speckled hind per vessel per trip). Deepwater species that met the criterion of at least 20% positive trips were speckled hind, snowy grouper, and blueline tilefish. All southern species met the 20% positive trip criterion, however small sample sizes of these species north of Cape Canaveral, Florida, necessitated combining geographic areas into two regions: southern Florida and all other areas. Northern species that met the 20% criterion were white grunt, gag, tomtate, black sea bass, vermilion snapper, and gray triggerfish.

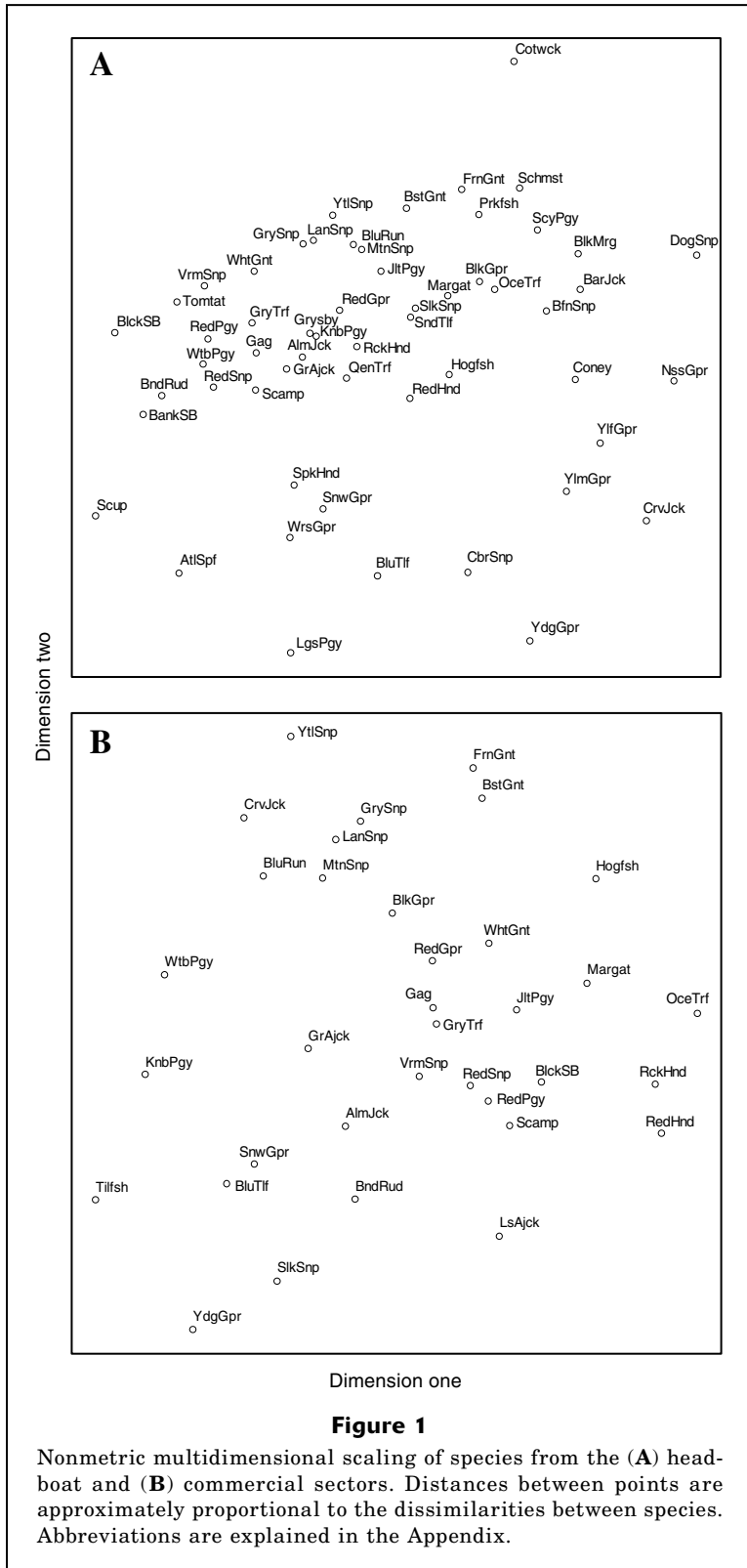


Figure 1

Nonmetric multidimensional scaling of species from the (A) headboat and (B) commercial sectors. Distances between points are approximately proportional to the dissimilarities between species. Abbreviations are explained in the Appendix.

