



Evidence of shared trends in juvenile fish recruitment to nearshore seagrass habitats of the eastern Gulf of Mexico

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ABSTRACT: Monitoring abundance of juveniles over time is fundamental to effective fisheries management, especially when juvenile abundance may be used to predict future productivity. Yet, the mechanisms underlying variation in fish recruitment remain a source of uncertainty for fully understanding population dynamics. Given the interest in progression from single-species to ecosystem-based fisheries management, tracking multiple species over time and determining overall trends becomes a key component of management. Therefore, we (1) examined potential temporal synchrony among recruitment of juvenile fish species to seagrass habitats along the West Florida Shelf (WFS) in the eastern Gulf of Mexico and (2) sought to identify potential environmental covariates driving shared trends among species. Dynamic factor analysis identified 3 shared trends among catch-per-unit-effort (CPUE) time series of 11 species from a 2008–2018 trawl survey. The first and third trends had similar bimodal patterns with high CPUEs at the beginning of the time series, a decline, and then an increase near the end of the time series. The second trend had increasing CPUEs for the first 2 yr, a stable but variable trend in the middle, and an increase thereafter. Within the annual trends, most species' seasonal CPUEs mimicked seasonal variability of seagrass biomass. Furthermore, southeast to westerly winds along the WFS 1 mo prior to sampling coincided with increased juvenile fish abundance for multiple species. Although the model is not without its limitations, there is evidence of shared recruitment patterns among fishes, which can inform multispecies survey design, habitat protection and restoration efforts, and management decisions for data-rich and data-limited species.

KEY WORDS: Dynamic factor analysis · Multispecies synchrony · Marine fisheries · Juvenile fish recruitment · Population dynamics · Time-series analysis · Gulf of Mexico

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1. INTRODUCTION

The coincident changes in time-varying characteristics (e.g. abundance) of populations, termed synchrony (Liebhold et al. 2004), is a fundamental aspect of population dynamics and can play a significant role in conservation and management. In highly synchronized populations, population growth or decline generally occurs among all synchronized populations (Moran 1953, Descamps et al. 2013 and references

therein). After a period of initial growth among all populations, however, it is possible that some populations decline due to competitive disadvantages among species (Chagaris et al. 2015). Less synchronous and more heterogeneous populations, in contrast, tend to have greater recovery rates and are generally more resistant to massive population reductions (Schindler et al. 2010).

Understanding synchronous, and asynchronous, relationships and the mechanisms driving population

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[§]Author email was updated.
This corrected version: August 22, 2022

dynamics has important implications for species conservation and management (Liebhold et al. 2004, Linné Kausrud et al. 2007, Keller et al. 2017). This is especially relevant given the recent push for multi-species, and ultimately ecosystem-based, fisheries management (Lindeman et al. 2000, Hall & Mainprize 2004, Pikitch et al. 2004, Marasco et al. 2007, Dell’Apa et al. 2015, Chagaris et al. 2019, Dell’Apa et al. 2020). However, the causal forces driving many synchronous population fluctuations remain poorly understood (Bjørnstad et al. 1999, Liebhold et al. 2004, Walter et al. 2017).

For over 30 yr, recruitment variability has been a major source of uncertainty in fisheries management (Sissenwine 1984, Tableau et al. 2019). Variation in recruitment is largely related to life-history patterns and timing reproduction with favorable environmental conditions (both physical and biological), which affect population dynamics (e.g. Lindeman et al. 2000, Van der Veer et al. 2000, Ammann 2004, Pepin 2015, Bode et al. 2016). Abundance during early life-history stages can coincide with fishery year class strength (e.g. Caputi & Brown 1986, Bailey & Spring 1992, Van der Veer et al. 2000, Fitzhugh et al. 2003, Hanisko et al. 2007, Ingram et al. 2007) and may be useful for forecasting future fishery productivity (Zuur et al. 2003b, Johnson & Koenig 2005). Stock managers are better able to determine best management actions when year class abundance can be predicted a year or more prior to a cohort entering the fishery (Stige et al. 2013 and references within). While moving toward multispecies conservation and management, decision makers now need to simultaneously assess recruitment for multiple species representing various life-history patterns.

Understanding temporal synchrony in recruitment among fish species with similar juvenile habitat requirements can be instrumental for sound fisheries management. For example, multiple species use marine seagrass beds as juvenile habitat (e.g. Beck et al. 2001 and references within), including fishery species that live in offshore reef habitats as adults (e.g. members of the snapper–grouper complex) (Luo et al. 2009, Switzer et al. 2012) and nearshore species that may use seagrass habitats as transients or residents. Identifying and understanding potential synchronous patterns in juvenile recruitment of these species can provide information on community trends over time. This could lead to more effective monitoring and management decisions because if fisheries researchers and managers better understand the degree of synchrony among populations, they may be better equipped to implement multispecies monitor-

ing surveys and predict and understand how species will respond to fishing pressure and other anthropogenic or natural disturbances.

Because management and conservation decisions are fundamentally based on trends over time, it is important to recognize how various species abundances are collectively changing over time. Therefore, we set out to (1) assess whether there were common temporal patterns in recruitment of juvenile fishes to nearshore seagrass beds along the West Florida Shelf (WFS) in the eastern Gulf of Mexico and (2) identify potential environmental covariates driving shared trends among species. We focused on 11 species that could broadly be categorized as reef-associated and non-reef, or nearshore, species. Six are recreationally and commercially important reef fishery species with an estuarine- or nearshore-dependent juvenile life-history stage: black sea bass *Centropristis striata*, white grunt *Haemulon plumierii*, hogfish *Lachnolaimus maximus*, gray snapper *Lutjanus griseus*, lane snapper *Lutjanus synagris*, and gag *Mycteroperca microlepis*. Five are non-reef fishes that use nearshore seagrass beds during various life stages and co-occur with the juvenile reef species: silver perch *Bairdiella chrysoura*, spotted seatrout *Cynoscion nebulosus*, pinfish *Lagodon rhomboides*, pigfish *Orthopristis chrysoptera*, and Gulf flounder *Paralichthys albigutta*. This set of 11 species includes both economically important reef and non-reef fishery species that are predators in the ecosystem, as well as ecologically important forage species. The inclusion of reef, non-reef, predator, and prey species allowed us to examine potential synchrony among a variety of taxa, with varying life histories, that share a common habitat in the eastern Gulf of Mexico, which can ultimately inform multi-species survey design, conservation, and management decisions.

2. MATERIALS & METHODS

2.1. Trawl sampling

The Florida Fish and Wildlife Conservation Commission’s Fish and Wildlife Research Institute’s (FWC-FWRI) Fisheries-Independent Monitoring Program (FIM) conducts monthly, standardized, stratified-random, 6.1-m otter trawl (38-mm mesh with a 3.2-mm mesh liner) sampling in polyhaline (salinity >18) seagrass habitats in 5 estuarine regions of the eastern Gulf of Mexico: St. Andrew Bay (SA), Apalachicola Bay (AP), the Big Bend region (BB), Tampa Bay (TB), and Charlotte Harbor (CH) (Fig. 1). The survey began

