Similar habitats, different communities: fish and large invertebrate assemblages in eastern Gulf of Mexico polyhaline seagrasses relate more to estuary morphology than latitude

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Abstract

Seagrass habitats are a dominant component of coastal waters along the eastern Gulf of Mexico coast and are recognized as essential habitats for many species. Although various ecologically and economically important species depend on seagrass habitats at some life stages, these habitats are vulnerable to anthropogenic influences. As coastal human populations continue to grow, and nearshore habitats are affected, understanding the structure and function of assemblages associated with nearshore habitats is important for management and mitigation efforts. Therefore, we sampled estuarine and nearshore polyhaline seagrass beds monthly (May–November) from 2008 through 2015 using a 6.1-m otter trawl in seven estuaries in the eastern Gulf of Mexico. Despite latitudinal variability, assemblage structure of fishes and selected larger invertebrates was predominantly driven by estuary morphology—semi-enclosed estuaries had significantly higher catch-per-unit-effort (CPUE) of estuarine obligates and incidental marine taxa, whereas open estuaries had higher CPUE of small forage and cryptic species. Furthermore, abundances of several important fishery species differed markedly between semi-enclosed and open systems. Our results highlight (1) the relative importance of different scales of environmental factors' influence on communities, (2) the need for understanding how seemingly similar habitats in estuaries of differing morphologies can support different fishery species, and (3) the importance of regional-scale monitoring data and its value in tracking ecological changes.

Keywords: BIOENV, brackish water, environment management, estuarine fisheries, otter trawls, submerged aquatic vegetation; Gulf of Mexico, Florida

1. Introduction

Seagrass beds are often a dominant component of estuaries and nearshore waters and are essential habitats for many estuarine fishes and invertebrates. For some species, including estuarine-dependent reef-associated fishes, seagrass habitats provide valuable nursery areas (e.g., Beck et al. 2001; Jackson et al., 2001; Nagelkerken et al., 2001; Heck et al. 2003; Verweij et al., 2008; Bertelli and Unsworth, 2014; reviewed by Whitfield, 2017) and food sources (reviewed by Whitfield, 2017). These important nearshore habitats are also especially vulnerable to anthropogenic influences such as eutrophication (e.g., Duarte, 2002) and intense harvesting, both of which may alter coastal food webs and affect community structure (Heck and Valentine, 2007). With much of the human population living near the coast, and that population continuing to grow, estuarine and nearshore seagrass habitats, and their associated fauna, may be further affected. Localized changes in abundance and distribution could eventually translate to population impacts if alternative suitable habitat were unavailable or not located by the associated fauna.

Estuarine and nearshore seagrass habitats along Florida’s Gulf coast are extensive, spanning a latitudinal climatic gradient from warm-temperate in the north (panhandle) to subtropical in the central peninsula and tropical in the southern Florida Keys. Multiple estuaries have been identified as some of the most productive and biologically diverse systems of Florida’s Gulf coast (Geselbracht et al., 2009). These estuaries also have two distinct morphologies, referred to as semi-enclosed and open estuaries in this study. Semi-enclosed estuaries are coastal bodies of water with free connections to the sea; most of the freshwater is discharged at the head via river(s) and then a mouth is present between the body of the estuary and the coastal ocean. Open estuaries, on the other hand, generally lack land barriers, and freshwater mixes with marine waters along the coastline. Florida's Big Bend region is an example of an open estuary system where the low-relief coastline functions as an estuary because of extensive freshwater sheet flow entering the Gulf (Geselbracht et al., 2015). These two morphologies vary in sources and volumes of freshwater inflow and associated hydrodynamics, as well as the spatial extent of connection with marine waters (i.e. an open coastline as opposed to a mouth), so fish and invertebrate communities may differ based on species' salinity preferences and tolerances and settlement cues.

Different types, amounts, and spatial arrangements of submerged aquatic vegetation can also affect associated faunal communities (e.g., Steffe et al., 1989; Raposa and Oviatt, 2000; Jackson et al., 2006; Jelbart et al., 2007; Staveley et al., 2017; Scapin et al., 2018). There are seven seagrass species found in Florida but not all estuaries along the Gulf coast have all seven species. The northern estuaries tend to be characterized by *Halodule wrightii*, *Thalassia testudinum*, and *Syringodium filiforme*, and more southern estuaries along the central peninsular coast tend to be dominated by *Thalassia testudinum* and *Halodule wrightii*. Additionally, the seagrass habitat tends to be more fragmented in the semi-enclosed estuaries as opposed to the Big Bend region, which contains some of the largest contiguous seagrass beds in the continental United States (Carlson and Madley, 2006), and tend to have mixtures of seagrass species. The semi-enclosed estuaries can have more monotypic seagrass beds. Further details on these estuaries (e.g., shoreline vegetation, riverine influence) can be found in Switzer et al. (2012) and references within.

Although all estuaries in this study were relatively shallow (≤5 m depth), they vary in climatic regime, morphology and associated seagrasses and spatial arrangements, so seagrass-associated faunas presumably differ among estuaries and estuary morphology. To test this hypothesis, we used a fisheries-independent monitoring survey (otter trawl) to sample relatively deeper water (>1.0 m depth), non-shoreline, polyhaline (>18) seagrass beds in semi-enclosed and open estuaries in the eastern Gulf. Our objectives were to: 1) describe patterns in faunal assemblages associated with polyhaline seagrass beds of different estuaries (and latitudes) representing different morphologies, 2) identify variations in groups of environmental variables that correlate with patterns of faunal assemblages, and 3) evaluate the relative importance of different environmental variable groups relating to the seagrass-associated fauna.

2. Materials and Methods

2.1. Trawl Sampling

The Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute Fisheries-Independent Monitoring Program (FWC-FWRI) has conducted standardized stratified-random sampling in estuarine systems of the eastern Gulf of Mexico monthly since the late 1990s (e.g., McMichael,1991; 2009). The monitoring effort includes a multi-gear approach targeting a variety of habitats, but recent analyses indicated that the nearshore, deeper water polyhaline seagrass habitats had been under-sampled (Casey et al., 2007; De Angelo et al., 2014). Additional sampling was therefore initiated in 2008 to better characterize nekton assemblages associated with deeper water polyhaline seagrasses, also aspiring to obtain needed data on estuarine-dependent reef-associated fishes (e.g., Switzer et al., 2012; Flaherty et al., 2014; Flaherty-Walia et al., 2015b).

Polyhaline seagrass beds were sampled via bottom trawl by FWC-FWRI in seven estuaries along Florida's Gulf coast (Fig. 1, Table 1) from 2008 through 2015. Apalachicola Bay (AP), Charlotte Harbor (CH), and Tampa Bay (TB) have been routinely sampled since the late

1990s; St. Andrew Bay (SA) and three estuaries in the Big Bend (BB) region between Cedar Key and Cape San Blas (St. Marks [BBA], Econfina [BBB], Steinhatchee [BBD]) were added in 2008 for this study and have become part of the continuing survey.

Seagrass-associated fishes and large invertebrates were sampled monthly with a 6.1-m otter trawl (38-mm mesh with a 3.2-mm mesh liner) from May through November during 2008–2015. Sampling locations were selected from a stratified-random-sampling design based on 0.1-nautical mile × 0.1-nautical mile (1 nautical mile = 1.85 km) grid cells overlaid on polyhaline seagrass habitats in each estuary. Potential sampling sites were limited to generally polyhaline (>18) waters that contained at least 50% bottom coverage of submerged aquatic vegetation (SAV) and were between 1.0 and 7.6 m deep. Accordingly, the number of trawls sampled in an estuary varied (Table 1). When water clarity permitted visual assessment of SAV composition and coverage, assessment was done from the surface, via drop camera, or by a free-diving swimmer. When water clarity prevented visual assessment, tactile assessment was used at four equidistant points along the transect, with points within the transect assessed after trawling. The otter trawl was towed 0.1 nautical mile at 1.2 kts (i.e., a 5-min tow). When bycatch (e.g., algae, tunicates) quantity was exceptionally high and prevented safe retrieval of the trawl, tows were reduced to three minutes. If bycatch quantity was still too high, tows were reduced to two minutes. Tows in depths ≥1.8 m were done in a straight line; tows in depths <1.8 m were curved to reduce any disturbance caused by the boat engine propeller wash. To account for differences in tow times, effort was calculated by distance covered during each tow and standardized to 720 m^2, which is the area sampled by a standard, 5-min tow of 0.1 nautical miles. Catch-per-unit-effort (CPUE) is presented as the number of individuals per trawl.

All fish and selected invertebrates (e.g., *Callinectes* spp., *Farfantepenaeus* spp., and *Argopecten* spp.) were identified in the field to the lowest possible taxonomic unit and counted. A subset of individuals was retained for laboratory confirmation of field identifications; remaining individuals were returned to the water. Extremely large samples of a single dominant taxon were subsampled using a modified Motoda box splitter (Winner and McMichael, 1997) after bycatch and less abundant animals were removed. Bottom type, SAV descriptors (i.e., seagrass species, alga species, % cover), depth (m), slope, temperature (°C), salinity (practical salinity scale), and dissolved oxygen (mg/L) were recorded for each trawl. Bottom values of temperature, salinity, and dissolved oxygen were used in this study because nekton were collected via bottom trawl.

2.2. Data analysis

Variations in seagrass-associated communities were analyzed as described below with the PRIMER v7 multivariate statistics software package (Clarke and Gorley, 2015). Null hypotheses were rejected for $P < 0.05$.

2.2.1. Data pre-treatment

Catch-per-unit-effort for each sample was first dispersion weighted (Clarke et al., 2006) by dividing the CPUE for each taxon by its index of dispersion (variance to mean ratio, for each estuary × year × month combination) to differentially down-weight taxa with high variability, such as schooling species. All samples were then square-root-transformed to down-weight consistently highly abundant taxa and up-weight consistently less abundant taxa (Clarke et al., 2006). Shade plots were constructed and analyzed for multiple data-transformation options

(Clarke et al., 2014) and square-root transformation after dispersion weighting was deemed appropriate in this case.

Environmental data consisted of categorical and quantitative data (Table 2). Categorical variables were changed to binary codes, given a value of 1 if a category was applicable and 0 if it was not. For quantitative variables, skew was visually assessed using draftsman (scatter) plots to select an appropriate transformation and to calculate the correlation between the members of each pair of variables. The environmental variables were then grouped by similarity of information (i.e., SAV, bycatch, water quality, physical information, tidal cycle, latitude, estuary morphology) so we could assess which group of environmental data was most closely related to the patterns in seagrass-associated faunal communities. These groups represented environmental data relating to different spatial scales, ranging from regional to estuary-wide to local. All environmental data were then normalized, to place each variable on the same dimensionless scale, and weighted as in Valesini et al. (2010) to ensure that all environmental variable groups had equal opportunity to contribute to further analyses.

