Exploring Unexplained Variability in Stock-Recruitment Relationship Estimates for the Gulf of Mexico's Greater Amberjack (*Seriola dumerili*) Stock with Long-Term Ecological Time-Series

Technical Report Prepared by: Joshua P. Kilborn, Ph.D.

University of South Florida, College of Marine Science; St. Petersburg, FL

Original Submission: December 31, 2020

Updated: April 6, 2021

EXECUTIVE SUMMARY

The main objectives of this study were to investigate long-term, ecological time series and determine their ability to describe any unknown variability in the annual stock recruitment of Greater Amberjack (*Seriola dumerili*) in the Gulf of Mexico large marine ecosystem (Gulf LME), and to do so with respect to its particular Stock Synthesis management model's results. As an additional focus, the relationship between *Sargassum spp.* areal coverage was examined for its capacity to impact Greater Amberjack (GAJ) recruitment in both spatial and temporal contexts. Three more focused models were also developed to explore suites of factors hypothesized to affect the early life history stages of GAJ (i.e., ecosystem and climate status, habitat availability, and eutrophication), and all of which yielded some level of information that could be applied to future ecosystem considerations for this species. Finally, the last priority of this effort was to determine if there was an already-existing capacity to more readily estimate GAJ new recruits during periods between formal assessments or SS3 model updates, using existing data collection or monitoring efforts.

Overall, there were relationships uncovered between long-term, ecological time series and GAJ recruitment deviations. Four different time scales (1970-2015, 1982-2010, 1987-2014, and 2000-2015) were used to investigate GAJ recruitment deviations (i.e., unexplained variability in the formal stock assessment recruitment estimates), and all four showed between ~17-32% of the variability in those deviations could be explained by mostly decadal-scale trends, but by a ~25-year trend as well.

Five potential leading indicators were identified out of the 48 that were assessed. The Atlantic Multidecadal Oscillation (AMO) and the number of both active petroleum industry-related and -unrelated artificial reefs displayed the best capacity to account for the variability in GAJ recruitment deviations over time. The two models that identified these three indicators (oil-related artificial habitat being selected twice) accounted for 24% (ecological model) and 16% (habitat model) of the variability in the deviations over

their respective time periods. Two remaining models accounted for 7% (*Sargassum* model #1) and 5% (Eutrophication) of the new-recruit deviations, and they implicated the areal coverage of *Sargassum* in the Florida Middle Grounds during the peak spawning and larval dispersal period for GAJ (March-May), and the dissolved oxygen (DO) levels offshore Texas in the fall sampling season.

From a practical perspective, the DO indicator is likely to be the most straightforward to follow-up on due to the fact that it relates directly to the biology and physiology of the species, and it can be tested and constrained via laboratory experiments or focused *in situ* observational studies. The next most likely candidate for success would be related to the habitat concerns of GAJ, and specifically with respect to the species' association with artificial reef habitat. There appears to be a stronger association with oil- and gas-related infrastructure as opposed to that which is unrelated, but this may also be a consequence of recent changes in record keeping. Regardless, the association between both habitat types should be explored, as they are both likely to be important, and the current balance of their influence is not well understood. The *Sargassum* coverage in the Florida Middle Grounds also deserves additional consideration as it relates to GAJ, and these results further support the idea that *Sargassum* is an important habitat in the early life history of GAJ. As a leading population-level indicator for GAJ recruitment, however, it would likely require a better understanding of the utilization levels of *Sargassum* habitats in general, and which would then need to be extended to the range of the Gulf LME expected to support this habitat in any given year/season.

More abstractly, the AMO index and the synthetic temporal eigenfunctions described herein might be adequate mathematical models to add to the predictive capabilities of stock assessment methods. However, in the former case in particular (and as illustrated by the results of this study), it can be very difficult to discern the underlying mechanisms that support the dynamics observed. This is not to say that it is not worth exploration, but it is worth noting that mathematical models that are not supported by a solid understanding of the underlying mechanisms are subject to increased likelihood of displaying unexpected or chaotic dynamics. As such, the AMO index, or any other synthetic or conglomerate metric, should undergo extensive simulation testing with respect to the modeling predictions related to this species, and should also be continuously evaluated and updated to avoid being taken by surprise.

Unfortunately, it seems as though there is little capacity at this time to extend ecosystem monitoring efforts into interim assessment updates, and if there were any, it would be extremely limited. Conversely, there is ample evidence to support the notion that ecosystem considerations should begin to be incorporated into the formal assessment of GAJ as soon as possible. Granted, more work needs to be done prior to implementation in management decision making, but the latest assessment for GAJ completed at the same time as this project, and there are currently no indications of an upcoming assessment for this stock prior to 2025[1]. Ultimately, this report serves to outline several ecosystem-level priorities that could benefit from more directed effort, and which are likely to influence the understanding of the ongoing declines in the Greater Amberjack stock in the Gulf of Mexico large marine ecosystem.

[1] http://sedarweb.org/docs/page/project%20planning%20grid_Oct2020_meeting_outcome_SEFSC_update.pdf (Date accessed: Dec. 31, 2020).

1.0 INTRODUCTION

Given that stock-recruitment relationship estimates for Greater Amberjack (*Seriola dumerili*) contain large amounts of unexplained variability (SEDAR 2014, 2016)[2], and that the contemporary stock status has not recovered to pre-1985 levels (Karnauskas et al. 2017), this species represents an ideal candidate for the evaluation of non-traditional, stock-size determinants. In particular, environmental ecological factors may represent key overlooked aspects contributing to the recent declining stock trends for the Greater Amberjack (GAJ) population and its associated spawning biomass (SEDAR 2014, Karnauskas et al. 2017). Furthermore, preliminary fishery ecosystem models for the Gulf of Mexico (Kilborn *unplublished*) and prepared using the ecosystem-level management-indicator selection tool (Kilborn et al. 2018), showed that, while the overall, long-term trend has been weakly positive for the full GAJ stock since around the mid-1990s, it generally appears to be varying on a ~12.5 year "down-up" cycle since the mid-1980s (not surprising timing, given the magnitude of stock changes over the study period; Karnauskas et al., 2017). However, there appear to be no obvious, measured variable that captures the mechanism of this cyclical trend for GAJ except for, possibly, the number of Gulf-wide, artificial reef structures. Lastly, there is a body of evidence suggesting the importance of additional habitat considerations for early-life stages for GAJ, specifically, the presence of the brown macroalgae *Sargassum* (Wells and Rooker 2003, 2004b, a). With the current expectations for climate change and the likelihood of increased magnitude and frequency of brown-algae blooms in the region (Wang et al. 2019), understanding the baseline connectivity between this important GAJ habitat and its influence on year class strength will be key to estimating future variability in this important fishery resource.

1.1 Proposed Project Goals and Objectives

To address these considerations, the following objectives were proposed for this project to help better understand the ecosystem-level ecological impacts affecting GAJ populations in the Gulf of Mexico:

1. To determine the extent of the relationship between annual estimates for the GAJ stock's spawning biomass, and subsequent recruitment levels, that can be modeled using long-term, time series indicators representing the natural and artificial, multi-scale, environmental and climatic factors hypothesized to organize the living marine resources within the Gulf of Mexico large marine ecosystem (Gulf LME).

[2] See summary of SEDAR33 update to the Council here: http://archive.gulfcouncil.org/council_meetings/BriefingMaterials//BB-04-2017/B%20-%207(a)(2)-GAJ%20PPT%20April2017.pdf

2. To explicitly examine the most recently available Southeast Data, Assessment, and Review (SEDAR) model for the GAJ population's stock-recruitment relationship, and determine which environmental, climatic, and/or socio-ecological indicators best constrain the remaining residual variability (i.e., uncertainty). Primary focus will be given to GAJ early life stages' habitat considerations, particularly those provided by the brown algae *Sargassum*, using satellite-derived, multi-scale measurements of bloom magnitude and timing; additional habitats and management considerations comprising the recent ecosystem status reports for the region will also be investigated here for their relationship to GAJ productivity.
3. To develop leading ecosystem-level indicators useful to fisheries management for improving short-term assessments of GAJ recruitment in the Gulf LME during interim periods between formal stock assessments, with the ultimate, long-term goal of developing daily, or weekly, products to inform in-season decision making with up to date recruitment estimates derived from readily accessible system status observations.

1.2 Proposed Deliverables Contained Herein

The deliverables for this study contained in this document are: (1) a technical report summarizing Objectives 1-3 for the GMFMC; (2) an assessment of the future potential for creating a short-term, in-season, decision support tool to better inform fisheries managers seeking to predict future recruitment for GAJ based on the spatiotemporal dynamics of the brown macroalgae *Sargassum*, and/or other ecosystem considerations.

2.0 METHODS

All data compilation, pretreatment, and modeling were performed in MATLAB r2020a computing environment (MATLAB 2020a). In the cases where randomization testing (i.e., bootstrapping and permutation) were employed, 10,000 pseudo-random iterations were used, and statistical inferences were based on the calculation and interpretation of p-values using a critical threshold of $\alpha = 0.05$. Specialized functions were used from the MATLAB Econometrics Toolbox (MATLAB 2020b), along with the standalone Fathom (Jones 2017) and Darkside (Kilborn 2020) Toolboxes for MATLAB.

2.1 Data Sources and Compilation

2.1.1 Greater Amberjack Data

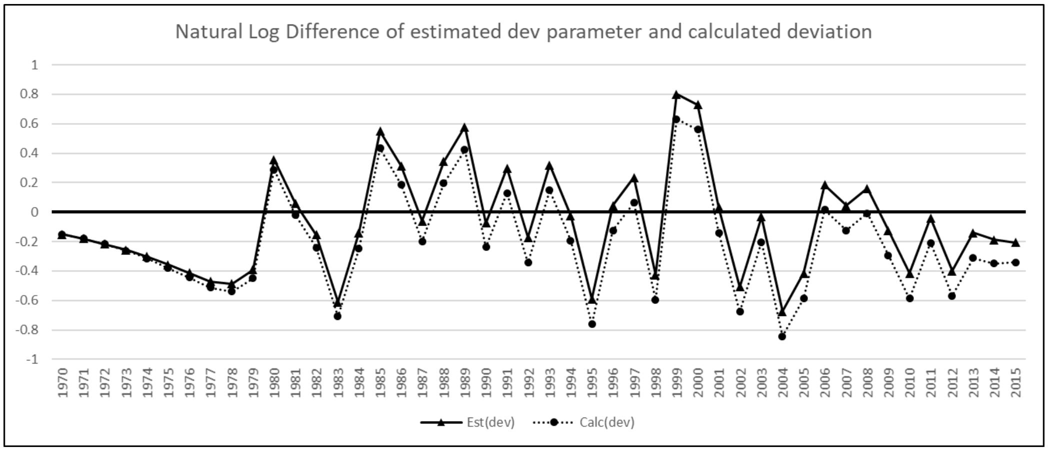
All GAJ data were drawn from the most recently updated report (SEDAR 2016) produced within the SEDAR process. The 2016 update to the full SEDAR 33 model (SEDAR 2014) contained the only GAJ-specific data available during the timeframe of this project, as the most recently performed full assessment model (SEDAR 70) had not been formally approved for distribution. Within GAJ's associated Stock Synthesis model (SS3, Methot 2000; Methot and Wetzel 2013), the stock-recruitment-relationship (SRR) was modeled using the standard Beverton-Holt (B-H) model with the log of unfished equilibrium recruitment and a virgin recruitment offset parameter estimated by the model (SEDAR 2014, 2016). The updated model was parameterized with a steepness value of $h = 0.85$ and unfished spawning stock biomass (SSB) of 18,835.9 (numbers in thousands). The GAJ SS3 model time series spans 1950-2015, but the "early" management era starts in 1970, and is the first year in which the model estimates the difference between modeled and predicted new recruits directly (i.e., *recruitment deviations*). Given that these recruitment deviations are constrained to sum to zero (Figure 1a), and in order to remove the effect of the SSB (Tolimieri et al. 2018), the recruitment deviations used here (Figure 1b) were derived directly, and calculated as the difference between the estimated recruits predicted by SS3 and by the B-H SRR model (Figure 2). Where appropriate, the recruitment deviation time series was reduced to be used in constrained analyses described below with environmental covariate datasets.

2.1.2 *Sargassum* Data

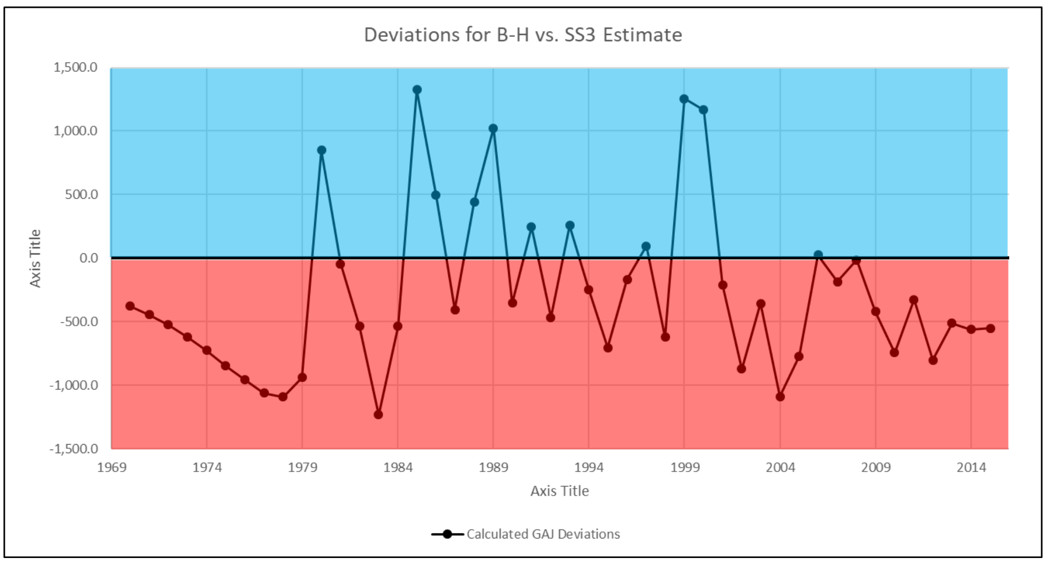
Data to describe the brown macroalgae *Sargassum spp.* (*S. natans* and *S. fluitans*) were provided by the Optical Oceanography Laboratory at the University of South Florida's College of Marine Science. For the period February 2000 through December 2018, *Sargassum* values were reported as monthly mean areal coverage (km^2), and were also translated into biomass estimates using a constant conversion factor of 3.34 $kg\ m^{-2}$ (Wang et al. 2018). The raw data were extracted in [0.5 x 0.5] degree (~56 km^2) grid cells across the entire aquatic area of the Gulf LME, and partitioned into specific regions of interest based on already established management areas and larger sub-basin scale areas (Table 1; Figure 3). Further, the data were temporally constrained for use with the GAJ deviation data ending in 2015, and to explicitly capture the assumed peak annual spawning and larval dispersal period from March-May (Fahay 1975, Wells and Rooker 2004b, a, Harris et al. 2007), as well as the pelagic feeding and new-recruit settlement period from June-August (Table 2; Wells and Rooker 2004a, b).