In general, indices of abundance were not synchronous (Table 2). Within the deepwater assemblage, snowy grouper was positively but not significantly correlated with blueline tilefish, and neither species was strongly correlated with speckled hind. Within the southern assemblage, correlations between species were mostly negative; however, those between yellowtail, lane, and gray snappers were positive and significant, indicating synchrony in this subset. Within the northern assemblage, about half of the correlations between species were negative, and only the correlation between vermilion snapper and black sea bass was positive and significant. These results offer little evidence of synchrony in population trends within assemblages.

Similarly, first-differenced indices of abundances were out of synchrony (Table 3). Correlations between species were both positive and negative; only one was significantly negative (between snowy grouper and speckled hind), and one was significantly positive (between gray triggerfish and vermilion snapper). These results from first-differenced time series do not support the hypothesis of synchrony in annual population growth rates within assemblages.

Discussion

It is unlikely that sufficient resources will ever be available to monitor, assess, and manage every fish stock individually. Thus, managing assemblages by means of indicator species has intuitive appeal. It begins a shift from single-species management toward ecosystem-based approaches and provides a scientific and managerial shortcut by supplanting the need to monitor and assess every managed stock. In the United States, for example, the Magnuson-Stevens Fishery Conservation and Management Reauthorization Act of 2006 (MSRA, 2006) requires that annual catch limits be established to end and prevent overfishing by 2011 in all fisheries (by 2010 for fisheries where overfishing is occurring), yet many stocks cannot be assessed and their status is therefore unknown. Conceivably, setting catch limits by assemblage rather than stock-by-stock could satisfy the statute 1) without substantial new resources devoted to both data collection programs and stock assessment and 2) within the time frame allowed.

Despite its possible appeal, the use of indicator species to extrapolate trends of other species should be viewed with considerable skepticism. From the perspective of niche theory, fishes that coexist are able to do so, in part, because they have adapted to use different niches in their shared environment (May and MacArthur, 1972; Leibold, 1995). Consequently, species within assemblages differ in reproductive characteristics, foraging behavior, habitat requirements, and population-level responses to such factors as competi-

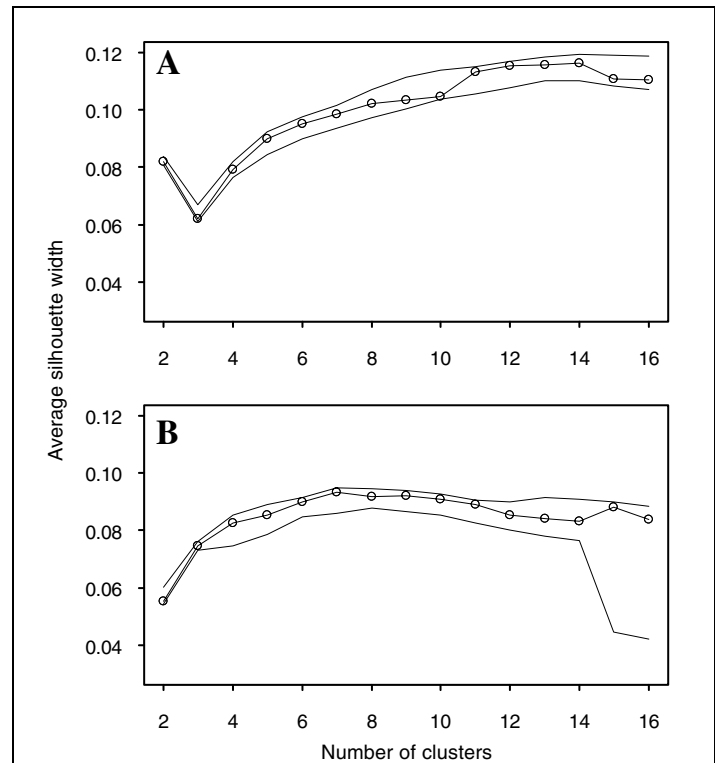


Figure 2

Average silhouette width (lines with circles) from k -medoid cluster analysis of species in (A) the headboat sector and (B) the commercial sector. Lower and upper lines (without circles) represent 5th and 95th percentiles, respectively, from $n=1000$ bootstrap replicates. Average silhouette width measures goodness of clustering; higher values indicate better concordance with data.

tion, predation, disease, and environmental variation (Landres et al., 1988). Because of these differences, population trends of one species (or stock) do not readily extrapolate to others in the assemblage (e.g., Niemi et al., 1997; Shaul et al., 2007). For empirical and theoretical reasons, several authors have concluded that the use of indicator species should be avoided, unless supported by strong evidence from the system in question (Landres et al., 1988; Niemi et al., 1997).

