Correlations in recruitment patterns of Atlantic reef fishes off the southeastern United States based on multi-decadal estimates from stock assessments

Kaitlynn J. Wade[1], Kyle W. Shertzer[2]*, J. Kevin Craig[2], Erik H. Williams[2]

1. University of Maryland Eastern Shore
Department of Natural Sciences
George Washington Carver Science Building, Room 1103
Princess Anne, Maryland 21853

2. National Oceanic and Atmospheric Administration
Southeast Fisheries Science Center
Beaufort Laboratory
101 Pivers Island Road
Beaufort, NC, USA 28516

*Corresponding author: Kyle.Shertzer@noaa.gov

Abstract

Atlantic reef fishes off the southeastern United States support a multispecies fishery important to both commercial and recreational fleets. Productivity of this reef-fish complex is driven to a large degree by recruitment of new individuals into their respective populations. In this study, we analyzed patterns in time series of annual recruitment of ten Atlantic reef-fish species, primarily snappers and groupers, that have been the subject of separate single-species stock assessments. Our focus was on identifying patterns in autocorrelation of recruitment within species and on uncovering patterns in correlation across species. We found that autocorrelation of recruitment deviations was evident in the majority (9/10) of species with a dominant lag of one year. Pairwise correlations between species were both positive and negative. Principal component analysis revealed two general groups of species: those that exhibited lower-than-expected recruitment in recent years and those that did not exhibit such low recruitment (either near expected or higher-than-expected). These results point toward common drivers of recruitment (e.g., environmental, ecological, exploitation) in this complex of reef-associated fishes, and they are a critical first step for developing hypotheses of underlying mechanisms. Additionally, they have practical importance for stock assessments that forecast recruitment when forming fishery management advice.

Keywords: Correlation, Recruitment, Reef fishes, Southeast United States Continental Shelf, Stock assessment

1. Introduction

Recruitment is a fundamental driver of population dynamics in marine fishes. Consequently, fishery science has devoted much attention over the past century toward understanding fluctuations in recruitment (Hjort, 1926; Ricker, 1954; Beverton and Holt, 1957; Thorson et al., 2014; Haltuch et al., 2019). Such efforts have practical importance, as the processes controlling recruitment are critical for gauging stock status and for predicting how populations will respond to management actions (Sharma et al., 2019; Van Beveren, 2021). The importance of understanding recruitment patterns is evident in many geographic regions (e.g., Friedland et al., 2009; Caselle et al., 2010; Ottmonn et al., 2018; Robitzch and Berumen, 2020), and the southeastern United States is no exception.

The southeast United States continental shelf is one of 50 large marine ecosystems (LMEs) recognized worldwide (Sherman and Duda, 1999; Craig et al., 2021). This LME is temperate in climate, spanning Atlantic waters from southern Florida to Cape Hatteras, North Carolina. It is characterized by high productivity, largely as a result of inputs from Gulf Stream upwelling and from the Albemarle-Pamlico Sound, the second largest estuary in the United States. In turn, this high productivity supports sizeable fisheries, including commercial fleets and the most active recreational fishing sector in the United States (Shertzer et al., 2019). Much of this commercial and recreational fishing effort targets reef-associated fishes, such as snappers and groupers (Coleman et al., 1999).

Reef-associated fishes in this region are federally managed by the South Atlantic Fishery Management Council as part of their Snapper Grouper Fishery Management Plan (https://safmc.net; website includes a map of the region). The Plan currently includes 55 species, of which approximately 25% have been the subject of formal stock assessments. The primary goals of those assessments are to estimate management quantities, such as population and fishing status, and to provide advice for setting future catch levels. Additionally, each assessment provides annual estimates of recruitment over multiple decades.

To date, recruitment estimates from those reef-fish stock assessments have primarily been considered on a species-by-species basis without any evaluation of time-series properties or cross-species relationships. However, comparing temporal patterns of recruitment across species can help identify common underlying mechanisms, such as similar responses to environmental drivers or exploitation (Bunnell, 2016; Hollowed et al., 2001; Szuwalski et al., 2014). Similarly, the presence of autocorrelation in recruitment time series can help better identify specific external drivers of recruitment (Thorson et al., 2014; Rindorf et al., 2020) and, if properly accounted for, can improve the short-term forecasts from assessment models that are used for catch advice (Johnson et al, 2016; Van Beveren et al., 2021).

Here, we evaluate time series of recruitment estimated by stock assessments of reef-associated fishes in the Southeast United States Continental Shelf LME. We have three primary goals: 1) to test for autocorrelation within each species' recruitment time series, 2) to test for correlation between species, and 3) to identify common patterns across species. Our methods synthesize decades of recruitment in this complex of marine fishes and could be utilized in other regions where properties of recruitment time series are of interest. We conclude by summarizing the practical implications of our findings for stock assessment and fishery management.

2. Materials and methods

2.1 Time series of recruitment estimates

To obtain time series of recruitment estimates, we accessed the most recent stock assessments of ten species in this complex of Atlantic reef fishes. The species analyzed were black sea bass (*Centropristis striata*; SEDAR, 2018a), gag grouper (*Mycteroperca microlepis*; SEDAR, 2021a), gray triggerfish (*Balistes capriscus*; SEDAR, 2016), greater amberjack (*Seriola dumerili*; SEDAR, 2020a), red grouper (*Epinephelus morio*; SEDAR, 2017), red porgy (*Pagrus pagrus*; SEDAR, 2020b), red snapper (*Lutjanus campechanus*; SEDAR, 2021b), scamp grouper (*Mycteroperca phenax*; SEDAR, 2021c), snowy grouper (*Hyporthodus niveatus*; SEDAR, 2021d), and vermilion snapper (*Rhomboplites aurorubens*; SEDAR, 2018b). All species were assessed using the Beaufort Assessment Model, an integrated, age-structured formulation (Williams and Shertzer, 2015; Li et al., 2021).

For each species, we analyzed recruitment deviations estimated (in log space) by the relevant stock assessment. For one of the species (black sea bass), deviations represented recruitment of age-0 fish, and for the other nine species, deviations corresponded to age-1 recruits. This difference in recruitment age for black sea bass does not preclude analysis, as recruitment strength should be apparent at age-0 or age-1 given that recruitment deviations are estimated from established cohorts (Rindorf et al., 2020). However, for temporal consistency, deviations for black sea bass were shifted one year later, such that all ten time series represent age-1 recruits. Recruitment deviations are similar to statistical residuals, in the sense that they represent variation from expected values. Our use of deviations, therefore, puts all species on a similar scale, centered on 0.0 and generally in the range of [-1,1]. Use of deviations also accounts for variation in recruitment due to changes in spawning potential, as an underlying spawner-recruit relationship (e.g., Beverton-Holt model) determines the expected values from which the recruitment deviations are computed. A positive deviation represents higher-than-expected recruitment given the current spawning potential (e.g., spawning biomass or population fecundity), and a negative deviation represents lower-than-expected recruitment given the current spawning potential. After extracting time series of recruitment deviations, we analyzed each for autocorrelation within species and temporal correlation between and among species.

2.2 Recruitment autocorrelation

For each of the ten species, recruitment autocorrelation was estimated to measure similarities between the time series and lagged versions of itself (Chatfield and Xing, 2019). The available years across species ranged from 1974 to 2019, but for any given species, the time series duration depended on the latest available stock assessment (mean duration of 38.4 yr, range of 27-44 yr). The autocorrelation for each species was calculated in R using the *acf* function with a maximum lag maximum of 15 years (R Core Team, 2022). Similarly, we computed partial autocorrelation using the *pacf* function in R. Similar to standard autocorrelation, partial autocorrelation measures the effect of lagged values, but additionally controls for the effects of all "other" possible lags. Because the dominant lag among species was 1 year (see Results), we plotted the lag-1 time series against the original time series to visually inspect the patterns in variability including possible outliers.

2.3 Recruitment correlation between and among species

Pairwise Pearson correlation coefficients were computed using the *cor.test* function in R applied to time series of recruitment deviations, to examine correlation between species (R Core Team, 2022). Given 10 species, there were 45 unique pairs. For each pair, the minimum and maximum year of analysis was determined by the earliest and latest year available for both species. For visualization, we plotted each pair as a scatter plot with linear regression.

