

ARTICLE

Coastal and Marine Ecology

Community dynamics of estuarine forage fishes are associated with a latitudinal basal resource regime

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Abstract

Forage fishes are an important component of marine, estuarine, and aquatic food webs that facilitate the transfer of energy and nutrients from primary producers to upper trophic levels. Previous studies of forage fishes have focused primarily on pelagic planktivorous species in pelagic environments. However, benthically associated taxa can be just as important as planktivorous species, particularly in highly productive estuarine environments that provide critical habitat for many predators. In this study, we analyzed a 20-year forage fish community composition and abundance dataset across four eastern Gulf of Mexico estuaries spanning a broad latitudinal gradient to investigate spatio-temporal variability in community structure and quantify associations with habitat. Our analyses revealed significant regional structuring of forage fish communities, coupled with a strong association with habitat characteristics related to latitudinal effects and basal resource regime. Communities in the two northern estuaries and two southern estuaries were associated primarily with planktonically reliant and benthically reliant taxa, respectively. Despite regional differences, we uncovered a coherent annual cycle in forage fish communities across all estuaries related to seasonal shifts in abundances of several abundant and ubiquitous species. We additionally revealed significant sub-decadal periodicity potentially associated with bottom-up effects of global climatic cycles. The significant association of forage fish communities with habitat regime shown in this study underlies the importance of continued monitoring of these communities. This study represents a novel approach to assess this critical ecosystem component in diverse estuarine systems globally.

KEYWORDS

ecosystem structure, hydrological variability, synchrony, time series, trophic channels

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INTRODUCTION

Lower trophic level species are an important link in the transfer of energy and nutrients through ecosystems (Polis & Strong, 1996). In marine and aquatic systems, this linkage between primary producers and higher-level consumers often includes forage fishes as a critical intermediate. Forage fishes are small- to medium-sized schooling species that are prey to many aquatic predators (Pikitch et al., 2014). Typically fast-growing, short-lived, highly fecund, and abundant, forage fishes make up a large portion of the diets of marine and aquatic fishes, seabirds, and mammals (Essington & Munch, 2014). Forage fishes can also provide large spatial subsidies of energy to a variety of systems through the movement of migratory species across ecosystem boundaries (Ziegler et al., 2019). In the subtropics, this subsidy from seagrass habitats can be as much as 25% of the total potential production of nearshore and offshore food webs (Nelson et al., 2011; Nelson et al., 2013). In high-productivity regions, particularly pelagic upwelling systems, forage fish communities are of particular concern due to their low taxonomic diversity, resulting in a “wasp-waist” trophic structure that can lead to complex bidirectional ecosystem regulation (Cury, 2000; Griffiths et al., 2012; Rice, 1995). By contrast, forage fish communities in near- and inshore coastal environments can be relatively diverse (Coll et al., 2011), particularly those in the subtropics where maintenance of prey diversity is an important component of food web stability (Petchey, 2000). Despite the value of forage fish communities in these lower latitude systems, we lack an understanding of their spatial patterns, temporal dynamics, and the processes that influence these attributes.

Much of the research on the role of forage fishes in marine and aquatic food webs to date has been focused on taxa that transfer energy and nutrients through phytoplankton-based pathways, particularly in pelagic environments. Pikitch et al. (2014) based their global study of forage fishes on this premise, constraining their definition to focus on planktivorous taxa. These planktonic pathways represent “fast” energy channels, which are highly efficient yet rely on patchy and episodic sources of primary production. By contrast, “slow” channels are less efficient, but more reliable spatially and temporally (Rooney et al., 2006). In marine and aquatic environments, slow energy channels are typically reliant on benthic sources of production. Benthic pathways, particularly those reliant on algae (e.g., epiphytes and turfs), are an important yet often overlooked component of coastal food webs that support many higher-level predators (MacIntyre et al., 1996; Radabaugh, 2013). Additionally, the coupling of fast and slow energy channels

through higher-level consumers has a stabilizing effect on food webs (Rooney et al., 2006; Vander Zanden & Vadeboncoeur, 2002; Wollrab et al., 2012). Thus, forage fishes that rely on benthic sources of production are likely just as important to maintaining coastal ecosystems as those that rely on planktonic pathways (Camp et al., 2019).

Estuarine habitats are highly productive systems that commonly support both planktonic and benthic channels of energy flow (Underwood & Kromkamp, 1999). Because of this, they can also support abundant and diverse assemblages of forage fishes (Stallings et al., 2015). Forage fishes in estuarine systems are of particular importance to ecosystem functioning (Hall et al., 2012). Moreover, estuarine ecosystems provide important ecological services, including several that are crucial for food web sustainability and the maintenance of fisheries (i.e., essential juvenile habitat, foraging habitat for adult populations of ecologically and economically important predator species, and reproductive habitat for both predators and prey species) (Barbier et al., 2011). Estuarine forage fishes not only serve as the primary prey for estuarine predators, they also provide an important source of energy for juveniles and subadults of marine consumers that use estuaries as essential early-life habitat (Camp et al., 2019). Additionally, many estuarine forage fishes undergo ontogenetic habitat shifts, thus serving as an important linkage between inshore and offshore habitats (Hall et al., 2012; Nelson et al., 2013). Because of the vital role that estuarine forage fish communities play in connecting planktonic and benthic pathways to both estuarine and marine predators through different life history stages, it is important to understand how these communities vary in composition and structure over space and time.

Forage fish populations can be influenced by spatiotemporal variability in habitat and climatic conditions, which can affect community structure and dynamics (Burghart et al., 2013; Chacin et al., 2016; Faletti et al., 2019; Lubbers et al., 1990; Simonis & Merz, 2019). For example, latitudinal gradients in community composition and species diversity are quite common in marine and estuarine environments (Hillebrand, 2004; Pease, 1999). However, this latitudinal effect is often overshadowed in estuarine habitats by characteristics such as morphology, size, and riverine input (Harrison & Whitfield, 2006; Ley, 2005; Schrandt et al., 2018). Indeed, in the eastern Gulf of Mexico (eGOM) spanning subtropical and temperate latitudes, Schrandt et al. (2018) showed that latitude had a minimal effect on estuarine seagrass-associated faunal communities, while estuary morphology and related factors explained much of the interestuarine variation in community composition. Differences among estuaries may also modulate inter- and intra-annual temporal variability in estuarine conditions affecting faunal communities (Travers et al., 2012).

Interannual cycles in population dynamics are commonly observed in estuarine species due to both ontogenetic migrations (Beck et al., 2001) and seasonal shifts in estuarine habitat conditions (Travers et al., 2012; Yanez-Arancibia et al., 1988). The timing of seasonal migrations and juvenile settlement to estuaries can vary across years and estuaries, which affect the degree of synchrony and asynchrony that occurs among populations and communities (Guichard et al., 2018; Hammond et al., 2020; Jarillo et al., 2020).