From another perspective, even without strong evidence of synchrony, indicator species may still be useful if applied in a restrictive sense. That is, if fishing effort occurs at the level of assemblages, regulations to reduce effort on one species (the indicator) could transmit to others of unknown status. The cost of this approach would be the forgone yield of any species that could sustain increased rates of exploitation. Ideally, the indicator species should be the weakest link of the assemblage, although defining weakest link could be problematic, along with choosing the correct species (Simberloff, 1998). Furthermore, there may be limited data for the species that is the weakest link of a marine fish assemblage. If achievable, however, such a

Table 1

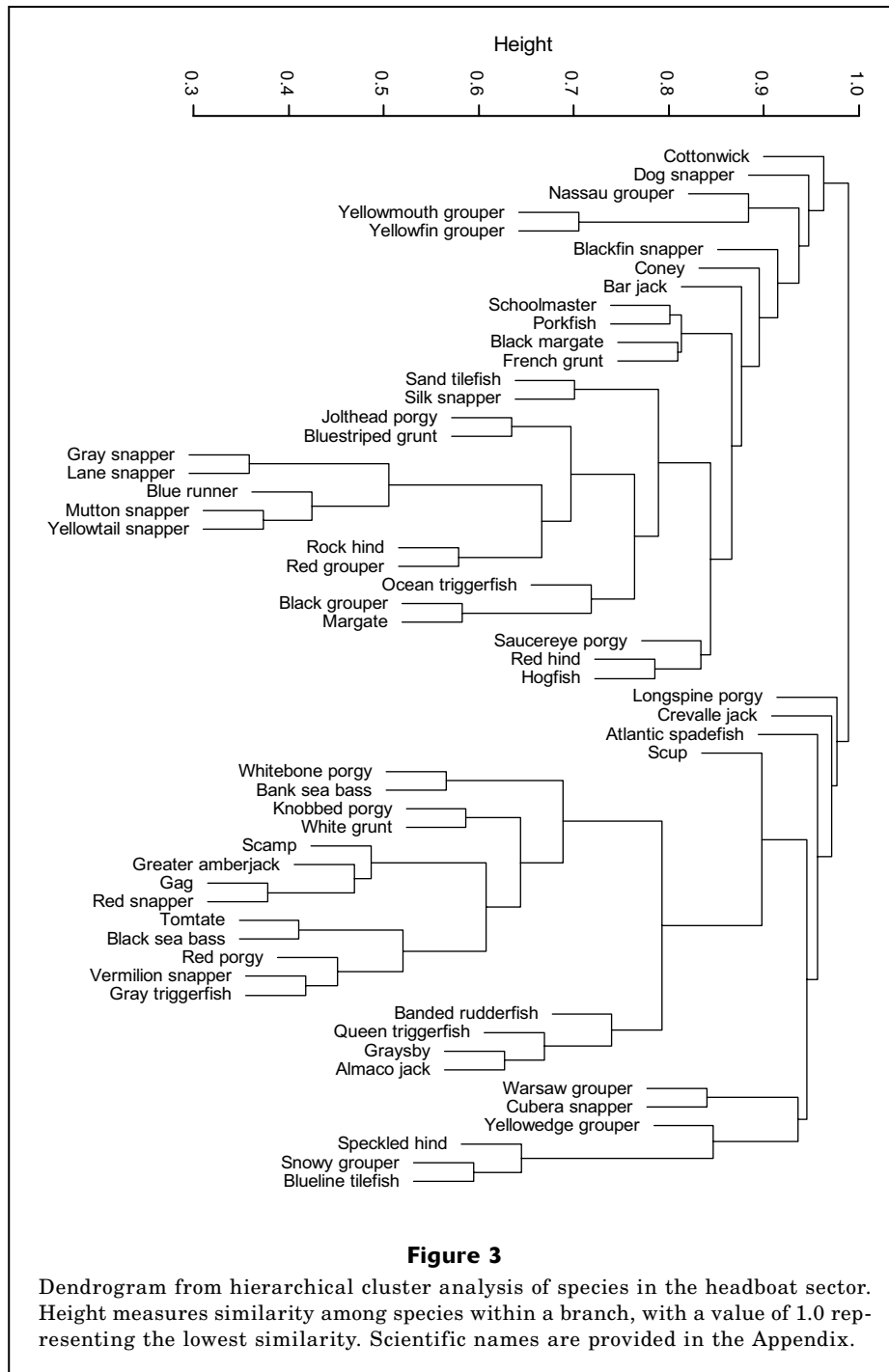
Clusters of species in headboat and commercial landings, listed in order of strongest to weakest cluster, as measured by each cluster's average silhouette width (in parentheses). Clusters were partitioned around $k=14$ (headboat) or $k=7$ (commercial) medoids—values determined by highest average silhouette widths computed from all species. See Appendix for the scientific names of species.