2.2.2. Multivariate analysis

Our main interest was the potential community differences among estuaries and estuary morphology, but we included year in the following two ANOSIM models because we had eight years of sampling data and temporal differences may have played a role. To analyze potential community differences among estuaries and years, a 2-way crossed Analysis of Similarities (ANOSIM) test was performed on the dispersion-weighted and square-root transformed CPUE data. The analysis was then repeated for estuary morphology (semi-enclosed vs. open) and year. Nonmetric multidimensional scaling (nMDS) ordination was used to illustrate the spatial pattern of community differences. Following ANOSIM, Similarity Percentage (SIMPER) analysis was used to assess which species were driving the similarities and differences among estuaries and between estuary morphologies.

Before exploring relationship with environmental data, we needed to reduce the taxa to a subset that was driving the overall spatial pattern of community differences to allow for more efficient models when relating the faunal data with the environmental data. We used the BVSTEP procedure in the BEST routine to reduce the taxa. We searched a subset of taxa using the BVSTEP forward selection/backward elimination algorithm (the resemblance worksheet was the resemblance matrix for the taxa data averaged by estuary and year, and the data worksheet was the pre-treated dataset averaged by estuary and year), repeated multiple times, starting with different, randomly selected subsets of one to six species. The correlation method was Spearman rank. This procedure minimizes the chances of failing to detect the most suitable subset (Clarke and Warwick, 1998). The CPUEs of selected taxa were then subjected to coherence plot analysis to visualize how CPUE varied.

To explore which environmental group, or combination of groups, had the highest correlation with the spatial pattern of differences among the species identified using the BVSTEP procedure, we used the Biota and Environment Matching Routine (BIOENV). We restricted this analysis to a maximum of four explanatory environmental groups so that groups explaining only a small percentage of any remaining variation were not included after the most explanatory groups. All possible environmental group combinations were individually examined for correlation with spatial patterns of the taxa subset. A separate Bray-Curtis similarity matrix was created that included only those taxa identified in the BVSTEP procedure above and was used as the reference data set. The treated environmental data was used as the secondary matrix, and Euclidean distances were calculated to produce a resemblance matrix. We used Spearman's rank correlation coefficient (ρ) to assess correlations between the matrices and subsequent permutation tests as in Valesini et al. (2014) to test the statistical significance of the identified environmental groups. Relationships between the community data and individual variables within the selected environmental groups were then assessed by performing separate principal components analysis (PCA) for the selected environmental groups. The number of principal components retained was the number of components needed to explain at least 75% of the variation.

3. Results

3.1. Faunal assemblages of nearshore polyhaline seagrass beds

The full data set comprised 3,445 trawl tows, which collected 52,420 individuals representing 212 taxa (Appendix 1). The 2-way crossed ANOSIM for estuary and year indicated a much greater difference in communities (5× higher R value) among estuaries ($R = 0.55$, $p = 0.001$) than among years ($R = 0.11$, $p = 0.001$) (Fig. 2a). Estuaries with the most similar communities were the Big Bend estuaries ($0.11 \leq R \leq 0.30$; $p < 0.003$) and CH and TB ($R = 0.18$; $p = 0.001$). Greatest differences in assemblages were between the Big Bend estuaries and CH ($0.84 \leq R \leq 0.91$). The second ANOSIM, focusing on estuary morphology and year, revealed significant differences between semi-enclosed and open estuaries ($R = 0.57$, $p = 0.001$) and relatively little variation among years ($R = 0.11$, $p = 0.001$). All semi-enclosed estuaries had faunal assemblages that were different than those of the open estuaries in the Big Bend. Among semi-enclosed estuaries, faunal assemblages varied latitudinally with separation in the nMDS plot between SA and AP in the panhandle and TB and CH in the peninsula. Because the two

ANOSIM analyses supported differences among estuaries and their morphologies but little differentiation among years, we focused our interpretation of results on regional differences among estuaries and morphologies. Data, however, are presented by estuary and year so that temporal variability can be visualized.

SIMPER analysis identified many species contributing to differences among estuaries, but the majority were present in multiple estuaries and changed in abundance, not presence or absence. (A list of all species and their CPUEs are presented in the Appendix.) More than 30 taxa contributed to 70% of the dissimilarities between estuary pairs. Dissimilarities between estuary morphologies were dependent on 28 taxa. Half of these taxa had CPUEs in semi-enclosed systems at least twice those in open estuary systems (e.g., *Orthopristis chrysoptera*, *Lagodon rhomboides*, *Paralichthys albigutta*, *Lutjanus synagris*, *Callinectes sapidus*, *Lutjanus griseus*; Fig. 3). Nine taxa had greater CPUEs in open systems than in semi-enclosed systems (e.g., *Centropristis striata*, *Monacanthus ciliatus*, *Calamus arctifrons*, *Diplodus holbrookii*, *Argopecten* spp.; Fig. 3).

The BVSTEP analysis identified 11 taxa that yielded a similar picture to the entire data set ($\rho = 0.951$), with nine distinguished groups (Fig. 2b). The nMDS resulting from these 11 taxa was comparable to the nMDS with all 212 taxa (Fig. 2a) with the exception that TB and CH assemblages were no longer distinct. Coherence plot analysis resulted in four groups, differing in the way in which CPUEs varied among estuaries and years (Fig. 4). *Archosargus probatocephalus* and *Eucinostomus gula* had relatively low CPUE in the panhandle and Big Bend regions (AP, BBA, BBB, BBD and SA), and higher, variable CPUE in the peninsular estuaries (CH and TB; Fig. 4a). *Argopecten* spp., *C. arctifrons*, *Centropristis striata*, and *D. holbrookii* had greatest CPUEs in the Big Bend estuaries and low CPUEs in others (Fig. 4b).

Chilomycterus schoepfii, *O. chrysoptera*, *P. albigutta*, and *S. hispidus* were present in all estuaries (lowest CPUE in BBB) and had high interannual variation in CPUE (Fig. 4c). Lastly, *Syngnathus louisianae* had greatest CPUE in AP and lower, less variable CPUEs in all the other estuaries (Fig. 4d).

3.2. Environmental correlations with faunal assemblages

Four environmental groups (estuary morphology, physical, water quality, and SAV), including estuary-wide and local scale variables, had a spatial pattern of differences that was best correlated with that among the taxa ($\rho = 0.74$; modified global BEST $p = 0.001$). Estuary morphology had the highest correlation with the taxa subset ($\rho = 0.72$), followed by the physical environmental group ($\rho = 0.58$), water quality ($\rho = 0.49$), and SAV ($\rho = 0.31$). Latitude was not identified as a significant environmental group relating to assemblage variations.

The PCA for the estuary morphology group resulted in a single principal component explaining 100% of the variation since there was only one variable. The PCAs for the remaining environmental groups each retained three principal components, explaining cumulative variations of 88.2% for the physical group, 87.6% for the water quality group, and 78.6% for the SAV group. Mean values of quantitative environmental variables are presented in Table 3. A descriptive summary of the PCA analyses of environmental variables of the open Big Bend estuaries compared to all semi-enclosed estuaries, as well as the semi-enclosed estuaries of the panhandle compared to the peninsula, can be found in Table 4. Detailed descriptions are below.

The first two physical PCs represented a combination of the presence of mud on the bottom and depth, with higher PC1 scores indicating mud and deeper water and higher PC2 scores indicating mud but shallower water. All open Big Bend estuaries were deeper with more mud (greater PC1 scores) than semi-enclosed estuaries. Additionally, CH and TB (peninsular estuaries) were deeper with more mud than SA and AP (panhandle estuaries). Scores from PC2 also characterized variability in mud and water depths within the Big Bend estuaries. The third PC was influenced almost equally by greater slope, more bottom structure, and less sand bottom. This third PC appeared to be most useful in distinguishing between TB and CH samples; TB samples had greater values.

The first water quality PC was characterized predominantly by lower bottom salinity (<30). Measured bottom salinities were lowest in BBB and BBA and greater in SA and AP. The remaining estuaries (TB and CH) typically had bottom salinities >30. The second PC was characterized mainly by a decreased Secchi depth; Secchi depth was less in semi-enclosed estuaries. Lastly, estuaries with greater loadings on the third PC had lower bottom dissolved oxygen readings (BBB, BBD, TB to lesser extent) and fewer instances of complete water clarity (i.e., Secchi disc visible on the bottom) (BBD, BBB, BBA).

The SAV environmental group consisted of the percentage of bottom vegetation cover as well as the different species of seagrass or alga present at each sample site. The first PC was heavily influenced by greater occurrences of mixed seagrass species and separated the open Big Bend estuaries from the others. The second PC was most strongly influenced by decreases in overall % cover and *Thalassia testudinum* but an increase in *Halodule wrightii.* This PC related most closely with the assemblages in AP with approximately 70% cover, the lowest *T. testudinum* occurrences, and the greatest *H. wrightii* occurrences. St. Andrew Bay also had elevated scores on this PC because it was the estuary with the second greatest occurrence of *H. wrightii*. The third PC helped further differentiate between SA and AP; more *Syringodium filiforme* and *Caulerpa* spp., and less *T. testudinum* were present in AP.

4. Discussion

4.1. Faunal communities of nearshore polyhaline seagrass beds

Nearshore polyhaline seagrass beds along Florida's Gulf coast support diverse nekton communities that vary among estuary and estuary morphology. We were able to detect ecological shifts among estuaries because of the rigorous and comparable regional sampling design among all seven estuaries—a sampling scale that has been considered a limitation for other studies examining large-scale influences on community assemblages (e.g., Edgar et al., 1999; Nicolas et al., 2010) but that, as we show, does have value. The most striking difference in seagrass-associated community composition was between semi-enclosed and open estuaries. To our knowledge, this is the first empirical evidence documenting regional differences in faunal assemblages in association with these estuary morphologies in the United States, although researchers have documented fish assemblage differences among estuary types in other systems. For example, Valesini et al. (2014) reported differences in juvenile fish assemblages among different estuary bar types along Australia's west coast. In South Africa, Vorwerk et al. (2001, 2003; juvenile) and Strydom et al. (2003; larvae and early juveniles) documented fish assemblage differences between permanently and temporarily open estuaries.