Understanding temporal synchrony among species and communities is important given its effects on community stability. Indeed, asynchronous species responses to habitat variability over space and time can promote stability within a community (McCann, 2000). Patterns of synchrony in community structure can also emerge from longer-term interannual variations in habitat and population demographics associated with broad-scale climatological phenomena. These phenomena may change the intensity of seasonal fluctuations in habitat (e.g., warmer summers and cooler winters or vice versa) that can affect faunal assemblages (Fiedler, 2002; Gordo et al., 2011; Ottersen et al., 2001; Rossi & Soares, 2017; Stenseth et al., 2004). The eGOM region is influenced by variation in both temperature and precipitation caused by the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO), which can drive decadal-scale variations in estuarine stream flow and salinity resulting in changes to estuarine faunal communities (Coleman & Budikova, 2013; Garcia et al., 2001; Schmidt & Luther, 2002).

Variations in the diversity, distribution, and relative abundances of forage species can influence the foraging behavior and demographics of their predators, affecting predator–prey interactions and food web stability (Chacin & Stallings, 2016; Cury, 2000; Leibold, 1996; Mason et al., 1998). Given the essential role of estuarine forage fishes in linking primary production and higher trophic levels throughout coastal ecosystems, it is important to understand how these communities are structured over space and time and how different components of their habitat are related to their spatiotemporal dynamics. In this study, we analyzed a long-term dataset of estuarine forage fish species composition and abundance in the eGOM to investigate their spatiotemporal dynamics across four distinct estuaries arranged along a broad latitudinal gradient. The coastal eGOM is a large system spanning two biogeographic provinces and two ecoregions from warm temperate to subtropical latitudes (Spalding et al., 2007), and includes a variety of estuarine environments supporting a diverse assemblage of predator and prey species. Specifically, we sought to answer three major questions related to estuarine forage fish communities: (1) How do

these communities vary spatially among four major estuaries arranged along a latitudinal gradient of the eGOM? (2) Do these communities exhibit predictable and synchronous patterns of temporal variability across the region? and (3) How does spatiotemporal variability in community assembly relate to biotic and abiotic components of forage fish habitat? We hypothesized that interestuary community structure would reflect the latitudinal, morphological, and hydrological differences among the estuaries tested. Although we expect both regional and local processes to contribute to community variability among estuaries, we did not explicitly measure the magnitude of these contributions. We also hypothesized that community structure would show consistent seasonal variability modulated by estuary location, hydrology, and morphology. Moreover, we predicted that communities would exhibit decadal-scale variability related to climatological effects of ENSO and NAO on estuarine habitats in the eGOM.

METHODS

Sampling design

Stratified random sampling was conducted monthly from 1998 to 2017 by the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWRI) Fisheries Independent Monitoring (FIM) program in each of four major eGOM estuaries: Apalachicola Bay, Cedar Key, Tampa Bay, and Charlotte Harbor (Figure 1 and Table 1). These estuaries were located along a latitudinal gradient, spanning over 500 km of coastline and varied in their morphologies and hydrologies. Sampling was conducted using three gears: (1) a 21.3-m center-bag seine restricted to depths less than 1.8 m; (2) a 183-m center-bag seine restricted to depths less than 2.5 m; and (3) a 6.1-m otter used in depths between 1 and 7.6 m (see Appendix S1: Section S1 for additional details on sampling design and protocol). Trained researchers identified all captured fish to the lowest practical taxonomic level and counted the number of individuals of each taxon. We identified forage fishes and their predators from net hauls using FishBase and available literature (see Appendix S1: Section S1 for details). We used catch data from the 21.3 m seine and 6.1 m otter trawl to estimate forage fish abundance because of their ability to catch small fishes due to small mesh sizes, while the larger meshed 183-m seine was used to estimate predator abundance. We converted the abundance data for all forage and predator taxa to catch-per-unit-effort (CPUE) by dividing the number of individuals caught for each taxon in each sampling event by the