2.1.3 Gulf of Mexico Ecological Data

Data representative of large-scale ecological characters within the Gulf LME were drawn from the two Ecosystem Status Reports (ESRs) created for the system in 2013 and 2017 (Karnauskas et al. 2013, Karnauskas et al. 2017). The ultimate suite of candidate indicators selected for this study were those that were hypothesized to be pertinent to the early life history stages of the GAJ stock in the Gulf (Table 3). The 2013 ESR data terminates in 2011, while the 2017 ESR Update has data that extend through 2015 in most cases; unfortunately, given the variability in time series start and end dates, it was not possible to create one large database that could be examined in one omnibus analysis. Therefore, the data were partitioned over various time periods to explore additional details related to their associations with GAJ recruitment levels and deviations (Table 4).



a.



b.

Figure 1. Greater Amberjack Stock Recruitment Deviations 1970-2015. (a.) Model estimated ('Est') vs. directly calculated ('Calc'). (b.) Raw calculated deviations between the Beverton-Holt (B-H) theoretical relationship and the Stock Synthesis ('SS3') outputs used for management.

2.2 Data Exploration and Detrending

2.2.1 Predictor Correlations

Correlations between various sets of predictor variables were checked using the Pearson's linear correlation coefficient (r; Legendre and Legendre 2012), and where variable pairs were excessively correlated ($r >$ 0.85), one was removed from the pool of indicators. In general, if the variables under consideration could be linked to a spatial extent, the one covering the larger extent was often removed in order to maintain relatively "fine" spatial resolution for hypotheses testing and interpretation purposes. In all cases the decision was based on the general predictor model under investigation and its requirements.

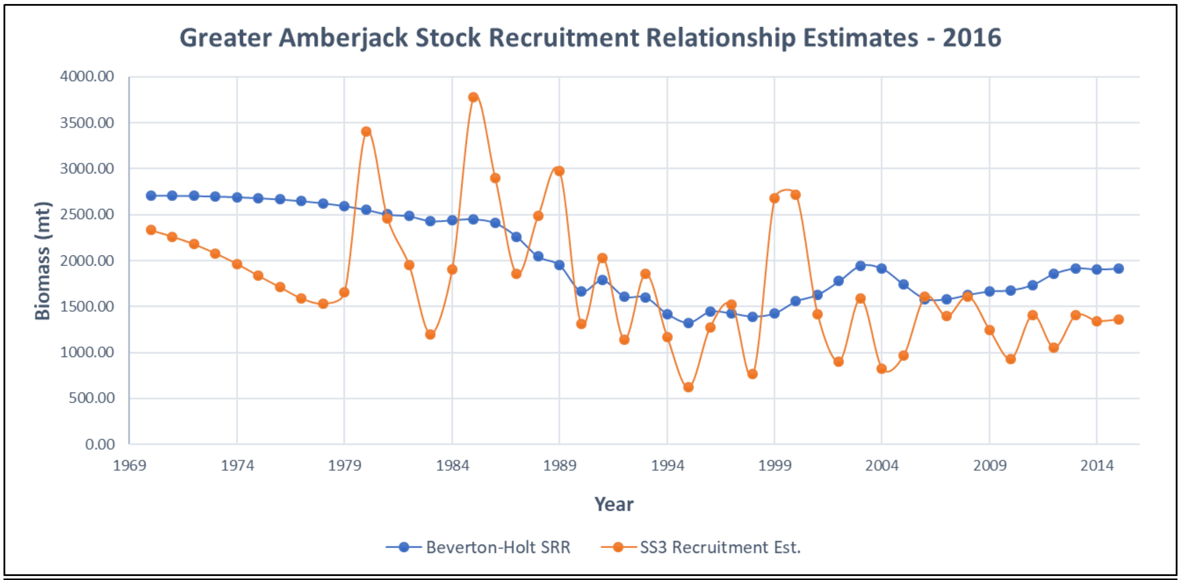


Figure 2. Greater Amberjack Stock Recruitment Relationship Estimates 1970-2015. Theoretical Beverton-Holt stock recruit relationship biomass estimates (metric of tons) over time (blue) plotted along with the Stock Synthesis output from the 2016 assessment update (orange).

Table 1. Spatial Areas Investigated for *Sargassum* Associations. Synthetic *Sargassum* experimental areas (see Figure 3) in the Gulf of Mexico and others based on existing management areas within the Gulf Council's jurisdiction.

Symbol	Description
coverALL	Mean annual coverage (km^2) for full Gulf LME
biomALL	Mean annual biomass (millions of tons) for full Gulf LME
edges	The Edges (40 Fathom Contour)
fgbE	Flower Garden Banks east
gom	Gulf-wide experimental area
gomC	Central Gulf experimental area
gomE	Eastern-central Gulf experimental area
gomW	Western-central Gulf experimental area
mouth	Gulf 'mouth' experimental area
madison	Madison Swanson Marine Reserve
mcgrail	McGrail Bank
middle	The Florida Middle Grounds
pulley	Pulley Ridge
efhRF	Essential fish habitat for reef fishes
steam	Steamboat Lumps Reserve

See: https://gulfcouncil.org/fishing-regulations/federal/#1567024726348-197a283c-476c for details of spatial boundary coordinates.

2.2.2 Recruitment Deviation Detrending

Given the temporal nature of stock assessment modeling, and the fact that SS3 recruitment data are based on a time-dependent model that incorporates the previous year's SSB, autocorrelation is expected in these data. Furthermore, a quick visual inspection of the recruitment deviations (Figure 2) under investigation

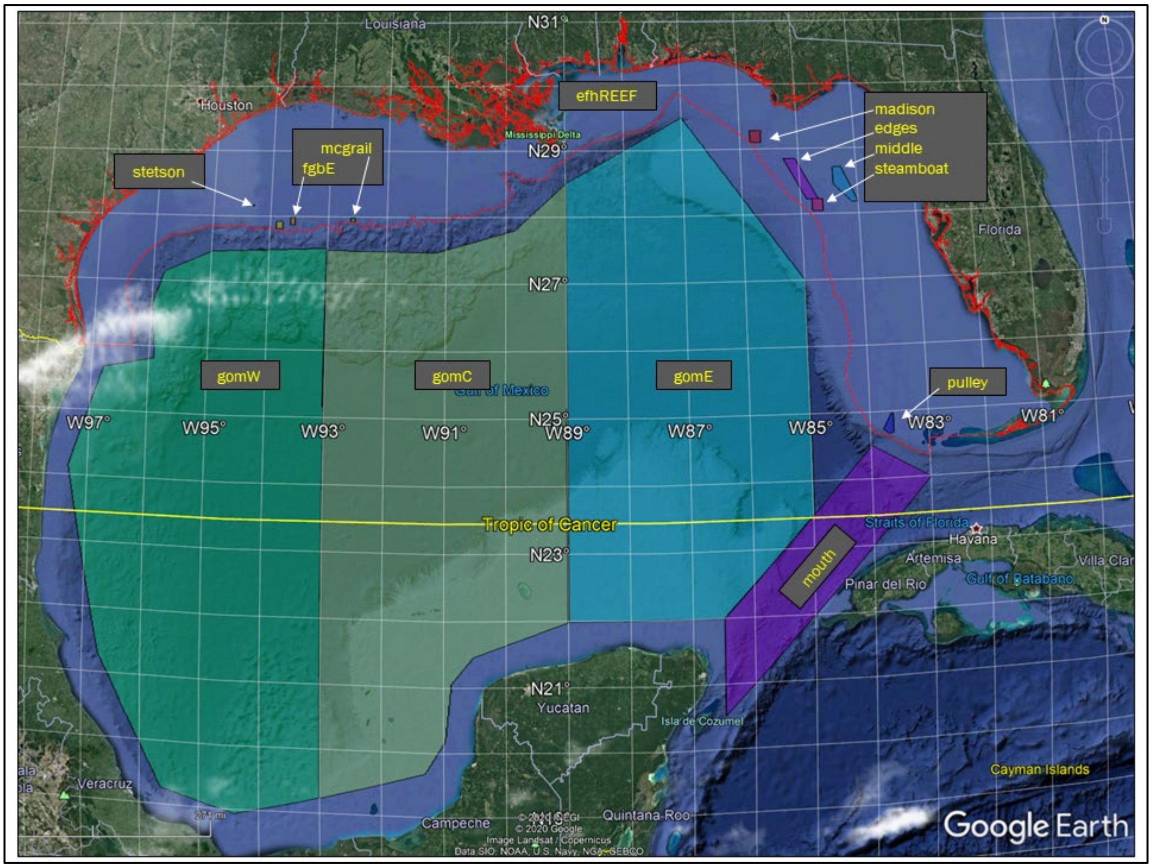


Figure 3. Gulf of Mexico LME and Experimental *Sargassum* and Existing Fisheries Management Areas. See Table 1 for details and label definitions.

revealed that there is at least some level of cyclicity in the response data that should be accounted for. Therefore, the GAJ recruitment deviations were first modeled using asymmetric eigenvector mapping (AEM; Blanchet et al. 2008, Blanchet et al. 2011). The AEM techniques decompose time series into patterns of autocorrelation that are representative of all possible temporal cycles available, given the length of the series and the minimum distance between observations (similar to spectral decomposition). For the purposes of this exercise, when any time series is converted, only the eigenvectors with eigenvalues greater-than zero were retained for modeling, since they represent the positive temporal autocorrelation. Recall that positive temporal autocorrelation dictates that successive years in a time series are more likely to have values similar to those values observed in years that are relatively close to the year of interest, as opposed to those years comparatively further away along the timeline (Legendre and Legendre 2012). As such, the

Table 2. Hypothesized Timing of Greater Amberjack Early Life History Stages. Estimates of the month in which each life stage listed occurs (X) and special emphasis (grey highlights) on the peak-spawning-period class's progress over the experimental periods used for data partitioning. 'Spawn/Dispersal' corresponds to the period where the newly-spawned and dispersed, whereas 'Pelagic/Recruit' refers to the period where larvae move through the earliest juvenile stages and recruit into the young-of-the-year (YOY) class > 150 days old. The months in *italics* are periods where commercial fishing is prohibited, and the underlined months represent recreational fishing closure periods.

			Spawn/Dispersal			Pelagic/Recruit						
Greater Amberjack Ontogenetic Stage	Jan.	Feb.	*Mar.*	*Apr.*	*May*	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Spawning			X	X	X	X						
Eggs			X	X	X	X						
Yolk-sack larvae				X	X	X	X					
Larvae (start feeding)				X	X	X	X					
Pelagic Juveniles (feeding pelagic)					X	X	X	X	X	X	X	X
Recruited stage (YOY > 150 days)								X	X	X	X	X

positive eigenvectors retained for analysis ($\mathbf{\Lambda}_i^+$) each represented a relative timescale over which the autocorrelation patterns may be manifest, and they also capture the cyclicity of the signal.

As part of the detrending process to remove and explain any autocorrelative dynamics within the GAJ recruit deviations, a forward variable selection method (Blanchet et al. 2008a), implemented in a redundancy analysis (RDA; Rao 1964) framework, was used to determine which time scales best accounted for the variability in the deviations. In this case, since the response variable was univariate, the RDA analysis reduced to what is, essentially, multiple linear regression (Quinn and Keough 2002, Legendre and Legendre 2012). Upon completion of the $\mathbf{\Lambda}_i^+$ selection, final models for the GAJ's recruitment response constrained by the temporal $\mathbf{\Lambda}_i^+$ predictors were developed, and from these models, two sets of information were retained for further analyses: (1) the modeled, or *fitted*, GAJ recruitment deviations, and (2) the remaining residual error (i.e., the *detrended* response data).

2.3 Predictor Models and Variable Selection

A second round of variable selection was utilized in order to determine which aspects of the temporally explained (i.e., fitted) and unexplained (i.e., detrended) GAJ recruitment response were explained by either *Sargassum* data, or those ecological characteristics extracted from the ESRs.

Table 3. List of Pertinent Ecological Predictor Indicators. Sources, observation years, and descriptions for all ecological variables considered for this study.