To explore potential groupings and relationships among all species, we used principal component analysis (PCA; Jolliffe and Cadima, 2016) on years that were common across all ten species (1990 to 2014). As is common practice, the recruitment deviations for each species were standardized for PCA by subtracting their mean and dividing by their standard deviation. PCA was based on Euclidean distance (similarity) and implemented with the R package *factoextra* (Kassambara and Mundt, 2020). In addition to groupings of species, we applied PCA to examine groupings of years, i.e., years that showed similarity in recruitment patterns across species. For visualization, we applied hierarchical clustering and show groupings of years with a dendrogram.

3. Results

3.1 Recruitment autocorrelation

All 10 species demonstrated positive autocorrelation at a lag of 1 year (Fig. 1). Indeed, nine of these 10 autocorrelation coefficients were statistically significant, with vermilion snapper the only exception. Three of the species─gag, scamp, and snowy grouper─demonstrated positive correlation coefficients for lags from 1 year to about 10 years, and then negative correlation coefficients for longer lags, suggesting a cyclic pattern of recruitment on a decadal time scale. Greater amberjack also showed a cyclic pattern, but on a shorter time scale (~4 years). Partial autocorrelation coefficients supported the findings of positive autocorrelation at a lag of 1 year and, again, all coefficients were statistically significant except for vermilion snapper (Fig. 1).

Regressing each time series of deviations on a lagged version of itself showed a wide range of variability across species (Fig. 2). Linear regression explained a minimum of 1.6% of the variation (vermilion snapper) to a maximum of 75% (snowy grouper), with remaining species ranging from 20% to 65%. The slopes of the regressions were all positive and all but that for vermilion snapper were statistically significant, as for the autocorrelation analysis. None of the relationships appeared to be driven by a small number of outliers or leverage points.

3.2 Recruitment correlation between and among species

Of the 45 relationships between species, a slight majority (26/45) of correlation coefficients were not statistically different from zero based on a p-value threshold of 0.05 (Appendix Table A1; Appendix Fig. A1); 13 relationships had positive correlations with a p-value ≤ 0.05, and 6 had negative correlations with similarly low p-values (Appendix Table A1; Appendix Fig. A1). Representative regressions and scatterplots demonstrate much variability in these relationships, even for those that were significantly correlated (Fig. 3), either negatively (red grouper and greater amberjack; red porgy and red snapper) or positively (vermilion snapper and red snapper; red grouper and scamp; red porgy and gag; snowy grouper and scamp). The strongest positive correlations were found between various combinations of gag, red grouper, red porgy, snowy grouper, and scamp (Fig. 4), all species that showed negative recruitment deviations near the end of their time series (Fig. 1). Red snapper showed the opposite pattern, i.e. positive recruitment deviations near the end of the time series (Fig. 1). This pattern resulted in red snapper recruitment being positively correlated with vermilion snapper and greater amberjack, but negatively correlated with all other species (Fig. 4).

In the PCA of species, the first principal component (axis 1) accounted for 43.8% of the variability and the second accounted for 22.7% (Appendix Fig. A2). This analysis showed similar groupings as did the correlation tests. Gag, red grouper, red porgy, snowy grouper, and scamp had positive values along the first principal component, with four of those species (all but red porgy) in the same quadrant. Greater amberjack, red snapper, and vermilion snapper were positively correlated, and all three showed negative values along the first principal component, with the two snappers in the same quadrant. Black sea bass and triggerfish did not strongly correlate with any of the other species, and these two clumped near each other along the principal component axes.

Given the recruitment pattern of black sea bass (Fig. 1), we were surprised that this species did not associate more strongly in the principal component analysis with those species that had negative deviations near the end of the time series (the “low recruitment” group). We suspected that this was due to using a terminal year of 2014, which was necessary to include all ten species. To test this, we removed the limiting species and re-ran the PCA using 7 species through 2016, and again using 6 species through 2017. In both cases, black sea bass did indeed associate with species in the low recruitment group (Appendix Fig. A3, A4).

In the PCA of species’ similarities across years, the first principal component accounted for 38.5% of the variance, and the second principal component accounted for 19.9% (Fig. 5). In general, the species with positively correlated negative recruitment deviations at the end of the time series clumped together, with negative values along the first principal component. Conversely, red snapper and correlated species (vermilion snapper and greater amberjack) clumped together in the fourth quadrant, with positive values along the first principal component and negative values along the second. Years in the most recent decade (since 2005) showed similarity in that they all had positive values along the first principal component; all other years, except 1998, had negative values along this axis.

Hierarchical clustering of the PCA revealed more nuanced relationships among years than did PCA alone (Fig. 6). The years branched into two main groups of 1990-1999 and 2000-2014. The latter period grouped into 2000-2009 and 2010-2014. The finding that years tended to group with surrounding years is consistent with the autocorrelation analysis identifying a lag of one year.

4. Discussion

4.1 Interpreting correlation patterns in recruitment

Our analysis revealed that autocorrelation in recruitment of Atlantic reef fishes is prevalent. Nine of the ten species examined demonstrated a statistically significant pattern of autocorrelation, with vermilion snapper being the only exception. For all other species, the dominant signature was autocorrelation with a lag of one year. In addition, PCA indicated that annual signals in recruitment tended to be most similar to those in nearby years, supporting the results from the single-species time-series analyses. Such autocorrelation could result from relationships between abundance (or spawning biomass) and recruitment, where high spawning biomass tends to produce high recruitment and vice versa. However, in this study, we analyzed recruitment deviations, which accounts for the effects of spawning biomass.

There are several plausible explanations for the patterns in recruitment autocorrelation documented here. One possibility is that the relative influence of different data sources in the stock assessment models influenced within-species correlation patterns in the estimated recruitment deviations. For example, lagged correlations could occur if annual recruitments estimated by the assessment model are influenced more by abundance indices, which typically encompass multiple age classes and therefore change gradually over time, than by annual age compositions, which often show large annual fluctuations of young fish. Alternatively, age at maturity and associated reproductive potential may contribute to the predominance of a one-year lag in recruitment correlations. For example, several species show substantial (>30%) female maturity at age-1 (red porgy, black seabass, red snapper, greater amberjack, gray triggerfish, vermilion snapper). Recruitment could be correlated at a lag of one year if a portion of recruits (i.e., age-1) also contribute offspring to the next year class. However, maturation may not be directly proportional to reproductive potential because spawning frequency, batch fecundity, and sperm/egg quality may vary with age and size (Sogard et al., 2008; Fitzhugh et al., 2012). Further, vermilion snapper, the only species that did not show a one-year lag in recruitment, had the highest estimated proportion of mature age-1 females (91%, SEDAR 2018b). A third possibility is that recruitment is affected by an exogenous environmental variable or ecological process with a dominant lag of one year. While such drivers of annual recruitment are not known for these species, possibilities include factors that influence growth and survival during the pelagic larval stage (temperature, zooplankton prey) or predation mortality (predator abundance and/or consumption rates) prior to or shortly after settlement on hard-bottom reef habitats (Szuwalski et al., 2014).

The 10 species considered here are part of an exploited, multi-species reef-fish complex that occurs predominantly on hard bottom habitat of the southeast United States continental shelf (Bacheler et al., 2016), and so we expected that patterns in recruitment might be correlated among species. Somewhat surprisingly, not all pairwise correlations were positive, suggesting considerable variability in recruitment patterns among species. Indeed, about half of the correlations among the 10 species were positive while the other half were negative, and four of the six strongest correlations were positive while the remaining two were negative. Given that all of the species considered here are exploited, similar patterns in fishing mortality and possible recruitment overfishing may lead to correlated patterns in recruitment. For example, red porgy recruitment decreased significantly from the 1970s to the 1990s associated with large increases in fishing mortality, consistent with recruitment overfishing (Vaughan and Prager, 2002). Similarly, many species in the reef-fish complex began to experience significant overfishing in the early 1980s (assessment reports available: https://sedarweb.org/). The strongest positive correlations in recruitment occurred among species that showed evidence of historical (since the 1980s) as well as recent (since the 2010s) overfishing based on stock assessments (gag, red porgy, snowy grouper). Similarly, the hierarchical cluster analysis differentiated a primary period between the 1990s (when annual recruitments were typically first estimated) and the 2000s, as well as a secondary period differentiating the early 2000s and the most recent decade (2010 onward), supporting the importance of both historical and recent recruitment to the positive correlation among some species. In contrast, species that showed negative or very weak correlations included one of these highly exploited species and a species with either little evidence of historical overfishing (greater amberjack, vermilion snapper) or recent (since 2010) reductions in fishing mortality due to management measures intended to promote stock recovery (red snapper). While fishing mortality may be a common driver of population dynamics across species in the reef-fish complex, it is unlikely to fully explain the patterns reported here, given the considerable variability in historical patterns of fishing, the relative importance of commercial versus recreational harvest, the efficacy of fisheries management measures, and the quality of data informing the stock assessments.