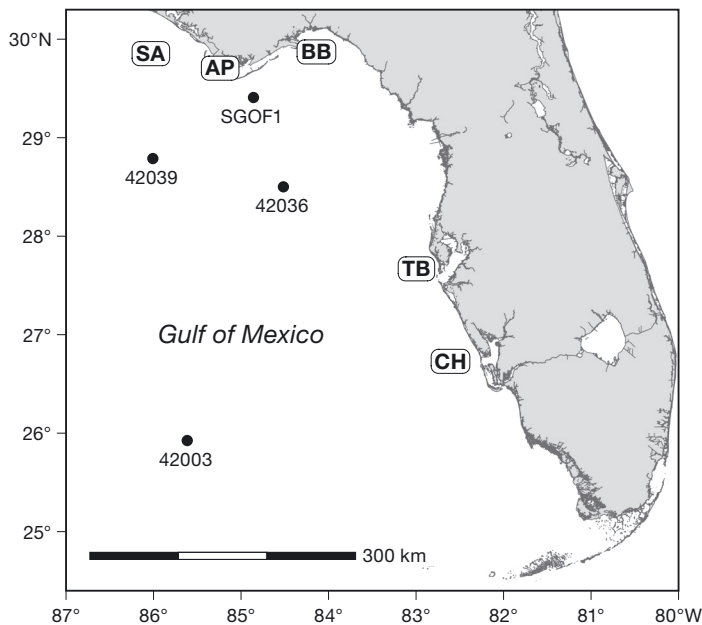


Fig. 1. Locations of the 5 eastern Gulf of Mexico estuaries, St. Andrew Bay (SA), Apalachicola Bay (AP), the Big Bend (BB) region, Tampa Bay (TB), and Charlotte Harbor (CH), sampled for juvenile reef fish abundance. The 4 offshore buoys used for wind data are denoted by filled black circles labeled with the buoy identification number from NOAA's National Data Buoy Center

in 2008 and was initially conducted from May through November to obtain data on juvenile estuarine-dependent, reef-associated fishes (e.g. Switzer et al. 2012, Flaherty et al. 2014, Flaherty-Walia et al. 2015). In 2016, monthly sampling was reduced to June through November to coincide with the predominant recruitment season of juvenile reef-associated fishes. During the annual 6-mo sampling window, there were approximately 36 trawl tows in SA, 48 in AP, 180 in BB, 60 in TB, and 48 in CH. The number of sampling sites differed by estuary according to the extent of available habitat. The survey is ongoing, so we restricted our analyses to the subset of available data with the most consistent sampling design, June through November 2008 through 2018, resulting in a total of 4087 tows during the 11-yr time series.

In each estuary, sampling sites were selected using a stratified-random design based on 0.1×0.1 nautical mile (1 nautical mile = 1.85 km) grid cells overlaid on polyhaline submerged aquatic vegetation (e.g. seagrass, rooted macroalgae) habitats in 1.0–7.6 m of water. Sampling sites were restricted to areas with $\geq 50\%$ cover of submerged aquatic vegetation, confirmed on site prior to each trawl deployment, using methodologies that prevent or minimize disturbance to the area. Visual assessment of SAV composition and coverage

was done from the surface, via drop camera, or by a free-diving swimmer when water clarity permitted. If water clarity prevented a visual assessment, tactile assessment was used at 4 equidistant points along the transect, with points within the transect assessed after trawling. Each trawl was towed into the direction of the prevailing current, which varied with tide and wind conditions. Boat speed was maintained at roughly 0.6 m s^{-1} to cover approximately 185 m during a 5-min tow, while GPS coordinates were used to calculate the exact tow distance. Additional information on seagrass habitat trawl procedures can be found in Schrandt et al. (2018). All fish were identified and counted and up to 40 individuals of each species were measured to the nearest millimeter standard length (SL). All individuals were returned to the water as quickly as possible, except for a subsample of individuals that was retained for laboratory confirmation of field identifications.

2.2. Data analysis

Catch data for each species of interest were subset to retain only individuals considered to be young-of-the-year (YOY). Because a subset of individuals was measured, we first used the measured portion of each collection, combined with the total number collected, to assign ratios defining the proportion of the total catch falling within 10-mm size classes. These ratios were then used to extrapolate lengths to the unmeasured portion of each collection. Finally, we subset for YOY sizes. We designated YOY sizes (in mm SL) using published length-at-age estimates from scientific literature (Table 1). When published lengths were presented in fork length (FL) or total length (TL) and conversions were not presented, we consulted the FIM program's historical length database (>20 yr of length records from various studies) to supplement the literature conversions (Table 1). Because the literature predominantly contained information for age-1 individuals, we were conservative with our size classifications and used a YOY length less than the published age-1 length (Table 1). After each species was subset for YOY individuals, we calculated catch-per-unit-effort (CPUE) as the number of YOY fish 100 m^{-2} because tow distance, and therefore effort, varied among trawls. We then calculated average month \times year CPUEs, regardless of estuary, because (1) we were interested in temporal synchrony across the region and (2) single-species stock assessments for various reef species are conducted for the eastern Gulf of Mexico as a whole (e.g. SEDAR 2014, SEDAR

Table 1. Length at age and associated morphometric conversions (if length at age 1 was not provided in the literature) for juvenile fishes that inhabit nearshore seagrass beds in the eastern Gulf of Mexico. F: forage species; P: predator species; FL: fork length; SL: standard length; TL: total length; YOY: young-of-the-year; FWRI-FIM: Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Fisheries-Independent Monitoring program; DFA: dynamic factor analysis

Species (trophic category)	Estimated mean size at age 1 (mm)	Source: age 1	Morphometric conversion	Source: conversion	Estimated YOY SL (mm) for DFA
Reef					
<i>Centropristis striata</i> , black sea bass (P)	148 SL	Hood et al. (1994)			110
<i>Haemulon plumieri</i> , white grunt (F)	200 TL	Murie & Parkyn (2005)	TL = 1.3 (SL) – 1.85	FWRI-FIM	150
<i>Lachnolaimus maximus</i> , hogfish (P)	150 FL	McBride & Richardson (2007), Collins & McBride (2011)	FL = 1.26 (SL) – 1.19	FWRI-FIM	120
<i>Lutjanus griseus</i> , gray snapper (P)	150 TL	Burton (2001)	TL = 1.27 (SL) – 0.689	FWRI-FIM	115
<i>Lutjanus synagris</i> , lane snapper (P)	150 TL	Johnson et al. (1995)	TL = 1.27 (SL) – 0.530	FWRI-FIM	115
<i>Mycteroperca microlepis</i> , gag (P)	383 TL	Hood & Schlieder (1992)	TL = 1.147 (SL) + 30.299	Hood & Schlieder (1992)	300
Non-reef					
<i>Bairdiella chrysoura</i> , silver perch (F)	126 SL	Grammer et al. (2009)			110
<i>Cynoscion nebulosus</i> , spotted seatrout (P)	350 TL	Murphy & Taylor (1994)	TL = 1.16 (SL) + 4.07	FWRI-FIM	295
<i>Lagodon rhomboides</i> , pinfish (F)	100 SL	Nelson (2002)			100
<i>Orthopristis chrysoptera</i> , pigfish (F)	125 TL	Hildebrand & Cable (1930)	TL = 1.19 (SL) + 10.2	FWRI-FIM	90
<i>Paralichthys albigutta</i> , Gulf flounder (P)	275 TL	Fitzhugh et al. (2008)	TL = 1.17 (SL) + 13.4	FWRI-FIM	220

2018a,b). This resulted in 11 time series, one for each species. We chose to use month \times year averages (6 mo \times 11 yr = 66 data points) so we could assess intra- and inter-annual temporal trends and to meet sample size recommendations (≥ 25 data points) of the selected statistical analyses if they are to be used in the future for predicting fishery productivity (Zuur et al. 2003b).

To assess whether there were common temporal juvenile recruitment patterns among species along the WFS, we used dynamic factor analysis (DFA; Zuur et al. 2003a). This analysis can be likened to a principal components analysis for time series data (Zuur et al. 2003a,b) and has been previously used to identify common trends in fisheries time series data (e.g. Zuur et al. 2003b, Zuur & Pierce 2004, Vânia et al. 2014, Sathianandan et al. 2016, Tableau et al. 2019, Ward et al. 2019). It also has the benefit of being applicable to relatively shorter time series (Zuur et al. 2003a). A detailed, technical description of DFA can be found in Zuur et al. (2003a). Briefly, DFA uses multivariate autoregressive state-space (MARSS) models, which cope with non-stationary data, and treats every time series as a linear combination of multiple state processes (Holmes et al. 2012). DFA estimates the number of common trends (i.e. state processes) and their weightings among the time series that explain the larger data set, like a dimension-reduction analysis. The collection of time series is modeled as a linear combination of common trends + factor loadings (+ covariates) + error terms. The amount each time series resembles each trend is described by the factor loadings; loadings in opposite directions for different trends indicate the time series resembles one trend more than another. Multiple species loading in the same direction for a single trend indicates similarity, or synchrony, in the species time series. Covariates (i.e. environmental or explanatory variables) can be included in the model but only one time series per covariate per model (i.e. a model with 11 species time series can have only one time series for each covariate). Various combinations of these models can be applied, including varying the number of trends, changing explanatory variables, and varying the structure of the error covariance matrix. A model selection procedure (e.g. comparison of Akaike's information criterion) can then be used to select the best-fitting model.