Source	Symbol	Description	Observation Years
ESR 2017	amo	Mean annual Atlantic multidecadal oscillation index	1970-2015
ESR 2017	artREEF	Annual Gulf-wide number of artificial reefs (non-oil) present	1970-2015
ESR 2017	doLAf	Annual mean dissolved O_2 off Louisiana in fall	1987-2015
ESR 2017	doLAs	Annual mean dissolved O_2 off Louisiana in summer	1987-2015
ESR 2017	doTXf	Annual mean dissolved O_2 off Texas in fall	1987-2015
ESR 2017	doTXs	Annual mean dissolved O_2 off Texas in summer	1987-2015
ESR 2013	flood	Marsh flooding rate in Barataria Bay, LA	1981-2011
ESR 2013	flowMS	Mean streamflow for Mississippi River	1980-2011
ESR 2013	hurr	ACE index of hurricane activity	1980-2011
ESR 2017	nit	Annual Gulf-wide nitrogen input from Mississippi-Atchafalaya River Basin (MARB)	1980-2014
ESR 2017	nOx	Annual Gulf-wide nitrogen oxides input from the MARB	1980-2014
ESR 2017	oilPLT	Annual Gulf-wide number of active oil platforms	1970-2015
ESR 2013	oilSPL	Number of U.S. Gulf LME oil spills	1980-2011
ESR 2017	phos	Annual Gulf-wide phosphate input from the MARB	1980-2014
ESR 2013	precip	Total precipitation for Mississippi River watershed	1980-2011
ESR 2017	sea	Mean annual change in sea level for all Gulf states	1970-2015
ESR 2017	sstC	Mean annual monthly sea surface temperature anomaly for central Gulf	1982-2015
ESR 2017	sstE	Mean annual monthly sea surface temperature anomaly for eastern Gulf	1982-2015
ESR 2017	sstW	Mean annual monthly sea surface temperature anomaly for western Gulf	1982-2015
ESR 2017	zoopS	Average zooplankton volume in the spring	1982-1984; 1986-1990; 1992-2015

In all cases, a stepwise selection process with Akaike's information criterion (AIC; Akaike 1974) was used in conjunction with RDA (Godinez-Dominguez and Freire 2003), and an AIC cutoff (Δ_{AIC}) of Δ_{AIC} = 2 was used for optimal model selection and comparison using an information theoretic approach. Model selection was undertaken across a series of model matrices accounting for the hypothesized characteristics of the Gulf LME. These models were explicitly developed to capture the following overarching themes: (1) *Sargassum* related, (2) ecosystem-wide ecological and habitat characters, and (3) metrics for eutrophication associated with the Mississippi-Atchafalaya River basin (MARB) and hypoxia in the northwestern Gulf (Table 4).

Table 4. List of Experimental Models, Variables Included, and Dates Covered. The following parameterizations were used to determine the extent of hypothesized relationships between the listed variable types (**boldface**) and the Greater Amberjack recruitment deviations over the time periods noted. Where indicated by an asterisk (*) the variables were included in an alternate model over the stated interval. All labels correspond to those listed in Table 1 and Table 3.

	Sargassum (2000-2015)	**Ecological** (1982-2010) (1970-2015)*	**Eutrophication** (1987-2014)
1	biomALL	amo	doLAf
2	coverALL	artREEF*	doLAs
3	edges	flood	doTXf
4	efhRF	flwMS	doTXs
5	fgbE	hurr	nit
6	gom	oilPLT*	nOx
7	gomC	oilSPL	phos
8	gomE	precip	
9	madison	sea*	
10	mcgrail	sstC	
11	middle	sstE	
12	mouth	sstW	
13	pulley	zoopS	
14	steam		

3.0 RESULTS

3.1 Predictor Correlations and Model Compilations

3.1.1 Sargassum Model #1 – Peak GAJ Spawning/Dispersal Period

The *Sargassum* cover data collated for the peak spawning and larval dispersal period from March-May showed very high correlations (Figure 4) among the Gulf-wide and experimental areas in the central Gulf LME, and between those regions and three other predefined management areas (McGrail Bank, Pulley Ridge, and the reef fish essential fish habitat [EFH]). Thus, all Gulf-wide and newly-developed experimental areas were removed, with the exception of the region that spans the 'mouth' of the Gulf LME where the basin meets the Caribbean Sea and the Straits of Florida (Figure 3). Additionally, the *Sargassum* cover data from the eastern Flower Garden Banks was removed for this seasonal subset. For the *Sargassum* variables removed during the spawning/dispersal period, the remaining reef fish EFH indicator was at least

85% correlated with the truncated data in all cases but that of the eastern-central Gulf region, an area which was itself strongly correlated (r = 0.85) with the retained 'mouth' index for *Sargassum* coverage (Figure 4). One very highly significant correlation (r = 0.98) was allowed to remain, that between McGrail Bank and Pulley Ridge, as they are geographically separated by ~950 km (~512 nautical miles) and in physically distinct areas of the Gulf LME (Figure 3).

3.1.2 Sargassum Model #2 – GAJ Pelagic Feeding and Settlement Period

In the case of the hypothesized pelagic/recruitment period from June-August, as with the spawning/dispersal period, many variables displayed significant correlations (Figure 4 and Figure 5). However, only four variables required removal due to violations of the pre-selected correlation threshold (Figure 5), the Gulf-wide and eastern-central Gulf indicators for *Sargassum* areal coverage, and those for the Middle Grounds and Steamboat Lumps management areas (Figure 3). As before, all removed indicators had a complimentary variable that was retained, but it was not universal in this case. The fact that the vast majority of the regional data remained "in play" during the pelagic/settlement period implies that there was more spatial variability over this sub-annual period than the spawning/dispersal period; in short, the areal coverall of *Sargassum* Gulf LME was relatively less homogeneous over time during the months June-August than in March-May.

3.1.3 Ecological Models

The ecological dataset extracted from both the 2013 and 2017 ESRs (Karnauskas et al. 2013, Karnauskas et al. 2017) consisted of 20 different indicators with observations beginning from 1970-1987, and ending between 2011-2015 (Table 3). These variables were further reduced to represent three ecological control systems hypothesized to affect GAJ recruitment levels and which may, therefore, better explain the SS3 recruitment deviations for GAJ. First, only four variables from the ecological dataset were recorded over the full 1970-2015 time period (Table 3), and of those four, three of them could conceivably be hypothesized to represent habitat considerations for GAJ, the annual number of artificial reefs and oil platforms, and the mean annual Gulf-wide sea level change. Therefore, these habitat considerations comprised one model pursued over the full-term of the GAJ recruitment data (Table 4). A second ecological model that was considered also included these three indicators for habitat, but was built along with other ecosystem-level factors whose date ranges precluded inclusion in a longer-term model. This second model covering 1982-2010 contained several indicators of sea surface temperature and marine ecosystem warming, including the north Atlantic basin-scale measure the Atlantic multidecadal oscillation (AMO), along with others describing hurricane activity, Mississippi River flow and related coastal marsh flooding, and springtime zooplankton bloom dynamics (Table 3, Table 4).

The correlation plots for these two models suggested that, over the 45-year term, sea level rise is strongly correlated with the installation of artificial reef structures (r = 0.85, Figure 6), and is only slightly less-so over the relatively shorter 28-year period (r = 0.81, Figure 7). Thus, the index of sea level change was removed from the pool of predictors in both models prior to further analyses, as the more direct-habitat related metric was preferable in this case. Additionally, the indicator for sea surface temperature in the western portion of the Gulf LME was removed due to its high correlation with the same metric in the central portion of the Gulf. This latter decision was relatively arbitrary, as both areas' metrics were significantly correlated with a total of seven other metrics in the ecological suite of predictors (Figure 7).

3.1.4 Eutrophication and Hypoxia Model

The fourth, and final, model derived from the ESR's ecological data was one that explicitly captured the effects of both eutrophication in the northern portion of the Gulf LME, particularly that associated with the MARB, and hypoxia in marine waters offshore Louisiana and Texas (Table 3, Table 4). Among those indicators representative of the characteristics that define marine eutrophication (Table 3), only those for total nitrogen ('nit') and "all nitrogen oxides" ('nOx') were correlated above the 0.85 level (r = 0.95; Figure 8). As such, since the information content of 'nit' was more general than 'nOx' (Karnauskas et al. 2013, Karnauskas et al. 2017), only the more focused 'nOx' was retained for further analyses. This model implicitly embeds both spatial and temporal considerations, since the dissolved oxygen indicators were dichotomized across seasons (fall and summer) and locations (Louisiana and Texas). Furthermore, the eutrophication metrics are explicitly derived from MARB outflow and, thus, are most relevant to the northern or north-western portions of the Gulf LME (Figure 3).

3.2 Greater Amberjack Recruitment Deviations and Detrending Exercises

Reliable GAJ stock recruitment deviations were available for the period 1970-2015 for this study (Figure 1b), however, given the four separate time scales dictated by the models described above, four independent detrending processes (Supplemental Figures S1-S4; Supplemental Tables S1-S4) for the various temporally constrained deviations (Table 5) were undertaken using AEM techniques. These exercises elucidated the long-term trends in autocorrelation underlying the GAJ recruitment deviations over the time periods of interest, and given that all four models selected at least one eigenvector map accounting for ~17-32% of the unexplained stock recruitment variability (Table 6), each GAJ recruit deviation time-series was reduced to their fitted and detrended component parts (Figure 9). Note that, together these two components comprise 100% of the variability in the time series of recruitment deviations, and the fitted, or modeled, portion is that which can be explained by the GAJ RDA model constrained by the selected $\mathbf{\Lambda}_i^+$ (i.e., the remaining

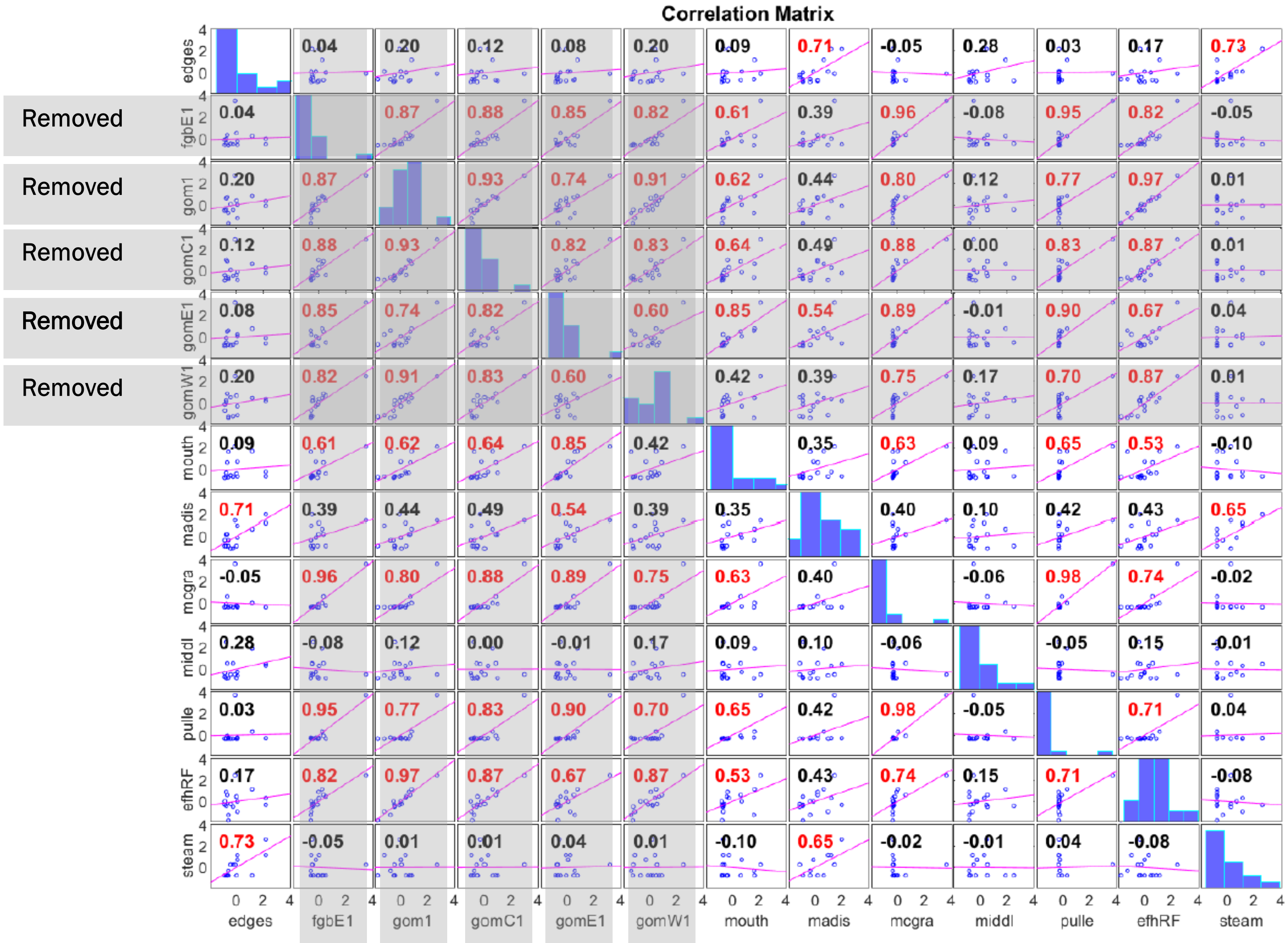


Figure 4. Correlation Matrix for *Sargassum* Coverage in Peak Spawning Season, 2000-2015. Pearson linear correlations between time series of mean annual areal coverage of *Sargassum* (km^2) in March-May across experimental treatment and existing management areas. Significant correlations are noted in red lettering, pink lines illustrate linear regressions, and histograms along the diagonal represent the indicators' value distributions. Data are Z-score standardized, and indicators that were removed prior to subsequent analysis are noted with gray bars.