Identifying the mechanisms underlying recruitment variability is important for understanding population dynamics, and the exploratory correlational analyses presented here are a useful first step (Szuwalski et al., 2014; Rindorf et al., 2020). Many of the species showing low recruitment are protogynous hermaphrodites or form spawning aggregations, supporting the possibility that particular life-history traits may make some species more vulnerable to recruitment overfishing (Coleman et al., 1999). Alternatively, abiotic factors or species interactions may also play a role in recruitment dynamics. For example, invasive lionfish occur in the same offshore hard-bottom habitats occupied by early juveniles of many reef-associated species, and they may be an additional source of natural mortality suppressing the recruitment of newly settled fish (Munoz et al., 2011; Ballew et al., 2016). Similar predation mortality on newly settled juveniles is an important factor influencing the population dynamics of reef-associated fishes inhabiting mesophotic coral reef ecosystems (Almany and Webster, 2006). Temperatures have also increased in the U.S. South Atlantic (Craig et al., 2021) and the Atlantic Multidecadal Oscillation (AMO), a temperature-based indicator of decadal-scale climate variability, shifted from a cool phase to a warm phase in the mid-1990s (Frajka-Williams et al., 2017). Temperature and related oceanographic processes potentially influence growth and survival during the pelagic larval stage through effects on larval transport and productivity at the base of the food web (Stegmann and Yoder, 1996; Signorini and McClain, 2007). While not documented for the southeast United States Atlantic, the mid-1990s shift in the AMO was correlated with changes in multiple ecosystem indicators (including fishing and species abundance indicators) in the Gulf of Mexico, supporting this possibility (Karnauskas et al., 2015).

4.2 Use of stock assessment output and management implications

The primary caveat when interpreting our results is that we do not have direct observations of recruitment. Rather, annual recruitment deviations were estimated from integrated assessment models that did not include direct information on recruitment (e.g., an age-0 or age-1 index). For oceanic fishes, direct observations are rarely available and recruitment indices of relative juvenile abundance when available, typically have high uncertainty (e.g., Adamski et al., 2011). While the recruitment estimates considered here are not 'data' in the true sense (Dickey-Collas et al., 2014; Brooks and Deroba, 2015), the use of estimated recruitments from scientifically reviewed stock assessments is a common practice (e.g., Szuwalski et al., 2014; Thorson et al., 2014; Rindorf et al., 2020), and the only source of stock-wide annual recruitment variability for most species. Further, the stock assessments used here estimated annual recruitment values by fitting multiple data sources (e.g., landings, abundance indices, age and length compositions) integrated into a single population model, and so are less subject to the limitations of any particular data source. In the assessments, most information about year-class strength (recruits) comes from indices of abundance and age compositions. Indices in the stock assessments considered here were standardized to account for covariates, such that estimated trends are more likely to represent dynamics in abundance, and ages used for compositions were subjected to age-validation studies. Despite the caveats, stock assessment outputs are the most comprehensive source of information about long-term trends in recruitment of U.S. Atlantic reef fishes. Additional work is needed to determine the extent to which patterns in recruitment investigated here are influenced by data or other factors internal to the assessment models (maturity, abundance indices, age compositions) versus exogenous factors not currently included in the assessments, but potentially influencing the recruitment dynamics of these species.

Despite the value of investigating alternative hypotheses to explain patterns in recruitment, a full mechanistic understanding is not necessary for improving short-term (i.e., 3-5 years) forecasting of recruitment to inform fisheries management decisions. The predominant pattern of autocorrelation with a lag of one year indicates that recruitment "this year" is a good predictor of recruitment "next year." This information can be incorporated into the short-term projections used for catch advice (Johnson et al., 2016; Van Beveren et al., 2021), and doing so can reasonably be expected to improve the management of Atlantic reef fishes. Further, if the recent period of low recruitment represents a regime shift (Klaer et al., 2015), future stock assessments might relax the assumption of stationarity in the stock-recruitment relationship and account for potential change in productivity on key management quantities, such as maximum sustainable yield.

4.3 Conclusions

The population dynamics of marine fishes depend fundamentally on recruitment. Given that importance, we attempted to synthesize recruitment time series of Atlantic reef fishes off the southeastern United States. The primary findings were that 1) recruitment deviations for most species were autocorrelated with a dominant lag of one year, 2) recruitment deviations were correlated between species, and 3) species could be categorized into two groups: those that demonstrated lower-than-expected recruitment in recent years and those that did not. The latter two findings suggest at least one common, exogenous driver of recruitment in this complex of reef-associated fishes, and further study is warranted to evaluate alternative mechanisms.

However, even without a mechanistic understanding of recruitment drivers, the first primary finding could be utilized immediately to improve the short-term forecasts from stock assessments that are used for resource management.

CRediT authorship contribution statement

KJW: Formal analysis, Software, Visualization, Writing – Original draft. KWS and JKC: Conceptualization, Methodology, Data curation, Writing – original draft, Writing – review & editing, Project administration. EHW: Conceptualization, Methodology, Writing – Review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

The time series of recruitment estimates analyzed in this study can be found in the stock assessment reports of each species, which are publically availabe from http://sedarweb.org/.

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References

Adamski, K.M., Buckel, J.A., Shertzer, K.W., Bath Martin, G., Taylor, J.C., 2011. Developing fishery-independent indices of larval and juvenile gag abundance in the southeastern United States. Trans. Am. Fish. Soc. 140, 973-983.

Almany, G.R., Webster, M.S., 2006. The predation gauntlet: early post-settlement mortality in reef fishes. Coral Reefs 25, 19-22.

Bacheler, N.M., Schobernd, Z.H., Berrane, D.J., Schobernd, C.M., Mitchell, W.A., Teer, B.Z., Gregalis, K.C., Glasgow, D.M., 2016. Spatial distribution of reef fish species along the southeast US Atlantic coast inferred from underwater video survey data. PLoS One 11(9): e0162653. https://doi.org/10.1371/journal.pone.0162653

Ballew, N.G., Bacheler, N.M., Kellison, G.T., Schueller, A.M., 2016. Invasive lionfish reduce native fish abundance on a regional scale. Sci Rep. 6, 32169, doi:10.1038/srep32169.

Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II 19, 1-533.

Brooks, E.N., Deroba, J.J., 2015. When "data" are not data: the pitfalls of post hoc analyses that use stock assessment model output. Can. J. Fish. Aquat. Sci. 72, 1-8.

Bunnell, D.B., Höök, T.O., Troy, C.D., Liu, W., Madenjian, C.P., Adams, J.V., 2017. Testing for synchrony in recruitment among four Lake Michigan fish species. Can. J. Fish. Aquat. Sci. 74, 306-315.

Caselle, J.E., Kinlan, B.P., Warner, R.R., 2010. Temporal and spatial scales of influence on nearshore fish settlement in the southern California Bight. Bull. Mar. Sci. 86, 355-385.

Chatfield, C., Xing, H., 2019. The Analysis of Time Series: An Introduction with R, 7th Ed. CRC Press,

Coleman, F.C., Koenig, C.C., Eklund, A., Grimes, C.B., 1999. Management and conservation of temperate reef fishes in the grouper-snapper complex of the Southeastern United States. In: Music, J.A. (Ed.), Life in the Slow Lane. American Fisheries Society Symposium, vol. 23. Bethesda, Maryland, pp. 233-242.

Craig, J.K., and 25 coauthors, 2021. Ecosystem Status Report for the U.S. South Atlantic Region. NOAA Technical Memorandum NMFS-SEFSC-753, 145 p. https://doi.org/10.25923/qmgr-pr03.

Dickey-Collas M., Hintzen, N.T., Nash, R.D.M, Schön, P-J., Payne, M.R., 2014. Quirky patterns in time-series of estimates of recruitment could be artefacts. ICES J. Mar. Sci. 72, 111-116.

Fitzhugh, G.R., Shertzer, K.W., Kellison, G.T., Wyanski, D.M., 2012. Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity. Fish. Bull. 110, 413-425.