We explored 3 environmental variables (i.e. covariates) for correlation with the CPUE dynamics, given their potential to affect juvenile and adult population dynamics in the eastern Gulf of Mexico: (1) the Atlantic Multidecadal Oscillation (AMO), which has been demonstrated to affect the frequency of major hurricane events in the Gulf of Mexico (Poore &

Brock 2011); (2) the El Niño Southern Oscillation Index (SOI), which affects weather patterns in the Gulf of Mexico; and (3) the prevailing wind direction for the WFS, which can influence larval transport, the movement of mobile refuge habitats (e.g. drift algae, bryozoans), water mixing patterns, and particulate resuspension in the Gulf of Mexico (Pederson & Peterson 2002, Jackson 2004, Johnson et al. 2005, 2009, 2017, Yeager et al. 2005). The AMO and SOI data were obtained from the NOAA Physical Sciences Laboratory page (<https://psl.noaa.gov/data/climateindices/>) and wind information was collected from 4 buoys (42039, SGOF1, 42036, 42003) along the WFS that are part of NOAA's National Data Buoy Center (<https://www.ndbc.noaa.gov/>) (Fig. 1). The buoys were selected for their proximity to the studied estuaries and likelihood of representing wind conditions on the majority of the WFS. All 4 buoys measured both components of wind, speed and direction, but not all had data for every sampling month and year between 2008 and 2018. Therefore, we calculated year \times month average wind for each buoy following Grange (2014) by separating the wind into its vector components and using vector functions. Average wind was positively correlated ($r = 0.44\text{--}0.88$, $p < 0.05$) among buoys so we averaged data among all 4 buoys following methods by Grange (2014) to obtain a single, complete year \times month time series to use in the DFA models. The AMO and SOI data were also averaged by year and month to produce a time series of the same resolution as the CPUE data.

In addition to obtaining environmental data for the month of sampling, we calculated 1, 2, 3, 4, and 5 mo lags for each of the 3 covariates to determine (via model selection) if conditions in the months prior to sampling better fit the catch data. With peak spawning times for the species of interest ranging from a few months to year-round (Darcy 1983, Manickhand-Dass 1987, Hood & Schlieder 1992, Hood et al. 1994, Murie & Parkyn 2002, Brown-Peterson et al. 2002, Nelson 2002, Fitzhugh et al. 2008, Allman & Goetz 2009, Grammer et al. 2009, Collins & McBride 2015), it was not possible to test environmental variables at a single peak-spawning time. Testing a range of lags from 1 to 5 mo encompassed the estimated time from spawning to size of recruitment to the sampling gear in polyhaline seagrass beds for multiple reef species: approximately 2–3 mo for *Lutjanus griseus* (Allman & Grimes 2002) and *L. synagris* (Mikulas & Rooker 2008), 3 mo for *Centropristis striata* (Able & Hales 1997), 4 mo or less for *Haemulon plumierii* (Saksena & Richards 1975), and 4–5 mo for *M. microlepis* (Strelcheck et al. 2003). Approximate size of recruitment to the sam-

pling gear was informed by length–frequency distributions from the same polyhaline seagrass survey, presented by Schrandt et al. (2021).

DFA was implemented with the MARSS (v. 3.11.4) package (Holmes et al. 2012) in R version 4.0.5 (R Core Team 2019). Each time series, CPUE and covariates, was first standardized by subtracting the mean and dividing by the standard deviation so the interpretation of common trends and factor loadings was comparable among time series. DFA was originally applied to the 11 CPUE time series to select the best-fitting model for CPUE data alone. We tested up to 10 possible trends (11 time series minus 1) with 4 different structures for the covariance matrix (same variances and no covariance, different variances and no covariance, same variances and same covariance, and different variances and covariances); the full complement (40 models) of trends and matrix variance structures were fit to select the best-fitting model for CPUE data alone (Table 2). Model selection was based on Akaike's information criterion as in Zuur et al. (2003a,b) for small sample size correction (AICc), with the model having the smallest AICc value selected as the most appropriate model for the CPUE time series alone.

After selecting the best DFA model for the CPUE time series, we assessed whether the model could be improved with the addition of covariates (Zuur et al. 2003a,b, Zuur & Pierce 2004). We did this in a 2-step approach. First, we modeled each of the 6 (current month + 5 lags) covariate time series with the CPUE time series and selected the best-fitting model for each covariate (Table 3), resulting in 3 (1 for each covariate) best-fit models. Second, we modeled all possible combinations (1, 2, or 3 covariates) of the best-fitting covariate models and calculated AICc. The final model was the model with the best AICc value overall (Table 3) to prevent over-fitting of the DFA model. To assist in biological interpretation of the full suite of information from the final DFA model, the error covariance matrix, \mathbf{R} , was transformed into a dissimilarity matrix via absolute correlations and visualized with multidimensional scaling (MDS) (Zuur et al. 2003b), displaying the degree of absolute correlation among species. As this is an MDS plot based on the error term of the DFA, clusters of species on the MDS plot indicate the species share some amount of information not explained by the DFA model's common trends and covariate(s) (Zuur et al. 2003b). Groups of species may have other attributes in common (e.g. similar life-history strategies, functional guild, geographic proximity) that influence the shared trends among species.

Table 2. Dynamic factor analysis (DFA) models applied to 11 time series for young-of-the-year polyhaline seagrass-associated fish species in the eastern Gulf of Mexico to determine the best-fit model of the time series data, prior to adding covariates

	Model	Covariance matrix, \mathbf{R}
1	Data = 1 common trend + noise	Diagonal and equal
2	Data = 2 common trends + noise	Diagonal and equal
3	Data = 3 common trends + noise	Diagonal and equal
4	Data = 4 common trends + noise	Diagonal and equal
5	Data = 5 common trends + noise	Diagonal and equal
6	Data = 6 common trends + noise	Diagonal and equal
7	Data = 7 common trends + noise	Diagonal and equal
8	Data = 8 common trends + noise	Diagonal and equal
9	Data = 9 common trends + noise	Diagonal and equal
10	Data = 10 common trends + noise	Diagonal and equal
11	Data = 1 common trend + noise	Diagonal and unequal
12	Data = 2 common trends + noise	Diagonal and unequal
13	Data = 3 common trends + noise	Diagonal and unequal
14	Data = 4 common trends + noise	Diagonal and unequal
15	Data = 5 common trends + noise	Diagonal and unequal
16	Data = 6 common trends + noise	Diagonal and unequal
17	Data = 7 common trends + noise	Diagonal and unequal
18	Data = 8 common trends + noise	Diagonal and unequal
19	Data = 9 common trends + noise	Diagonal and unequal
20	Data = 10 common trends + noise	Diagonal and unequal
21	Data = 1 common trend + noise	Equal variances and covariances
22	Data = 2 common trends + noise	Equal variances and covariances
23	Data = 3 common trends + noise	Equal variances and covariances
24	Data = 4 common trends + noise	Equal variances and covariances
25	Data = 5 common trends + noise	Equal variances and covariances
26	Data = 6 common trends + noise	Equal variances and covariances
27	Data = 7 common trends + noise	Equal variances and covariances
28	Data = 8 common trends + noise	Equal variances and covariances
29	Data = 9 common trends + noise	Equal variances and covariances
30	Data = 10 common trends + noise	Equal variances and covariances
31	Data = 1 common trend + noise	Unconstrained
32	Data = 2 common trends + noise	Unconstrained
33	Data = 3 common trends + noise	Unconstrained
34	Data = 4 common trends + noise	Unconstrained
35	Data = 5 common trends + noise	Unconstrained
36	Data = 6 common trends + noise	Unconstrained
37	Data = 7 common trends + noise	Unconstrained
38	Data = 8 common trends + noise	Unconstrained
39	Data = 9 common trends + noise	Unconstrained
40	Data = 10 common trends + noise	Unconstrained

3. RESULTS

Monthly CPUE for reef and non-reef species had similar, cyclical patterns with high CPUEs in the beginning of each year's sampling season, followed by a decline as the year progressed (Fig. 2A,C). Annual CPUE trends varied among the 11 species (Fig. 2B,D). Annual CPUEs for non-reef fish (Fig. 2D) were less variable among species than the reef fish (Fig. 2B) and most had similar temporal trends. Overall, there was an increasing trend in annual CPUE of non-reef

species from 2008 to 2018 (Fig. 2D). Notably, 2010, 2013, and 2014 were high recruitment years for non-reef species: *Lagodon rhomboides* in 2010, *Orthopristis chrysoptera* and *L. rhomboides* in 2013, and *Cynoscion nebulosus* and *Paralichthys albigutta* in 2014. The same years had low CPUEs for some reef species, including *Haemulon plumieri* and *Lachnolaimus maximus*, and to a lesser extent, *Lutjanus synagris*.