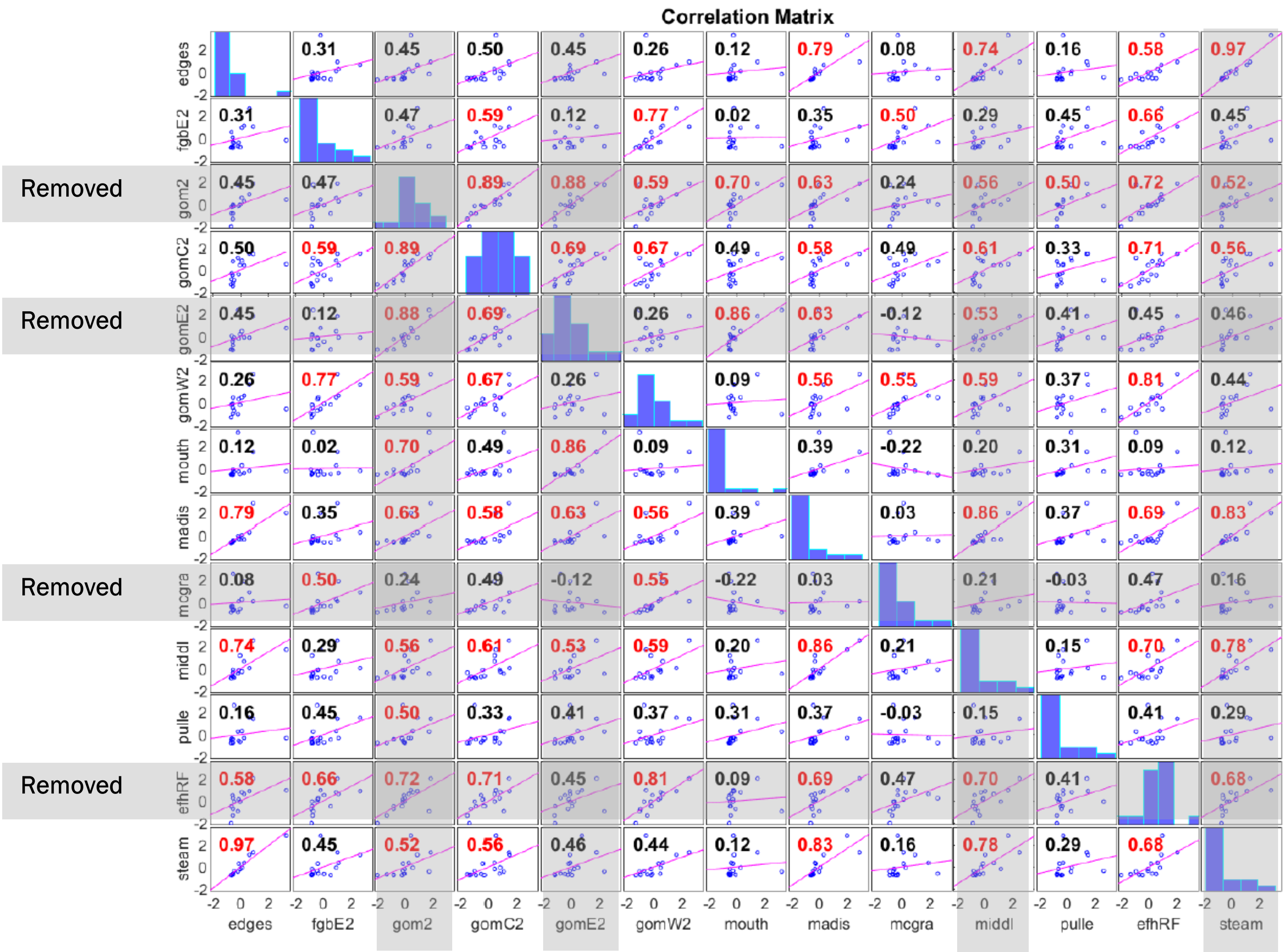


Figure 5: Correlation Matrix for *Sargassum* Coverage in Pelagic/Recruitment Period, 2000-2015. Pearson linear correlations between time series of mean annual areal coverage of *Sargassum* (km^2) in June-August across experimental treatment and existing management areas. See Figure 4 for additional details.

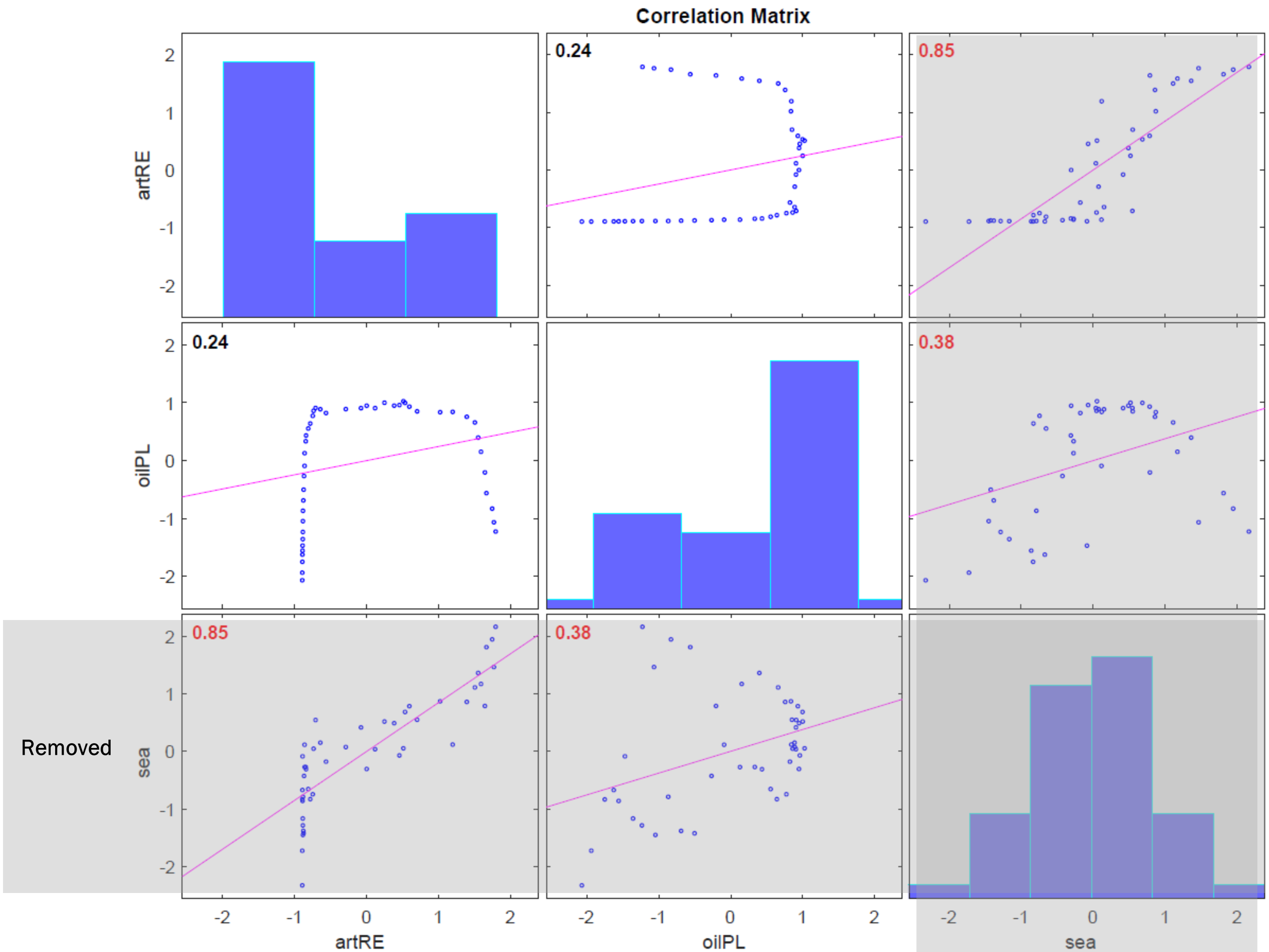


Figure 6: Correlation Matrix for Habitat Model Indicators, 1970-2015. Pearson linear correlations between time series related to artificial reefs ('artRE'), petroleum platforms ('oilPL') and sea level rise ('sea'). See Figure 4 for additional details.

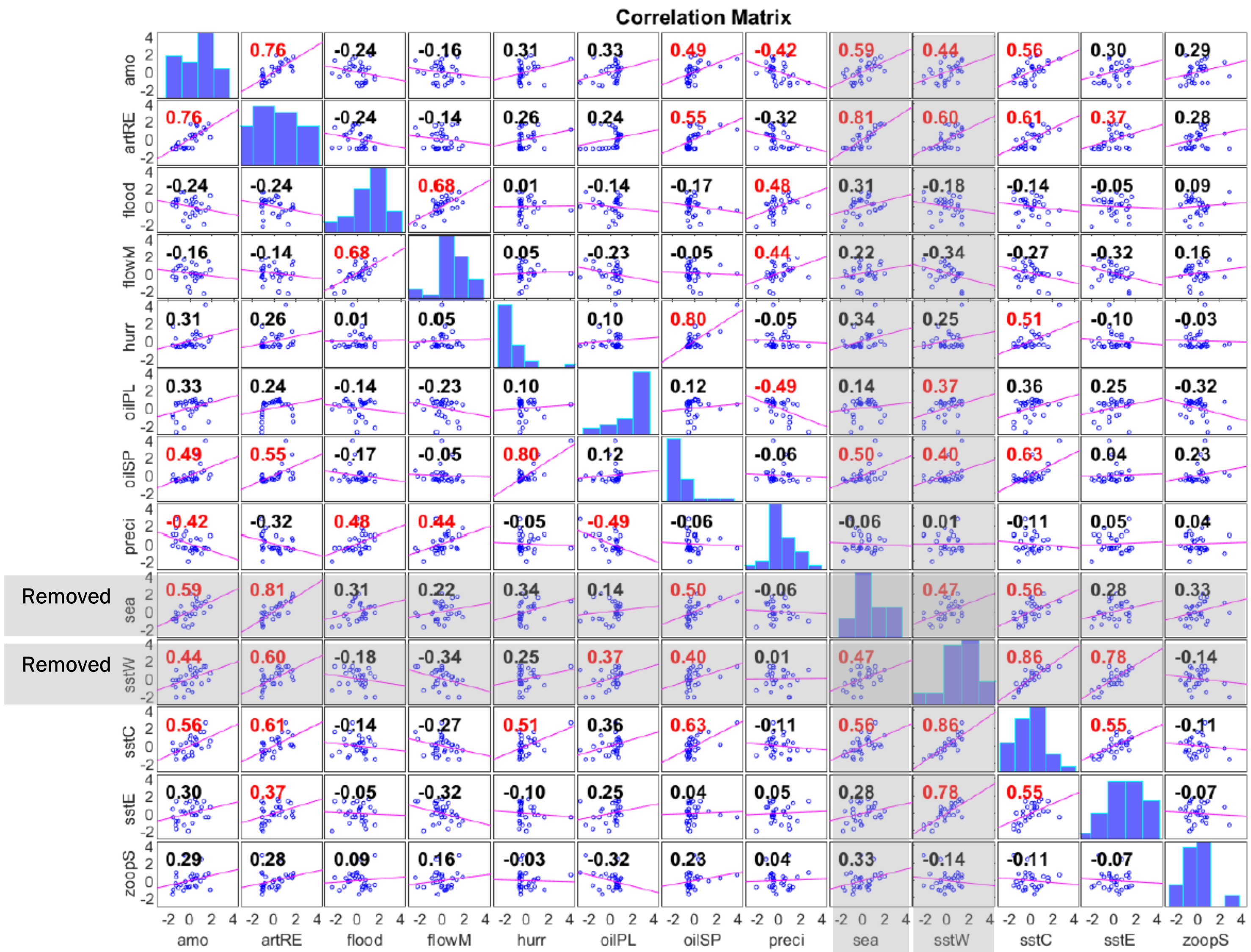


Figure 7: Correlation Matrix for Ecological Model Indicators, 1982-2010. Pearson linear correlations between time series related to all ecological indicators extracted from the two ecosystem status reports for the Gulf LME. See Table 3 for information on labels, and Figure 4 for additional figure details.