Frajka-Williams, E., Beaulieu, C., Duchez, A., 2017. Emerging negative Atlantic Multidecadal Oscillation index in spite of warm subtropics. Sci. Rep. 7, 11224, https://doi.org/10.1038/s41598-017-11046-x.

Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., Maoiléidigh, N.Ó., McCarthy, J.L., 2009. The recruitment of Atlantic salmon in Europe. ICES J. Mar. Sci. 66, 289-304.

Haltuch, M.A., Brooks, E.N., Brodziak, J., Devine, J.A., Johnson, K.F., Klibansky, N., Nash, R.D.M., Payne, M.R., Shertzer, K.W., Subbey, S., Wells, B.K., 2019. Unraveling the recruitment problem: A review of environmentally informed forecasting and management strategy evaluation. Fish. Res. 217, 198-216.

Hjort, J., 1926. Fluctuations in the year classes of important food fishes. ICES J. Mar. Sci. 1, 5-38.

Hollowed, A.B., Hare, S.R., Wooster, W.S., 2001. Pacific Basin climate variability and patterns of Northeast Pacific marine fish production. Prog. Oceangr. 49, 257-282.

Johnson, K.F., Councill, E., Thorson, J.T., Brooks, E., Methot, R.D., Punt, A.E., 2016. Can autocorrelated recruitment be estimated using integrated assessment models and how does it affect population forecasts? Fish. Res. 183, 222-232.

Jolliffe, I.T., Cadima, J., 2016. Principal component analysis: a review and recent developments. Phil. Trans. R. Soc. A 374, 20150202.

Karnauskas, M., Schirripa, M.J., Craig, J.K., Cook, G.S., Kelble, C.R., Agar, J.J., Black, B.A., Enfield, D.B., Lindo-Atichati, D., Muhling, B.A., Purcell, K.M., Richards, P.M., Wang, C., 2015. Evidence of climate-driven ecosystem reorganization in the Gulf of Mexico. Glob. Chang. Biol. 21, 2554-2568.

Kassambara, A., Mundt, F., 2020. Factoextra: Extract and visualize the results of multivariate data analysis. R package version 1.0.7, https://CRAN.R-project.org/package=factoextra.
Klaer, N.L., O'Boyle, R.N., Deroba, J.J., Sayte, S.E., Little, L.R., Alade, L.A., Rago, P.J., 2015. How much evidence is required for acceptance of productivity regime shifts in fish stock assessments: Are we letting managers off the hook? Fish. Res. 168, 49-55.
Li, B., Shertzer, K.W., Lynch, P.D., Ianelli, J.N., Legault, C.M., Williams, E.H., Methot Jr., R.D., Brooks, E.N., Deroba, J.J., Berger, A.M., Sagarese, S.R., Brodziak, J.K.T., Taylor, I.G., Karp, M.A., Wetzel, C.R., Supernaw, M., 2021. A comparison of 4 primary age-structured stock assessment models used in the United States. Fish. Bull. 119, 149-167.
Munoz, R.C., Currin, C.A., Whitfield, P.E., 2011. Diet of invasive lionfish on hard bottom reefs of the Southeast USA: insights from stomach contents and stable isotopes. Mar. Ecol. Prog. Ser. 432, 181-193.
Ottmann, D., Grorud-Colvert, K., Huntington, B., Sponaugle, S., 2018. Interannual and regional variability in settlement of groundfishes to protected and fished nearshore waters of Oregon, USA. Mar. Ecol. Prog. Ser. 598, 131-145.
R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
Rindorf, A., Cadigan, N., Howell, D., Eero, M., Gislason, H., 2020. Periodic fluctuations in recruitment success of Atlantic cod. Can. J. Fish. Aquat. Sci. 77, 236-246.
Robitzch, V., Berumen, M.L., 2020. Recruitment of coral reef fishes along a cross-shelf gradient in the Red Sea peaks outside the hottest season. Coral Reefs 39, 1565-1579.
SEDAR, 2016. SEDAR 41 – South Atlantic Gray Triggerfish Assessment Report. SEDAR, North Charleston SC. 428 pp. available online at: http://sedarweb.org/sedar-41.

SEDAR, 2017. SEDAR 53 – South Atlantic Red Grouper Assessment Report. SEDAR, North Charleston SC. 159 pp. available online at: http://sedarweb.org/sedar-53.

SEDAR, 2018a. SEDAR 56 – South Atlantic Black Sea Bass Assessment Report. SEDAR, North Charleston SC. 164 pp. available online at: http://sedarweb.org/sedar-56.

SEDAR, 2018b. SEDAR 55 – South Atlantic Vermilion Snapper Assessment Report. SEDAR, North Charleston SC. 170 pp. available online at: http://sedarweb.org/sedar-55.

SEDAR, 2020a. SEDAR – South Atlantic Greater Amberjack Stock Assessment Report. SEDAR, North Charleston SC. 142 pp. available online at: http://sedarweb.org/sedar-59.

SEDAR, 2020b. SEDAR 60 South Atlantic Red Porgy Stock Assessment Report. SEDAR, North Charleston SC. 181 pp. available online at: http://sedarweb.org/sedar-60.

SEDAR, 2021a. SEDAR 71 South Atlantic Gag Stock Assessment Report. SEDAR, North Charleston SC. 164 pp. available online at: http://sedarweb.org/sedar-71.

SEDAR, 2021b. SEDAR 73 South Atlantic Red Snapper Stock Assessment Report. SEDAR, North Charleston SC. 194 pp. available online at: http://sedarweb.org/sedar-73.

SEDAR, 2021c. SEDAR 68 South Atlantic Scamp Grouper Stock Assessment Report. SEDAR, North Charleston SC. 397 pp. available online at: http://sedarweb.org/sedar-68.

SEDAR, 2021d. SEDAR 36 Update South Atlantic Snowy Grouper Stock Assessment Report. SEDAR, North Charleston SC. 118 pp. available online at: http://sedarweb.org/sedar-36u.

Sharma, R. Porch, C.E., Babcock, E.A., Maunder, M.N, Punt, A.E., 2019. Recruitment: Theory, estimation, and application in fishery stock assessment models. Fish. Res. 217, 1-4.

Sherman, K., Duda, A.M., 1999. An ecosystem approach to global assessment and management of coastal waters. Mar. Ecol. Prog. Ser. 190, 271-287.

Shertzer, K.W., Williams, E.H., Craig, J.K., Fitzpatrick, E.E., Klibansky, N., Siegfried, K.I., 1999. Recreational sector is the dominant source of fishing mortality for oceanic fishes in the Southeast United States Atlantic Ocean. Fish. Manag. Ecol. 26, 621-629.

Signorini, S.R., McClain, C.R., 2007. Large-scale forcing impact on biomass in the South Atlantic Bight. Geophys. Res. Lett. 34, L21605, doi:10.1029/2007GL031121.

Sogard, S.M., Berkeley, S.A., Fisher, R., 2008. Maternal effects in rockfishes *Sebastes* spp.: a comparison among species. Mar. Ecol. Prog. Ser. 360, 227-236.

Stegmann, P.M., Yoder, J.A., 1996. Variability of sea-surface temperature in the South Atlantic Bight as observed from satellite: Implications for offshore-spawning fish. Cont. Shelf Res. 16, 843-861.

Szuwalski, C., Vert-Pre, K.A., Punt, A.E., Branch, T.A., Hilborn, R., 2014. Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. Fish Fish. 16, 633-648.

Thorson, J.T., Jensen, O.P., Zipkin, E.F., 2014. How variable is recruitment for exploited marine fishes? A hierarchical model for testing life history theory. Can. J. Fish. Aquat. Sci. 71, 973-983.

Vaughan, D.S., Prager, M.H., 2002. Severe decline in abundance of the red porgy (*Pagrus pagrus*) population off the southeastern United States. Fish. Bull. 100, 351-375.

Van Beveren, E., Benoît, H.P., Duplisea, D.E., 2021. Forecasting fish recruitment in age-structured population models. Fish Fish. 22, 941-954.

Williams, E.H., Shertzer, K.W., 2015. Technical documentation of the Beaufort Assessment Model (BAM). U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SEFSC-671. 43 p.

Figure legends

Figure 1. Time series of recruitment deviations, autocorrelation (ACF), and partial autocorrelation of ten species in the southeastern United States Atlantic reef-fish complex. Dashed lines in autocorrelation and partial autocorrelation panels indicate 95% confidence intervals.