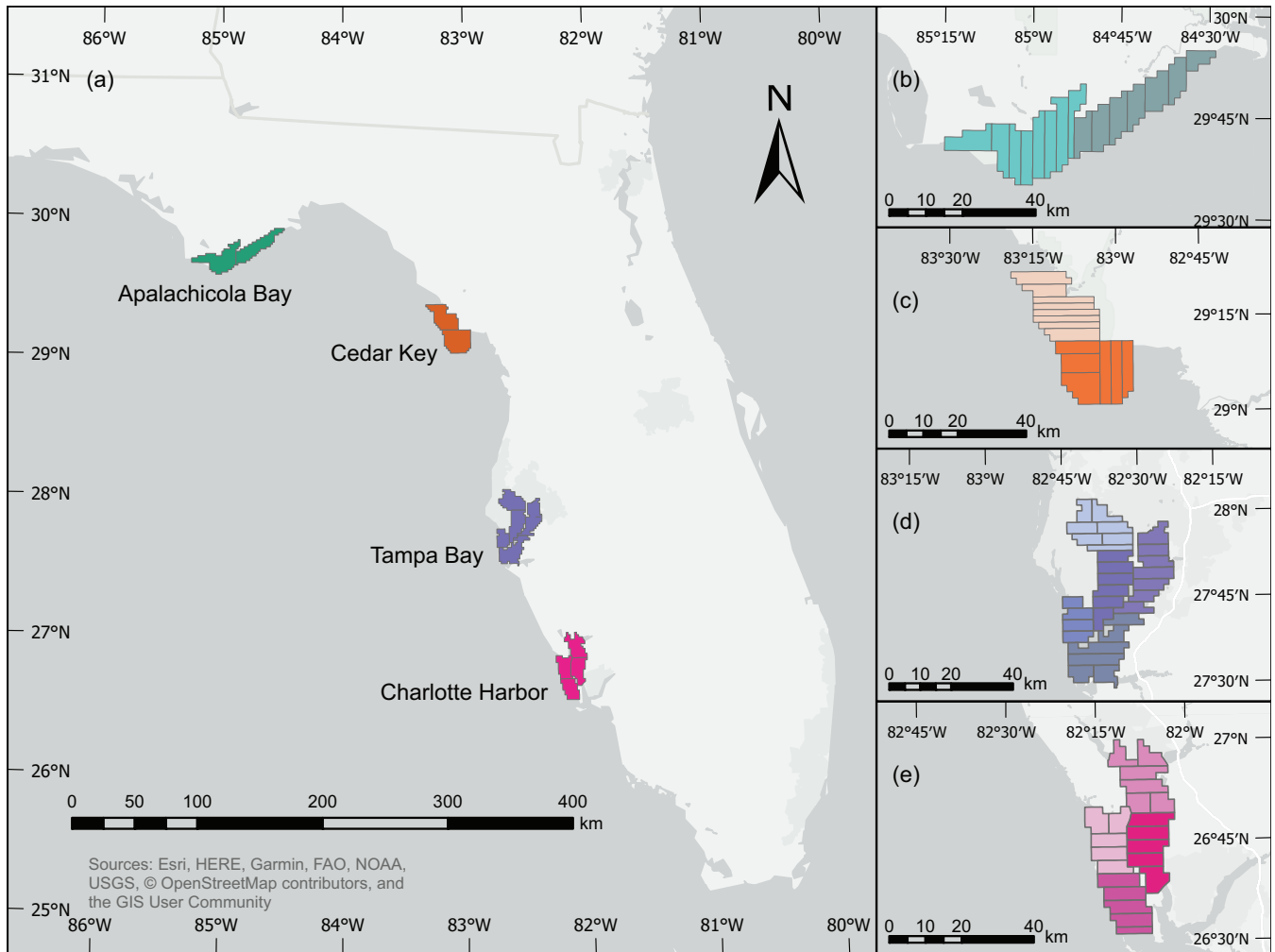


FIGURE 1 Map of sampling areas in the eastern Gulf of Mexico (eGOM). Filled polygons (a) represent areas sampled by Fish and Wildlife Research Institute's (FWRI) Fisheries Independent Monitoring (FIM) program from 1998 to 2016 in four eGOM estuaries. Apalachicola Bay (AB; b) is a semi-enclosed estuary at the terminus of the fluvial Apalachicola River, which supplies a large amount of sediment and nutrients to the area. Cedar Key (CK; c) is located at the effluent of the blackwater Suwannee River, which provides a large amount of freshwater and nutrients to the area with minimal sediment flux, resulting in a relatively high-nutrient, low-salinity open estuarine system. Tampa Bay (TB; d), the largest open-water estuary in Florida, is a semi-enclosed estuary supplied primarily by four low-flow rivers: the Hillsborough River, which flows into Hillsborough Bay at its northernmost tip; the Alafia River, which flows into south Hillsborough Bay; the Little Manatee River, which supplies Middle Tampa Bay; and the Manatee River, which flows into Lower Tampa Bay at the southern mouth of Tampa Bay. Charlotte Harbor (CH; e) is a semi-enclosed estuary supplied by the low-flow Myakka River and Peace River in the north and the Caloosahatchee River near its mouth. Outlined areas (b–e) represent subzones over which catch and environmental data were aggregated, shaded by stratified spatial zones

total area sampled during each sampling event. We then used multigear mean standardization (Gibson-Reinemer et al., 2017) to standardize and aggregate forage fish CPUE across gear types. We aggregated net hauls spatially by subdivisions of the stratified spatial zones and temporally by 3-month periods (winter: January–March; spring: April–June; summer: July–September; and fall: October–December). While the relatively coarse resolutions at which the data were aggregated limited our ability to investigate subseasonal patterns of community variability or lagged environmental effects, we chose this

approach since we were primarily interested in large-scale patterns of spatiotemporal variability that may have been masked by fine-scale variations. Aggregated hauls for each subzone and season served as the basis for our analyses and will be denoted as “samples” for the remainder of the manuscript (Table 1 and Appendix S1: Section S1).

At each sampling site, FWRI researchers collected data on environmental variables including salinity, water temperature (in degrees Celsius), pH, and dissolved oxygen (in milligrams per liter) with a handheld

TABLE 1 Attributes of the four major eastern Gulf of Mexico estuaries analyzed

Attribute	Apalachicola Bay (AB)	Cedar Key (CK)	Tampa Bay (TB)	Charlotte Harbor (CH)	Overall
Latitude (decimal degrees N)	29.7	29.3	27.7	26.8	
Climate	Temperate	Temperate/ Subtropical	Subtropical	Subtropical	
Estuary morphology	Semi-enclosed	Open	Semi-enclosed	Semi-enclosed	
Total estuarine surface area (km ²)	804.3	697.8	937.5	801.3	
Average annual riverine inflow (m ³ /s)	647 ^a	287 ^b	39 ^c	150 ^d	
Years sampled	1998–2017	2001–2017	2001, ^e 2005–2017	2003–2004, ^e 2005–2017	
Total samples	885	918	688	843	3334
Samples per year (min, med, max)	16, 48, 53	34, 41, 46	3, ^e 66, 82	4, ^e 69, 73	
Species richness	45	42	41	39	50
Chao's Index	47	44	45	41	50

^aAnnual discharge of Apalachicola River at Sumatra, FL (U.S. Geological Survey, 2019).

^bAnnual discharge of Suwannee River at Wilcox, FL (U.S. Geological Survey, 2019).

^cEstimated total stream flow discharge across four largest drainages: Hillsborough, Alafia, Little Manatee, Manatee (Schmidt & Luther, 2002; Zarbock et al., 1995).

^dEstimated total stream flow discharge across three largest drainages: Peace, Myakka, Caloosahatchee (Hammett, 1990).

^eAlthough seine sampling occurred from 1998 to 2017 in all estuaries, trawl sampling was limited in Tampa Bay and Charlotte Harbor prior to 2005 to river zones, several of which overlap estuary zones used in this study. These years contributed 3, 4, and 17 samples, respectively. Because of the reduced number of samples in each of these years compared to the total pool of samples, these years were excluded from time series analyses, but included in all other analyses. The inclusion of these years did not substantially bias any of these analyses.

multiparameter water quality meter, and visually estimated the percent cover of submerged aquatic vegetation (SAV) in 10% increments. While FIM researchers record the presence of hard-bottom habitat types, such as oysters, corals, rocks, and mussel reef, that are encountered during a seine or trawl sample, these habitats are not targeted due to gear limitations and their abundances are not quantified. Due to the presence-only nature of these data and the aggregated nature of our samples, the relative cover of these habitats was not included in our analyses. We used vertical visibility, estimated from Secchi disk depth measurements, as a proxy for water clarity. Secchi measurements for samples where the Secchi disk reached the bottom prior to loss of visibility were not included in calculating mean vertical visibility. We averaged all environmental variables and CPUE values for each predator taxon by sample.

Univariate statistical analyses

We conducted all univariate and multivariate analyses using R Statistical Computing Environment v4.0.0 (R Core Team, 2020) unless otherwise stated, and an alpha of 0.05 was used for all significance testing. We implemented a modified indicator value (IV) analysis (adapted from Dufrene & Legendre, 1997) to determine

relative predominance of forage fish taxa across estuaries and within each estuary. We calculated IV for each taxon as follows:

$$IV_i = F_i \times N_i, \quad (1)$$

where F_i is the frequency of occurrence for taxon i across samples, and N_i is the relative abundance of taxon i across all samples, including those where taxon i was not observed, calculated as the abundance of each taxon as a proportion of the total sum of relative abundances of all taxa (note that these are not equivalent to true frequency of occurrence and relative abundance across raw net hauls; see Appendix S1: Section S1).

We calculated forage fish taxonomic richness (S , total number of taxa) and evenness for each sample using PRIMER v7 analytical software (Clarke & Gorley, 2015). Pielou's taxonomic evenness index was calculated as follows:

$$J' = \frac{-\sum P_i \ln P_i}{\ln S}, \quad (2)$$

where P_i is the relative abundance of taxon i and S is the number of taxa. We compared richness and evenness across estuaries and seasons using analyses of variance.

We corrected richness for varying effort per sample prior to analysis (Appendix S1: Section S1).

Multivariate statistical analyses

We used a multifactor mixed-effects permutational multivariate analysis of variance (PERMANOVA; Anderson & Willis, 2003) conducted through the PERMANOVA+ add-on (Anderson et al., 2008) for PRIMER v7 (Clarke & Gorley, 2015) to assess spatiotemporal variability in forage fish communities. The study design consisted of four explanatory factors: estuary, season, zone, and year (see Appendix S1: Section S1 for factorial design details). We conducted canonical analysis of principal coordinates using the *vegan* package in R (Oksanen et al., 2019) to examine differences among significant factors (see Appendix S1: Section S1 for details on test assumptions). We additionally conducted a principal coordinates analysis (PCoA) to visualize multivariate patterns of species composition and abundance by estuary over time.