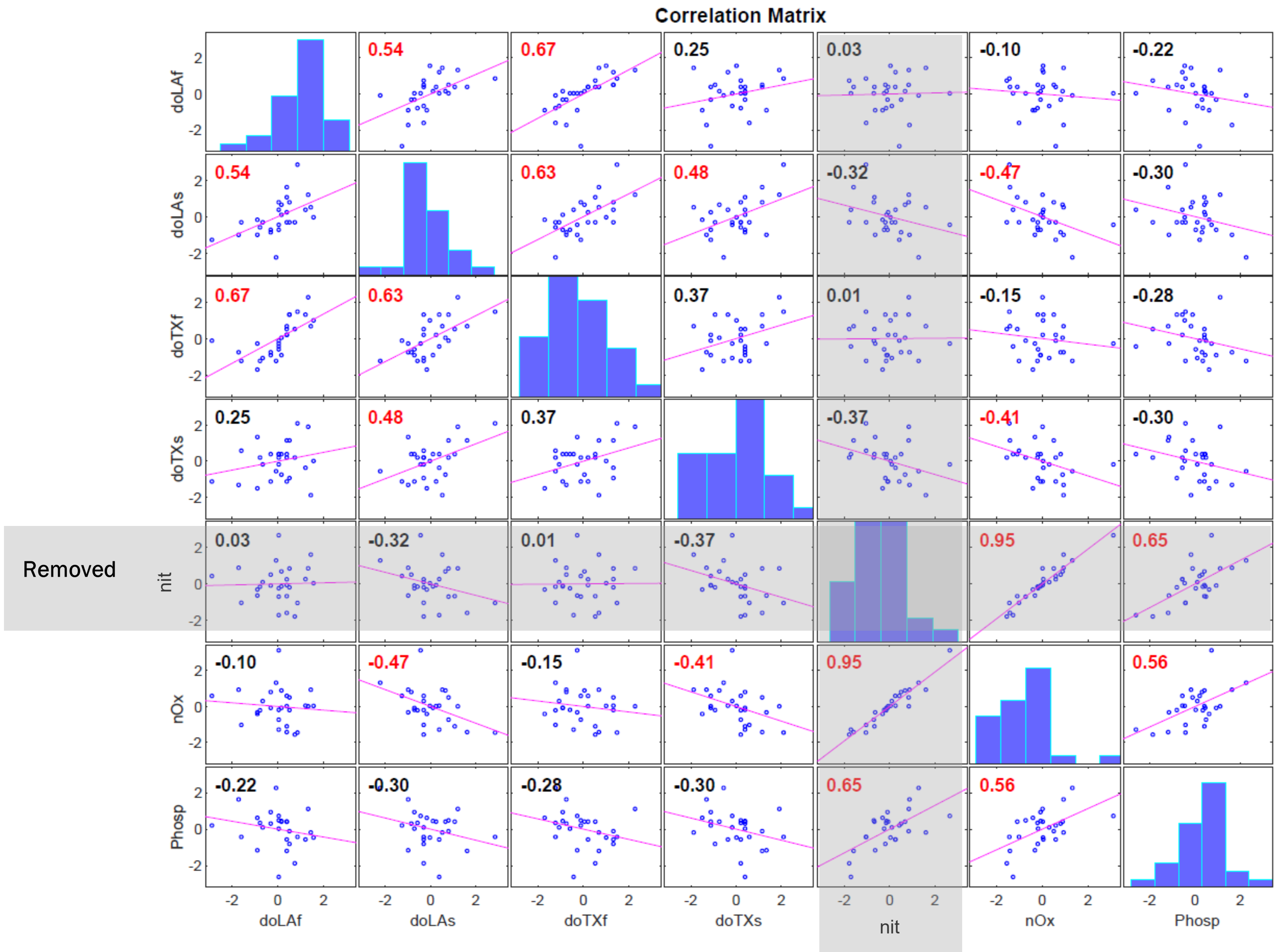


Figure 8: Correlation Matrix for Eutrophication Model Indicators, 1987-2014. Pearson linear correlations between time series related to all ecological indicators related to eutrophication and hypoxia that were extracted from the two ecosystem status reports for the Gulf LME. See Table 3 for information on labels, and Figure 4 for additional figure details.

proportion of the variability that is unaccounted for by the temporal model is retained in the "detrended" components). In all cases, the detrended component retained the vast majority of the recruitment deviations' variabilities (Supplemental Tables S1-S4), but, as noted above, in at least one case (the *Sargassum* model) the temporally autocorrelated variability represented 31.6% of the modeled variability (Table 6). All four models' fitted values displayed periodic trends (Figure 9) matching the periodicity of the autocorrelation eigenfunctions retained to constrain them, and, for three models (*Sargassum*, ecological, and habitat), this periodicity was driven by only one $\mathbf{\Lambda}_i^+$ pattern (Table 6; Figure 9a-c). The temporal expression within the eutrophication model, however, not only displayed a relatively short 8-year cycle, but it also incorporated a very long-term declining trend (Figure 9d). Lastly, it should be further noted that these four models' temporal trends were all derived from the same data partitioned over different time periods as dictated by the ecosystem-level characteristics compiled to assess each related hypothesis (e.g., eutrophication as driver of GAJ recruitment variability). Thus, as always, the interpretation of these models and results should be tempered by the knowledge that there is an implicit problem of pattern and scale (Levin 1992) underlying this, or any, ecological investigation, and that the time scales selected are not necessarily representative of the "real" underlying dynamics and controls within the system, but, rather, are artifacts of the selected time frame for investigation. Having said that, it is also important to note that this is wholly unavoidable, especially in a management context where decisions must be made regardless of clarity.

3.3 Predictor Variable Selections

All models, both fitted and detrended variants, were submitted to the AIC variable selection process (Tables S5-S9), however, only one set of detrended recruitment deviations returned an optimal model (Table 7). Of the 48 ecosystem-level, ecological predictors examined, only seven were ultimately selected to explain the deviations in GAJ recruitment levels over their respective time periods, and two of those were deemed statistically insignificant via randomization methods (Table 7).

3.3.1 *Sargassum* Models

The two pools of indicators representing mean seasonal areal coverage (km^2) across the Gulf LME for two dominant *Sargassum spp.,* when selected for against the fitted 2000-2015 GAJ recruitment deviations, both returned optimal models with one regional *Sargassum* metric. However, only model #1 representing the peak spawning and dispersal period displayed statistical significance, and it was best described by the *Sargassum* coverage in the FL Middle Grounds (Table 7). The two detrended recruitment deviation models did not return optimal models. Recall that the fitted model in this case accounted for ~32% of the variability in the original GAJ recruitment deviations and was primarily described by an 8-year cyclical trend (Table 6, Figure 9a). This model's adjusted coefficient of determination (R^2_{adj} = 0.2167) suggested that

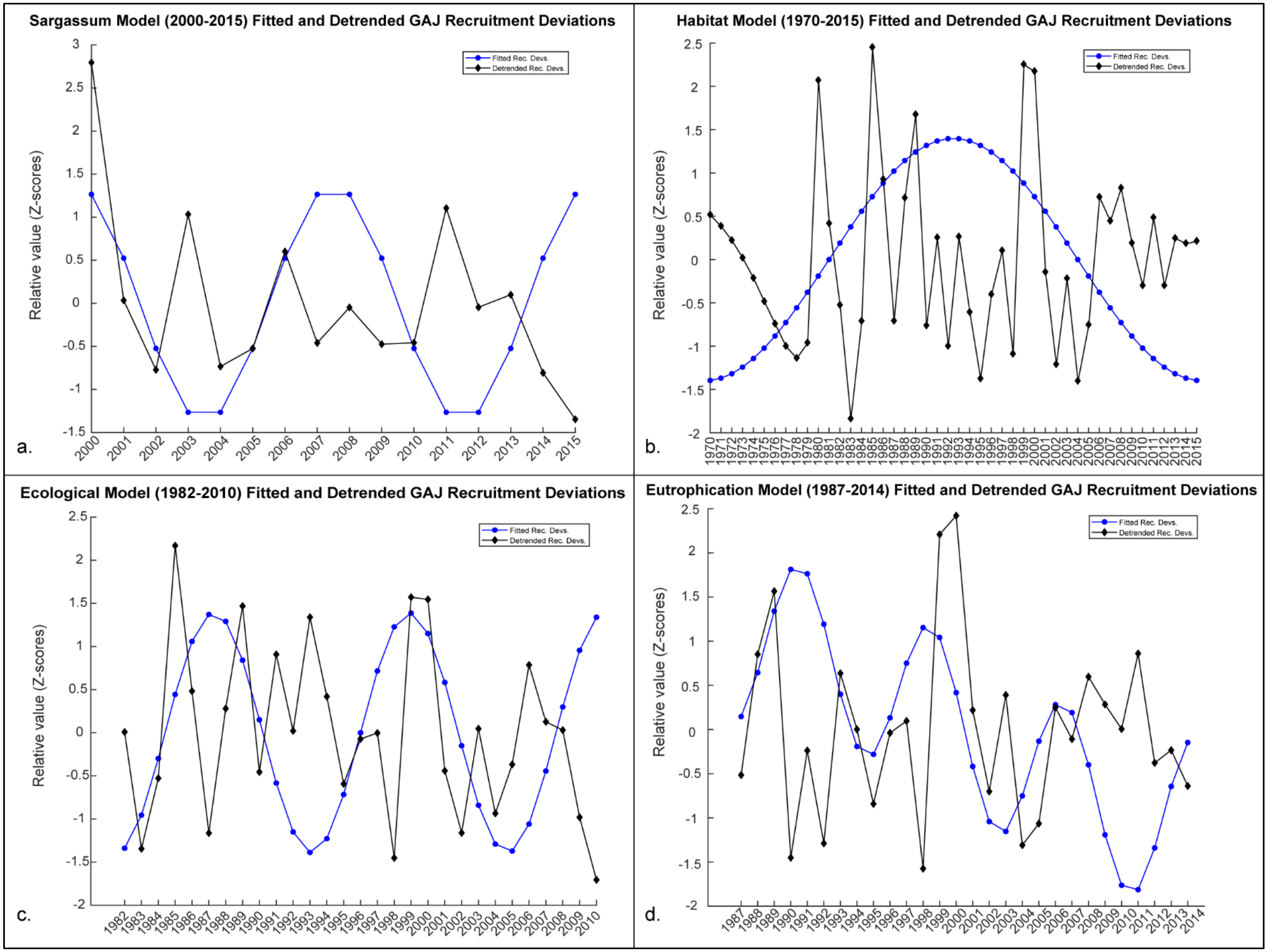


Figure 9. Fitted vs. Detrended Greater Amberjack Recruitment Deviations. Time series plots of the fitted (circles) vs. detrended (diamonds) recruitment deviation values after accounting for selected asymmetric eigenvector maps. Data are Z-score standardized, and model and time period are noted in each panel.

Table 5. Descriptive Statistics for Greater Amberjack Recruitment Deviations. Descriptive statistics for each model's subsample of Greater Amberjack recruitment deviations according to the time periods listed. Tests for normality were performed using the Lilliefors test where the *null* hypothesis is that of no difference from a normal distribution. 'StndDev.' = standard deviation, and 'StndErr.' = standard error.

Model	Period	*n*	Minimum	Mean	Median	Maximum	StndDev.	StndErr.	Normal	*p*-value
Habitat	1970-2015	46	-1233.4	-286.2	-434.4	1324.6	638.25	94.12	No	0.0069
Ecological	1982-2010	29	-1233.4	-124.6	-250.0	1324.6	679.16	126.12	Yes	0.1097
Eutrophication	1987-2014	28	-1089.1	-190.5	-339.9	1254.6	595.89	112.61	Yes	0.0511
Sargassum	2000-2015	16	-1089.1	-389.4	-467.1	1165.6	519.35	129.84	Yes	0.3259

Table 6. Selected Asymmetric Eigenvector Maps and Optimal RDA Model Results. Optimal RDA models for selected eigenfunctions (Λ_i^+) used to detrend and fit Greater Amberjack recruitment deviations among the four experimental model treatments' time periods. The temporal patterns' scales are related in the 'Period #' column.

Model	Period	*n*	Λ_i^+ (Period 1)	Λ_i^+ (Period 2)	*F*	R^2	R^2_{adj}	*p*-value
Habitat	1970-2015	46	Λ_2^+ (23 years)	-	10.5	0.1922	0.1738	0.0029
Ecological	1982-2010	29	Λ_5^+ (11 years)	-	7.0	0.2067	0.1773	0.0141
Eutrophication	1987-2014	28	Λ_1^+ (28 years)	Λ_7^+ (8 years)	4.9	0.2794	0.2218	0.0169
Sargassum	2000-2015	16	Λ_4^+ (8 years)	-	7.9	0.3621	0.3165	0.0071

Table 7. Optimal Predictor Models Developed via Variable Selection. Final predictors selected via Akaike's information criterion to model the fitted ('Fit') and detrended ('Dtrnd.') Greater Amberjack recruitment deviations according to experimental treatments. The adjusted coefficients of determination (R^2_{adj}) for the temporally constrained models are in the second column, and the R^2_{adj} for each subsequent optimal predictor model in the penultimate pair of columns are to be interpreted with respect to the original models' proportion of explained variability (extended values are presented in Table 8). See Table 1 and Table 3 for predictor labels and details. Models with **boldface** predictor labels and *p*-values were statistically significant ($\alpha = 0.05$).

			Selected Predictors		*F*		R^2_{adj}		*p*-Value	
Model	Fit R^2_{adj} (Dtrnd.)	Period	*Fit*	*Dtrnd.*	*Fit*	*Dtrnd.*	*Fit*	*Dtrnd.*	*Fit*	*Dtrnd.*
Habitat	0.1738 (0.8262)	1970-2015	**'oilPLT' + 'artReef'**		239.12	-	0.9137	-	**0.0001**	-
Ecological	0.1773 (0.8227)	1982-2010	'precip'	**'amo' + 'oilPLT'**	3.94	6.75	0.0949	0.2910	0.0586	**0.0050**
Eutrophication	0.2218 (0.7782)	1987-2014	**'doTXf'**		9.69	-	0.2434	-	**0.0045**	-
Sargassum #1	0.3165 (0.6835)	2000-2015	**'middle1'**		5.15	-	0.2167	-	**0.0378**	-
Sargassum #2	0.3165 (0.6835)	2000-2015	'mouth2'		-	2.57	-	0.0949	-	0.0884

approximately 22% of that 32%, or ~7% of the original total unexplained GAJ recruitment variability, could be explained by this management area's seasonal *Sargassum* coverage metric (Table 8).

3.3.2 Ecological and Habitat Models

The models developed for the ecosystem-level ecological characteristics drawn from the ESRs for the region were the most complex of all. This complexity was relative, though, as the two statistically significant models only selected two variables apiece. However, the ecological and habitat models together were additionally unique in that they had significant models for the detrended and fitted GAJ recruitment deviations, respectively (Table 7). When considering the habitat model, which covered the longest study period (1970-2015), the fitted recruit deviations were best explained by the annual number of oil platforms and non-petroleum industry artificial reefs present Gulf-wide (Table 7). This model displayed, by far, the best relationship between explained to unexplained variability (F = 239.12) compared to all others developed, and also had the lowest p-value, implying that the observed relationship was not only great in magnitude, but also that it was highly unlikely to have presented via random processes alone (Table 7). Additionally, while the strength and significance of this model were legitimate, the proportion of the total variability accounted for in the original GAJ recruitment deviations was the second highest modeled (~16%; Table 8). Finally, it is important to recall that this model was derived from the 23-year autocorrelation signal uncovered using AEM analysis (Figure 9b).