Figure 2. Linear regressions (line) and 95% confidence intervals (shaded) of recruitment deviations "next" year (t+1) regressed on deviations "this" year (t), computed for species in the southeastern United States Atlantic reef-fish complex. In each panel, the R^2 value is the coefficient of determination and the p-value represents a test for whether the slope is statistically different from zero.

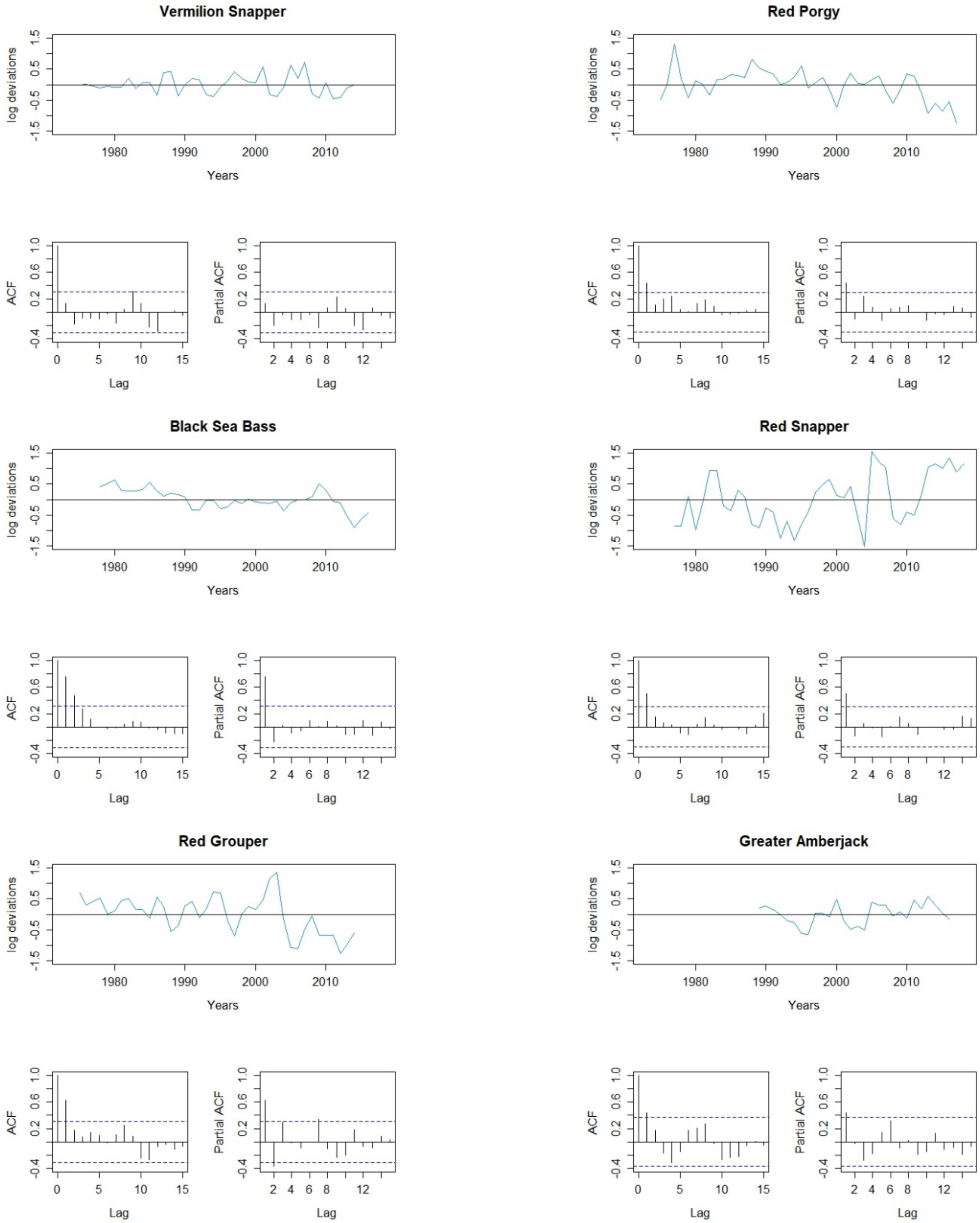
Figure 3. Linear regressions (line) and 95% confidence intervals (shaded) of recruitment deviations for pairs of species in the southeastern United States Atlantic reef-fish complex, with two pairs exhibiting statistically significant ($p\text{-value}<0.05$) negative correlation and four pairs exhibiting statistically significant positive correlation. Points are labeled with years and color coded by decade: pre-1990 (dark purple), 1990s (light purple), 2000s (pink), and 2010s (yellow). The full set of years is 1974 to 2019, but those plotted for any given pair of species depends on the years modeled in those particular stock assessments. In each panel, the R^2 value is the coefficient of determination and the p-value represents a test for whether the slope is statistically different from zero.

Figure 4. Pearson correlation coefficients computed from recruitment deviations for pairs of species in the southeastern United States Atlantic reef-fish complex. The shading of each square indicates the strength of correlation, with red for negative values and blue for positive values. Asterisks indicate that the value is statistically different from zero, with significance at the 0.01 (***), 0.05 (**), or 0.1 (*) levels. The species analyzed were black sea bass (BSB), gag grouper (GAG), gray triggerfish (TR), greater amberjack (GAJ), red grouper (RG), red porgy (RP), red snapper (RS), scamp grouper (SCG), snowy grouper (SG), and vermilion snapper (VS).

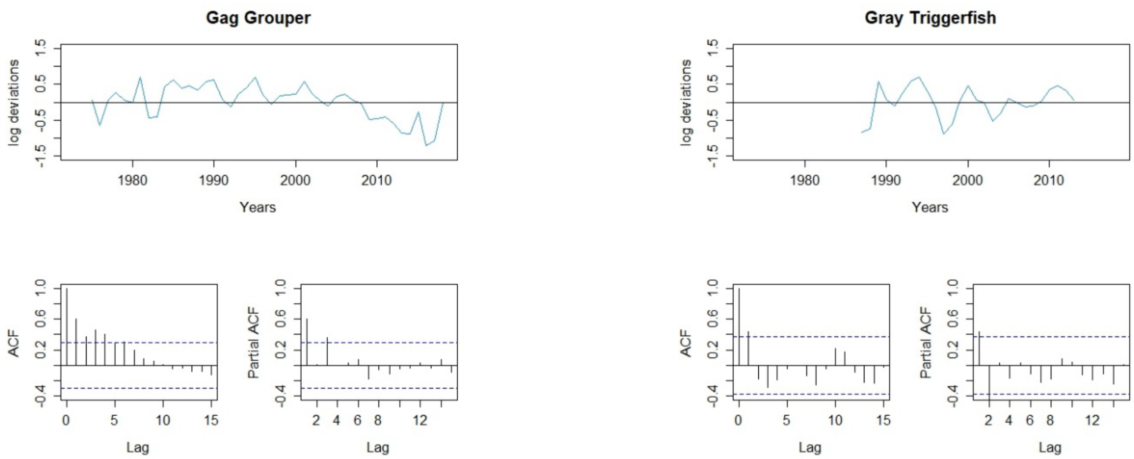
Figure 5. Principal component analysis of standardized recruitment deviations for all species with a range of years from 1990 to 2014, with PC1 and PC2 indicating the first two axes of the analysis. The years are color coded by decade, with the darker blue representing early years and lighter blues representing more recent years. The species analyzed were species in the southeastern United States Atlantic reef-fish complex, including black sea bass (BSB), gag grouper (GAG), gray triggerfish (TR), greater amberjack (GAJ), red grouper (RG), red porgy (RP), red snapper (RS), scamp grouper (SCG), snowy grouper (SG), and vermilion snapper (VS).

Figure 6. Dendrogram of years based on similarity in standardized recruitment deviations for species in the southeastern United States Atlantic reef-fish complex. The years included, 1990 to 2014, are those of overlap for all ten species included in the analysis.