To explore the effects of environmental variables on forage fish community composition, we performed a distance-based redundancy analysis (dbRDA; McArdle & Anderson, 2001) using the *vegan* package in R (Oksanen et al., 2019). Explanatory variables included water temperature, pH, salinity, dissolved oxygen, water clarity, and percent cover of SAV. We determined the most appropriate model using the Akaike information criterion (AIC) and stepwise model selection. We used a similar approach to explore the relationship between forage fish and predator communities (Appendix S2: Section S1).

We conducted all multivariate methods using a square-root-transformed Bray-Curtis dissimilarity matrix derived from fourth-root-transformed species composition and abundance data (see Appendix S1: Section S1 for transformation and dissimilarity metric details).

Time series analyses

We constructed seasonal time series for richness, evenness, and principal coordinate scores. We then used power spectral density estimation to detect periodicity within each time series via the Lomb-Scargle method of least-squares spectral analysis using the *spectral* package for R (Seilmayer, 2019). We performed cross-correlation analyses to assess potential variation in forage fish communities related to NAO and ENSO (see Appendix S1: Section S1).

To test for synchrony in forage fish community composition among estuaries, we also performed cross-correlation analyses for each estuary pair on richness,

evenness, and principal coordinate scores. To investigate interannual synchrony, we first detrended data to remove seasonal signals. For intra-annual synchrony, we focused only on the seasonal signals.

RESULTS

From the 300 total taxa collected by FIM sampling, we identified 50 as forage fishes spanning 14 families. Of the 50 forage fish taxa, seven were found only in either Apalachicola Bay or Cedar Key, while one taxon was found exclusively in Tampa Bay or Charlotte Harbor (Figure 2). Bay Anchovy (*Anchoa mitchilli*) were the most abundant forage fish, and Pinfish (*Lagodon rhomboides*) were the most ubiquitous among all samples (Appendix S1: Table S1). Forage fish composition and total richness differed among the four estuaries (Table 1 and Figure 2), as did the top taxa by abundance and frequency of occurrence (Appendix S1: Table S2). Over 90% of taxa estimated by Chao's Index were sampled in each estuary, indicating sampling was sufficient (Table 1). Average local richness differed among estuaries ($F = 77.59$, $p < 0.001$). Pairwise tests further indicated that local richness was higher in the northern estuaries than the southern ones ($t > 9.06$, $p < 0.001$). Richness was similar between the two northern estuaries (Apalachicola Bay and Cedar Key; $t = 1.54$, $p > 0.05$) and the two southern ones (Tampa Bay and Charlotte Harbor; $t = 1.41$, $p > 0.05$). Local richness differed among all seasons ($F = 183.12$, all pairwise $t > 5.53$, all $p < 0.001$) and was lowest in the winter, highest in the summer, and intermediate in the fall and spring (Appendix S1: Figure S2b). Evenness varied about a global average of 0.52. Average local evenness did not differ among estuaries ($F = 0.37$, $p > 0.05$) and differed among seasons but to a small degree ($F = 6.79$, $p < 0.001$; Appendix S1: Figure S2).

Forage fish assemblages significantly varied both intra- and interannually among estuaries (significant Season \times Estuary \times Year interaction term; Table 2). This broad-scale variation was modulated by significant fine-scale within-estuary variation (significant Season \times Zone [Estuary] \times Year interaction term; Table 2). The greatest multivariate variability occurred at the scale of individual samples (residuals), then across seasons, and finally across estuaries (Table 2). Pairwise tests indicated that forage fish assemblages were similar between the two northern estuaries in all seasons, and between the two southern estuaries in winter, summer, and fall (Appendix S1: Table S3). Forage fish assemblages in northern estuaries were significantly different from southern estuaries in all four seasons (Appendix S1: Table S3). Among-estuary differences accounted for

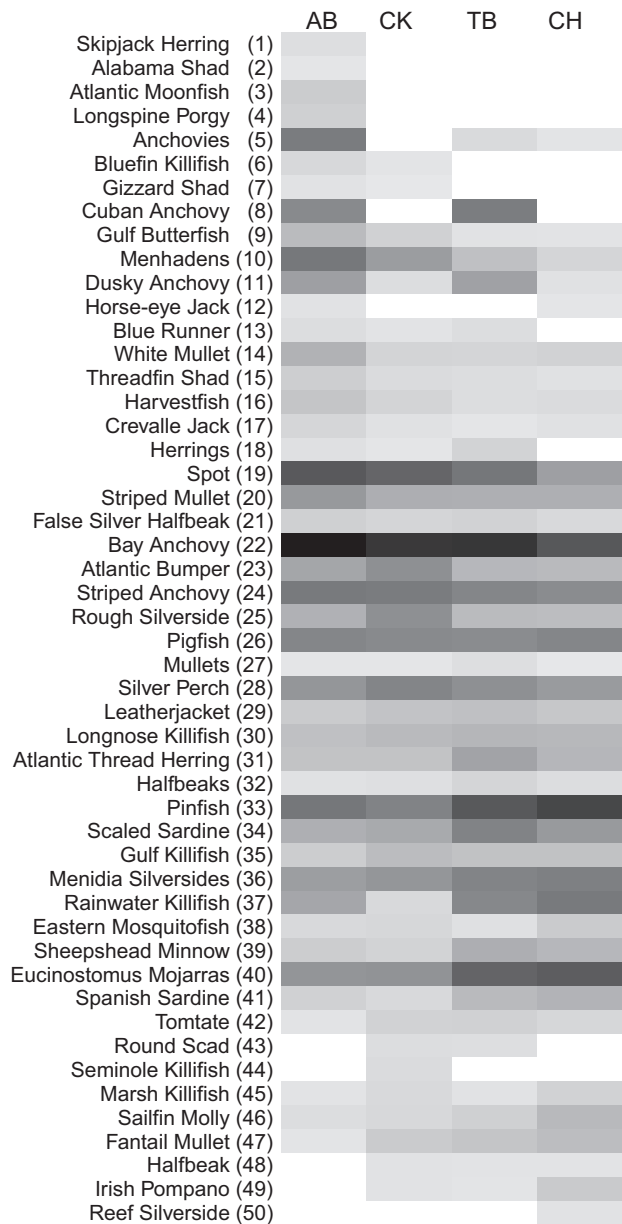


FIGURE 2 Distribution of forage fish taxa, sorted by similarity of taxa distributions, across all estuaries: Apalachicola Bay (AB; $n = 45$ species), Cedar Key (CK; $n = 42$), Tampa Bay (TB; $n = 41$), and Charlotte Harbor (CH; $n = 39$). Shading indicates relative abundance across all samples; white indicates taxa were not found in any sample in this estuary

2.05%–15.85% of within-season variability in forage fish assemblages. Constrained ordination resulted in three significant canonical axes within each season. The first canonical axis (CA1), which separated the northern and southern estuaries for each season, accounted for 67.68%–78.25% of among-group variability. The second canonical axis (CA2), which separated Apalachicola Bay and Cedar Key for each season, accounted for 15.78%–21.63% of among-group variability. The taxa most related to the separation between the northern and southern

estuaries along CA1 across all seasons were Pinfish, *Eucinostomus* mojarras (*Eucinostomus* spp.), and Rainwater Killifish (*Lucania parva*), while the taxa most related to the separation between Apalachicola Bay and Cedar Key along CA2 varied by season (Figure 3a–d). Assemblages were significantly different among all seasons in each of the four estuaries (Appendix S1: Table S3) and accounted for 0.26%–15.28% of within-estuary variability in forage fish assemblages. The taxa most related to seasonal differences across all estuaries were *Eucinostomus* mojarras, Spot (*Leiostomus xanthurus*), and Pinfish (Figure 3e–h).