The period 1982-2010, for which the full ecological model was developed for the Gulf LME, was unique in that these series of GAJ recruitment deviations could only be accounted for in the non-temporal, or detrended, sense. Thus, none of the predictor variables appeared to be sufficiently varying on the 11-year autocorrelation scale (Figure 9c) to be able to describe ~18% of the new recruit deviations accounted for by that model, but two were competent enough to capture ~29% of the remaining 82% of the deviations' variability observed over that same time period. This implies that the model accounted for ~24% of the total GAJ recruitment deviation variability over that 29-year period of GAJ monitoring and management model (Table 8), and which is potentially non-trivial. Furthermore, of the two variables selected, one was also retained in the habitat model, the number of oil platforms. The other selected metric was a basin-scale climatic variable associated with temperature changes in the north Atlantic Ocean, the AMO (Table 7).

3.3.3 Eutrophication Model

Much like the *Sargassum* models, the model exploring the effects of eutrophication in the northern and north-western Gulf LME yielded one indicator that explained a statistically significant portion of the GAJ

Table 8. Modeled Proportions of the Total Variability in Greater Amberjack Recruitment Deviations. Total percentage accounted for of the original Greater Amberjack population's recruitment deviation's variability ('Total % Modeled') by each experimental model. Totals are derived from the temporal models' (using fitted or *detrended values) 'Proportion of Total' variability, and their associated predictor model's proportions accounted for ('Modeled Prop.').

	Temporal	*Predictor*	
Model	**Proportion of Total**	**Modeled Prop.**	**Total % Modeled**
Habitat	0.1738	0.9137	16%
Ecological*	0.8227	0.291	24%
Eutrophication	0.2218	0.2434	5%
Sargassum #1	0.3165	0.2167	7%

recruitment deviations over the period 1987-2014 (Table 7), and it too was associated only with the temporally constrained model. Recall that this temporal model was derived from two AEMs representing a long-term continuous 28-year trend and a cyclical 8-year repeating pattern (Figure 9d), resulting in the most complex temporal dynamics observed in GAJ recruitment deviations over any time scale investigated. In this model, the dissolved oxygen levels offshore Texas in the fall sampling season best captured the recruitment dynamics, but, also like the *Sargassum* model, the overall measured effect was relatively small (~5%, Table 8).

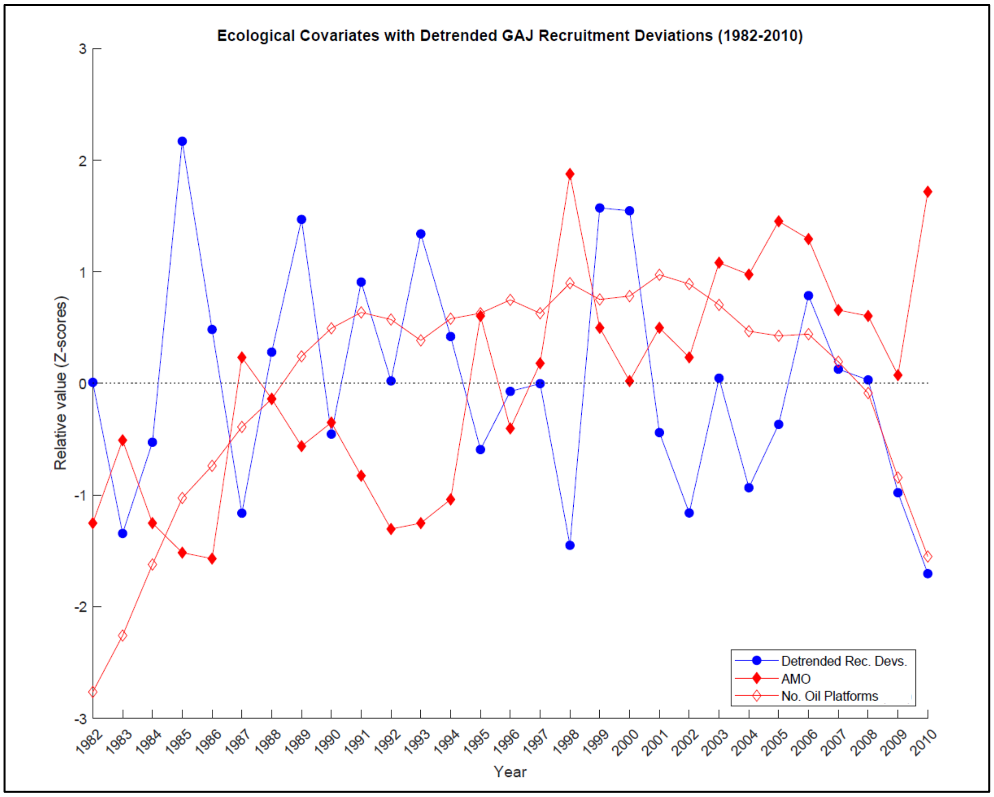
4.0 DISCUSSION

4.1 Climate and Habitat Considerations

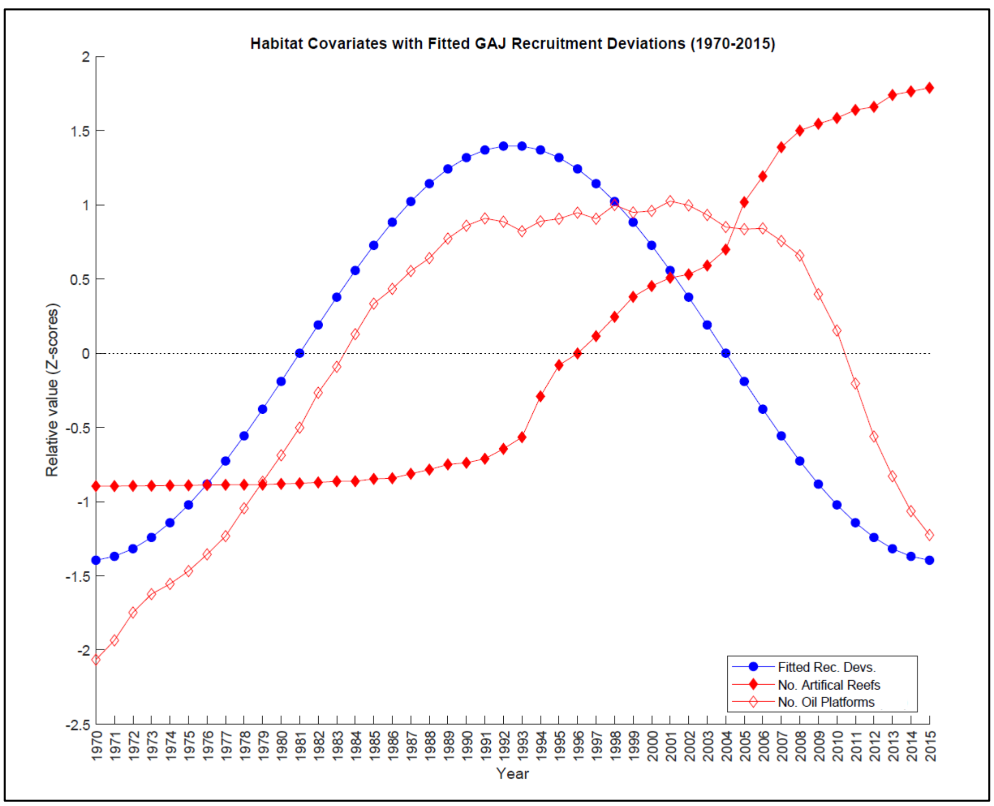
The model that described the greatest proportion of the GAJ recruitment deviations over time was the 1982-2010 ecological model with AMO and the number of oil platforms present Gulf-wide. While this model accounted for ~24% of the recruitment variability, it was the only model that explained non-temporally structured deviations in the GAJ stock recruitment levels. In conjunction with the original autocorrelation model based on its $\mathbf{\Lambda}_5^+$, and which captured a repeating decadal cycle (Figure 9c), these three components captured approximately 41% of the total variability in the GAJ recruitment deviations over that time scale. The first variable selected in the non-temporal model was the AMO (Table S6), and it appeared to have an inverse relationship with recruitment deviations (Figure 10a), implying that higher AMO values correspond with below-average (and negative) deviations and, therefore, overestimated recruitment levels. Given that the AMO is a measure of warming surface waters in the northern Atlantic Ocean (Nye et al. 2014), and is known to have numerous teleconnections across great spatial scales (Enfield et al. 2001, Zhang et al. 2012, Nye et al. 2014), including within the Gulf LME and its related fisheries (Karnauskas et al. 2015, Kilborn et al. 2018), it is not surprising that it has been identified as a notable climate-related predictor for GAJ recruitment. It also implies that there is a forcing relationship that is unaccounted for, and which could serve to explain why the recruitment levels in certain years are being misrepresented. What is not obvious, however, is what the nature of this relationship is, and what the mechanisms at play are. For example, given that GAJ are known to spawn offshore (Fahay 1975, Wells and Rooker 2004a), and AMO is thought to affect large-scale circulation patterns (Nye et al. 2014), it is conceivable that physical advection of larvae could play a role in the success or failure (Johnson et al. 2017) of any given year class, and that this could ultimately be ascribed to movement of the AMO. This is only one of many possible scenarios that might be at play.

In addition to the AMO, the number of active oil platforms in the Gulf LME was also selected for this model, and seemed to display a somewhat mixed relationship with recruitment deviations over time. In this instance, the oil platform metric showed two very clear periods of below-average numbers (1982-1988 and 2008-2010) and the 1989-2007 period displaying well above-average patterns, and all while the recruitment deviations displayed both above- and below-average activity over the same timespans, respectively (Figure 10a). Decomposing the relationship between GAJ and oil installations does become more complicated by the fact that it is a Gulf-wide metric that cannot be interpreted spatially, thus reducing to a general implication of the importance of this underwater infrastructure as a habitat, but not which particular physical or chemical conditions might also be attractive in these environments (e.g., deep water platforms vs. shallow, eastern Gulf vs. western).

Furthermore, when examining all 46 years of recruitment data for autocorrelative dynamics, the ~11-year cycle captured by $\mathbf{\Lambda}_5^+$ over the 1982-2010 period does not present itself, and instead that period's $\mathbf{\Lambda}_2^+$ is selected as the only temporally relevant trend, and which models a 23-year, unimodal up-down pattern for GAJ recruit deviations (Figure 9b). Fortunately, the number of oil platforms was selected for this optimal model as well, and which implies that either this metric does encapsulate a real effect toward the recruitment success (or failure) of GAJ conferred by installing offshore habitats, or it embodies a mathematical artefact or temporal coincidence. The long-term model adds further support for the argument in favor of oil platforms as important habitats for GAJ recruitment as it appears that, in addition to tracking closely with the temporally constrained trends in recruitment deviations throughout the entire 46-year time series, the only divergence between the two appears after the stark increases in artificial reefs not related to petroleum production in the mid-1990s. Interestingly, that "divergence" manifests more as a delay in the response, and the current status of the matter is that oil platforms continue to track closer than ever with GAJ recruitment deviations (Figure 10b). Other artificial reefs, on the other hand, seem to have a mostly negative relationship with GAJ new recruit estimate deviations, and their dynamics appear to support the idea that the growth in these aquatic habitats, while still increasing, has mostly level-off. Currently, while non-



a.



b.

Figure 10. Time Series Plots of Model Recruit Deviations and Ecological Covariates. Time series of the temporally constrained Greater Amberjack recruit deviations (circles) plotted along with selected covariate predictors (diamonds) for the ecological (a.) and habitat (b.) models. Data are Z-score standardized, temporal scale is noted on the x-axis, and panel legend's contain predictor details. See Table 3 for more descriptor details.

petroleum related artificial reefs are at a relative all-time high, the 23-year period model's fitted recruitment estimates are below average, and this may imply that by considering increasing levels of this habitat when estimating GAJ recruitment, it may help reduce the frequency of overestimations.

4.2 Sargassum Considerations

Another primary focus of this project was to assess the relationship between floating *Sargassum* mats in the greater Gulf LME and unexplained GAJ recruitment variability. In order to do this, remote-sensed satellite data were used to estimate the areal surface expression of the macroalgae across major sections of the Gulf, at monthly intervals, for the period 2000-2018. The GAJ recruitment data were only available through 2015, and, unfortunately, the SS3 products were temporally limited by the fact that only annual estimates are obtained through the model's outputs. Additionally, the satellite data were observed at the relatively course spatial resolution of ~56 km^2 $pixel^{-1}$. For reference, the Gulf LME covers ~1.5 million km^2 (Kumpf et al. 1999), the GMFMC's jurisdictional area is ~628,830 km^2 and the area designated to EFH for reef fish is ~349,136 km^2 (GMFMC 2016), the FL Middle Grounds[3] covers ~1,193 km^2, and the total area ascribed to all artificial reef structures (within the reef fish EFH) was ~21 km^2 (GMFMC 2016). Further spatial complications included, for example, that both of the Flower Garden Banks' eastern and western locations were contained within a single pixel, or that The Edges was contained within four pixels, but Steamboat Lumps resides within the lower right quadrant of that 2 x 2 grid (Figure 3). Nevertheless, it was instructive to explicitly test each of the management areas noted in Table 1, and to provide at least some spatial context to the question of *Sargassum*'s influence on GAJ recruitment.

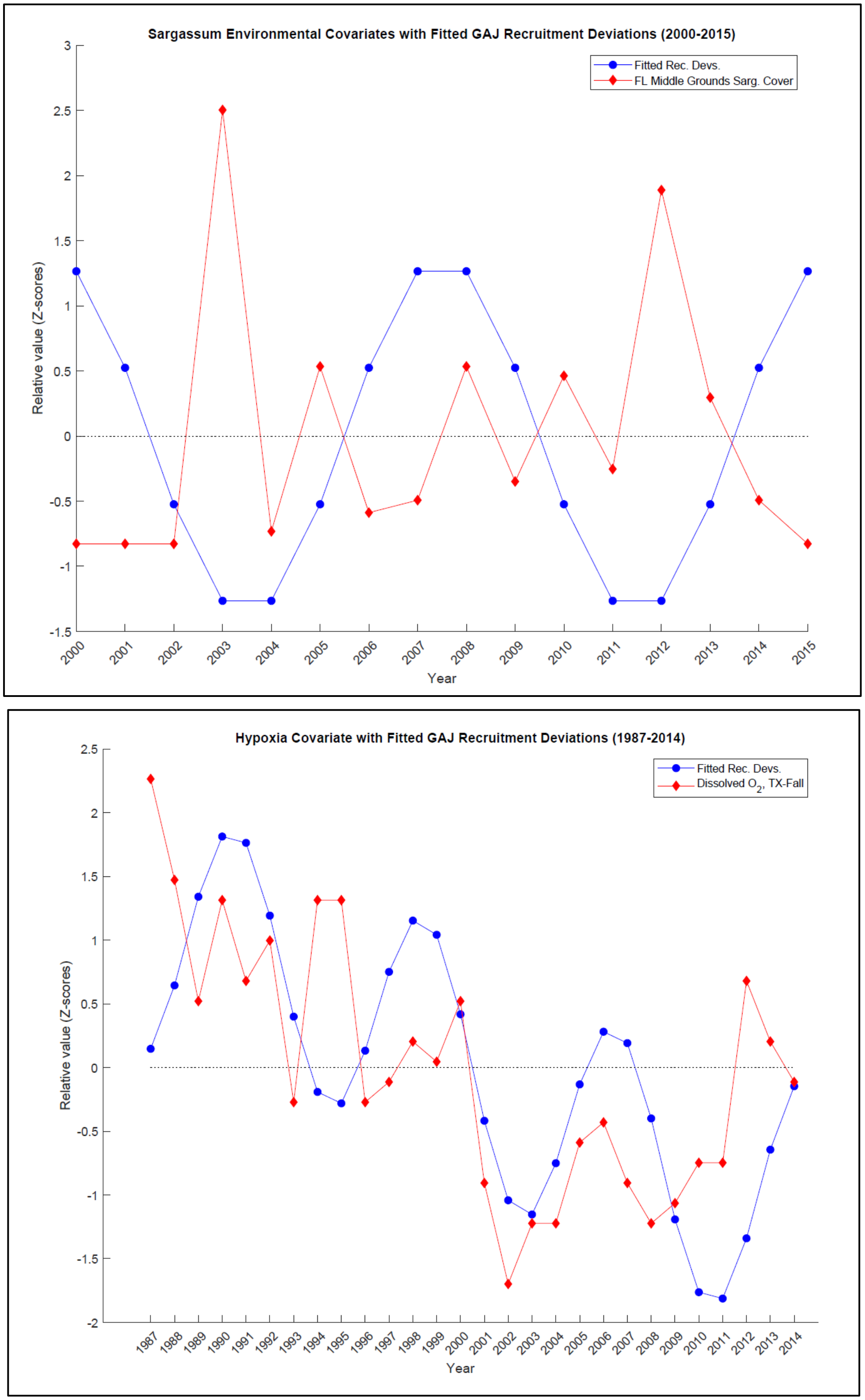
The two models considered not only contained the implicit spatial hypotheses that any area selected could be presumed as important to the overall recruitment dynamics, but given the separation of data across seasons, there were implied temporal hypotheses under investigation as well. The seasonal periods March-May and June-August, were selected to capture the peak spawning and larval dispersal period (Fahay 1975, Wells and Rooker 2004a, Harris et al. 2007) and the pelagic feeding and young-of-the-year settlement period (Wells and Rooker 2004a, b), respectively. Greater Amberjack are thought to associate with *Sargassum* in the earliest portions of their life history and after the first 6-months it has been suggested that they switch to a more demersal existence (Wells and Rooker 2004a). Thus, there was some expectation that a fair number of associations would be borne out across a variety of spatial scales, or at least in some of the more offshore regions, as there have also been notable associations with greater juvenile GAJ abundance and spawning activity with increasing distances from shore (Fahay 1975, Wells and Rooker 2004a).

[3] https://gpsfishingmaps.wordpress.com/florida-middle-grounds-map/

Unfortunately, only two regions were selected, and only one in each of the two seasonal models. Furthermore, the latter model (i.e., the pelagic/settlement period) was deemed insignificant given that over 800 of the 10,000 randomized models produced results as extreme as those observed in the data collected. Thus, the only *Sargassum*-related metric that was retained was the areal macroalgal coverage in the FL Middle Grounds management area during the spawning/larval period March-May. Notably, this model was an extension of the temporal model used to detrend the data, and was based on the fitted scores that followed the 8-year cycle of autocorrelation that accounted for ~32% of the original GAJ recruitment deviations over the period 2000-2015. Therefore, no additional explanatory capacity is gained by this model than that which was provided by the associated eigenfunction, except to discern that while 35% of the recruitment variability can be explained by the temporal signal, only ~7% of the total variability (i.e., ~22% of that 35%) is accounted for by this region's *Sargassum* coverage parameter. "Why the FL Middle Grounds?" and "Why during March-May?" is not immediately clear. It is notable, though, that another inverse relationship between GAJ recruitment deviations and the selected predictor was present (Figure 11a). Over the 15-year period of the model, it appears as though relatively high *Sargassum* coverage in the FL Middle Grounds translates to negative GAJ recruitment deviations, implying that greater coverage leads to lower recruitment than expected by B-H during that year.

4.3 Eutrophication and Hypoxia Considerations

The final model that was presented in this analysis covered the period 1987-2014, and focused on the effects of both eutrophication in the system as well as the effects of hypoxia in offshore demersal waters of the shelf ecosystems associated with Louisiana and Texas. This model identified the dissolved oxygen (DO) levels in benthic waters offshore of Texas in the fall sampling season to be the most useful metric for accounting for GAJ stock recruitment deviations. Overall, this model accounted for the least amount of total variability in recruitment deviations, but it did have the second highest ratio of explained to unexplained variability and the second lowest randomized *p*-value. Together, these do seem to imply that this model is notable, and upon further inspection it can be seen that the DO trends in Texas track very closely with both the 8-year repeating cyclical and the 28-year steadily declining trends captured by the eigenvectors used as the basis for this model (Figure 11b). Within this temporally constrained model, Texas's marine DO levels in the fall accounted for ~5% of the total recruitment deviations for GAJ, but they appear to do so very well. This is notable as there is evidence that suggests low DO levels (~12.5% saturation) can lead to birth defects and increased instances of larval failure (Sawada et al. 2006). Furthermore, when rearing GAJ in aquaculture settings, an optimal range for DO is ~6.0-7.0 mg l^{-1} (Papandroulakis et al. 2005), however, the DO conditions in the western Gulf LME in the fall have notably been below the 6.0 mg l^{-1} range since the early portion of the 2000s (Karnauskas et al. 2017). Given that



a.

b.

Figure 11. Time Series Plots of Model Recruit Deviations with *Sargassum* and Hypoxia Covariates. Time series of the temporally constrained Greater Amberjack recruit deviations (circles) plotted along with selected covariate predictors (diamonds) for the *Sargassum* (a.) and hypoxia (b.) models. Data are Z-score standardized, temporal scale is noted on the x-axis, and panel legend's contain predictor details. See Table 3 for more descriptor details.

the DO conditions across the range of spawning area for GAJ have deteriorated over time (Karnauskas et al. 2017), it is plausible that there has been a long-term effect on the recruitment capacity of the GAJ stock. Unfortunately, the timing of the indicator selected in this model (i.e., the fall season) does not match the temporal hypotheses set out above with respect to the *Sargassum* models (i.e., spawning/dispersal vs. pelagic/settlement phases).

4.4 Leading Indicators for Greater Amberjack Recruitment

Over the course of this study, five ecological indicators were selected as having some level of capacity to constrain the unexplained variability in GAJ recruitment deviations: (1) the AMO index, (2) the number of active oil platforms in the Gulf LME, (3) the number of non-petroleum industry artificial reefs, (4) the mean annual areal coverage of *Sargassum* in the Florida Middle Grounds in the March-May spawning and larval dispersal period for GAJ, and (5) the DO levels offshore Texas in the fall. On the surface, all of these metrics appear to be reasonable candidates for leading indicators of recruitment success for GAJ, but the reliability of each, and the full dynamical range of their relationships with GAJ, are not fully understood at the level of predictability, especially not in a management context. Nevertheless, there are some apparent weightings that can be estimated with respect to the likelihood of success in determining mechanistic support for the high-level linkages uncovered here.

<u>4.4.1 Leading Environmental Indicators</u>

The indicator that can be most directly related back to physiological constraints on the species would be that for the DO levels in Texas's waters. Therefore, even though this particular measure was in one of the least explanatory models, it still represents the best lead in terms of understanding the true nature of the success or failures conveyed by changes in this environmental parameter. For example, in addition to tank experiments and laboratory studies that could estimate the physical tolerance and response ranges for a compliment of GAJ life-stages across a range of activity levels, temperatures, and oxygen concentrations, simulation studies such as management strategy evaluations can be performed to estimate the impacts of those experimentally-derived ranges on fecundity, larval survival, and subsequent population statuses and future planning scenarios. This type of work could be extended into follow-up investigations regarding the influence of the AMO on recruitment levels, however this would require a much more detailed and nuanced analysis incorporating the relationship between the AMO and DO in the Gulf LME.

As previously stated, the AMO index reflects a natural environment that has the potential to alter a number of different physical and chemical processes in the Gulf LME by way of altered temperature, circulation, precipitation, or freshwater inflow patterns. All of which is to state, once again, that changes in the AMO represent a complex amalgamation of symptoms manifest in the marine ecosystem of the Gulf, and to determine which of those signals is actually impacting the GAJ stock in the LME is an equally complex task that likely requires focused *in situ* and laboratory studies. Once again, however, simulation studies could be performed to assess the effective capacity of the metric to account for recruitment variability simply as a mathematical construct, and not as a mechanistic information criterion. Caution should be employed in all cases, however, because the nature, magnitude, and internal dynamics of the teleconnections associated with the AMO are often variable over time in fisheries contexts (Nye et al. 2009, Alheit et al. 2014, Nye et al. 2014, Karnauskas et al. 2015, Kilborn et al. 2018).

4.4.2 Leading Habitat Indicators

The remaining ecological factors that were flagged as potential leading indicators for GAJ recruitment were mostly related to habitat considerations. Much like the AMO, however, habitat represents a complex tapestry of actual mechanisms and interactions that could underly the nature of the true relationship. Thus, while underwater structure and artificial habitat appears to be a very powerful factor for GAJ as a species, it is unclear how this influences recruitment, and even when only exploring the unexplained deviations in the SS3 model (i.e., a small component of the estimated recruitment from the model). This can be seen in the apparent oppositional effects on stock recruitment deviations due to changes in artificial reefs that either are, or are not, associated with the petroleum and gas industry. As mentioned above, it is encouraging that both the AMO and the number of oil platforms in the Gulf LME were both able to explain detrended variability in the deviations, as this implies that this is actually wholly new explained variability for this species that was not driven by temporally-associated processes. Unlike the AMO, however, the effects of oil industry infrastructure on GAJ has been studied to some degree, and there is a known association between this species and the habitat (Seaman et al. 1989, Stanley and Wilson 1997, Franks 2000, Reynolds et al. 2018).

Considering *Sargassum* as habitat for GAJ is also not unreasonable, as there are documented associations with this species and the floating macroalgae as well (Bortone et al. 1977, Wells and Rooker 2004b, a). Once again, though, this is very likely to be a more nuanced relationship due to the fact that *Sargassum* habitats foster a large diversity of fishes (Bortone et al. 1977, Wells and Rooker 2003). Therefore, in addition to the provision of refugia, a variety of other interspecific and density-dependent considerations (e.g., predator-prey dynamics, competition for resources or space) become worthy of investigating to disentangle the true advantages (or disadvantages) that are associated with annual variation in the availability of this form of aquatic habitat. The models developed here identified, specifically, the FL Middle Grounds as a notable location to monitor *Sargassum*, and particularly during the spawning season for GAJ. This information could be the basis for designing a more focused study within that area, or the larger Gulf region surrounding it, but it also points to a gap in the understanding of the impacts of spatial constraints on fish species, particularly habitat-associated ones, in the LME. There is some evidence to suggest that the FL Middle Grounds benefits from weak larval dispersal effects (Johnson et al. 2017), and so this is a plausible mechanism that could contribute to this areas apparent importance to GAJ recruitment, but more investigation into that matter would be required. Therefore, while this work showed promise for *Sargassum* as a leading indicator, considerably more observational work may need to be undertaken in order to ascertain which spatiotemporal factors better suit for predictive purposes. Since *Sargassum* is itself a passive agent with respect to mobility, simulation studies related to physical dispersal patterns of the surface expression of algal mats would be beneficial to management, provided a more detailed understanding of the utilization of these habitats can be incorporated as well.

4.4.3 Autocorrelation and Periodic Signals

It should be noted that the data used for these studies were derived from those used in management decision making, and are themselves the product of a very complex data collection, validation, and subsequent modeling process. As such, they constitute the best available science and knowledge concerning the stock, at least until a new (or updated historical) model is developed. Additionally, and as previously noted, given the nature of the time-series models used for those efforts, some level of temporal autocorrelation might be expected. It does come as somewhat of a surprise, however, to see that no less than ~17% of the adjusted variability (max $R^2_{adj} \cong 32\%$) in any time series of GAJ recruitment deviations could be explained by wholly synthetic AEM models derived from the annualized period of study. In all cases, the relatively short-term and repeating period of ~8-11 years (potentially a decadal cycle) was prevalent across three of the five temporal models, and two of those with $n > 25$ years displayed longer temporal trends as well (averaging ~25 years between them).