Estuary morphology, regardless of latitude, was the most influential variable structuring faunal assemblages of Florida's Gulf coast polyhaline seagrass beds. The degree of openness of an estuary and hence, the connectivity between the estuary and coastal waters, can affect the ability of marine organisms to be transported or migrate into the estuary (e.g., Kirby-Smith et al., 2001; Peterson, 2003). This is supported by Vorwerk et al. (2001, 2003), Strydom et al. (2003) and Valesini et al. (2014), who reported differences in fish assemblages among estuary types that varied in their degree of connection to the ocean, and generally documented greater fish diversity and more estuarine opportunists in more open estuaries. Although the semi-enclosed and open estuaries examined here both maintained permanent connections with the sea, one might expect a similar gradient in assemblages. Therefore, completely open estuarine systems like the Big Bend estuaries may be expected to have greater diversity and support more estuarine opportunists compared to semi-enclosed estuaries because of seemingly greater accessibility to estuarine waters. Interestingly, we found the opposite: the greatest number of taxa observed (90 vs. 81 taxa) and the greatest average taxon richness (73 vs. 67) were greater in semi-enclosed estuaries than in open estuaries. This may be because open estuarine systems can experience fewer extremes in water quality conditions, as suggested by Hoeksema et al. (2006) and Potter et al. (2010), and thereby could support a more constant community composition. Estuaries of different morphological types may also have different nearshore habitats, water clarity, wave action, ambient noise, etc., which may interact to influence fish recruitment and settlement. Zoogeography may also play a role, but this was not detected in our analyses because all open estuaries were in the Big Bend, spanning a smaller latitudinal range than the semi-enclosed estuaries along the panhandle and peninsula.

Overall, semi-enclosed estuaries in this study were distinguished by higher CPUEs of estuarine obligates (e.g., *Callinectes sapidus*, *F. duorarum, Cynoscion nebulosus*), which ranged from invertebrates to forage fish to commercially or recreationally important species. In addition to estuarine obligates, some reef-associated fishes (e.g., *Lutjanus synagris, L. griseus*) with estuarine dependency as juveniles (e.g., Beck et al., 2001; McMahon et al., 2011) had greater CPUEs in semi-enclosed estuaries. Open estuaries, on the other hand, had fewer estuarine obligates, incidental marine species and commercially or recreationally important species.

Instead, these estuaries had more cryptic or small forage fish, an observation similar to that by Salita et al. (2003), which probably depend on seagrass as refugia from predation (e.g., Beck et al., 2001; Shoji et al., 2017). Indeed, the open estuaries sampled in this study comprise some of Florida's largest continuous seagrass beds (Carlson and Madley, 2006), providing a complex habitat for refugia from predation. The vast expanse of continuous seagrass beds may allow some fishes, especially larger ones, to disperse themselves throughout the bed, resulting in lower CPUEs than fragmented beds, where fishes would tend more to aggregate in seagrass patches. The lack of fragmentation, while benefitting species seeking refuge from predation, may also inadvertently result in lower species diversity in trawl samples because of reduced habitat diversity. Habitat heterogeneity has been reported to increase the number of niches and species richness (e.g., Ferreira et al., 2001; Tews et al., 2004; Willis et al., 2005), which is further supported by our findings of greater taxon richness in seagrass beds of semi-enclosed estuaries with more fragmented landscapes. We do acknowledge the limitations of trawl sampling, especially regarding our lack of catches of larger, more mobile animals that can escape the gear, have greater presence at night (e.g., Shoji et al., 2017), or occupy deeper waters (e.g., Blaber et al., 1992); however, we feel this does not alter our comparison of communities in these estuaries as the gear and methods were standardized among all estuaries.

Although many of the commercially or recreationally important taxa had greater CPUEs in semi-enclosed estuaries, a few had greater CPUEs in open estuaries, including *Centropristis striata* and *Argopecten* spp. *Centropristis striata* is typically found in the lower reaches of Florida's west coast estuaries (Hood et al., 1994), and most juveniles (<19 cm total length) settle in coastal areas, moving later into estuaries (Steimle et al., 1999). This use pattern corresponds to greater abundance of juveniles in open estuarine seagrass beds. The other dominant taxa in open estuaries was *Argopecten* spp., bay scallops. Typically confined to shallow water seagrass, greater CPUEs of *Argopecten* spp. in the Big Bend estuaries was expected because population declines among already disjunct populations along Florida's coast have left relatively high-density local populations restricted to areas north and west of the Suwannee River (Arnold et al., 1997), corresponding to the Big Bend area.

4.2. Environmental correlations with community assemblages

The successful reduction of the taxon data set to 11 taxa ultimately allowed for a more rigorous test of how the measured environmental variables correlated with the pattern of variation in community assemblages. Although assemblage structure could be attributed primarily to differences in general estuary morphology, water quality was also an important contributing factor. Salinity was the main explanatory factor in the water quality group, and the proximity of seagrass beds to freshwater input can influence their use by fish (Flaherty-Walia et al., 2015a). The Big Bend estuaries are farther from freshwater influence because they are farther offshore, but salinities were lower in the Big Bend estuaries than the semi-enclosed estuaries, indicating a relatively constant influence of freshwater or a well-mixed system. This could be expected because the Big Bend has rather significant sheet flow of groundwater (Geselbracht et al., 2015) and multiple rivers with ground- and spring-water influence (e.g., Suwannee River). The semi-enclosed estuaries in the panhandle and peninsular regions of Florida, in contrast, do not have enough freshwater flow to exceed the tidal influence—marine influence generally exceeds that of freshwater in these estuaries (Harte Research Institute for Gulf of Mexico Studies, 2016), which could help explain the greater CPUEs of fully marine species in semi-enclosed estuaries. In addition to salinity differences, water clarity was greater in the Big Bend region. This may be related to the sheet flow derived from spring-fed rivers (Geselbracht et al., 2015) that typically do not transport sediment-laden waters into estuaries.

The physical factors correlating to community assemblages appeared to be more variable, with separation among estuaries based on small differences. These factors probably indirectly affect the seagrass-associated fauna by dictating the environmental factors affecting SAV. The presence of different types, amounts, and spatial arrangements of aquatic vegetation (seagrass and algae) can affect associated faunal communities (e.g., Steffe et al., 1989; Raposa and Oviatt, 2000; Jackson et al., 2006; Jelbart et al., 2007). We found different faunal communities associated with the more diverse, continuous, and higher-cover seagrass beds in the Big Bend estuaries than in the panhandle and peninsular estuaries. As discussed above, more cryptic species and small fish were collected from these seagrass beds. In the panhandle, the presence of *T. testudinum* and the overall percent cover of SAV tended to be lower, resulting in different seagrass-associated nekton communities from SA and AP than from the Big Bend or peninsula estuaries. Ultimately, our results consistently show that seagrass-associated communities in open estuaries with continuous, mixed-species seagrass beds (more small forage fishes and cryptic species) differ from those in semi-enclosed estuaries with less percent cover and more monotypic beds (more estuarine obligate and facultative species).

4.3. Management and conservation implications

Variability of estuarine nekton assemblages is valuable as an indicator of environmental quality (Whitfield and Elliott, 2002). Therefore, the patterns discerned during this study have important implications for managers of these resources and coastal development. Urbanization, and associated sediment and nutrient loading in coastal waters, has been linked to declines in seagrass coverage (Short and Wyllie-Echeverria, 1996). In Florida, the seagrass beds in the Big Bend estuaries have been less strongly affected by urbanization and development (Mattson et al., 2007), but as Florida's population continues to increase (Carr and Zwick, 2016), the Big Bend area could become threatened by increased anthropogenic pressures that could alter the assemblages. This study also highlights that seagrass beds in open and semi-enclosed estuaries function differently in terms of the fauna they support. Successful management strategies for conservation of these vital habitats and associated fishery species will require understanding that, although seagrass beds in estuaries of different morphologies may appear similar, they support different fishery species.

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References

Arnold, W.S., Marelli, D.C., Hagner, K., Harrison, M., Hoffman, P., 1997. Annual report of the bay scallop project, 1996. Florida Department of Environmental Protection, Florida Marine Research Institute, St. Petersburg.

Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein, M.P., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51, 633–641.

Bertelli, C.M., Unsworth, R.K., 2014. Protecting the hand that feeds us: Seagrass (Zostera marina) serves as commercial juvenile fish habitat. Marine Pollution Bulletin 83, 425–429.

Blaber, S.J.M, Brewer, D.T., Salini, J.P, Kerr, J.D., Conacher, C., 1992. Species composition and biomasses of fishes in tropical seagrasses at Groote Eylandt, Northern Australia. Estuarine, Coastal and Shelf Science 35, 605–620.

Carlson, P.R., Madley, K., 2006. Statewide summary for Florida. In: Handley L., Altsman D., DeMay R. (Eds.), Seagrass Status and Trends in the Northern Gulf of Mexico: 1940–2002. US Environmental Protection Agency, Washington, DC, Vol. 885-R-04–003, pp. 100–113.

Carr, M.H., Zwick, P.D., 2016. Technical Report: Water 2070, Mapping Florida’s Future: Alternative Patterns of Water Use in 2070. A research project prepared for the Florida Department of Agriculture and Consumer Services and 1000 Friends of Florida, 53 pp.

Casey, J.P., Poulakis, G.R., Stevens, P.W., 2007. Habitat use by juvenile gag, *Mycteroperca microlepis* (Pisces: Serranidae), in subtropical Charlotte Harbor, Florida (USA). Gulf and Caribbean Research 19, 1–9.

Clarke, K.R., Chapman, M.G., Somerfield, P.J., Needham, H.R., 2006. Dispersion-based weighting of species counts in assemblage analyses. Marine Ecology Progress Series 320, 11–27.

Clarke, K.R., Gorley, R.N., 2015. PRIMER v7. User Manual/Tutorial. PRIMER-E, Plymouth Marine Laboratory, Plymouth, England, UK. 296 pp.

Clarke, K.R., Tweedley, J.R., Valesini, F.J., 2014. Simple shade plots aid better long-term choices of data pre-treatment in multivariate assemblage studies. Journal of the Marine Biological Association of the United Kingdom 94, 1–16.

Clarke, K.R., Warwick, R.M., 1998. Quantifying structural redundancy in ecological communities. Oecologia 113, 278–289.

De Angelo, J.A., Stevens, P.W., Blewett, D.A., Switzer, T.S., 2014. Fish assemblages of shoal- and shoreline-associated seagrass beds in eastern Gulf of Mexico estuaries. Transactions of the American Fisheries Society 143, 1037–1048.

Duarte, C.M., 2002. The future of seagrass meadows. Environmental Conservation 29, 192–206.

Edgar, G.J., Barrett, N.S., Last, P.R., 1999. The distribution of macroinvertebrates and fishes in Tasmanian estuaries. Journal of Biogeography 26, 1169–1189.