Headboat clusters		Commercial clusters	
<u>One (0.22)</u>	<u>Six (0.07)</u>	<u>One (0.17)</u>	<u>Six (0.01)</u>
Bank sea bass	Cubera snapper	Black sea bass	Bluestriped grunt
Black sea bass	Warsaw grouper	Gag	Crevalle jack
Gag		Gray triggerfish	French grunt
Gray triggerfish	<u>Seven (0.04)</u>	Margate	Lane snapper
Greater amberjack	Blackfin snapper	Red grouper	Whitebone porgy
Knobbed porgy	Cottonwick	Red porgy	
Red porgy	Sand tilefish	Red snapper	<u>Seven (0.00)</u>
Red snapper	Silk snapper	Scamp	Lesser amberjack
Scamp		Vermilion snapper	
Tomtate	<u>Eight (0.03)</u>	White grunt	
Vermilion snapper	Black margate		
White grunt	Coney	<u>Two (0.14)</u>	
Whitebone porgy	Porkfish	Black grouper	
		Blue runner	
<u>Two (0.19)</u>	<u>Nine (0.00)</u>	Gray snapper	
Blue runner	Bar jack	Greater amberjack	
Bluestriped grunt	Black grouper	Mutton snapper	
French grunt	Hogfish	Yellowtail snapper	
Gray snapper	Margate		
Jolthead porgy	Ocean triggerfish	<u>Three (0.07)</u>	
Lane snapper	Red hind	Almaco jack	
Mutton snapper	Saucereye porgy	Banded rudderfish	
Red grouper	Schoolmaster	Blueline tilefish	
Yellowtail snapper		Silk snapper	
	<u>Ten (0.00)</u>	Snowy grouper	
<u>Three (0.18)</u>	Atlantic spadefish	Tilefish	
Blueline tilefish		Yellowedge grouper	
Snowy grouper			
Speckled hind	<u>Eleven (0.00)</u>	<u>Four (0.04)</u>	
Yellowedge grouper	Crevalle jack	Hogfish	
		Jolthead porgy	
<u>Four (0.11)</u>	<u>Twelve (0.00)</u>	Rock hind	
Almaco jack	Dog snapper		
Banded rudderfish		<u>Five (0.02)</u>	
Graysby	<u>Thirteen (0.00)</u>	Knobbed porgy	
Queen triggerfish	Longspine porgy	Ocean triggerfish	
Rock hind		Red hind	
	<u>Fourteen (0.00)</u>		
<u>Five (0.09)</u>	Scup		
Nassau grouper			
Yellowfin grouper			
Yellowmouth grouper			

restrictive use of indicator species could be considered a precautionary approach to management.