Power spectral density analyses revealed strong significant annual periodicity in richness for all estuaries. Charlotte Harbor was the only estuary where evenness exhibited significant annual periodicity. The first four principal coordinates (PCO) axes revealed strong significant annual periodicity in all estuaries, although strongest in the northern estuaries. Relatively strong, significant subdecadal periodicity of 3–7 years was observed among several PCO axes in Cedar Key, Tampa Bay, and Charlotte Harbor (Appendix S1: Figure S3). Strong, significant associations were found between NAO and each of the estuaries (1 season lag) along the first PCO axis, and between NAO and the southern estuaries (1 season lag) along the second PCO axis. There was also a significant association between the Multivariate ENSO Index and each of the estuaries (lag 0–1 seasons) among the first four PCO axes (Appendix S1: Table S4).

Positive interannual synchrony in richness (lag 0–1 seasons) occurred between Apalachicola Bay and Cedar Key ($r = 0.28$), Apalachicola Bay and Charlotte Harbor ($r = 0.29$), and Cedar Key and Tampa Bay ($r = 0.37$). Evenness was positively synchronous between Apalachicola Bay and Cedar Key ($r = 0.29$) and between Cedar Key and Charlotte Harbor ($r = 0.35$), and negatively synchronous between Tampa Bay and Charlotte Harbor ($r = -0.28$). There was positive interannual synchrony (lag 0–1 seasons) between the two northern estuaries ($r > 0.43$ – 0.51) in the first two PCO axes and between the two southern estuaries ($r = 0.64$ – 0.74) in the first three PCO axes. Weak but significant positive synchrony also occurred between Tampa Bay and each of the two northern estuaries in the first two PCO axes ($r = 0.35$ – 0.54 ; Appendix S1: Table S5). Significant positive intra-annual synchrony occurred among all estuaries in richness and each of the first four PCO axes ($r = 0.34$ – 0.99 ; Appendix S1: Table S5). Evenness was positively synchronous between Cedar Key and Tampa Bay ($r = 0.40$) and between Tampa Bay and Charlotte Harbor ($r = 0.63$), and negatively synchronous between Apalachicola Bay and Cedar Key ($r = -0.33$) and between Apalachicola Bay and Tampa Bay ($r = -0.69$; Appendix S1: Table S5).

TABLE 2 Nonparametric multivariate analysis of variance of 50 fish taxa abundance variables, based on square-root-transformed Bray-Curtis dissimilarity derived from fourth-root-transformed species composition and abundance data, including estimated pseudo-variance components for noncovariate fixed and random factors

Source	df	Sum of Squared Deviations	Mean Square	Pseudo- <i>F</i>	<i>p</i>	Variance estimate	Percent of total
No. seines (NS) ^a	1	527.16	527.16	5.2293	0.0001	N/A	N/A
No. trawls (NT) ^a	1	316.9	316.9	4.2042	0.0001	N/A	N/A
Year covariate (YearC) ^a	1	740.36	740.36	5.8773	0.0001	N/A	N/A
Estuary (Est)	3	6389.3	2129.8	3.8676	0.0002	1.46	10.45
Season (Se)	3	6931.9	2310.6	21.432	0.0001	1.64	11.68
Year	18	1635.9	90.883	3.1136	0.0001	0.62	4.43
Zone (Estuary) [Zo(Est)]	9	3966	440.66	16.469	0.0001	1.33	9.44
Est × Se	9	2113.3	234.82	2.8738	0.0001	0.92	6.55
Est × Year	43	1940.6	45.129	1.5941	0.0001	0.60	4.26
Se × Year	56	2080.6	37.153	1.5241	0.0001	0.59	4.17
Se × Zo(Est)	27	1301.1	48.189	2.0415	0.0001	0.66	4.68
Zo(Est) × Year	121	3186.7	26.336	1.2054	0.0001	0.53	3.76
Est × Se × Year	123	3309	26.903	1.1452	0.0001	0.55	3.95
Se × Zo(Est) × Year	354	8053.7	22.75	1.0412	0.0006	0.47	3.37
Residual	2564	56,022	21.849			4.67	33.27
Total	3333	98,514				14.05	100

Note: All variance components are random except for Season, Estuary, and Est × Se which are sums of squared fixed effects.

^aCovariate effects were removed prior to analysis of fixed and random effects.

All habitat parameters were selected through AIC selection as having a substantial contribution to the explained variation in forage fish community composition and abundance. There was a significant effect of habitat on forage fish community composition and abundance ($F = 71.68$, $p < 0.001$), accounting for 11.82% of the total variability in forage fish assemblages. Each sequentially added term explained a significant portion of the variability (all $p < 0.001$). Temperature ($F = 160.66$) and salinity ($F = 150.90$) had the strongest effects, followed by bottom vegetation ($F = 66.80$) and water clarity ($F = 40.90$) each with moderate effects, while pH ($F = 7.06$) and dissolved oxygen ($F = 3.79$), although significant, had relatively weak effects. Constrained ordination resulted in six significant canonical axes ($F = 1.62$ – 247.27 , $p < 0.05$). The first and second canonical axes explained 6.80% and 3.77% of the variation in forage fish assemblages, respectively (Figure 4). Variable associations with CA1 showed that high levels of salinity, bottom vegetation, and water clarity were characteristic of the two southern estuaries (Tampa Bay and Charlotte Harbor) and that these conditions were related to high relative abundance of benthivorous taxa such as *Eucinostomus* mojarras, Pigfish (*Orthopristis chrysoptera*), and Pinfish. By contrast, lower levels of salinity, bottom vegetation, and water clarity were characteristic of the two northern

estuaries (Apalachicola Bay and Cedar Key), and these conditions were related to high relative abundances of planktivorous taxa such as Bay Anchovy, Striped Mullet (*Mugil cephalus*), and menhadens (*Brevoortia* spp.), as well as the omnivorous Spot. Dissolved oxygen and temperature were associated with seasonal differences along CA2, where winter and spring were characterized by high dissolved oxygen and low temperatures and higher abundances of Pinfish, Spot, and Striped Mullet, while summer and fall were characterized by low dissolved oxygen, higher temperatures, and higher abundances of *Eucinostomus* mojarras, Pigfish, Scaled Sardine (*Harengula jaguana*), and Silver Perch (*Bairdiella chrysoura*; Figure 4). After accounting for habitat effects, there was a significant but weak association of predator community assemblage with forage fish assemblages, accounting for an additional 3.64% of variability in forage fish community composition and abundance (Appendix S2: Figure S1).

DISCUSSION

Forage fish communities are fundamental to maintaining bottom-up connections throughout many marine and

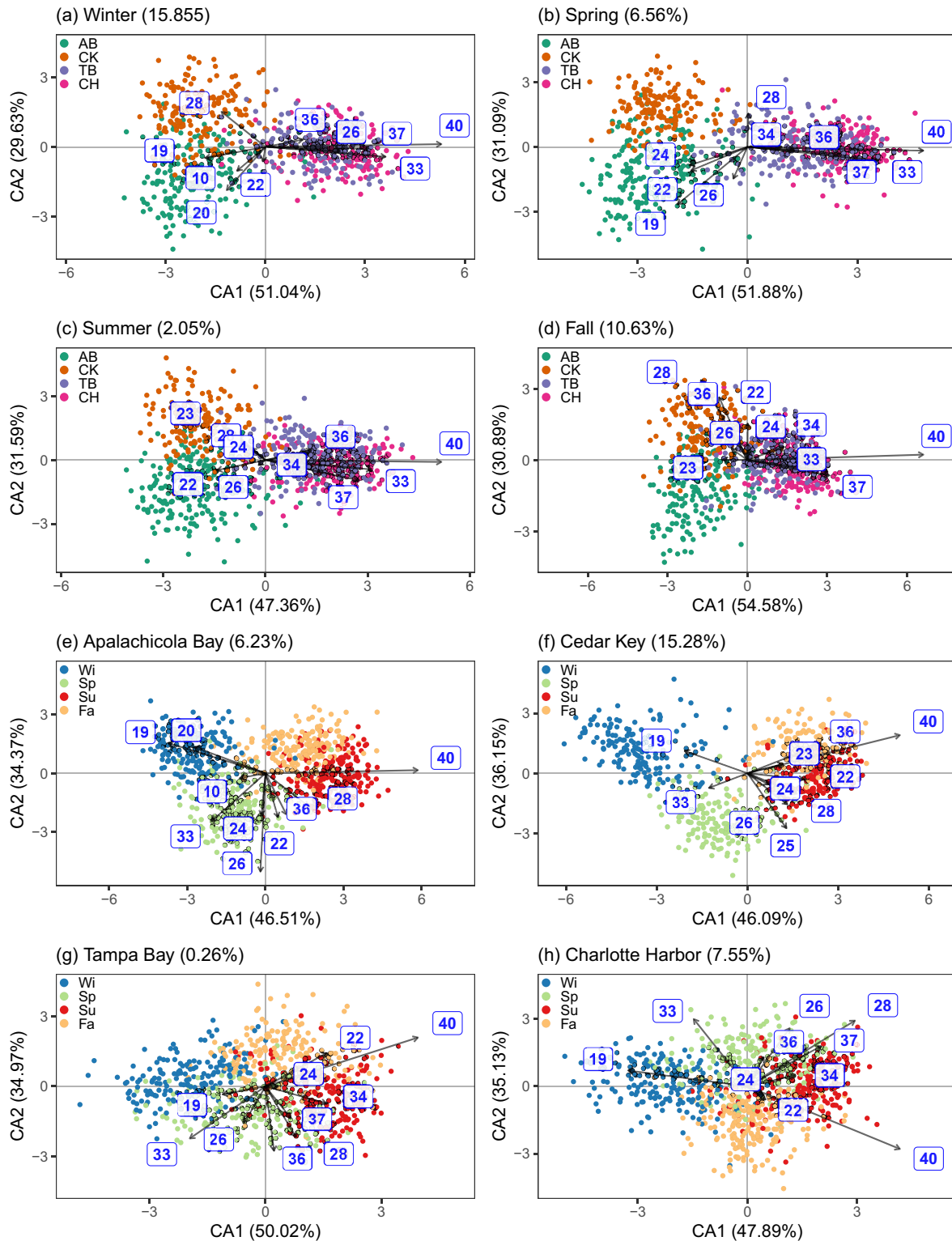


FIGURE 3 Canonical analysis of principal coordinates (CAP) ordination diagrams of estuary (AB: Apalachicola Bay; CK: Cedar Key; TB: Tampa Bay; CH: Charlotte Harbor) by season (a–d) and season (Wi: winter; Sp: spring; Su: summer; Fa: fall) by estuary (e–h). Percentages shown next to each group signify the total percentage of variability explained by the CAP model. Total among-group variance explained by each canonical axis (CA) is shown next to the axis title. Taxa associations are shown as vectors corresponding to correlation of the taxon to the canonical axes scores. These are shown for the top 10 taxa by relative abundance and frequency of occurrence among samples in each group. Number of labels correspond to taxa as shown in Figure 2. Note that only the first two canonical axes are shown for each diagram, corresponding to the two axes of greatest group separation, and thus, each ordination diagram does not depict the full extent of among-group separation. In both sets of ordination diagrams, the third canonical axis (not shown) further explained approximately 4%–11% of among-group variability

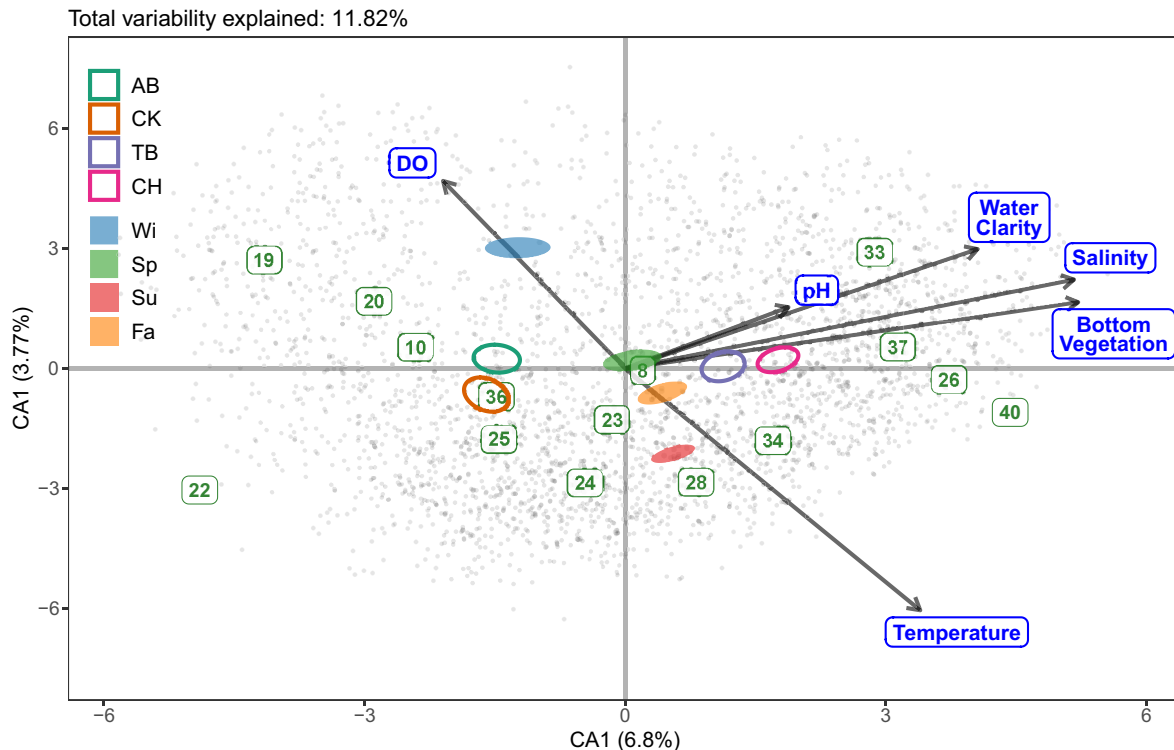


FIGURE 4 Distance-based redundancy analysis (RDA) ordination diagram for habitat parameters. Percentages shown signify the total variation in forage fish communities explained by each canonical axis (CA). Vectors represent the correlation of each habitat variable (DO: dissolved oxygen) with each CA, and taxa are plotted as weighted average scores, with relative position along each CA reflecting the “ideal” habitat conditions for a given taxon along that axis. Ellipses represent 95% CI for the centroid location of each estuary (open; AB: Apalachicola Bay; CK: Cedar Key; TB: Tampa Bay; CH: Charlotte Harbor) and each season (filled; Wi: winter; Sp: spring; Su: summer; Fa: fall). Forage fishes are represented as numbers corresponding to taxa as shown in Figure 2

estuarine food webs (Cury, 2000; Essington & Munch, 2014; Pikitch et al., 2014). Here, we have conducted an expansive analysis of the patterns and dynamics of forage fish communities across a broad latitudinal gradient spanning subtropical and temperate estuaries. Our efforts have also sought to better understand the processes that affected the observed patterns and dynamics. Our results revealed significant regional structuring of forage fish communities between the two northern and two southern estuaries, coupled with differential associations of fishes with habitat characteristics between regions. These results further suggested that the regional structuring was related to the combined effects of latitude and variation in basal resources, most likely related to differences in riverine input to the estuaries. Our analyses additionally uncovered a consistent seasonal cycle in forage fish communities across the region, modulated by a long-scale periodicity potentially associated with the NAO and the global ENSO cycle.

One of the defining characteristics of eGOM estuarine forage fish communities revealed in this study was a clear latitudinal distinction between the two northern and two southern estuaries, both in richness and in the

composition and abundance of forage fish taxa. Local richness was higher in the northern estuaries than in the southern estuaries. While this pattern was statistically significant, the average magnitude of these differences was relatively small, with only two to three additional taxa typically observed in northern estuaries. The small magnitude of difference in richness may explain the apparent similarity in evenness between the northern and southern estuaries despite the observed latitudinal differences across other analyses. Differences in richness appeared to be driven by higher summer and fall richness in the northern estuaries, as winter richness was similar across all estuaries (Appendix S1: Figure S3). Apalachicola Bay and Cedar Key are located in the confluence between temperate and subtropical ecoregions. This may allow for higher taxonomic diversity through a mixture of species (Waugh et al., 2019), as temperate residents comingle with seasonally ephemeral subtropical taxa during warmer months. Indeed, seven of the 50 taxa were found only in either Apalachicola Bay or Cedar Key, while only one taxon was found exclusively in Tampa Bay or Charlotte Harbor. Alternatively, greater primary productivity in the northern estuaries during warmer

months may be able to support higher planktonic biomass and thus greater taxonomic diversity (Castillo-Rivera et al., 2002; Yanez-Arancibia et al., 1988). The separation between northern and southern estuaries also accounted for a large percent of the variation in forage fish community composition and abundance. Much of this separation was attributed to variation in abundances of several common and ubiquitous taxa primarily based on basal resource use. Several common taxa with higher observed abundances in the northern estuaries such as Bay Anchovy, Striped Anchovy (*Anchoa hepsetus*), Rough Silverside (*Membras martinica*), and menhadens rely primarily on planktonic production (Lucas, 1982; Olsen et al., 2014; Sheridan, 1978). By contrast, the southern estuaries had higher abundances of small sparids (Pinfish and Pigfish) and *Eucinostomus* mojarras, taxa that rely on a benthic source of production (Carr & Adams, 1973; Darcy, 1985).

Interestingly, and perhaps surprisingly, estuary morphology did not appear to have a strong effect on forage fish community composition, as no significant differences were observed between Cedar Key (open estuary) and Apalachicola Bay (semi-enclosed estuary) among all seasons. While this may seem to contradict findings from Schrandt et al. (2018), there are several important distinctions between these two studies that may explain the apparently different findings. The current study focused primarily on forage fishes and investigated estuary-wide variations across all habitats. Conversely, Schrandt et al. (2018) included a broader variety of taxa spanning several trophic levels, and limited samples to habitats that contained at least 50% bottom coverage of seagrasses. Additionally, our study included samples from both seines and trawls to encompass a variety of depths and habitats over a more coarse sampling grain, while Schrandt et al. (2018) exclusively used trawls to sample primarily seagrass habitats in depths greater than 1 m. These discrepancies suggest either that forage fish communities are less affected by hydrographic processes governed by estuarine morphology or that the response of forage fishes to estuarine morphology is dependent on habitat type at a patch scale finer than the broader scales over which samples were aggregated for the present study.

A significant portion of the difference in taxonomic composition between the northern and southern estuaries was associated with habitat characteristics that further supports the hypothesis of regional variation in basal resource use. Specifically, salinity, water clarity, and availability of SAV varied between the regions and are associated with the relative proportions of planktonic and benthic production. Apalachicola Bay is a semi-enclosed bay fed primarily by the alluvial Apalachicola

Chattahoochee-Flint (ACF) watershed, while Cedar Key is an open estuarine region fed primarily by the blackwater Suwannee River. Both the ACF watershed and Suwannee River are high-discharge systems with watersheds that extend into Georgia, and are characterized by high-nutrient loads. Tampa Bay and Charlotte Harbor are both semi-enclosed bays fed primarily by blackwater rivers: Tampa Bay by the Alafia, Little Manatee, Manatee, and Hillsborough Rivers, and Charlotte Harbor by the Myakka and Peace Rivers. These rivers have much lower discharge rates than the ACF watershed and Suwannee River (U.S. Geological Survey, 2019). Thus, the northern estuaries receive a much higher nutrient flux than the southern estuaries, which can affect patterns of basal resource dominance. Apalachicola Bay, in particular, also experiences large fluxes of sediments from the ACF, further limiting light availability for benthic production. Indeed, we found lower water clarity, salinity, and SAV in the northern estuaries. This can lead to low benthic production due to light attenuation, allowing phytoplankton to outcompete benthic species for available nutrients (Sand-Jensen & Borum, 1991). Conversely, the southern estuaries had a high proportion of SAV coupled with high water clarity and high salinity, which allows for enhanced benthic growth as light is less attenuated and bottom vegetation provides a suitable substrate for benthic algal growth. The lower nutrient requirement of benthic microalgae allows them to outcompete phytoplankton, leading to dominance of benthic production in this region (Sand-Jensen & Borum, 1991; Snow & Adams, 2007).

The distinction between the northern and southern estuaries observed in this study could be related to both regional and local processes structuring these communities. Regional effects, such as latitudinal patterns in temperature and species ranges, have been documented in other broadly located estuarine systems (Pease, 1999; Vasconcelos et al., 2015). Additionally, a north-south gradient in basal resource dominance has been documented in eGOM shelf waters previously by Radabaugh (2013), who also found basal resource shifts between nearshore and offshore shelf environments of the eGOM related to variation in light attenuation via depth gradients. Burghart et al. (2013) found variations in basal resource dependence of macrofaunal communities between surface-fed (eutrophic, phytoplankton dominance) and spring-fed (oligotrophic, benthic dominance) systems, with associated abrupt shifts in faunal communities. Our findings suggest that the latitudinal shift in faunal communities in eGOM estuaries is related to comparable basal resource dominance shifts driven largely by hydrological differences among estuaries. Although our results indicated that differences in local habitat had a strong effect on forage fish communities in this region, we did

not measure the relative strength of regional and local drivers of community variability. Further studies of these communities that consider more explicit measures of spatially structured processes, such as those using variation partitioning techniques or joint species distribution models (e.g., HMSC, Ovaskainen et al., 2017), could expand on our results to better parse these components of forage fish community structure.

Despite the observed regional differences, forage fish communities displayed similar seasonal dynamics among all estuaries. Seasonality was particularly strong in the northern estuaries, consistent with what we expect for higher latitudes. This strong seasonal signal was also reflected in the positive intra-annual synchrony among all estuaries in the first four PCO axes (Appendix S1: Table S5) and primarily related to seasonal abundances of *Eucinostomus* mojarras, Spot, and Pinfish (Figure 3e–h). Seasonal periodicity may be related to differing life history strategies among forage fish taxa. For example, Faletti et al. (2019) and Chacin et al. (2016) found that Pinfish in the eGOM were most abundant in late winter and early spring due to postspawning recruitment, while Godefroid et al. (2001) found that juvenile abundance of *Eucinostomus* mojarras peaked in summer and early fall following early-summer spawning. Both of these patterns are reflected in eGOM forage fish community seasonal associations shown in this study. Seasonal periodicity may also be related to shifts in habitat suitability. For example, variations in riverine discharge could cause shifts in salinity, sediment, and nutrient levels, thus causing short-term seasonal shifts in the dominance of benthic versus planktonic production. This is of particular concern in the more temperate northern estuaries where seasonal shifts in temperature and salinity are more extreme (Bianchi et al., 1999; Orlando, 1993) and where seasonal decreases of aboveground seagrass biomass reduce available substrate for benthic growth (Dawes et al., 1985).

Time series analyses also revealed significant sub-decadal periodicity which, upon further analysis, was related to both the NAO index and MEI, an indicator of the relative state of the ENSO global cycle. These climatological phenomena have documented global effects throughout both terrestrial and marine ecosystems (Fiedler, 2002; Gordo et al., 2011; Holmgren et al., 2001; Ottersen et al., 2001; Rossi & Soares, 2017; Stenseth et al., 2004; Zhang et al., 2017). NAO has a strong effect on temperature primarily in the temperate north Atlantic, but in the southeastern United States, both NAO and ENSO have a strong interannual effect on precipitation, influencing stream flow and seasonal salinity variability in surface-fed eGOM estuaries (Coleman & Budikova, 2013; Schmidt & Luther, 2002). Salinity variability related

to large-scale climatological oscillations can in turn have a strong effect on western Atlantic estuarine fish communities (Garcia et al., 2001). El Niño Southern Oscillation, in particular, was also shown to have a significant effect on phytoplankton biomass variability in the northern Gulf of Mexico, resulting in higher planktonic production in El Niño winters (Gomez et al., 2019) potentially driving an increase in forage fish oil content (Leaf, 2017), and may have an additive effect on the interannual viability of forage communities to support upper trophic level taxa in these systems. Additionally, ENSO can drive shifts in coastal circulation (Gomez et al., 2019), which could influence the larval supply of forage fishes that spawn in nearshore areas. Despite the relatively strong association of estuarine forage fish communities with NAO revealed in this study, very little research has been done on the effects of NAO on these communities in this region. Our findings warrant further study into the effects of NAO, ENSO, and other large-scale climatological phenomena on estuarine food webs in the eGOM.

We examined community dynamics across a broad range of estuarine taxa in the eGOM by combining data from two different gears, each of which surveyed specific habitat types and selected different forage fishes. It is possible that portions of the community were underrepresented in the combination of gears used. For example, the relative size of these gears, speed of collection, and small mesh sizes of the netting used in each gear focused primarily on smaller species of forage fishes and the juvenile stages of larger species. Although the inclusion of larger gears may have allowed for a broader investigation of forage fishes across all life stages, several species are considered forage fishes early in their life history but no longer fit the criteria in later life stages. Indeed, Pigfish (*O. chrysoptera*) feed primarily on plankton and small benthic invertebrates as juveniles and subadults before transitioning to a higher trophic role as adults (Darcy, 1983). Likewise, jacks such as Blue Runner (*Caranx crysos*) and Crevalle Jack (*Caranx hippos*) feed on zooplankton in estuarine nursery habitats (Austin & Austin, 1971; Keenan, 2002; Mirto et al., 2002) but reach sizes as adults generally considered too large to serve as a trophic intermediary. Additionally, neither gear included in this study sampled pelagic waters in depths greater than 2 m, which represent a potentially key habitat for forage fishes in estuarine systems. For example, Atlantic Thread Herring (*Opisthonema oglinum*) are commonly found in the upper 3 m of the water column in depths greater than 5 m (Lieske & Myers, 1994) and thus were potentially underrepresented in this study. Further studies are needed to investigate whether forage fishes primarily inhabiting pelagic estuarine habitats follow similar patterns revealed in this study.

Due to the role of forage fishes as a key link between primary production and higher trophic levels, it is important to continue studying these communities to predict how future changes in estuarine environments will propagate through the ecosystem. For example, shifts in water quality could cause the loss of benthically associated forage fishes (Lapointe et al., 2015), which subsequently could lead to bottom-up food web effects (Rooney et al., 2006) such as has occurred in Florida's Indian River Lagoon (Adams et al., 2019). This is of particular concern in the context of anthropogenic eutrophication, which can potentially lead to light-attenuating harmful algal blooms. Moreover, the effects of global ocean change through the individual and interactive effects of warming and acidification may lead to shifts in composition (Blowes et al., 2019) and reductions of trophic web integrity, particularly for primary consumers (Nagelkerken et al., 2020). Thus, continued monitoring of forage fish communities is necessary to ensure their future sustainability and that of the ecosystems they support.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Jonathan A. Peake and Christopher D. Stallings conceived the idea; Timothy C. MacDonald and Kevin A. Thompson collated and provided raw data; Jonathan A. Peake processed and analyzed all data and produced all figures; and Jonathan A. Peake and Christopher D. Stallings lead writing. All authors contributed edits and comments toward the final manuscript.

DATA AVAILABILITY STATEMENT

Data and code (Peake, 2021) are available from Zenodo: <https://doi.org/10.5281/zenodo.5711374>.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

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