Ferreira, C.E.L., Gonçalves, J.E.A., Coutinho, R., 2001. Community structure of fishes and habitat complexity on a tropical rocky shore. Environmental Biology of Fishes 61, 353–369.

Flaherty, K.E., Switzer, T.S., Winner, B.L., Keenan, S.F., 2014. Regional correspondence in habitat occupancy by gray snapper (*Lutjanus griseus*) in estuaries of the southeastern United States. Estuaries and Coasts 37, 206–228. doi:10.1007/s12237-013-9652-x

Flaherty-Walia, K.E., Matheson, R.E. Jr., Paperno R., 2015a. Juvenile spotted seatrout (*Cynoscion nebulosus*) habitat use in an eastern Gulf of Mexico estuary: the effects of seagrass bed architecture, seagrass species composition, and varying degrees of freshwater influence. Estuaries and Coasts 38, 353–366.

Flaherty-Walia K.E., Switzer, T.S., Winner, B.L., Tyler-Jedlund, A.J., Keenan, S.F., 2015b. Improved ability to characterize recruitment of gray snapper in three Florida estuaries along the Gulf of Mexico through targeted sampling of polyhaline seagrass beds. Transactions of the American Fisheries Society 144, 911–926. doi:10.1080/00028487.2015.1054516

Geselbracht, L., Torres, R., Cumming, G., Dorfman, D., Beck, M., Shaw, D., 2009. Identification of a spatially efficient portfolio of priority conservation sites in marine and estuarine areas of Florida. Aquatic Conservation: Marine and Freshwater Ecosystems 19, 408–420.

Geselbracht, L.L., Freeman, K., Birch, A.P., Brenner, J., Gordon, D.R., 2015. Modeled sea level rise impacts on coastal ecosystems at six major estuaries on Florida’s Gulf coast:

implications for adaptation planning. PLoS ONE 10, e0132079. doi:10.1371/journal.pone.0132079

Harte Research Institute for Gulf of Mexico Studies, 2016. GulfBase: Resource Database for Gulf of Mexico Research, Education, and Management. Texas A&M University–Corpus Christi. http://www.gulfbase.org.

Heck, K.L., Hays, G., Orth, R.J., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series 253, 123–136.

Heck, K.L., Valentine, J.F., 2007. The primacy of top-down effects in shallow benthic ecosystems. Estuaries and Coasts 30, 371–381.

Hoeksema, S.D., Chuwen, B.M., Potter, I.C., 2006. Massive mortalities of the black bream *Acanthopagrus butcheri* (Sparidae) in two normally-closed estuaries, following extreme increases in salinity. Journal of the Marine Biological Association of the United Kingdom 86, 893–897.

Hood, P.B., Godcharles, M.F., Barco, R.S., 1994. Age, growh, reproduction, and the feeding ecology of black sea bass, *Centropristis striata* (Pisces: Serranidae), in the eastern Gulf of Mexico. Bulletin of Marine Science 54, 24–37.

Jackson, E.L., Attrill, M.J., Rowden, A.A., Jones, M.B., 2006. Seagrass complexity hierarchies: influence on fish groups around the coast of Jersey (English Channel). Journal of Experimental Marine Biology and Ecology 330, 38–54.

Jackson, E.L., Rowden, A.A., Attrill, M.J., Bossey, S.J., Jones, M.B., 2001. The importance of seagrass beds as a habitat for fishery species. Oceanography and Marine Biology 39, 269–303.

Jelbart, J.E., Ross, P.M., Connolly, R.M., 2007. Patterns of small fish distributions in seagrass beds in a temperate Australian estuary. Journal of the Marine Biological Association of the United Kingdom 87, 1297–1307.

Kirby-Smith, W.W., Lebo, M.E., Herrmann, R.B., 2001. Nekton variations in tributaries along a hydrologically modified North Carolina estuary. Estuaries 24, 59–68.

Mattson, R.A., Frazer, T.K., Hale, J., Blitch, S., Ahijevych, L., 2007. The Big Bend. In: Handley, L., Altsman, D., DeMay, R. (Eds.), Seagrass Status and Trends in the Northern Gulf of Mexico: 1940–2002. US Geological Survey Scientific Investigations Report No. 2006-5287. US Geological Survey, 2007. pp. 171–188.

McMahon, K.W., Berumen, M.L, Mateo, I., Elsdon, E.S., Thorrold, S.R., 2011. Carbon isotopes in otolith amino acids identify residency of juvenile snapper (Family: Lutjanidae) in coastal nurseries. Coral Reefs 30, 1135–1145.

McMichael, R.H. Jr., 1991. Florida’s marine fisheries-independent monitoring program. Pages 255-261 in S.F. Treat and P.A. Clark, editors. Proceedings, Tampa Bay area Scientific information symposium 2 (BASIS). Tampa Bay Regional Planning, Tampa Florida.

McMichael, R.H. Jr., 2009. Fisheries-independent monitoring program 2008 annual data summary report. Report to the Florida Fish and Wildlife Conservation Commission from the Florida Fish and Wildlife Research Institute, Fish and Wildlife Research Institute in-house report 2009-002, St. Petersburg.

Nagelkerken, I., Kleijenen, S., Klop, T., van den Brand, R.A., Cocheret, C.J., de la Morinière, E., van der Velde, G., 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Marine Ecology. Progress Series 214, 225–235.

Nicolas, D., Lobry, J., Lepage, M., Sautour, B., Le Pape, O., Cabral, H., Uriarte, A., Boë, P., 2010. Fish under influence: a macroecological analysis of relations between fish species richness and environmental gradients among European tidal estuaries. Estuarine, Coastal and Shelf Science 86, 137–147.

Peterson, M.S., 2003. A conceptual view of environment–habitat–production linkages in tidal river estuaries. Reviews in Fisheries Science 11, 291–313.

Potter, I.C., Chuwen, B.M., Hoeksema, S.D., Elliott, M., 2010. The concept of an estuary: a definition that incorporates systems which can become closed to the ocean and hypersaline. Estuarine, Coastal and Shelf Science 87, 497–500.

Raposa, K.B., Oviatt, C.A., 2000. The influence of contiguous shoreline type, distance from shore, and vegetation biomass on nekton community structure in eelgrass beds. Estuaries 23, 46–55.

Salita, J.T., Ekau, W., Saint-Paul, U., 2003. Field evidence on the influence of seagrass landscapes on fish abundance in Bolinao, northern Philippines. Marine Ecology Progress Series 247, 183–195.

Scapin, L., Zucchetta, M., Sfriso, A., 2018. Local habitat and seascape structure influence fish assemblages in the Venice Lagoon: the importance of conservation at multiple spatial scales. Estuaries and Coasts 1–16.

Shoji, J., Mitamura H., Ichikawa K., Kinoshita, H., Arai, N., 2017. Increase in predation risk and trophic level induced by nocturnal visits of piscivorous fishes in a temperate seagrass bed. Nature Scientific Reports 7, 1–10.

Short, F.T., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbances of seagrasses. Environmental Conservation 23, 17–27.

Staveley, T.A., Perry, D., Lindborg, R., Gullström, M., 2017. Seascape structure and complexity influence temperate seagrass fish assemblage composition. Ecography 40, 936–946.

Steffe, A.S., Westoby, M., Bell, J.D., 1989. Habitat selection and diet in two species of pipefish from seagrass: sex differences. Marine Ecology Progress Series 55, 23–30.

Steimle, F., Zetlin, C., Berrien, P., Chang, S., 1999. Essential Fish Habitat Source Document: Black Sea Bass, *Centropristis striata*, Life History and Habitat Characteristics. NOAA Technical Memorandum NMFS-NE 143. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA. 50 pp.

Strydom, N.A., Whitfield, A.K., Wooldridge, T.H., 2003. The role of estuarine type in characterizing early stage fish assemblages in warm temperate estuaries, South Africa. African Zoology 38, 29–43.

Switzer, T.S., MacDonald, T.C., McMichael, R.H., Keenan, S.F., 2012. Recruitment of juvenile gags in the eastern Gulf of Mexico and factors contributing to observed spatial and temporal patterns of estuarine occupancy. Transactions of the American Fisheries Society 141, 707–719. doi:10.1080/00028487.2012.675913

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, J., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31, 79–92.

Valesini, F.J., Hourston, M., Wildsmith, M.D., Coen, N.J., Potter, I.C., 2010. New quantitative approaches for classifying and predicting local-scale habitats in estuaries. Estuarine, Coastal and Shelf Science 86, 645–664.

Valesini, F.J., Tweedley, J.R., Clarke, K.R., Potter, I.C., 2014. The importance of regional, system-wide and local spatial scales in structuring temperate estuarine fish communities. Estuaries and Coasts 37, 525–547.

Verweij, M.C., Nagelkerken, I., Hans, I., Ruseler, S.M., Mason, P.R., 2008. Seagrass nurseries contribute to coral reef fish populations. Limnology and Oceanography 53, 1540–1547.

Vorwerk, P.D., Whitfield, A.K., Cowley, P.D., Paterson, A.W., 2001. A survey of selected Eastern Cape Estuaries with particular reference to the ichthyofauna. Ichthyological Bulletin of the J.L.B Smith Institute of Ichthyology 72, 1–52.

Vorwerk, P.D., Whitfield, A.K., Cowley, P.D., Paterson, A.W., 2003. The influence of selected environmental variables on fish assemblage structure in a range of southeast African estuaries. Environmental Biology of Fishes 66, 237–247.

Whitfield, A.K., 2017. The role of seagrass meadows, mangrove forests, salt marshes, and reed beds as nursery areas and food sources for fishes in estuaries. Reviews in Fish Biology and Fisheries 27, 75–110.

Whitfield, A.K., Elliott, M., 2002. Fishes as indicators of environmental and ecological changes within estuaries: a review of progress and some suggestions for the future. Journal of Fish Biology 61 (Supplement A), 229–250.

Willis, S.C., Winemiller, K.O., Lopez-Fernandez, H., 2005. Habitat structural complexity and morphological diversity of fish assemblages in a neotropical floodplain river. Oecologia 142, 284–295.

Winner, B.L, McMichael, R.H., 1997. Evaluation of a new type of box splitter designed for subsampling estuarine ichthyofauna. Transactions of the American Fisheries Society 126, 1041–1047.

Appendix. Average CPUE (individuals/trawl) of all species recorded from 2008-2015 during polyhaline seagrass bed trawling in seven estuaries along Florida's Gulf coast. AP=Apalachicola Bay, SA=St. Andrew Bay, BBA=St. Marks, BBB=Econfina, BBD=Steinhatchee, TB=Tampa Bay, CH=Charlotte Harbor. AP and SA are estuaries located in the panhandle region of Florida; BBA, BBB, and BBD are in the Big Bend region of Florida; TB and CH are in the peninsula region of Florida. Specimens that could not be identified to species are found listed alphabetically by their genus or family.