Although the time series of standardized CPUEs were variable among the 11 species, the DFA detected 3 common trends among the suite of seagrass-associated species. The DFA reduced the dimensionality to provide fewer time series that represent the community, thereby suggesting evidence of temporal synchrony in juvenile abundance for various seagrass-associated species. The best model for the time series (AICc = 1831) had 3 common trends, a covariance matrix that allowed for different variances and covariances, and a 1-mo lag in average wind (Table 2). Unlike the standardized monthly CPUE trends (Fig. 2A,C), the DFA trends did not exhibit consistent intra-annual patterns for any of the 3 common trends; seasonal peaks occurred at the beginning, middle, or end of each sampling season (Fig. 3A,C,E; shaded areas).

Annual trends from the DFA, in contrast, were more pronounced. The first and third trends had similar bimodal patterns (Fig. 3A,E), while the second trend was more stable (Fig. 3C). All 3 common trends had an overall increase in CPUEs (although the authors do acknowledge some single-year variability) for the last 4 to 5 yr of the time series.

The first common trend depicted the highest CPUEs between 2008 and 2011, followed by an overall decline to the lowest CPUE in 2015, and then an overall increase through 2018 (Fig. 3A). The second trend was more stable than the first, starting with an increase in CPUE from 2008 to 2009, followed by a stable but variable trend from 2009 to 2014, and an overall increase thereafter, with 2018 CPUEs being the highest for the trend (Fig. 3C). The third common trend overall had 2 divergent CPUE trends: a decline from 2008 to 2014, followed by an increase through

Table 3. Dynamic factor analysis (DFA) models applied to 11 time series for young-of-the-year polyhaline seagrass-associated fish species in the eastern Gulf of Mexico. All listed models were fit after selecting the most appropriate CPUE-only (catch-per-unit-effort) model (3 common trends and an unconstrained covariance matrix) via DFA. We used a 2-step approach to first select the best model for each of 3 covariates and then examine model fits with different combinations of covariates. AICc values in bold are the best-fitting model for each environmental variable (Analysis Step 1) or analysis step (Analysis Step 2). The model name in bold is the best-fit model overall. AICc: Akaike's Information Criterion (small sample size correction); AMO: Atlantic Multidecadal Oscillation; SOI: Southern Oscillation Index; WIND: average wind

Model	AICc
Data = 3 common CPUE trends + noise	1871
Analysis Step 1:	
Data = 3 common CPUE trends + AMO + noise	1882
Data = 3 common CPUE trends + AMO_Lag 1 month + noise	1880
Data = 3 common CPUE trends + AMO_Lag 2 months + noise	1876
Data = 3 common CPUE trends + AMO_Lag 3 months + noise	1882
Data = 3 common CPUE trends + AMO_Lag 4 months + noise	1885
Data = 3 common CPUE trends + AMO_Lag 5 months + noise	1886
Data = 3 common CPUE trends + SOI + noise	1889
Data = 3 common CPUE trends + SOI_Lag 1 month + noise	1892
Data = 3 common CPUE trends + SOI_Lag 2 months + noise	1892
Data = 3 common CPUE trends + SOI_Lag 3 months + noise	1893
Data = 3 common CPUE trends + SOI_Lag 4 months + noise	1876
Data = 3 common CPUE trends + SOI_Lag 5 months + noise	1881
Data = 3 common CPUE trends + WIND + noise	1838
Data = 3 common CPUE trends + WIND_Lag 1 month + noise	1831
Data = 3 common CPUE trends + WIND_Lag 2 months + noise	1867
Data = 3 common CPUE trends + WIND_Lag 3 months + noise	1880
Data = 3 common CPUE trends + WIND_Lag 4 months + noise	1871
Data = 3 common CPUE trends + WIND_Lag 5 months + noise	1885
Analysis Step 2:	
Data = 3 common CPUE trends + AMO_Lag 2 months + SOI_Lag 4 months + noise	1885
Data = 3 common CPUE trends + AMO_Lag 2 months + WIND_Lag 1 month + noise	1834
Data = 3 common CPUE trends + SOI_Lag 4 months + WIND_Lag 1 month + noise	1837
Data = 3 common CPUE trends + AMO_Lag 2 months + SOI_Lag 4 months+ WIND_Lag 1 month + noise	1843

2018. Abundances at the beginning and end of this trend were nearly similar in magnitude (Fig. 3E).

The amount each species' time series resembled the common trends was described by the factor loadings, whereby each species could have loadings on multiple trends, with the direction and strength indicating which common trend most resembled the species' time series (Fig. 3B,D,F). There was evidence of temporal synchrony in recruitment of juvenile fishes to nearshore seagrass beds because multiple species had positive loadings on the same common trend, for each of the 3 common trends. The time series for *Centropristis striata*, *L. rhomboides*, and *Mycteroperca microlepis* all resembled Trend 1 (Fig. 3B). Similarly, *C. striata*, *C. nebulosus*, and, to a lesser extent, *L. maximus* resembled Trend 2 (Fig. 3D). Although Trend 3 had resemblances to *L. maximus*, *L. synagris*, and *O. chrysoptera*, *L. maximus* had the strongest resemblance to the common trend (Fig. 3F). Three species' time series did not strongly resemble any of the

3 common trends: *Bairdiella chrysoura*, *Haemulon plumierii*, and *Paralichthys albigutta*.

Ultimately, all 3 common trends played a role in describing synchrony in this suite of species as each trend resembled multiple species' time series, but there was no clear pattern between trends and life-history characteristics (e.g. not all reef species loaded in the same direction on each of the trends). Model results indicated broad confidence intervals for multiple species but most species' time series fits were within those confidence intervals (Fig. 4), with cyclical patterns reflecting the seasonal recruitment cycle of the survey's target species. The model fit for *L. maximus* was nearly perfect; *L. maximus* is also the only species where catch data were modeled for a single estuary (BB) because they were almost exclusively collected in the BB region. Model fits were suboptimal for *B. chrysoura*, *O. chrysoptera*, *L. synagris*, and, to a lesser extent, *L. rhomboides* (Fig. 4). Ultimately, the fitted values (Fig. 4) suggest that