Figure 1



Vermilion Snapper
Red Porgy
Black Sea Bass
Red Snapper
Red Grouper
Greater Amberjack
log deviations
Years
ACF
Partial ACF
Lag
1.5
0.5
-0.5
-1.5
1980
1990
2000
2010
1.0
0.6
0.2
-0.4
0
5
10
15
2
4
6
8
12


Gag Grouper
Gray Triggerfish
log deviations
Years
ACF
Partial ACF
Lag

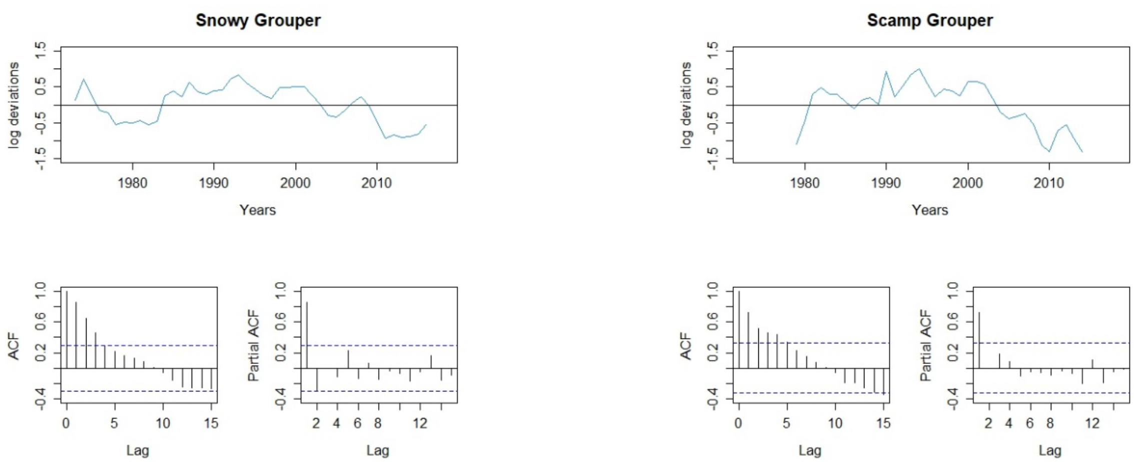

Snowy Grouper
Scamp Grouper
log deviations
Years
ACF
Partial ACF
Lag

Figure 2

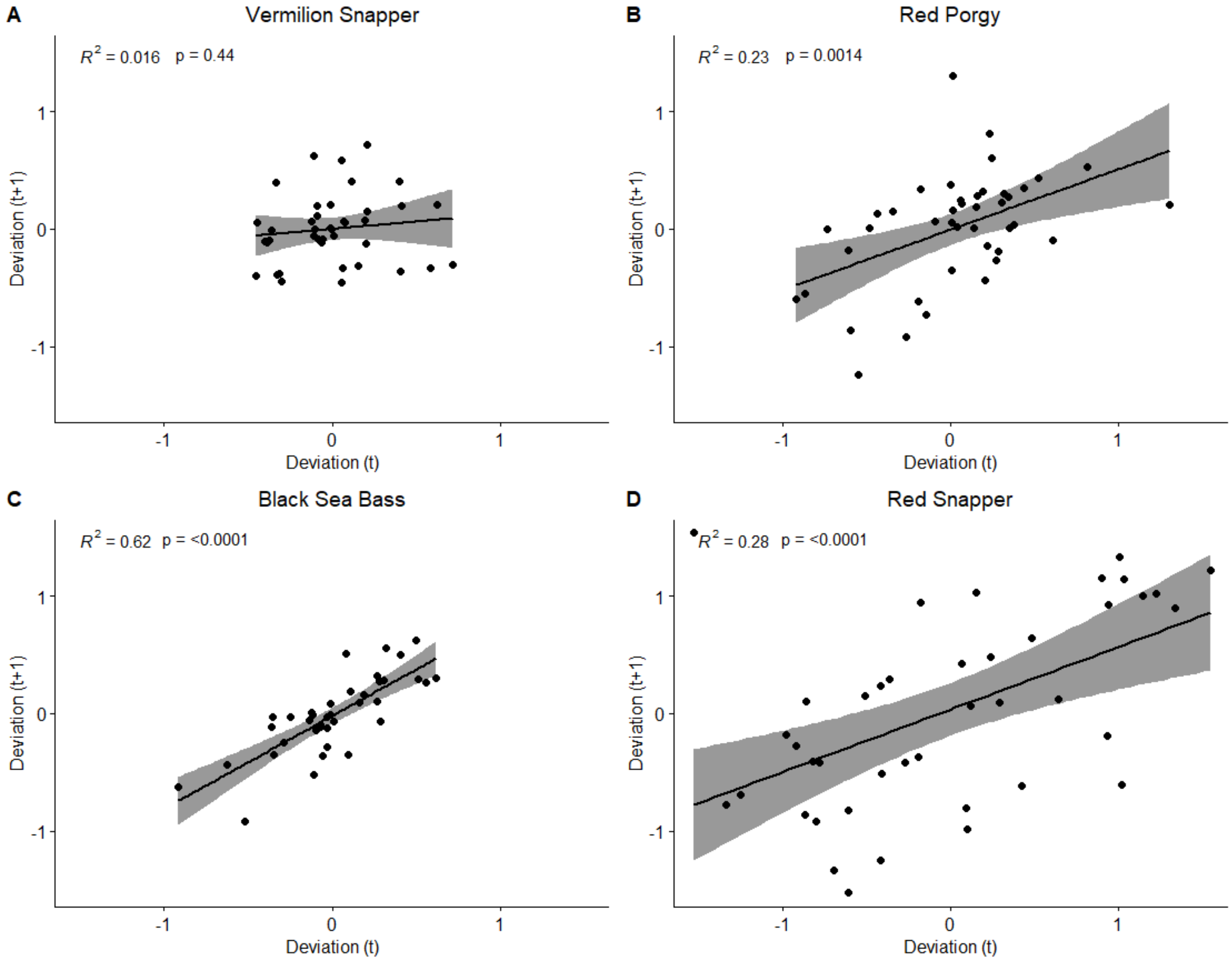

A
Vermilion Snapper
R^2 = 0.016 p = 0.44
B
Red Porgy
R^2 = 0.23 p = 0.0014
C
Black Sea Bass
R^2 = 0.62 p = <0.0001
D
Red Snapper
R^2 = 0.28 p = <0.0001
Deviation (t+1)
Deviation (t)
-1
0
1

Figure 2 (continued)