Scientific Name	**AP**	**SA**	**BBA**	**BBB**	**BBD**	**TB**	**CH**
Acanthostracion quadricornis	0.626	0.468	1.007	0.285	0.377	2.114	0.779
Acanthostracion spp.	0.000	0.000	0.000	0.003	0.000	0.000	0.000
Acanthurus chirurgus	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Achirus lineatus	0.027	0.224	0.109	0.037	0.075	0.053	0.092
Albula vulpes	0.003	0.000	0.000	0.000	0.000	0.000	0.000
Alosa alabamae	0.003	0.000	0.000	0.000	0.000	0.000	0.000
Alosa chrysochloris	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Aluterus schoepfii	0.100	0.248	0.343	0.224	0.247	0.111	0.079
Anarchopterus criniger	0.037	0.031	0.266	0.863	0.308	0.072	0.183
Anchoa cubana	2.754	0.072	0.017	0.000	0.000	1.646	0.000
Anchoa hepsetus	5.245	0.175	0.799	0.079	0.041	0.085	0.321
Anchoa lyolepis	0.117	0.180	0.039	0.001	0.000	0.002	0.000
Anchoa mitchilli	18.564	1.151	6.403	2.031	1.558	10.611	6.011
Anchoa spp.	0.000	0.046	0.000	0.000	0.000	0.000	0.000
Ancylopsetta quadrocellata	0.042	0.000	0.041	0.009	0.023	0.006	0.015
Anguilliformes spp.	0.000	0.004	0.000	0.000	0.000	0.000	0.000
Apogonidae spp.	0.004	0.000	0.000	0.000	0.000	0.000	0.000
Archosargus probatocephalus	0.166	0.128	0.002	0.010	0.015	1.145	1.035
Argopecten spp.	0.323	0.390	4.036	2.242	4.635	0.341	0.339
Ariopsis felis	0.275	0.036	0.023	0.029	0.114	0.112	0.252
Astrapogon alutus	0.004	0.000	0.000	0.000	0.002	0.000	0.000
Astroscopus y-graecum	0.002	0.006	0.000	0.002	0.002	0.002	0.000
Bagre marinus	0.000	0.000	0.000	0.000	0.002	0.002	0.000
Bairdiella chrysoura	18.540	10.316	10.514	5.428	6.380	22.600	13.922
Blenniidae spp.	0.004	0.000	0.000	0.000	0.000	0.000	0.000
Bothus robinsi	0.000	0.009	0.000	0.000	0.000	0.000	0.000
Brevoortia spp.	0.000	0.000	0.000	0.000	0.016	0.000	0.000
Calamus arctifrons	0.175	0.005	3.063	2.060	2.444	0.270	0.023
Calamus penna	0.000	0.000	0.000	0.000	0.000	0.010	0.017
Calamus proridens	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Calamus spp.	0.004	0.003	0.000	0.000	0.000	0.011	0.028
Callinectes ornatus	0.008	0.003	0.002	0.000	0.000	0.012	0.118
Callinectes sapidus	1.965	5.211	0.927	0.179	0.174	1.806	1.325
Callinectes similis	0.019	0.020	0.009	0.015	0.002	0.000	0.000
Caranx hippos	0.000	0.009	0.000	0.000	0.000	0.000	0.002
Centropomus undecimalis	0.000	0.000	0.000	0.000	0.000	0.000	0.002

Scientific Name	AP	SA	BBA	BBB	BBD	TB	CH
Centropristis philadelphica	0.029	0.052	0.013	0.000	0.000	0.000	0.000
Centropristis spp.	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Centropristis striata	4.582	0.668	12.158	6.018	8.501	1.685	0.460
Chaetodipterus faber	0.050	0.050	0.109	0.067	0.031	0.057	0.069
Chasmodes saburrae	0.123	0.443	0.298	0.040	0.063	0.334	0.162
Chilomycterus schoepfii	1.650	3.420	2.422	0.936	1.272	4.488	4.382
Chloroscombrus chrysurus	0.095	0.025	0.084	0.138	0.070	0.009	0.026
Citharichthys macrops	0.058	0.066	0.041	0.016	0.080	0.057	0.026
Citharichthys spilopterus	0.018	0.011	0.002	0.000	0.000	0.000	0.000
Clupeidae spp.	0.000	0.000	0.002	0.000	0.000	0.000	0.000
Cosmocampus albirostris	0.002	0.012	0.000	0.002	0.000	0.000	0.000
Cosmocampus spp.	0.000	0.004	0.000	0.000	0.000	0.000	0.000
Cryptotomus roseus	0.000	0.013	0.000	0.000	0.000	0.000	0.000
Ctenogobius boleosoma	0.162	0.557	0.004	0.000	0.000	0.000	0.000
Cynoscion arenarius	0.133	0.003	0.022	0.009	0.036	0.005	0.004
Cynoscion nebulosus	2.413	1.364	0.817	0.443	0.516	1.372	1.172
Dasyatis americana	0.013	0.010	0.004	0.010	0.004	0.009	0.011
Dasyatis sabina	0.226	0.097	0.104	0.027	0.030	0.159	0.039
Dasyatis say	0.073	0.040	0.007	0.000	0.012	0.028	0.017
Decapterus punctatus	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Diodon holocanthus	0.000	0.000	0.000	0.000	0.000	0.000	0.004
Diodon spp.	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Diplectrum bivittatum	0.000	0.004	0.000	0.024	0.004	0.000	0.000
Diplectrum formosum	0.190	0.116	0.261	0.162	0.125	0.038	0.047
Diplectrum spp.	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Diplodus holbrookii	0.258	0.057	8.074	7.779	12.199	2.340	0.202
Diplogrammus pauciradiatus	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Dorosoma petenense	0.000	0.003	0.004	0.000	0.000	0.000	0.000
Echeneis neucratoides	0.004	0.006	0.002	0.004	0.002	0.002	0.000
Elacatinus macrodon	0.000	0.000	0.004	0.012	0.002	0.000	0.000
Elops saurus	0.002	0.000	0.000	0.000	0.002	0.004	0.000
Epinephelus morio	0.002	0.025	0.000	0.000	0.008	0.024	0.070
Etropus crossotus	0.384	0.035	0.075	0.076	0.181	0.022	0.032
Etropus cyclosquamus	0.017	0.015	0.011	0.005	0.007	0.000	0.000
Etropus spp.	0.000	0.007	0.000	0.000	0.000	0.000	0.000
Eucinostomus argenteus	0.272	0.281	0.058	0.000	0.005	0.002	0.000
Eucinostomus gula	0.885	0.638	0.909	0.344	0.879	7.255	7.713
Eucinostomus harengulus	0.185	0.174	0.070	0.063	0.033	0.077	0.115
Eucinostomus spp.	6.298	13.419	1.287	0.891	0.999	35.730	18.949
Farfantepenaeus aztecus	0.086	0.000	0.000	0.000	0.000	0.000	0.000
Farfantepenaeus duorarum	0.860	1.039	1.758	1.005	0.601	1.946	1.367
Farfantepenaeus spp.	3.639	3.088	0.516	0.706	0.369	0.000	0.000

Scientific Name	AP	SA	BBA	BBB	BBD	TB	CH
Fistularia spp.	0.000	0.006	0.000	0.000	0.000	0.000	0.000
Floridichthys carpio	0.000	0.000	0.000	0.000	0.000	0.006	0.000
Fundulus similis	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Ginglymostoma cirratum	0.000	0.000	0.000	0.000	0.000	0.000	0.009
Gobiesox strumosus	0.000	0.000	0.000	0.004	0.009	0.000	0.000
Gobiidae spp.	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Gobiosoma bosc	0.005	0.012	0.002	0.009	0.003	0.000	0.000
Gobiosoma longipala	0.002	0.003	0.000	0.008	0.005	0.004	0.004
Gobiosoma robustum	0.118	0.208	0.090	0.047	0.021	0.256	0.427
Gobiosoma spp.	0.025	0.099	0.057	0.076	0.025	0.183	0.597
Gymnachirus melas	0.000	0.000	0.000	0.000	0.000	0.002	0.000
Gymnothorax saxicola	0.000	0.000	0.005	0.005	0.009	0.000	0.002
Gymnachirus spp.	0.000	0.000	0.000	0.000	0.000	0.000	0.002
Gymnura micrura	0.011	0.003	0.005	0.002	0.002	0.017	0.010
Haemulidae spp.	0.000	0.000	0.002	0.000	0.000	0.000	0.000
Haemulon aurolineatum	0.002	0.000	0.028	0.063	0.035	0.004	0.000
Haemulon plumierii	0.086	0.219	0.802	2.571	1.317	1.514	1.236
Haemulon spp.	0.000	0.000	0.002	0.000	0.000	0.000	0.000
Halichoeres bivittatus	0.256	0.482	0.077	0.133	0.326	0.009	0.019
Harengula jaguana	0.313	0.411	0.115	0.039	0.871	0.760	0.262
Hemicaranx amblyrhynchus	0.027	0.000	0.000	0.000	0.002	0.000	0.000
Hippocampus erectus	0.034	0.262	0.054	0.015	0.043	0.094	0.060
Hippocampus zosterae	0.012	0.033	0.026	0.004	0.004	0.028	0.058
Holocentridae spp.	0.000	0.000	0.003	0.000	0.000	0.000	0.000
Hypleurochilus caudovittatus	0.000	0.000	0.020	0.021	0.018	0.009	0.025
Hypleurochilus spp.	0.000	0.000	0.002	0.000	0.000	0.000	0.000
Hypsoblennius hentz	0.183	0.016	0.069	0.002	0.010	0.101	0.047
Lachnolaimus maximus	0.011	0.000	0.163	0.582	0.197	0.022	0.006
Lactophrys trigonus	0.008	0.011	0.000	0.000	0.000	0.009	0.004
Lagodon rhomboides	99.729	289.993	104.162	51.503	61.853	321.676	232.360
Larimus fasciatus	0.002	0.004	0.000	0.000	0.000	0.000	0.000
Leiostomus xanthurus	0.758	1.182	0.547	0.045	0.126	0.252	0.073
Lepisosteus osseus	0.002	0.000	0.006	0.000	0.000	0.002	0.002
Limulus polyphemus	0.002	0.000	0.000	0.000	0.002	0.009	0.006
Litopenaeus setiferus	0.035	0.000	0.000	0.000	0.000	0.000	0.000
Lucania parva	0.146	1.185	0.362	0.007	0.311	0.156	0.245
Lutjanus analis	0.000	0.000	0.000	0.000	0.000	0.002	0.006
Lutjanus griseus	0.268	0.567	0.050	0.020	0.060	1.774	3.217
Lutjanus synagris	2.715	0.756	0.772	0.663	0.794	1.865	2.855
Menidia spp.	0.000	0.006	0.000	0.000	0.000	0.000	0.006
Menippe spp.	0.252	0.026	0.506	0.178	0.312	0.293	1.526
Menticirrhus americanus	0.194	0.003	0.022	0.011	0.048	0.011	0.002