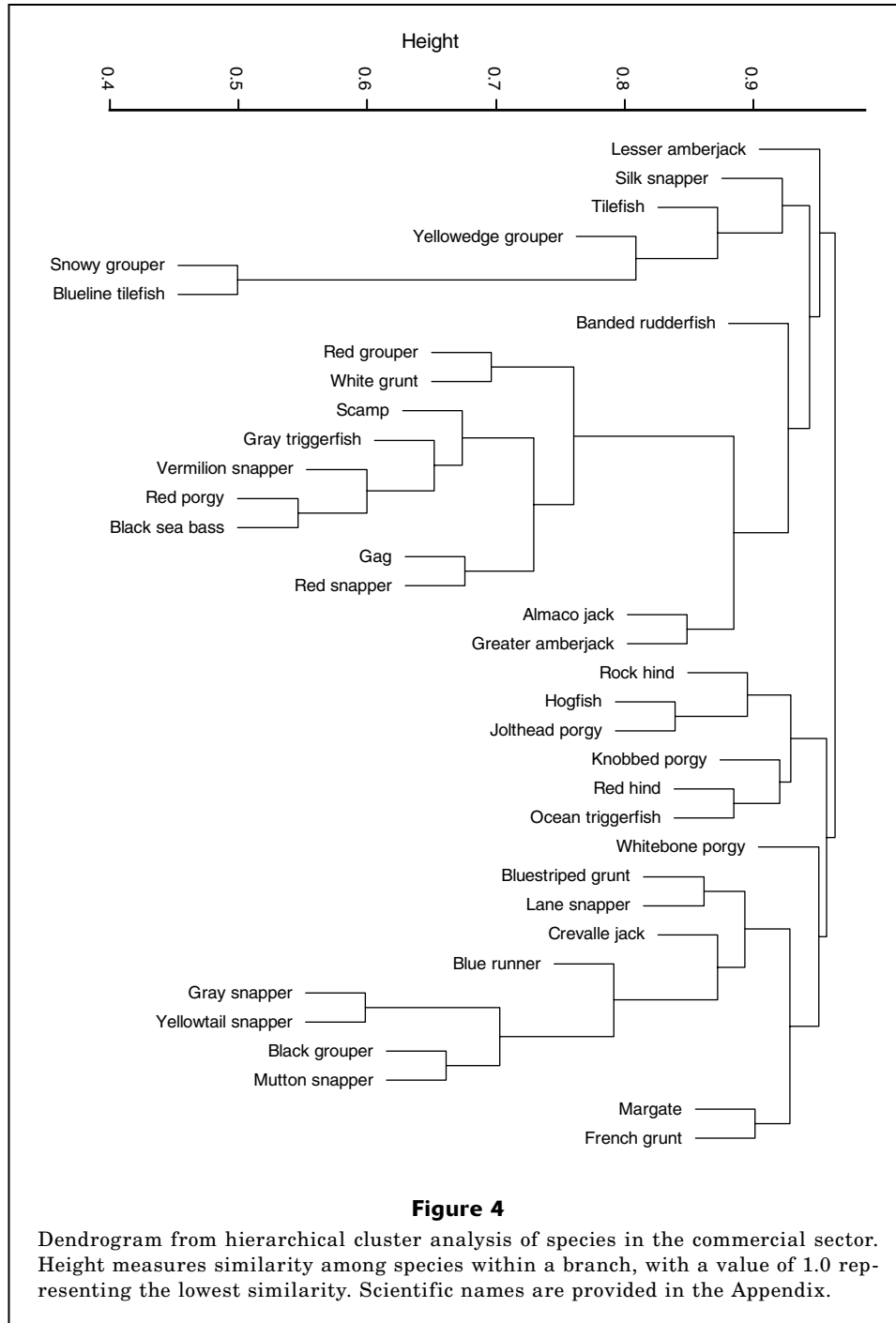
In this study of reef fishes off the southeastern United States, we found little evidence of synchrony in population dynamics, and thus, no support for the use of

indicator species. One possible reason for these negative results is that the study area was too broad; however, similar findings have been documented at smaller spatial scales (Parker and Dixon, 1998). A second reason is that the indices of abundance did not accurately



represent actual relative abundances because indices were computed from fishery-dependent (headboat) data (Arreguin-Sánchez, 1996; Harley et al., 2001). Fishery-independent data would have been preferable; however, for most species in this study, such data were of small sample size, short survey duration, or were nonexistent. We contend that the headboat data set was the best available for computing indices of abundance because of its relatively large sample size, long duration, and

wide geographic coverage. In addition, headboat effort is expended generally toward a complex of species rather than specific stocks, and that generality minimizes any confounding effect of density-dependent catchability. A third possible reason for the negative results is that the population dynamics were truly out of synchrony. From a practical perspective, the actual reason, whether it stemmed from inadequate data or real dynamics, is of secondary concern. Foremost, positive evidence of



synchrony in this reef fish complex has yet to be established, and we therefore urge precaution before using indicator species.

We did find positive evidence of species assemblages on the basis of landings, but these were not necessarily ecological assemblages. Although assemblages in landings may reflect those in nature, the two could differ if some species are preferentially retained from the catch or are more vulnerable to exploitation. Still,

assemblages in landings have direct implications from the perspective of managing fisheries, in terms of reducing bycatch and controlling fishing effort across species.

Nondimensional scaling analysis revealed that the species assemblages are not strongly coherent. Such loose structure has also been found in assemblages north of our study area (Mahon et al., 1998). Nonetheless, agreement between the headboat and commer-

Table 2

Synchrony in indices of abundance of reef fishes off the southeastern United States from headboat data. Assemblages are labeled as Deepwater, Southern (south of Cape Canaveral, Florida), and Northern (north of Cape Canaveral, Florida). Values are correlation coefficients and proportions of coefficients (in parentheses) from $n=10,000$ randomizations that were smaller than the correlations presented, such that values near 1.0 indicate significance of positive coefficients and values near 0.0 indicate significance of negative coefficients. Asterisks note significance at the $\alpha=0.1$ level after Bonferroni correction (two-tailed test). Abbreviations for species names are explained in the Appendix.

Deepwater	SnwGpr	BluTlf	SpkHnd			
SnwGpr	1.00	0.45 (0.96)	0.08 (0.62)			
BluTlf	—	1.00	-0.06 (0.41)			
SpkHnd	—	—	1.00			
Southern	BluRun	YtlSnp	LanSnp	GrySnp	MtnSnp	
BluRun	1.00	-0.16 (0.21)	-0.06 (0.38)	-0.11 (0.28)	-0.23 (0.11)	
YtlSnp	—	1.00	0.73*(1.00)	0.78*(1.00)	-0.56*(0.00)	
LanSnp	—	—	1.00	0.82*(1.00)	-0.65*(0.00)	
GrySnp	—	—	—	1.00	-0.64*(0.00)	
MtnSnp	—	—	—	—	1.00	
Northern	BlckSB	WhtGnt	Tomtat	GryTrf	VrmSnp	Gag
BlckSB	1.00	-0.67*(0.00)	0.24 (0.89)	-0.35 (0.04)	0.47*(0.99)	0.37 (0.97)
WhtGnt	—	1.00	-0.41 (0.02)	0.43 (0.99)	-0.35 (0.04)	-0.35 (0.03)
Tomtat	—	—	1.00	0.03 (0.56)	0.36 (0.97)	0.19 (0.83)
GryTrf	—	—	—	1.00	-0.08 (0.34)	-0.14 (0.23)
VrmSnp	—	—	—	—	1.00	-0.04 (0.42)
Gag	—	—	—	—	—	1.00

cial data sets implies that the assemblages, although loosely structured, are not arbitrary. Moreover, additional analyses conducted as part of this study revealed assemblages that were quite similar to those presented. These analyses included the use of an alternative transformation [$\log(x+1)$], alternative measure of distance (binary dissimilarities), alternative linkage method with the hierarchical analysis (average linkage), commercial data from multiday trips (two, three, or four-plus days), and data by trip (i.e., trips not aggregated over months).

The three clusters with the most coherence were deepwater, southern, and northern assemblages. The ranges of these assemblages likely correlate with physical characteristics (as our chosen labels imply). Several of the assemblage species have been found to be linked through latitude, depth, and hard bottom habitat (Sedberry and Van Dolah, 1984; Cuellar et al., 1996). Such information should be beneficial for managing assemblages as units, allowing regulations to be focused on relevant geographic areas.

Although the status of many stocks in the snapper-grouper complex is unknown, it is evident from most stock assessments that overfishing is occurring. In aggregate, these assessment results indicate overfishing of the ecosystem in general (Murawski, 2000). The average level of overfishing and its variance, along with

considerations of life histories and vulnerabilities, may indicate appropriate degrees of reduction in fishing effort across assemblages. The use of multiple species as probes into ecosystem health is likely more robust than the use of a single indicator species.