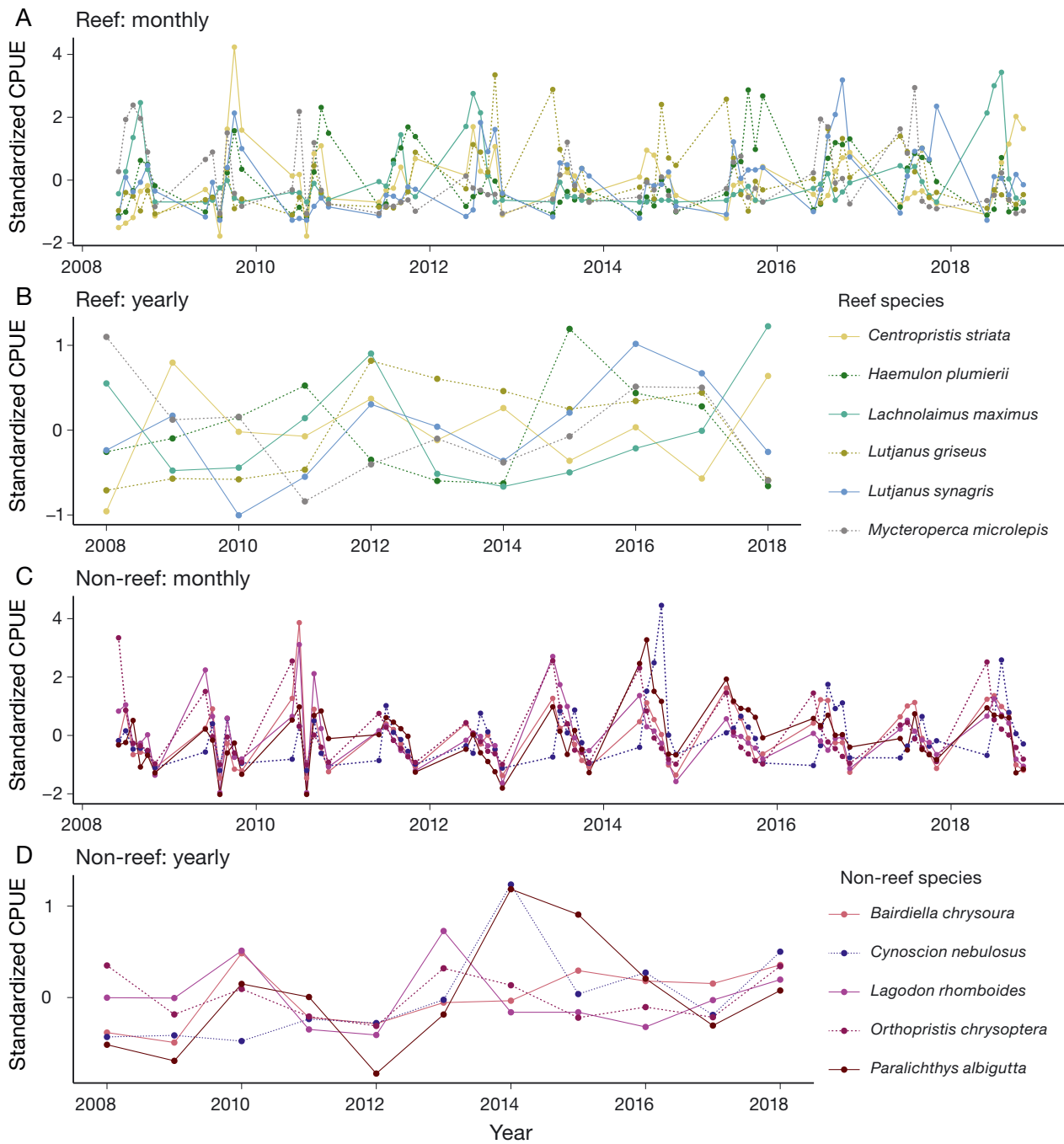


Fig. 2. Standardized (A,C) monthly and (B,D) yearly catch-per-unit-effort (CPUE) time series for the 6 reef fish species and 5 non-reef fish species collected in West Florida Shelf seagrass beds from 2008 to 2018. The time series are standardized and therefore unitless. Note the different scales on the y-axis

some of the species' time series or multiple months within the time series are not fitted well, as many observations do not fall on the fitted line even though they are within the 95% confidence intervals. Therefore, we calculated the ratio of the sum of squared observed totals and the sum of squared residuals for

each species, where a high ratio indicated either the species' or a few time points within the species' time series were not fitted well. Of the 11 species, 2 reef fish had ratios < 0.5 (*L. maximus*, ratio = 0.36; *C. striata*, ratio = 0.48). All other ratios indicated a significant amount of variation (ratio ≥ 0.68) was present in

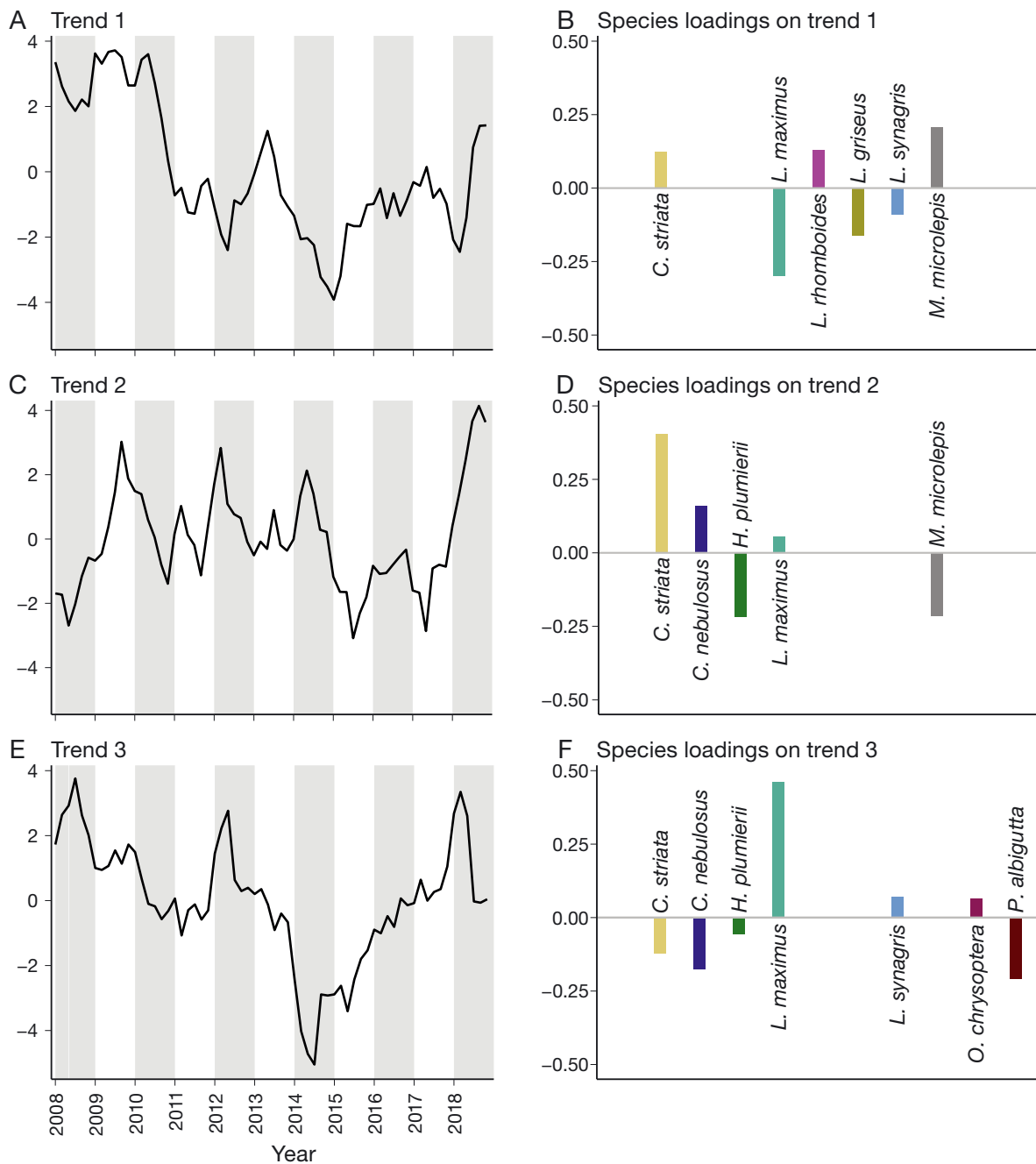


Fig. 3. (A,C,E) Common trends for the seagrass-associated species' CPUE time series obtained by the dynamic factor analysis (DFA) model containing 3 common trends, a 1-mo lag average wind direction covariate, and an unconstrained matrix, and (B,D,F) factor (i.e. species) loadings obtained by the same DFA model. Sampling years are alternately shaded (A,C,E) to aid in comparing intra-annual trends among panels. Species loadings <0.05 were not plotted. Common trends and species loadings are unitless

the error term of the model, suggesting that multiple time points were not fitted well; the extent and variability of the seasonality in the time series (Fig. 4) was not captured well by the model.

A single environmental covariate improved the model fit for the CPUE time series: a 1-mo time lag

of the average wind (Table 2) on the WFS. To visualize the relationship between wind direction 1 mo prior to sampling and CPUEs, we plotted wind roses for each species and the fitted values from the best-fit model (Fig. 5). The effect of wind direction on fish CPUE was context dependent. For reef

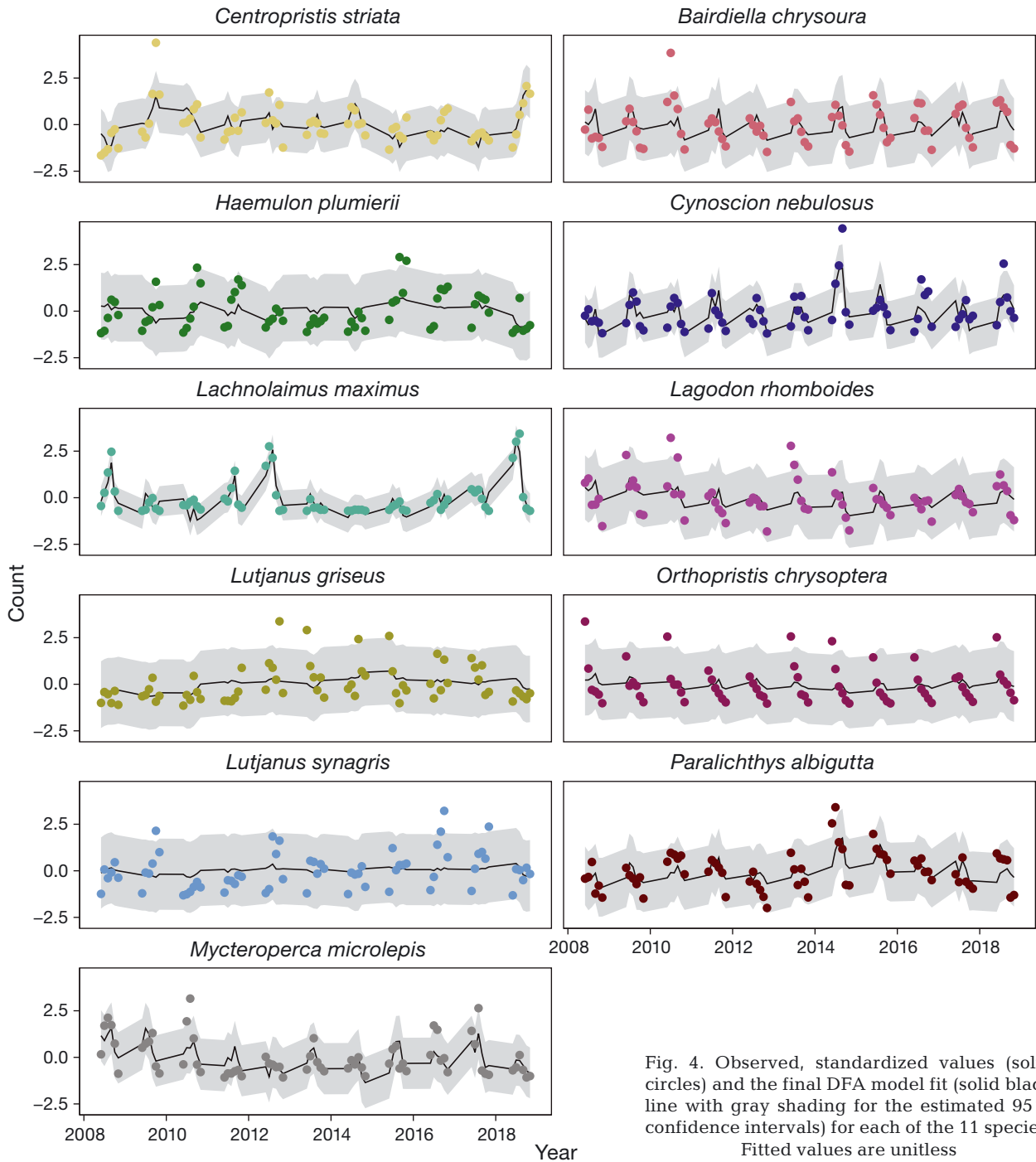


Fig. 4. Observed, standardized values (solid circles) and the final DFA model fit (solid black line with gray shading for the estimated 95% confidence intervals) for each of the 11 species. Fitted values are unitless

fishes, the relationship between the prevailing wind direction and CPUE differed by species, whereas for non-reef species, the pattern was consistent among species (Fig. 5). For reef fishes, *C. striata* had higher catch rates with east through southeast winds (~90–135 deg from true north). *Mycteroperca microlepis* and *L. maximus* catch rates were relatively greater with winds from the

east to southeast through the west (~135–270 deg from true north) (Fig. 5). *Lutjanus griseus*, *L. synagris*, and *H. plumierii* catch rates were comparatively less influenced by wind direction. The suite of non-reef species' catch rates was higher with west and southwesterly winds (~180–270 deg from true north) and lower with north and northeasterly winds (0–90 deg from true north).

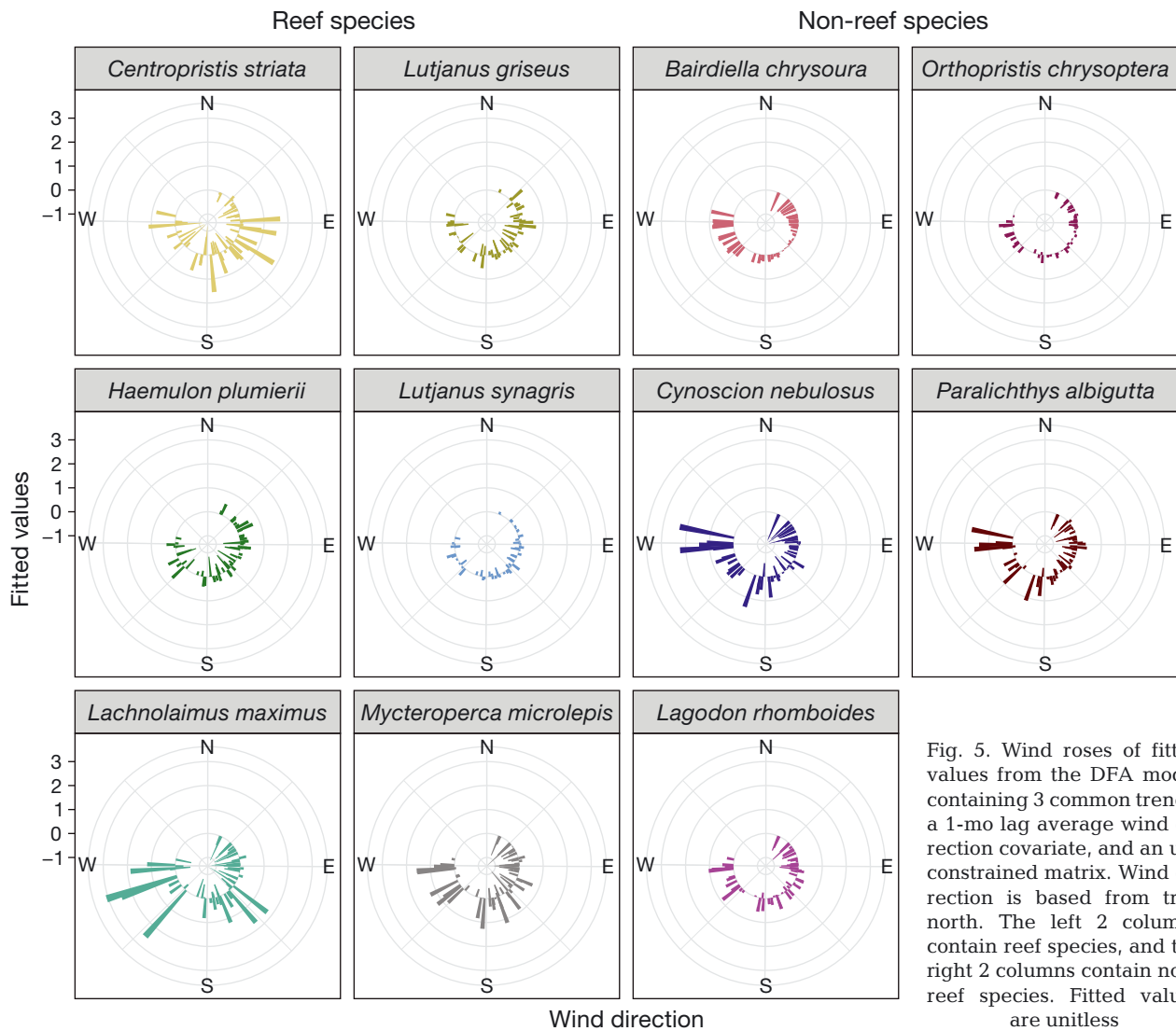
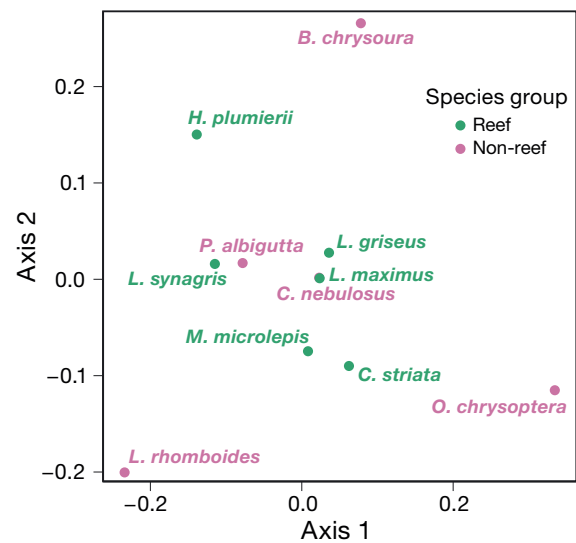


Fig. 5. Wind roses of fitted values from the DFA model containing 3 common trends, a 1-mo lag average wind direction covariate, and an unconstrained matrix. Wind direction is based from true north. The left 2 columns contain reef species, and the right 2 columns contain non-reef species. Fitted values are unitless

The MDS results (Fig. 6) indicate 7 species, representing reef and non-reef species, share information not accounted for by the common trends and explanatory variable, wind. All species in this group were predators (Table 1), and 5 of the 7 were reef species. Contrastingly, all species positioned away from the center, toward the edges, were forage (prey) fish. Furthermore, 3 of the 4 forage fish along the edges had time series that did not resemble the common trends.

Fig. 6. Multidimensional scaling of the error covariance matrix, \mathbf{R} , that was transformed into a dissimilarity matrix via absolute correlations. Species names are indicated on the graphic, with reef species in green and non-reef species in pink



4. DISCUSSION

We detected some evidence of synchrony in juvenile reef and non-reef fish recruitment to nearshore, polyhaline seagrass beds in the eastern Gulf of Mexico using DFA. The individual species' time series resembled the trends detected by the DFA but also had intra-annual trends. Many of the species examined in this study, especially the predatory species (Table 1), had consistent seasonal CPUE patterns, with peak abundance occurring between July and September, when seagrass productivity is typically greatest in Florida waters (Zieman & Zieman 1989). Juvenile fish commonly use seagrass habitats as shelter from predators and as a source of food (Zieman & Zieman 1989, Beck et al. 2001, Nagelkerken et al. 2001, Obaza et al. 2015). Therefore, seasonal peaks in production may play a role in the timing of seagrass habitat use by fishes, contributing to the observation of similar CPUE patterns among reef and non-reef species alike. Similar seasonal patterns in reef fish CPUE were expected because the survey was designed for juvenile reef fish recruitment, which spans the summer and fall months in the eastern Gulf of Mexico (e.g. Switzer et al. 2012, Flaherty-Walia et al. 2015). Most non-reef species and prey species (Table 1) also had seasonal abundance patterns, but peak abundances tended to occur within the first or last month of the sampling season, depending on species, suggesting we may have missed the true abundance peak for some prey species. Several of the prey species recruit to seagrass habitats during the fall to winter (i.e. *Haemulon plumieri*) and winter to spring months (i.e. *Lagodon rhomboides* and *Orthopristis chrysoptera*) (Poulakis et al. 2003, Gloeckner & Luczkovich 2008), which were not sampled with this survey. Although we may have missed the true recruitment peak for some species, reef and non-reef species have considerable overlap in seagrass habitat residency during their juvenile life stage.

Evidence of shared inter-annual trends among the species time series was detected with DFA, which simultaneously analyzed all 11 species' time series and identified 3 underlying, shared time series trends, 2 of which had similar patterns. Five reef-associated fishes had positive loadings on the first and third trends identified by DFA, indicating that their time series resembled these very similar trends. The time series of one reef species (*Centropristis striata*) and one non-reef species (*Cynoscion nebulosus*) most closely resembled the second trend. Positive loadings of multiple reef species on one trend and

reef and non-reef fishes on another trend may be influenced by shared spawning and recruitment windows. In the eastern Gulf of Mexico, the reef fishes and *C. nebulosus* share spawning and recruitment windows (Manickhand-Dass 1987, Saucier & Baltz 1993, Hood et al. 1994, Coleman et al. 1996, Brown-Peterson et al. 2002, Murie & Parkyn 2005, Waggy et al. 2006, Allman & Goetz 2009, Collins & McBride 2015), so seasonal fluctuations in abundance likely influence the shared trends as multiple species recruit concurrently.

There is also support for trophic dynamics to influence the shared trends. The clustering of several predator species in the center of the MDS plot for the off-diagonal element of the covariance matrix suggests these species' time series are influenced by variables not explained by the DFA common trends or covariate(s), which in this case may be trophic level. For example, years of high *Mycteroperca microlepis* juvenile recruitment to seagrass habitats, which happen periodically (e.g. Switzer et al. 2012), can affect foraging preferences of other juvenile predatory fishes (K. Thompson, unpubl. data), altering trophic dynamics of the ecosystem. Similar interactions are also present in adult habitats. The presence of *M. microlepis* reduces *C. striata* abundance in adult, offshore reef habitats where *C. striata* is at a competitive disadvantage in the presence of large piscivores such as *M. microlepis* (Chagaris et al. 2015). These types of trophic and competitive interactions likely contribute to multispecies temporal synchrony in abundance at various life stages.

The positive loadings of both forage fish (e.g. *L. rhomboides* and *O. chrysoptera*) and piscivorous fish (e.g. *C. striata*, *M. microlepis*, *C. nebulosus*, and *Paralichthys albigutta*) on 2 of the 3 shared trends suggests that predator-prey dynamics may also influence recruitment synchrony trends. Several of the species we examined are prey of the predators we examined (Moody 1949, Carr & Adams 1973, Stallings 2010), and prey population structure changes have been shown to affect predator populations, although the reverse has also been documented (e.g. Hairston & Hairston 1993, Menge 2000). An influx of migratory predators, such as *P. albigutta*, during the spring and summer months into inshore environments from their wintering grounds (Fitzhugh et al. 2008) may concentrate some forage fish (e.g. *L. rhomboides*) into seagrass habitats, where they attempt to escape predation by using cover provided by seagrass meadows (Harter & Heck 2006). These trophic

dynamics can affect multiple species simultaneously, influencing the level of synchrony among species occupying similar habitats.

In addition to biological interactions influencing species abundance, environmental factors can play a role. We did not find evidence of large-scale drivers (i.e. AMO or SOI) but, in nearshore seagrass habitats of the eastern Gulf of Mexico, temporal synchrony in recruitment of seagrass-associated species may be influenced by a regional- or local-scale variable: a 1-mo lag of the prevailing wind patterns along the WFS. Some reef species' abundances were positively correlated with southerly and southwesterly winds (e.g. *L. maximus* and *M. microlepis*) or southeasterly winds (i.e. *C. striata*). Multiple non-reef species had greater abundances with southwesterly winds, supporting the idea that southwesterly winds along the WFS could assist in larval retention for these inshore or nearshore spawning species. The 1-mo lag time frame coincides with the range in larval duration, 20–43 d, of most reef fish species we evaluated (Koenig & Coleman 1998, Lindeman et al. 2001, Tzeng et al. 2003, Edwards et al. 2008, Seyoum et al. 2015) and wind, either alone or in conjunction with other transport processes, is an important component of larval fish dispersal (Sissenwine 1984, Hare et al. 1999, Luettich et al. 1999, Johnson et al. 2017). However, most individuals collected were more than 1 mo post-settlement, suggesting that a direct influence of wind on larval transport is unlikely.

Prevailing winds 1 mo prior to sampling are potentially confounded with other environmental factors that relate to juvenile abundance in nearshore seagrass habitats of the eastern Gulf of Mexico. For example, prevailing winds may influence localized circulation and mixing of water masses (e.g. Yang & Weisberg 1999, Jackson 2004, Yeager et al. 2005) and shift physical locations of favorable physicochemical conditions for various species, which can affect fish abundance. Altering the physicochemical properties of the water also affects primary productivity and resuspension of particulate matter (Jackson 2004, Yeager et al. 2005). This could provide additional food resources or additional particulates in the water column that affect visual predator success rates (Jackson 2004), which may be one of the processes affecting juvenile reef fish abundance. Likewise, wind forcing can affect movements of drift algae (Virnstein & Carbonara 1985, Pederson & Peterson 2002), which may serve as additional refuge from predation or additional food or nutrient sources (Gore et al. 1981, Pederson & Peterson 2002). The direct mechanistic link between prevailing wind

direction 1 mo prior to sampling and multispecies synchrony in juvenile fish abundance along the WFS is not yet clear, but this presents an interesting avenue for future research.

To our knowledge, this is the first time DFA has been applied to monthly time series of multiple fish species in the eastern Gulf of Mexico. Early use of DFA focused on various zoobenthic (Zuur et al. 2003a) and phytoplankton (e.g. Holmes et al. 2012) species, as well as multiple populations or stocks of a single species (e.g. Zuur et al. 2003b, Zuur & Pierce 2004). More recently, DFA has been applied, as in our study, to multiple fish taxa within a region (e.g. Castillo-Jordán et al. 2015 in the southern hemisphere, Latour et al. 2017 in Chesapeake Bay, Lima et al. 2017 in a tributary of the Amazon). Compared to these previous works, we took note of a few findings in our DFA. First, although we used monthly CPUEs, as opposed to yearly, for the same 6 mo of each year, fitted values from the model fell within the 95% confidence interval for most species. This is encouraging because it could extend the use of DFA to other time series, if time steps follow a consistent, repetitive pattern. Second, some species had positive or negative loadings on multiple trends, and no single shared trend had positive loadings for more than 3 species. This indicates that all 3 shared trends played a role in characterizing synchrony among this set of species. We believe this is related to trying to fit a model to 11 different species, with various biological and ecological characteristics, all producing variability in juvenile fish abundance over time, which can lead to variable and conflicting trends among species. Furthermore, variability in seagrass density, drift algae, and other environmental variables can alter the abundance of seagrass-associated species in the Gulf of Mexico (Belgrad et al. 2021). Third, the species' loadings for our final model were in the range of loadings from other work, including Zuur et al. (2003a) and Zuur & Pierce (2004), suggesting DFA is a viable analytical technique for our research objective.

Overall, we were able to detect evidence of common temporal recruitment patterns in the eastern Gulf of Mexico, a spatial resolution that matches the management scale for many Gulf of Mexico fishery species (e.g. SEDAR 2014, 2018a,b). The 3 common trends had some similarities (Fig. 3), with 2 having an overall decline from 2008 to 2014 or 2015, and all 3 having an overall increase from 2014 through 2018. Although the mechanisms for these long-term trends are not yet fully elucidated, large-scale disturbances can influence annual trends. For example,

following the 2010 Deepwater Horizon oil spill, reef fish abundance and diversity declined on the WFS, with some species (including piscivores) showing little indication of recovery to pre-disturbance status after 7 yr (Lewis et al. 2020). Although the oil spill occurred after the onset of the decline in abundances in our analyses, oil-spill-related reductions in offshore spawning stocks could lead to reduced juvenile abundances inshore (ca. 2010–2015), followed by increases after the spawning stocks began to recover (ca. 2014–2018).

Limitations of our model are important to note to inform future monitoring and research. Multiple time steps were not fitted well by the model, resulting in a model with much variance remaining in the error term. However, we have multiple lines of evidence pointing toward some synchrony in juvenile fish recruitment along the WFS, including similarities in monthly and yearly CPUEs among multiple species, multiple species loading in the same direction on multiple common trends, and clustering of several predator species in the center of the MDS plot for the error term of the model, suggesting the species share some amount of information not explained by the DFA model's common trends and covariate. The lack of fit for multiple time steps for multiple species may result from the variability in the extent of seasonality (i.e. abundances vary widely within a season), variability among years, and among estuaries along the WFS. As the WFS juvenile reef fish survey continues with additional monthly trawl samples (Schrandt et al. 2021), inter-annual synchrony may be assessed with DFA, and we would expect model fits to be better than those from monthly time steps as variability in annual catch estimates should decrease.

Identifying evidence of shared trends can be advantageous for conservation and management. For example, when considering conservation actions, habitat protection generally serves to attempt to protect species at multiple life stages and can help promote abundance of individuals. Our results suggest that prevailing southwest to west winds are correlated with increased juvenile abundance in nearshore seagrass habitats for about half of the fish examined here. If the winds from this direction were significantly greater in one year compared to another, we could speculate that juvenile recruitment to the seagrass habitat would increase, thereby resulting in a subsequent increase in recruitment to the adult population in offshore reef habitats. Indeed, the connection between juvenile and adult fish abundances has been previously demonstrated in the WFS ecosystem. Juvenile *M.*

microlepis abundance in seagrass habitats is positively correlated to fishery year class strength in the eastern Gulf of Mexico (Johnson & Koenig 2005), providing support for habitat conservation influencing multiple life stages.

Identifying evidence of shared trends in recruitment of juveniles can also inform design of monitoring surveys and management decisions. At a minimum, synchrony in recruitment allows for a single monitoring survey to collect information for a suite of species, which improves efficiency of monitoring efforts and can provide baseline information for multiple single-species stock assessments and data-limited species. Indices of juvenile abundance may be a suitable proxy for predicting future year class strength (Adamski et al. 2011, Switzer et al. 2012), which can inform co-management of various species. Ultimately, different species in the same ecosystem may have patterns of abundance that covary in time (Tableau et al. 2019), and identifying synchrony among species moves management closer to multi-species fisheries management, with an end goal of ecosystem-based fisheries management (e.g. Lindeman et al. 2000, Hall & Mainprize 2004, Pikitch et al. 2004, Marasco et al. 2007, Dell'Apa et al. 2015, 2020, Chagaris et al. 2019). Furthermore, understanding synchrony among species may also allow for inferences to be made for data-deficient or data-limited species (Tableau et al. 2019) if they are highly synchronous with more well-studied species.

Acknowledgements. We thank all Florida Fish and Wildlife Conservation Commission staff and volunteers who have assisted with the collection and processing of data since the inception of this survey, and the Florida State University Coastal Marine Lab for permitting us free use of their boat ramp for nearby sampling. We also thank the two anonymous reviewers, whose comments greatly improved this manuscript. This project was supported in part by proceeds from state of Florida saltwater recreational fishing licenses, from the Department of the Interior, US Fish and Wildlife Service, Federal Aid for Sportfish Restoration (grants F14AF00328, F15AF01222, F16AF00898, F17AF00932, and F18AF00665), from the US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service (grants NA08NMF4720645 and NA09NMF4330152), and from the National Fish and Wildlife Foundation Gulf Environmental Benefit Fund (grants FL 40624, FL 45766, FL 50347, FL 54269, and FL 58101). The statements, findings, views, conclusions, and recommendations contained in this document are those of the authors and do not necessarily reflect the views of the US Department of the Interior or the US Department of Commerce and should not be interpreted as representing the opinions or policies of the US government. Mention of trade names or commercial products does not constitute their endorsement by the US government.

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*Editorial responsibility: Simon Pittman,
Oxford, UK
Reviewed by: K. Darnell and 2 anonymous referees*

*Submitted: April 19, 2021
Accepted: May 17, 2022
Proofs received from author(s): July 21, 2022*