Scientific Name	AP	SA	BBA	BBB	BBD	TB	CH
Menticirrhus saxatilis	0.032	0.000	0.007	0.005	0.020	0.002	0.000
Mercenaria mercenaria	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Microgobius gulosus	0.032	0.701	0.093	0.006	0.000	0.111	0.109
Microgobius spp.	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Microgobius thalassinus	0.005	0.003	0.000	0.000	0.004	0.000	0.000
Micropogonias undulatus	0.071	0.018	0.021	0.000	0.000	0.000	0.000
Monacanthus ciliatus	0.684	0.076	6.382	4.068	4.001	0.572	0.296
Mugil cephalus	0.000	0.003	0.000	0.002	0.000	0.000	0.002
Mugil curema	0.000	0.000	0.000	0.002	0.000	0.000	0.000
Mullus auratus	0.000	0.000	0.002	0.017	0.009	0.005	0.004
Mycteroperca microlepis	0.301	0.184	0.042	0.025	0.145	0.393	0.567
Mycteroperca spp.	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Myrophis punctatus	0.005	0.007	0.000	0.002	0.000	0.002	0.002
Nicholsina usta	0.067	1.345	0.040	0.084	0.235	2.156	2.041
Ocyurus chrysurus	0.000	0.007	0.000	0.000	0.000	0.000	0.028
Ogcocephalus corniger	0.000	0.000	0.002	0.000	0.000	0.000	0.000
Ogcocephalus cubifrons	0.022	0.000	0.039	0.013	0.013	0.017	0.021
Ogcocephalus parvus	0.000	0.000	0.000	0.003	0.000	0.000	0.000
Oligoplites saurus	0.000	0.000	0.002	0.000	0.002	0.000	0.000
Ophidion holbrookii	0.000	0.000	0.083	0.058	0.028	0.004	0.000
Opisthonema oglinum	0.000	0.191	0.011	0.019	0.002	0.031	0.019
Opistognathus robinsi	0.000	0.014	0.000	0.000	0.000	0.000	0.000
Opsanus beta	1.280	2.018	2.370	1.936	2.445	0.791	0.825
Orthopristis chrysoptera	80.976	98.652	25.423	8.997	24.792	53.978	30.115
Ostraciidae spp.	0.000	0.000	0.000	0.000	0.000	0.023	0.000
Parablennius marmoreus	0.028	0.009	0.000	0.009	0.013	0.000	0.000
Paraclinus fasciatus	0.000	0.000	0.279	1.570	0.266	0.000	0.000
Paraclinus marmoratus	0.002	0.000	0.000	0.097	0.002	0.241	0.409
Paraclinus spp.	0.000	0.000	0.002	0.000	0.000	0.000	0.000
Paralichthys albigutta	1.998	2.802	1.182	0.483	0.759	2.181	1.275
Paralichthys lethostigma	0.014	0.003	0.006	0.004	0.000	0.000	0.000
Penaeidae spp.	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Peprilus burti	0.007	0.000	0.000	0.002	0.000	0.000	0.000
Pogonias cromis	0.000	0.000	0.000	0.000	0.000	0.002	0.000
Portunidae spp.	0.000	0.006	0.000	0.000	0.000	0.000	0.000
Portunus spp.	0.270	0.322	0.135	0.200	0.207	0.281	0.415
Prionotus longispinosus	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Prionotus martis	0.000	0.000	0.000	0.005	0.003	0.000	0.000
Prionotus rubio	0.000	0.000	0.000	0.000	0.000	0.000	0.002
Prionotus scitulus	0.234	0.132	0.226	0.135	0.211	0.181	0.142
Prionotus tribulus	0.050	0.053	0.022	0.030	0.067	0.005	0.006
Pseudupeneus maculatus	0.000	0.000	0.000	0.000	0.000	0.002	0.000

Scientific Name	AP	SA	BBA	BBB	BBD	TB	CH
Rachycentron canadum	0.004	0.000	0.000	0.000	0.000	0.000	0.000
Raja eglanteria	0.004	0.000	0.000	0.002	0.000	0.000	0.000
Raja texana	0.000	0.000	0.000	0.000	0.003	0.005	0.000
Rhinobatos lentiginosus	0.000	0.000	0.000	0.000	0.002	0.000	0.000
Rhizoprionodon terraenovae	0.000	0.000	0.002	0.000	0.000	0.000	0.000
Rimapenaeus constrictus	0.095	0.048	0.011	0.000	0.006	0.000	0.002
Sardinella aurita	0.002	0.000	0.010	0.005	0.028	0.000	0.000
Scarus spp.	0.000	0.007	0.000	0.000	0.000	0.000	0.000
Sciaenops ocellatus	0.011	0.010	0.000	0.002	0.002	0.006	0.071
Scomberomorus maculatus	0.000	0.000	0.000	0.000	0.002	0.000	0.000
Scorpaena brasiliensis	0.096	0.139	0.034	0.016	0.053	0.176	0.455
Scorpaena plumieri	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Selene vomer	0.009	0.000	0.014	0.009	0.013	0.004	0.002
Serraniculus pumilio	0.080	0.009	0.007	0.002	0.019	0.000	0.006
Serranus subligarius	0.095	0.021	0.016	0.010	0.017	0.050	0.221
Sicyonia brevirostris	0.000	0.015	0.000	0.000	0.000	0.000	0.000
Sicyonia laevigata	0.002	0.006	0.000	0.000	0.004	0.006	0.000
Sicyonia parri	0.000	0.000	0.000	0.000	0.000	0.000	0.006
Sicyonia spp.	0.000	0.003	0.000	0.000	0.000	0.000	0.002
Sicyonia typica	0.000	0.004	0.000	0.003	0.000	0.002	0.000
Sparidae spp.	0.000	0.015	0.002	0.000	0.000	0.000	0.000
Sparisoma chrysopterum	0.000	0.015	0.000	0.000	0.000	0.000	0.000
Sparisoma radians	0.000	0.051	0.000	0.000	0.000	0.000	0.000
Sparisoma spp.	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Sphoeroides nephelus	0.742	0.555	1.226	0.387	0.481	0.804	0.819
Sphoeroides spengleri	0.002	0.008	0.005	0.019	0.018	0.073	0.041
Sphoeroides spp.	0.048	0.000	0.003	0.000	0.000	0.000	0.000
Sphyraena barracuda	0.004	0.000	0.000	0.000	0.000	0.009	0.000
Sphyraena borealis	0.067	0.663	0.063	0.079	0.160	0.060	0.030
Sphyraena guachancho	0.000	0.000	0.002	0.000	0.000	0.000	0.011
Sphyraena spp.	0.000	0.000	0.000	0.000	0.000	0.000	0.006
Stegastes variabilis	0.000	0.006	0.000	0.000	0.000	0.000	0.000
Stephanolepis hispidus	9.359	8.276	9.393	2.402	6.166	7.998	4.698
Strongylura spp.	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Syacium papillosum	0.000	0.000	0.000	0.000	0.000	0.000	0.002
Symphurus plagiusa	0.084	0.031	0.082	0.067	0.082	0.014	0.017
Syngnathidae spp.	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Syngnathus floridae	3.709	6.903	10.874	5.181	6.345	3.871	2.726
Syngnathus louisianae	1.294	0.166	0.169	0.145	0.086	0.247	0.195
Syngnathus scovelli	2.880	2.247	1.372	0.370	0.159	2.887	3.048
Syngnathus spp.	0.000	0.000	0.000	0.005	0.000	0.002	0.000
Syngnathus springeri	0.000	0.000	0.000	0.000	0.005	0.000	0.002

Scientific Name	AP	SA	BBA	BBB	BBD	TB	CH
Synodus foetens	1.236	0.756	0.732	0.266	0.378	0.801	0.446
Trachinotus carolinus	0.000	0.000	0.000	0.003	0.000	0.000	0.000
Trinectes maculatus	0.203	0.009	0.117	0.004	0.011	0.024	0.043
Urophycis floridana	0.000	0.000	0.002	0.004	0.000	0.000	0.000
Xiphopenaeus kroyeri	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Xyrichtys novacula	0.000	0.009	0.000	0.002	0.000	0.000	0.000

Table 1. Number of trawls sampled in polyhaline seagrass beds in each estuary along Florida's Gulf coast, by year (2008–2015).

Estuary	Coast (Latitude)	Type	Number of trawls per year								
			2008	2009	2010	2011	2012	2013	2014	2015	Total
Apalachicola Bay (AP)	Panhandle	Semi-enclosed	55	55	55	56	56	56	56	56	445
St. Andrew Bay (SA)	Panhandle	Semi-enclosed	42	41	42	42	39	42	41	42	331
St. Marks (BBA)	Big Bend	Open	63	70	70	70	70	70	70	70	553
Econfina (BBB)	Big Bend	Open	68	69	70	70	70	70	70	70	557
Steinhatchee (BBD)	Big Bend	Open	63	70	70	70	70	70	70	70	553
Tampa Bay (TB)	Peninsula	Semi-enclosed	70	70	68	67	69	70	70	69	553
Charlotte Harbor (CH)	Peninsula	Semi-enclosed	61	56	56	56	56	56	56	56	453

Table 2. Environmental variables recorded for each trawl, 2008–2015, along Florida's Gulf coast, along with their associated group, data type and transformation.