As single-species management loses fashion, its ideal replacement of full ecosystem management remains theoretically appealing, yet impractical given current data and understanding of marine ecosystems. Progress toward ecosystem management will likely occur in increments (Hall and Mainprize, 2004). Where assemblages exist, managing them as such offers a practicable step for implementing ecosystem considerations, including bycatch and species interrelations. Although the results of our study do not support the use of indicator species, they provide information on fish communities fundamental to the judicious application of assemblage management.

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Table 3

Synchrony in first differences of indices of abundance of reef fishes off the southeastern United States from headboat data. Assemblages are labeled as Deepwater, Southern (south of Cape Canaveral, Florida), and Northern (north of Cape Canaveral, Florida). Values are correlation coefficients and proportions of coefficients (in parentheses) from $n=10,000$ randomizations that were smaller than the correlations presented, such that values near 1.0 indicate significance of positive coefficients and values near 0.0 indicate significance of negative coefficients. Asterisks note significance at the $\alpha=0.1$ level with Bonferroni correction (two-tailed test). Abbreviations for species names are explained in the Appendix.

Deepwater	SnwGpr	BluTlf	SpkHnd			
SnwGpr	1.00	0.31 (0.87)	-0.61*(0.01)			
BluTlf	—	1.00	-0.14 (0.31)			
SpkHnd	—	—	1.00			
Southern	BluRun	YtlSnp	LanSnp	GrySnp	MtnSnp	
BluRun	1.00	-0.25(0.11)	-0.10 (0.32)	-0.11 (0.31)	-0.25 (0.11)	
YtlSnp	—	1.00	0.24 (0.89)	-0.08 (0.35)	0.25 (0.90)	
LanSnp	—	—	1.00	-0.19 (0.17)	0.37 (0.97)	
GrySnp	—	—	—	1.00	-0.06 (0.38)	
MtnSnp	—	—	—	—	1.00	
Northern	BlckSB	WhtGnt	Tomtat	GryTrf	VrmSnp	Gag
BlckSB	1.00	0.05 (0.61)	0.16 (0.78)	0.18 (0.82)	0.10 (0.70)	-0.06 (0.38)
WhtGnt	—	1.00	-0.09 (0.33)	0.20 (0.84)	-0.06 (0.37)	-0.22 (0.14)
Tomtat	—	—	1.00	0.08 (0.65)	0.23 (0.88)	0.02 (0.47)
GryTrf	—	—	—	1.00	0.50*(1.00)	-0.11 (0.28)
VrmSnp	—	—	—	—	1.00	0.21 (0.86)
Gag	—	—	—	—	—	1.00

headboat operators who submitted logbook data. The data sets were provided to us by K. Brennan (headboat) and K. McCarthy (commercial).

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Appendix

Species in the snapper-grouper complex off the southeastern United States, as managed under the Snapper Grouper Fishery Management Plan of the South Atlantic Fishery Management Council.

Common name	Scientific name	Short name
Almaco jack	<i>Seriola rivoliana</i>	AlmJck
Atlantic spadefish	<i>Chaetodipterus faber</i>	AtlSpf
Banded rudderfish	<i>Seriola zonata</i>	BndRud
Bank sea bass	<i>Centropristis ocyurus</i>	BankSB
Bar jack	<i>Caranx ruber</i>	BarJck
Black grouper	<i>Mycteroperca bonaci</i>	BlkGpr
Black margate	<i>Anisotremus surinamensis</i>	BlkMrg
Black sea bass	<i>Centropristis striatus</i>	BlckSB
Black snapper	<i>Apsilus dentatus</i>	BlkSnp
Blackfin snapper	<i>Lutjanus buccanella</i>	BfnSnp
Blue runner	<i>Caranx chrysos</i>	BluRun
Blueline tilefish	<i>Caulolatilus microps</i>	BluTlf
Bluestriped grunt	<i>Haemulon sciurus</i>	BstGnt
Coney	<i>Epinephelus fulvus</i>	Coney
Cottonwick	<i>Haemulon melanurum</i>	Cotwck
Crevalle jack	<i>Caranx hippos</i>	CrvJck
Cubera snapper	<i>Lutjanus cyanopterus</i>	CbrSnp
Dog snapper	<i>Lutjanus jocu</i>	DogSnp
French grunt	<i>Haemulon flavolineatum</i>	FrnGnt
Gag	<i>Mycteroperca microlepis</i>	Gag
Goliath grouper	<i>Epinephelus itajara</i>	GolGpr
Grass porgy	<i>Calamus arctifrons</i>	GrsPgy
Gray snapper	<i>Lutjanus griseus</i>	GrySnp
Gray triggerfish	<i>Balistes capriscus</i>	GryTrf
Graysby	<i>Epinephelus cruentatus</i>	GrySby
Greater amberjack	<i>Seriola dummerili</i>	GrAjck
Hogfish	<i>Lanchnolaimus maximus</i>	Hogfsh
Jolthead porgy	<i>Calamus bajonado</i>	JltPgy
Knobbed porgy	<i>Calamus nodosus</i>	KnbPgy
Lane snapper	<i>Lutjanus synagris</i>	LanSnp
Lesser amberjack	<i>Seriola fasciata</i>	LsAjck
Longspine porgy	<i>Stenotomus carprinus</i>	LgsPgy
Mahogany snapper	<i>Lutjanus mahogoni</i>	MhgSnp
Margate	<i>Haemulon album</i>	Margat
Misty grouper	<i>Epinephelus mystacinus</i>	MstGpr
Mutton snapper	<i>Lutjanus analis</i>	MtnSnp
Nassau grouper	<i>Epinephelus striatus</i>	NssGpr
Ocean triggerfish	<i>Canthidermis sufflamen</i>	OceTrf
Porkfish	<i>Anisotremus virginicus</i>	PrkFsh
Puddingwife	<i>Halichoeres radiatus</i>	Puddwf
Queen snapper	<i>Etelis oculatus</i>	QenSnp
Queen triggerfish	<i>Balistes vetula</i>	QenTrf
Red grouper	<i>Epinephelus morio</i>	RedGpr
Red hind	<i>Epinephelus guttatus</i>	RedHnd
Red porgy	<i>Pagrus pagrus</i>	RedPgy
Red snapper	<i>Lutjanus campechanus</i>	RedSnp
Rock hind	<i>Epinephelus adscensionis</i>	RckHnd
Rock sea bass	<i>Centropristis philadelphicus</i>	RockSB
Sailors choice	<i>Haemulon parrai</i>	SlsChc
Sand tilefish	<i>Malacanthus plumieri</i>	SndTlf
Saucereye porgy	<i>Calamus calamus</i>	ScyPgy

continued

Appendix (continued)

Common name	Scientific name	Short name
Scamp	<i>Mycteroperca phenax</i>	Scamp
Schoolmaster	<i>Lutjanus apodus</i>	Schmst
Scup	<i>Stenotomus chrysops</i>	Scup
Sheepshead	<i>Archosargus probatocephalus</i>	Shphed
Silk snapper	<i>Lutjanus vivanus</i>	SlkSnp
Smallmouth grunt	<i>Haemulon chrysargyreum</i>	SmtGnt
Snowy grouper	<i>Epinephelus niveatus</i>	SnwGpr
Spanish grunt	<i>Haemulon macrostomum</i>	SpnGnt
Speckled Hind	<i>Epinephelus drummondhayi</i>	SpkHnd
Tiger grouper	<i>Mycteroperca tigris</i>	TgrGpr
Tilefish	<i>Lopholatilus chamaeleonticeps</i>	Tilfsh
Tomtate	<i>Haemulon aurolineatum</i>	Tomtat
Vermilion snapper	<i>Rhomboplites aurorubens</i>	VrmSnp
Warsaw grouper	<i>Epinephelus nigritus</i>	WrsGpr
White grunt	<i>Haemulon plumieri</i>	WhtGnt
Whitebone porgy	<i>Calamus leucosteus</i>	WtbPgy
Wreckfish	<i>Polyprion americanus</i>	Wrkfsh
Yellow jack	<i>Caranx bartholomaei</i>	YelJck
Yellowedge grouper	<i>Epinephelus flavolimbatus</i>	YdgGpr
Yellowfin grouper	<i>Mycteroperca venenosa</i>	YlfGpr
Yellowmouth grouper	<i>Mycteroperca interstitialis</i>	YlmGpr
Yellowtail snapper	<i>Ocyurus chrysurus</i>	YtlSnp