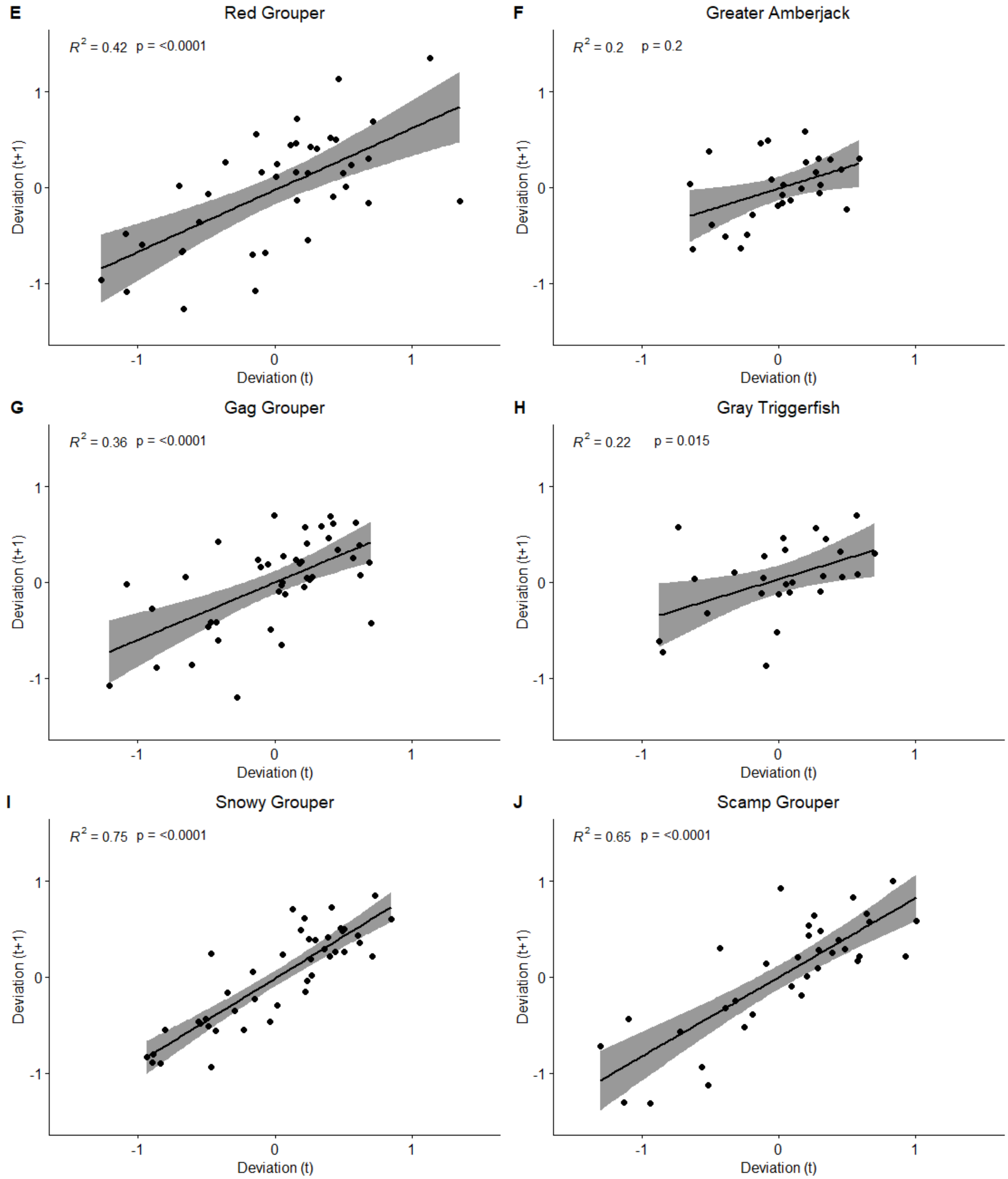


Figure 3

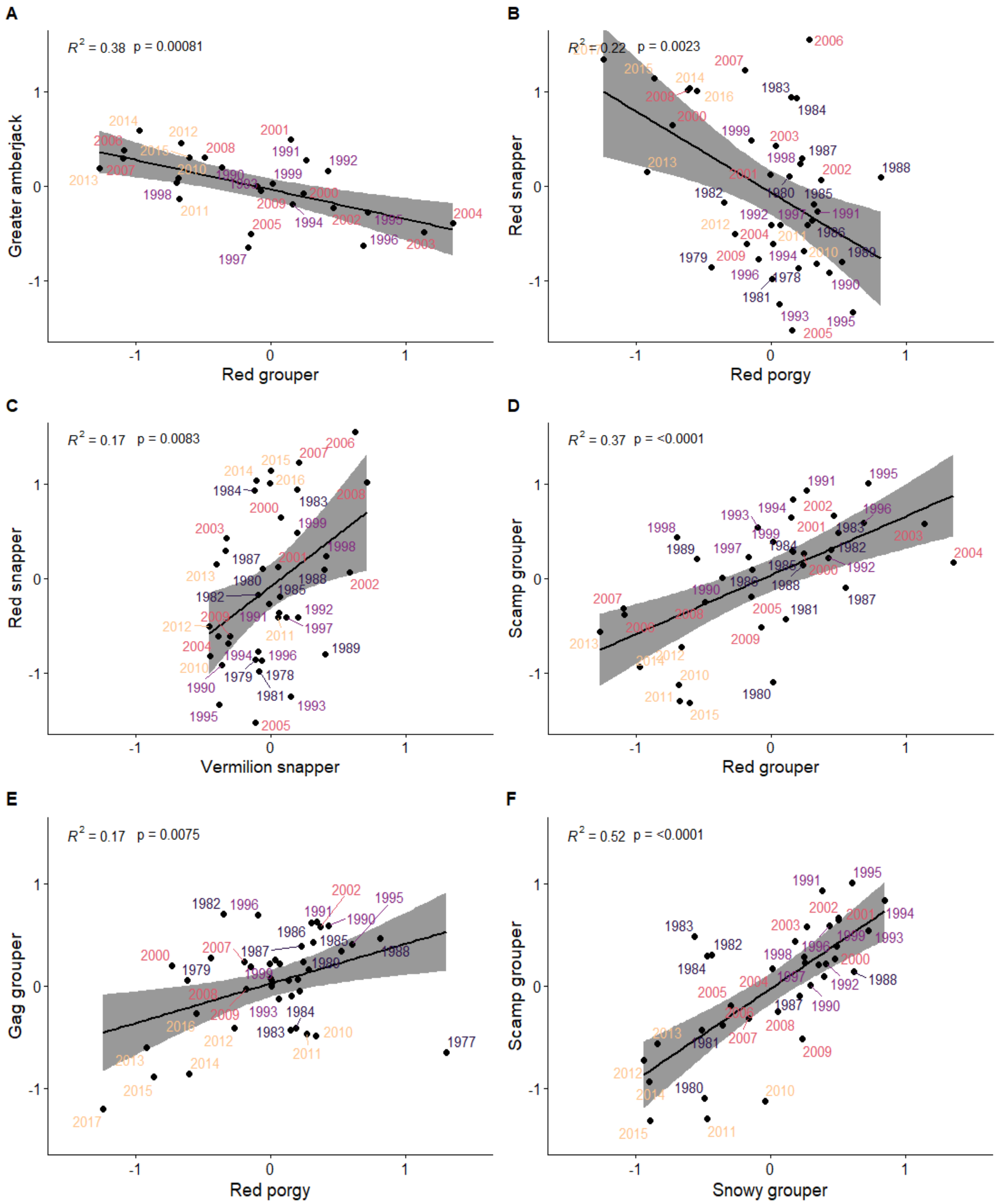

A
R^2 = 0.38 p = 0.00081
Greater amberjack
Red grouper
B
R^2 = 0.22 p = 0.0023
Red snapper
Red porgy
C
R^2 = 0.17 p = 0.0083
Red snapper
Vermilion snapper
D
R^2 = 0.37 p = <0.0001
Scamp grouper
Red grouper
E
R^2 = 0.17 p = 0.0075
Gag grouper
Red porgy
F
R^2 = 0.52 p = <0.0001
Scamp grouper
Snowy grouper