Environmental variable	Group	Data type	Transformation
CA (*Caulerpa* spp.)	SAV	categorical	none
GM (seagrasses, mixed)	SAV	categorical	none
GU (seagrasses, unidentified)	SAV	categorical	none
HA (*Halodule wrightii*)	SAV	categorical	none
HE (*Halophila engelmannii*)	SAV	categorical	none
HI (*Halophila* spp.)	SAV	categorical	none
HM (*Halimeda* spp.)	SAV	categorical	none
SG (*Sargassum* spp.)	SAV	categorical	none
SY (*Syringodium filiforme*)	SAV	categorical	none
TH (*Thalassia testudinum*)	SAV	categorical	none
Bottom Veg Cover (%)	SAV	quantitative	square root
Bycatch Quantity	Bycatch	quantitative	square root
Secchi depth (m)	Water Quality	quantitative	square root
Secchi on bottom	Water Quality	categorical	none
Temperature (°C)	Water Quality	quantitative	square root
Salinity	Water Quality	quantitative	square root
Dissolved oxygen	Water Quality	quantitative	square root
bSan (sand bottom)	Physical	categorical	none
bMud (mud bottom)	Physical	categorical	none
bStr (structure/rock bottom)	Physical	categorical	none
Slope	Physical	quantitative	square root
Depth (m)	Physical	quantitative	square root
LS (low slack)	Tide	categorical	none
LR (low rising)	Tide	categorical	none
MR (mid rising)	Tide	categorical	none
HR (high rising)	Tide	categorical	none
HS (high slack)	Tide	categorical	none
HF (high falling)	Tide	categorical	none
MF (mid falling)	Tide	categorical	none
LF (low falling)	Tide	categorical	none
Panhandle	Latitude	categorical	none
Big Bend	Latitude	categorical	none
Peninsula	Latitude	categorical	none
Semi-enclosed	Estuary Morphology	categorical	none
Open	Estuary Morphology	categorical	none

Table 3. Mean values (standard deviation in parentheses) of quantitative environmental parameters for each sampled estuary along Florida's Gulf coast, 2008–2015. AP=Apalachicola Bay, SA=St. Andrew Bay, BBA=St. Marks, BBB=Econfina, BBD=Steinhatchee, TB=Tampa Bay, CH=Charlotte Harbor.

	Environmental parameter							
Estuary	BottomVeg Cover (%)	Secchi depth (m)	Temperature (°C)	Salinity (psu)	D.O. (mg/L)	Slope	Depth (m)	Bycatch quantity (L)
AP	71.42 (19.67)	1.41 (0.44)	26.53 (4.03)	29.45 (4.30)	7.12 (1.55)	0.27 (0.31)	1.49 (0.43)	33.46 (45.69)
SA	82.93 (16.75)	1.55 (0.47)	26.61 (4.15)	29.25 (5.46)	6.98 (1.39)	0.42 (0.47)	1.51 (0.45)	35.88 (32.86)
BBA	89.39 (16.96)	1.99 (0.72)	26.34 (4.05)	28.27 (3.82)	6.91 (1.79)	0.22 (0.32)	2.15 (0.79)	58.43 (68.26)
BBB	95.70 (11.27)	2.07 (0.77)	25.71 (5.02)	27.98 (3.97)	6.80 (1.43)	0.15 (0.19)	2.34 (0.69)	77.68 (56.05)
BBD	90.22 (16.71)	1.81 (0.72)	26.74 (4.24)	30.49 (2.95)	6.56 (1.82)	0.23 (0.26)	2.12 (0.78)	47.22 (46.79)
TB	79.15 (17.12)	1.52 (0.45)	27.74 (3.42)	31.63 (3.13)	6.80 (1.58)	0.45 (0.58)	1.66 (0.54)	38.27 (47.67)
CH	90.26 (15.06)	1.42 (0.34)	28.20 (3.30)	32.88 (3.98)	7.14 (1.91)	0.23 (0.26)	1.50 (0.38)	58.23 (67.88)

Table 4. Descriptive results from the principal components analysis for the variables within environmental groups that correlated with the patterns of community composition for polyhaline seagrass beds along Florida's Gulf coast. The ↓ symbol indicates a lower value, the ↑ symbol indicates a higher value, and the ↔ symbol indicates a relatively even value for the comparison. The left column is the overall comparison between open estuaries and semi-enclosed estuaries. The right column is a descriptive comparison among semi-enclosed estuaries in the panhandle (north) and the peninsula (central) of Florida.

Open estuaries	Semi-enclosed estuaries
Big Bend compared to all semi-enclosed	Panhandle compared to peninsula
↓ salinity	↓ salinity
↓ dissolved oxygen	↔ dissolved oxygen
↑ mud	↓ mud
↑ depth	↓ depth
↑ mixed SAV	↓ *Thalassia testudinum*
↑ SAV % cover	↓ SAV % cover

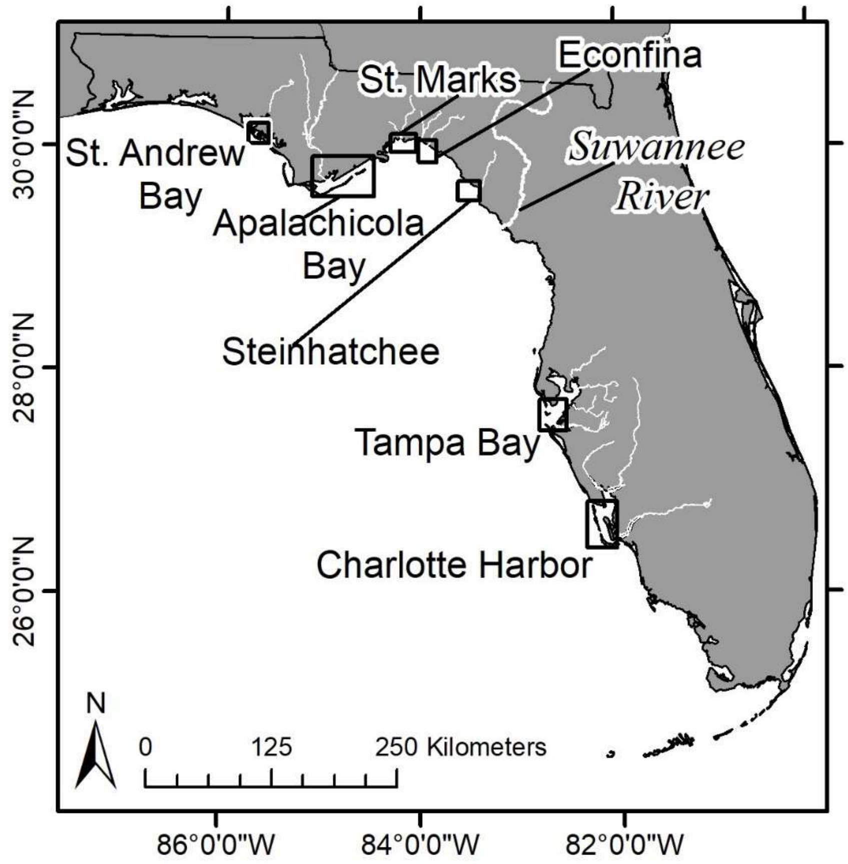


Fig. 1. Study area of polyhaline seagrass habitats sampled in estuarine systems in the panhandle (St. Andrew Bay [SA], Apalachicola Bay [AP]), Big Bend [BB] region (St. Marks [BBA], Econfina [BBB], and Steinhatchee [BBD]), and peninsula (Tampa Bay [TB] and Charlotte Harbor [CH]) of Florida, USA.

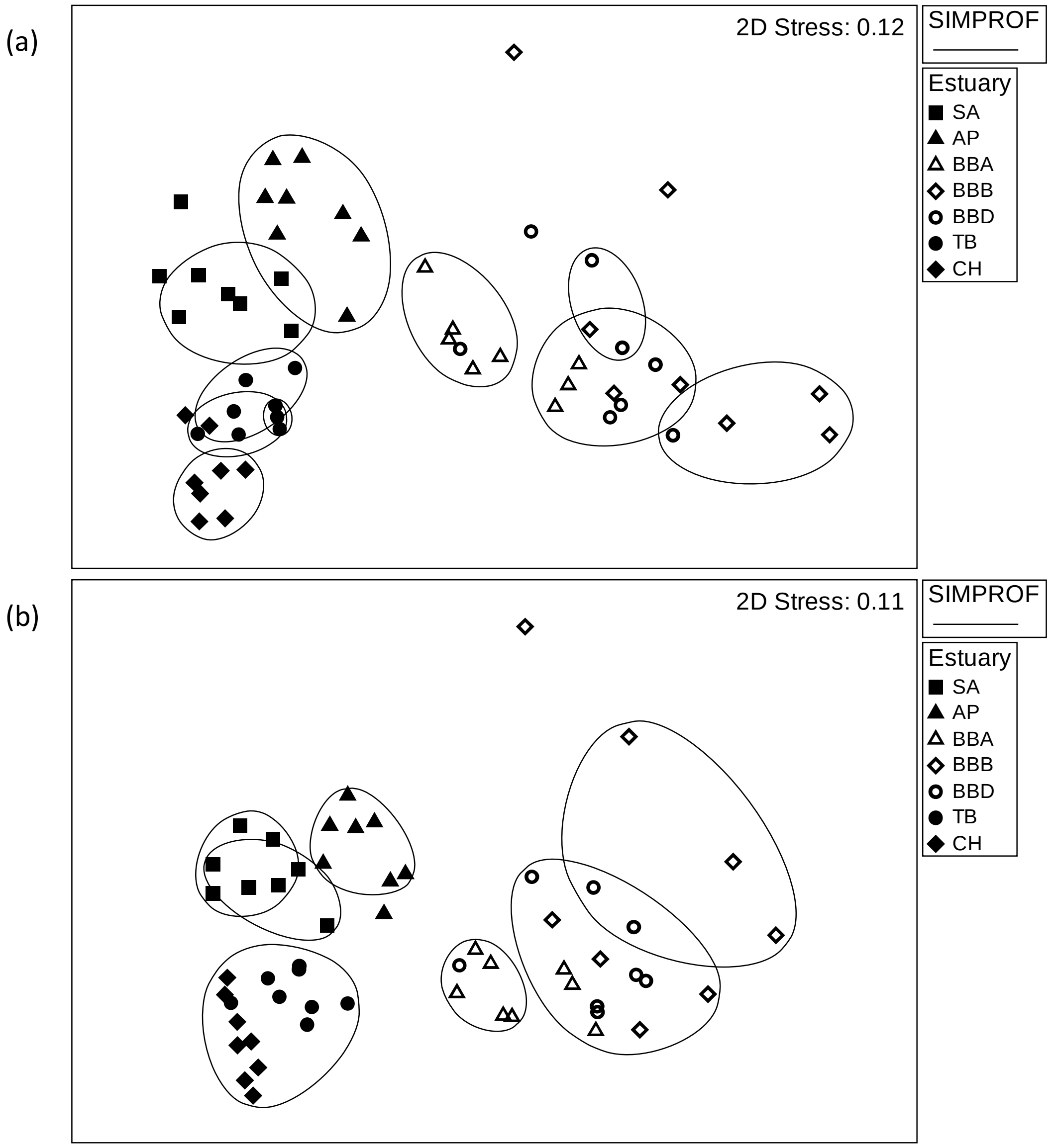


Fig. 2. nMDS ordination plots derived from dispersion-weighted taxon abundances averaged by estuary and year for (a) all 221 taxa and (b) the subset of 11 taxa identified by BEST analysis to serve as a proxy for the full data set. AP=Apalachicola Bay, SA=St. Andrew Bay, BBA=St. Marks, BBB=Econfina, BBD=Steinhatchee, TB=Tampa Bay, CH=Charlotte Harbor. The multiple symbols for each estuary represent different years (2008–2015). Symbols are grouped based on the SIMPROF test. Filled and open symbols represent semi-enclosed and open estuaries, respectively.