The persistence of these scales and trends across models implies one of two things, (1) there are unaccounted for factors that operate on these temporal scales, or (2) there is some sort of mechanistic bias imparted by the modeling process for SS3. The existence of significant synthetic temporal factors that can moderately predict portions of the SS3 model's error is not an indictment of the assessment model itself, but rather, it is a call to better understand the temporally structured drivers that are influencing the outcomes it predicts, and incorporate them into a better informed, next-generation stock assessment model. The eigenvector techniques used here can inform those models, and could even be used as standalone substitutes in the absence of real mechanistic indicators. However, constant monitoring and recursive updating would be required in order to avoid missing the replacement of one dominant temporal signal for another, in the cases where more than one time scale is relevant (e.g., eutrophication model).

5.0 CONCLUSIONS & RECOMMENDATIONS

The main objectives of this study were to investigate long-term, ecological time series and determine their ability to describe any unknown variability in the annual stock recruitment of Greater Amberjack in the Gulf LME, and to do so with respect to its particular SS3 management model's results. As an additional focus, the relationship between *Sargassum spp.* areal coverage was more closely examined for its capacity to impact GAJ recruitment in both spatial and temporal contexts. Three more focused models were also developed to explicitly explore other suites of factors hypothesized to affect the early life history stages of GAJ (e.g., habitat, water quality), and all of which yielded some level of information that could be applied to future ecosystem considerations for this species. Finally, the last priority of this effort, to determine if there was an already-existing capacity to estimate GAJ new recruits during periods between formal assessments or SS3 model updates using existing data collection or monitoring efforts, was somewhat more complex than expected, partly due to spatial and temporal mismatches in the available data.

In short, and to address the first main objective of this work, there does appear to be some capacity to compliment future stock assessment efforts by incorporating ecosystem considerations into the GAJ's stock dynamics. Unfortunately, the realization of this capacity may still require further investigation prior to implementation. For example, each of the significant models discussed here only accounted for < 25% of the variability in the deviations between the theorized B-H stock recruitment levels for GAJ and the bias-adjusted SS3-derived values (i.e., the reality at the time), and only one of those models actually spanned the entire 46-year time period for which recruitment deviation data were available. Thus, at a very general level, these models show that environmental considerations should be included in any conversation regarding a predictive model of GAJ recruitment levels. The modeling and variable selection processes outlined above were undertaken in an effort to explain both the temporal (i.e., fitted) and non-temporal (i.e., detrended) GAJ recruitment deviations, and to try to determine if there are any currently monitored ESR indicators or *Sargassum*-related metrics that could capture their unexplained dynamics. Where these models fall short implies more to learn, other important factors that are currently unmonitored, and relationships or dynamics yet to be uncovered.

The data for this work, aside from the *Sargassum* data collected specifically for the task, were all publicly available at the time of the investigation, and were intentionally limited to this scope due to the desire to determine if there were any immediate potential to inform GAJ management in between SEDAR events. One of the take-aways from this process is that the mismatched observation timescales across suites of related characteristics was problematic. For example, very few indicators were collected over the entire time series used for GAJ management. In other cases, as seen when comparing the periods actually modeled, while many variables ended ~2014-2015, the starting dates were not compatible (i.e., 1970 vs

1982 vs 1987 vs 2000). Further, to reduce the majority of the data such that it would all be able to be considered at once would mostly repeat similar analyses performed on 2013 ESR data (Karnauskas et al. 2013, Karnauskas et al. 2015, Kilborn et al. 2018). This highlights an existing problem in ecosystem-based management, where long-term monitoring data are not always sustained or funded to the level required for recurring reassessment and management uptake.

Out of all the ecosystem considerations modeled and selected for against the GAJ recruitment deviations, the *Sargassum* results were the least encouraging, presumably because they provided no real certainty except to say that more focused field work and monitoring research are required. Those variables most likely to produce immediate returns on research effort are related to the oxygen saturation of the aquatic environment, potentially offshore Texas in particular, and the association of the species with petroleum extraction infrastructure. This artificial structure work could also reasonably extend to other, non-oil related installations as well. Lastly, the effects of the AMO and its teleconnected processes are important to the GAJ stock recruitment relationship, however the extent of that relationship, and the mechanisms at play are not well understood and will require significant further effort to untangle.

The weight of evidence appears to imply that, in addition to the fishing-related considerations built into the high-complexity, age-structured SS3 model for GAJ, habitat and water-quality considerations may also benefit its predictive performance. While the largest gains in knowledge are likely to be tied to habitat-availability related concerns, the higher probability of successfully uncovering the magnitude, direction, and timing of the relationship for incorporation into mathematical modeling may lie with other, lower-impact parameters such as DO. Unfortunately, in all circumstances, more work will need to be done in order to produce interim, *sans*-SEDAR recruitment updates. Furthermore, far more spatially and temporally explicit sampling and modeling will need to be undertaken in order to better understand the level of usage of *Sargassum* habitats throughout the GAJ's ontogeny. This work provides greater insight into the trade-offs associated with GAJ recruitment and its aquatic environment and climate. Over time, and as more work focused on incorporating ecosystem-considerations into understanding the particular effects to the Gulf of Mexico's Greater Amberjack stock's population dynamics, demographics, and reproductive capacity emerges, how to incorporate these matters into decision support tools will become more apparent. For the moment, though, the first set of priorities has been identified via these analyses.

6.0 LITERATURE CITED

Akaike, H. 1974. A New Look at the Statistical Model Identification. Ieee Transactions on Automatic Control **AC19**:716-723.

Alheit, J., P. Licandro, S. Coombs, A. Garcia, A. Giraldez, M. T. G. Santamaria, A. Slotte, and A. C. Tsikliras. 2014. Atlantic Multidecadal Oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central Atlantic. Journal of Marine Systems **131**:21-35.

Blanchet, F. G., P. Legendre, and D. Borcard. 2008a. Forward selection of explanatory variables. Ecology **89**:2623-2632.

Blanchet, F. G., P. Legendre, and D. Borcard. 2008b. Modelling directional spatial processes in ecological data. Ecological Modelling **215**:325-336.

Blanchet, F. G., P. Legendre, R. Maranger, D. Monti, and P. Pepin. 2011. Modelling the effect of directional spatial ecological processes at different scales. Oecologia **166**:357-368.

Bortone, S. A., P. A. Hastings, and S. B. Collard. 1977. The Pelagic Sargassum Ichthyo Fauna of the Eastern Gulf of Mexico. Northeast Gulf Science **1**:60-67.

Enfield, D. B., A. M. Mestas-Nunez, and P. J. Trimble. 2001. The Atlantic multidecadal oscillation and its relation to rainfall and river flows in the continental US. Geophysical Research Letters **28**:2077-2080.

Fahay, M. P. 1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV DOLPHIN cruises between May 1967 and February 1968. Pages 1-39 *in* D. o. Commerce, editor. National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Franks, J. 2000. A review: pelagic fishes at petroleum platforms in the Northern Gulf of Mexico; diversity, interrelationships, and perspective.*in* Pêche thonière et dispositifs de concentration de poissons, Caribbean-Martinique, 15-19 Oct 1999.

GMFMC. 2016. Final Report 5-Year Review of Essential Fish Habitat Requirements. Pages 1-502 Including Review of Habitat Areas of Particular Concern and Adverse Effects of Fishing and Non-Fishing in the Fishery Management Plans of the Gulf of Mexico. Gulf of Mexico Fishery Management Council, Tampa, FL.

Godinez-Dominguez, E., and J. Freire. 2003. Information-theoretic approach for selection of spatial and temporal models of community organization. Marine Ecology Progress Series **253**:17-24.

Harris, P. J., D. M. Wyanski, D. B. White, P. P. Mikell, and P. B. Eyo. 2007. Age, growth, and reproduction of greater amberjack off the southeastern US Atlantic coast. Transactions of the American Fisheries Society **136**:1534-1545.

Johnson, D. R., H. M. Perry, G. Sanchez-Rubio, and M. A. Grace. 2017. Loop Current Spin-off Eddies, Slope Currents and Dispersal of Reef Fish Larvae from The Flower Gardens National Marine Sanctuary and The Florida Middle Grounds. Gulf and Caribbean Research **28**:10.

Jones, D. L. 2017. The Fathom Toolbox for MATLAB: Software for multivariate ecological and oceanographic analysis. University of South Florida, College of Marine Science, St. Petersburg, FL, USA. Available from: https://www.marine.usf.edu/research/matlab-resources/.

Karnauskas, M., C. R. Kelble, S. Regan, C. Quenée, R. Allee, M. Jepson, A. Freitag, J. K. Craig, C. Carollo, L. Barbero, N. Trifonova, D. Hanisko, and G. Zapfe. 2017. 2017 Ecosystem status report update for the Gulf of Mexico. Technical Memorandum NMFS-SEFSC-706, NOAA, Southeast Fisheries Science Center, Miami, FL.

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

Karnauskas, M., M. J. Schirripa, C. R. Kelble, G. S. Cook, and J. K. Craig. 2013. Ecosystem status report for the Gulf of Mexico. Technical Memorandum NMFS-SEFSC-653, NOAA, Southeast Fisheries Science Center, Miami, FL.

Kilborn, J. P. 2020. The Darkside Toolbox for MATLAB. University of South Florida, College of Marine Science, St. Petersburg, FL.

Kilborn, J. P. *unplublished*. Fisheries Ecosystem Trajectories in the Gulf of Mexico (1987-2013). Unpublished **n/a**.

Kilborn, J. P., M. Drexler, and D. L. Jones. 2018. Fluctuating fishing intensities and climate dynamics reorganize the Gulf of Mexico's fisheries resources. Ecosphere **9**:e02487.

Kumpf, H., K. A. Steidinger, and K. Sherman. 1999. The Gulf of Mexico large marine ecosystem : assessment, sustainability, and management. Blackwell Science, Malden, Mass., USA.

Legendre, P., and L. Legendre. 2012. Numerical Ecology. Third English edition edition. Elsevier, Amsterdam, The Netherlands.

Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology. Ecology **73**:1943-1967.

MATLAB. 2020a. The MathWorks, Inc., Natick, Massachusetts, United States.

MATLAB. 2020b. Econometrics Toolbox. The MathWorks, Inc., Natick, Massachusetts, United States.

Nye, J. A., M. R. Baker, R. Bell, A. Kenny, K. H. Kilbourne, K. D. Friedland, E. Martino, M. M. Stachura, K. S. Van Houtan, and R. Wood. 2014. Ecosystem effects of the Atlantic Multidecadal Oscillation. Journal of Marine Systems **133**:103-116.

Nye, J. A., J. S. Link, J. A. Hare, and W. J. Overholtz. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series **393**:111-129.

Papandroulakis, N., C. C. Mylonas, E. Maingot, and P. Divanach. 2005. First results of greater amberjack (Seriola dumerili) larval rearing in mesocosm. Aquaculture **250**:155-161.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK ; New York.

Rao, C. R. 1964. The use and interpretation of principal component analysis in applied research. Sankhyā: The Indian Journal of Statistics, Series A:329-358.

Reynolds, E. M., J. H. Cowan, K. A. Lewis, and K. A. Simonsen. 2018. Method for estimating relative abundance and species composition around oil and gas platforms in the northern Gulf of Mexico, U.S.A. Fisheries Research **201**:44-55.

Sawada, Y., M. Hattori, M. Iteya, Y. Takagi, K. Ura, M. Seoka, K. Kato, M. Kurata, H. Mitatake, S. Katayama, and H. Kumai. 2006. Induction of centrum defects in amberjack Seriola dumerili by exposure of embryos to hypoxia. Fisheries Science **72**:364-372.

Seaman, J. W., W. J. Lindberg, C. R. Gilbert, and T. K. Frazer. 1989. Fish Habitat Provided by Obsolete Petroleum Platforms off Southern Florida. Bulletin of Marine Science **44**:1014-1022.

SEDAR. 2014. SEDAR 33 Stock Assessment Report - Gulf of Mexico Greater Amberjack. SEDAR, North Charleston, SC.

SEDAR. 2016. SEDAR 33 Stock Assessment Report Update - Gulf of Mexico Greater Amberjack. SEDAR, North Charleston, SC.

Stanley, D. R., and C. A. Wilson. 1997. Seasonal and spatial variation in the abundance and size distribution of fishes associated with a petroleum platform in the northern Gulf of Mexico. Canadian journal of fisheries and aquatic sciences **54**:1166-1176.

Tolimieri, N., M. A. Haltuch, Q. Lee, M. G. Jacox, and S. J. Bograd. 2018. Oceanographic drivers of sablefish recruitment in the California Current. Fisheries Oceanography **27**:458-474.

Wang, M., C. Hu, J. Cannizzaro, D. English, X. Han, D. Naar, B. Lapointe, R. Brewton, and F. Hernandez. 2018. Remote Sensing of Sargassum Biomass, Nutrients, and Pigments. Geophysical Research Letters **45**:12,359-312,367.

Wang, M. Q., C. M. Hu, B. B. Barnes, G. Mitchum, B. Lapointe, and J. P. Montoya. 2019. The great Atlantic Sargassum belt. Science **365**:83-+.

Wells, R. J. D., and J. R. Rooker. 2003. Distribution and abundance of fishes associated with Sargassum mats in the NW Gulf of Mexico. Gulf Caribbean Fisheries Inst Gcfi, Ft Pierce.

Wells, R. J. D., and J. R. Rooker. 2004a. Distribution, age, and growth of young-of-the-year greater amberjack (Seriola dumerili) associated with pelagic Sargassum. Fishery Bulletin **102**:545-554.

Wells, R. J. D., and J. R. Rooker. 2004b. Spatial and temporal patterns of habitat use by fishes associated with Sargassum mats in the northwestern Gulf of Mexico. Bulletin of Marine Science **74**:81-99.

Zhang, L. P., C. Z. Wang, and L. X. Wu. 2012. Low-frequency modulation of the Atlantic warm pool by the Atlantic multidecadal oscillation. Climate Dynamics **39**:1661-1671.