Figure 4

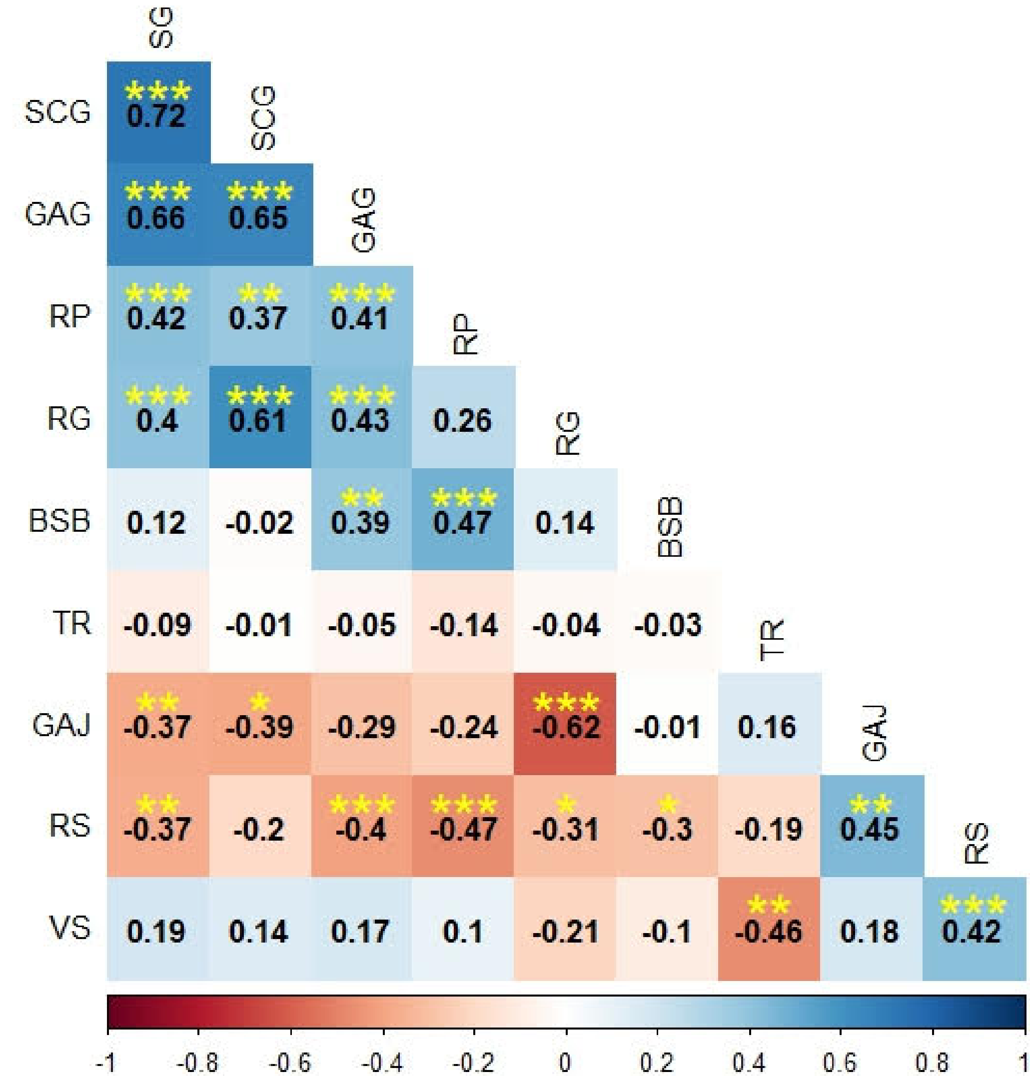
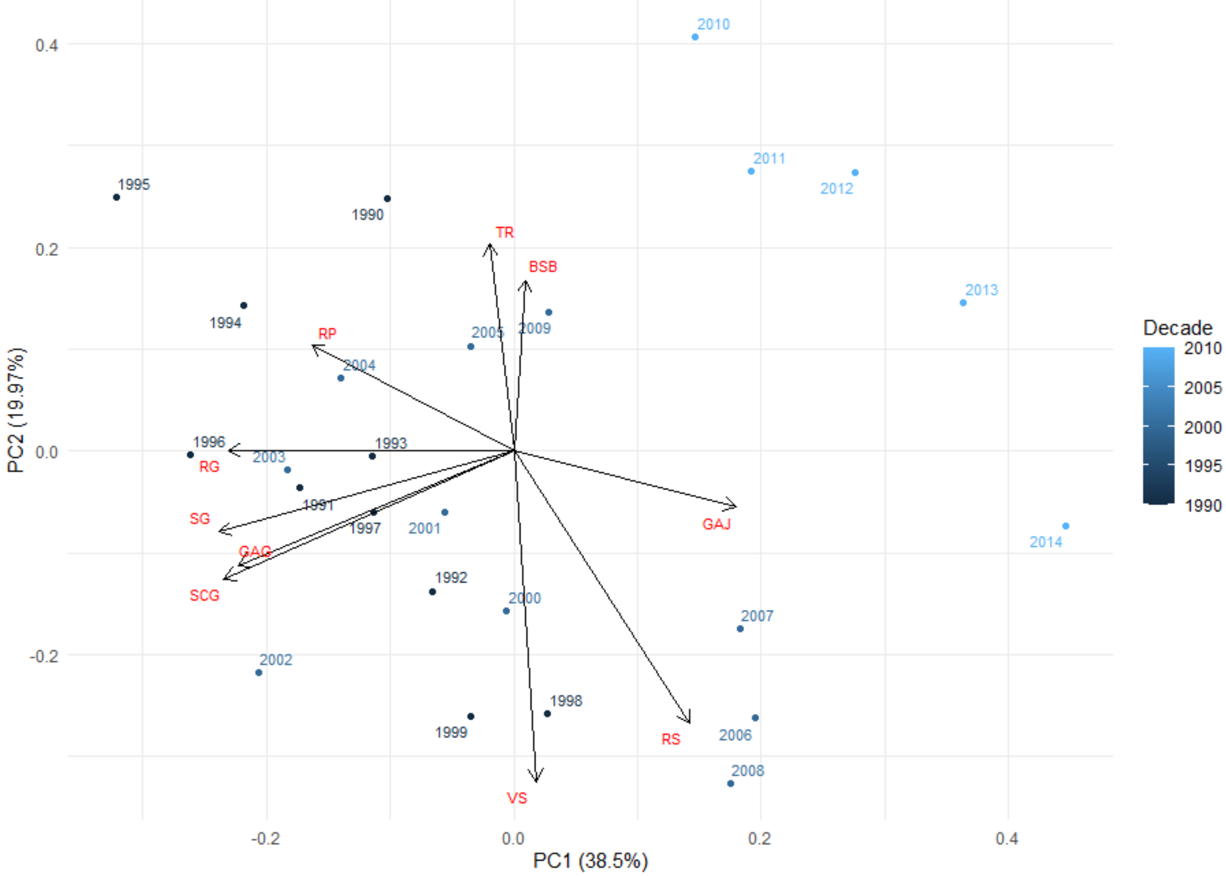
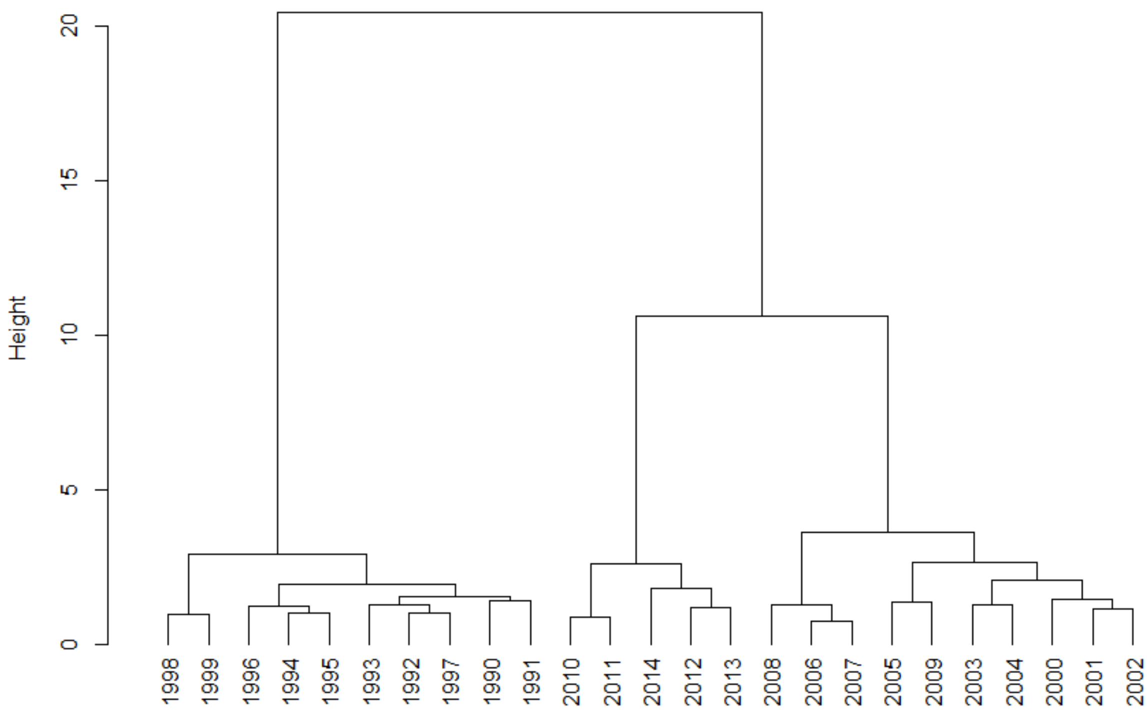

SG
SCG
GAG
RP
RG
BSB
TR
GAJ
RS
SCG *** 0.72
GAG *** 0.66 *** 0.65
RP *** 0.42 ** 0.37 *** 0.41
RG *** 0.4 *** 0.61 *** 0.43 0.26
BSB 0.12 -0.02 ** 0.39 *** 0.47 0.14
TR -0.09 -0.01 -0.05 -0.14 -0.04 -0.03
GAJ ** -0.37 * -0.39 -0.29 -0.24 *** -0.62 -0.01 0.16
RS ** -0.37 -0.2 *** -0.4 *** -0.47 * -0.31 * -0.3 -0.19 ** 0.45
VS 0.19 0.14 0.17 0.1 -0.21 -0.1 ** -0.46 0.18 *** 0.42
-1 -0.8 -0.6 -0.4 -0.2 0 0.2 0.4 0.6 0.8 1

Figure 5



PC1 (38.5%)
PC2 (19.97%)
0.4
0.2
0.0
-0.2
-0.2
0.0
0.2
0.4
Decade
2010
2005
2000
1995
1990
TR
BSB
RP
RG
SG
GAG
SCG
GAJ
RS
VS
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014

Figure 6


Height
0
5
10
15
20
1998
1999
1996
1994
1995
1993
1992
1997
1990
1991
2010
2011
2014
2012
2013
2008
2006
2007
2005
2009
2003
2004
2000
2001
2002