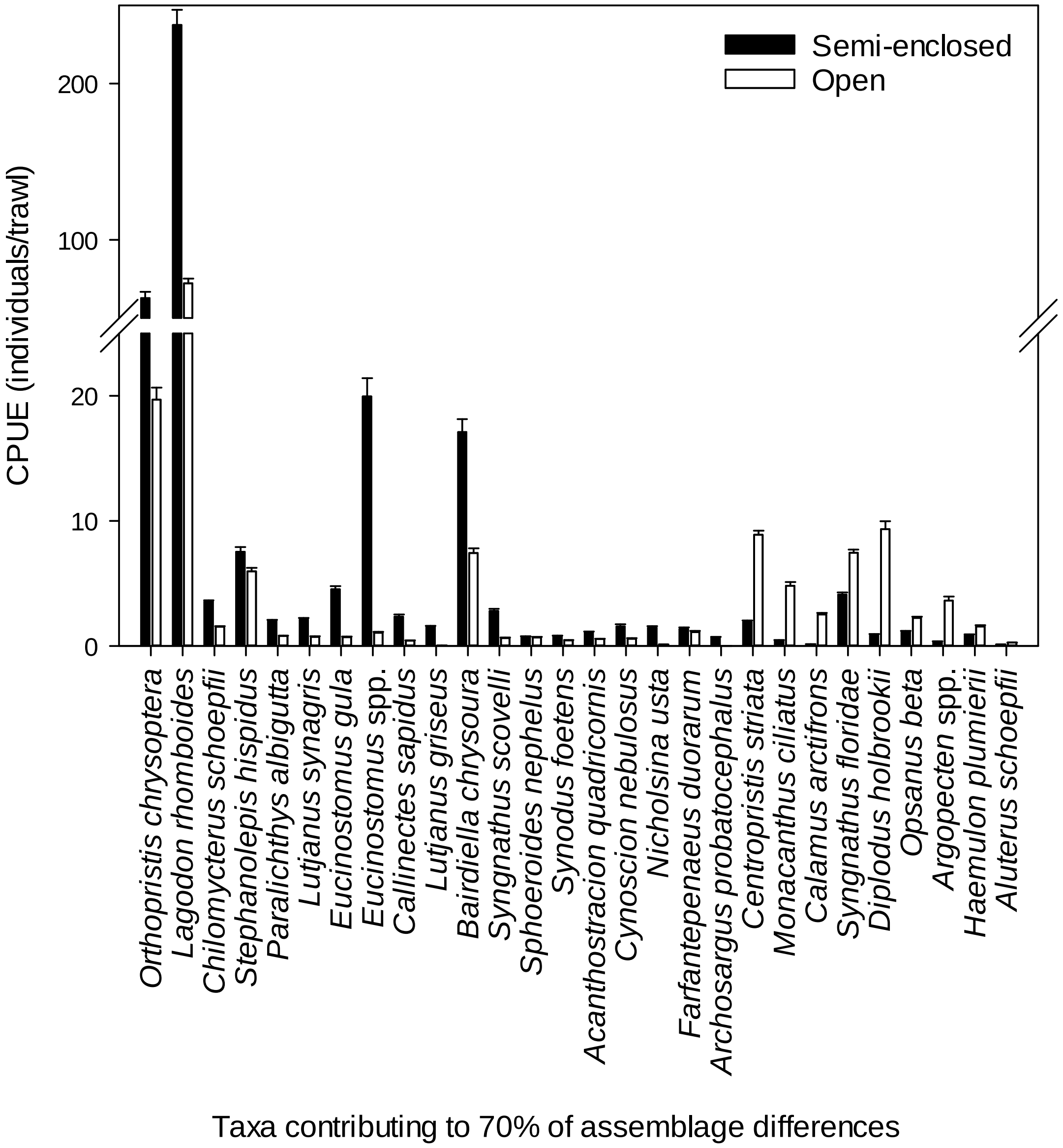


Fig. 3. Mean catch-per-unit-effort (CPUE) + SE for the 28 taxa contributing to 70% of the assemblage differences between semi-enclosed and open estuaries. Taxa toward the left had greater CPUE in semi-enclosed estuaries; those on the right had greater CPUE in open estuaries. Within each group (semi-enclosed vs. open), taxa are ordered from left to right based on their percent contribution to assemblage differences between semi-enclosed and open estuary morphologies.

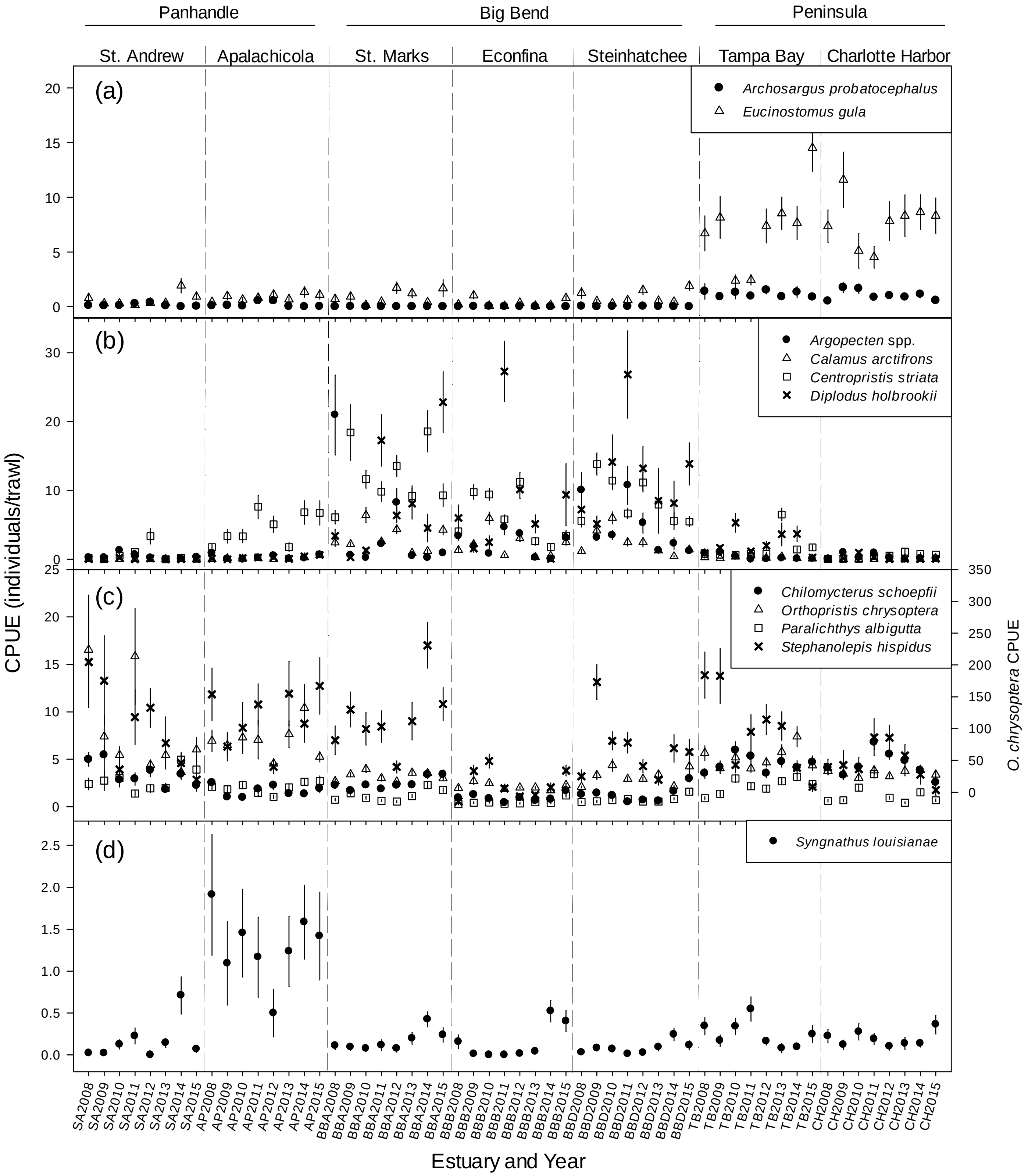
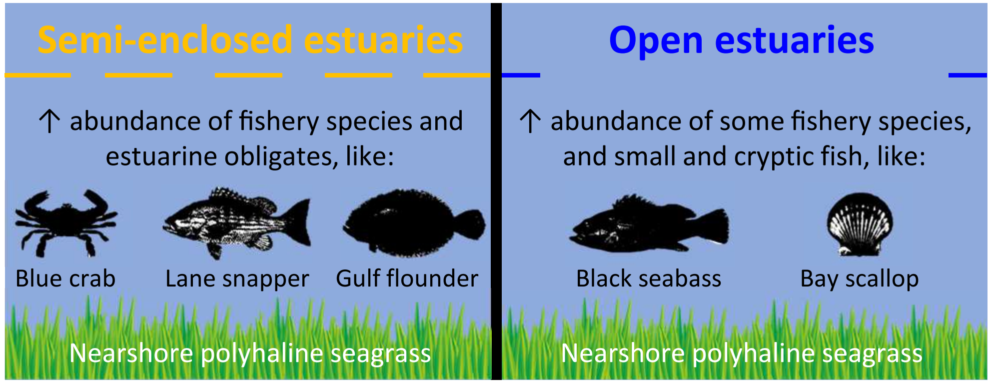


Fig. 4. Coherence plots of mean CPUE (individuals/trawl) ± SE for the 11 taxa identified by the BEST analysis that provide a similar resemblance structure as that of the entire 221-taxon data set. The 11 species were grouped by SIMPROF into four groups (a–d), depending on how CPUE varied spatially and temporally. Note CPUE of *Orthopristis chrysoptera* is on the right y-axis in (c) because of the disparity in scale.

Highlights:

- Eastern Gulf of Mexico estuary morphology affects faunal community composition
- Physiochemical parameters and submerged aquatic vegetation play secondary role
- Fishery species' abundances differ between semi-enclosed and open estuaries
- Regional scale monitoring data is valuable for assessing inter-estuary patterns



Semi-enclosed estuaries

↑ abundance of fishery species and estuarine obligates, like:

Open estuaries

↑ abundance of some fishery species, and small and cryptic fish, like: