ORIGINAL RESEARCH

Biodiversity of forage fishes in the Lower Laguna Madre, southernmost Texas

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ABSTRACT. Coastal estuarine ecosystems serve as nursery habitats for many commercially and recreationally important fishes. Biodiversity is a structural indicator and has been used as a metric for conservation and management. In the hypersaline Lower Laguna Madre of Texas, a variety of organisms makes their living in and around the dominant seagrass vegetation. This study provides a general assessment of forage fishes biodiversity collected seasonally with bag seines in two sites: Holly Beach (HB) and South Bay (SB) within the most southern Texas bay system as part of a broader study on fish biology. A total of 15,880 fishes representing 32 species were collected during four quarterly samplings through a year (11,795 from HB and 4,085 from SB). Both sites are interconnected as no fishes similarities difference were found, nonetheless, the sites' variable characteristics (i.e. basin area, seagrasses coverage, connection to the Gulf of Mexico) resulted in significant greater species richness, relative abundances, and diversity in HB than SB for most of the year, suggesting differences in habitat quality or at the very least variation in the availability of habitat types, which are known to contribute to differences in fish diversity attributes.

Key words: Fishing gear, estuaries, coastal fishes, baitfish, nursery habitat.

Biodiversidad de peces de forraje en la Laguna Madre Inferior, en el extremo sur de Texas

RESUMEN. Los ecosistemas de estuarios costeros sirven como hábitats de crianza para muchos peces de importancia comercial y recreativa. La biodiversidad es un indicador estructural y se ha utilizado como métrica para la conservación y la gestión. En la hipersalina Laguna Madre Inferior de Texas, una variedad de organismos vive en y alrededor de la vegetación de pastos marinos dominante. Este estudio proporciona una evaluación general de la biodiversidad de peces de forraje recolectados estacionalmente con redes de cerco en dos sitios: Holly Beach (HB) y South Bay (SB) dentro del sistema de bahías al sur de Texas, como parte de un estudio más amplio sobre la biología de peces. Durante cuatro muestreos trimestrales a lo largo de un año, se recolectaron un total de 15.880 peces (11.795 de HB y 4.085 de SB) que representan 32 especies. Ambos sitios están interconectados, ya que no se encontraron diferencias en las similitudes de peces; sin embargo, las características variables de los sitios (es decir, área de la cuenca, cobertura de pastos marinos, conexión con el Golfo de México) dieron como resultado una riqueza de especies, abundancias relativas y diversidad significativamente mayores en HB que en SB durante la mayor parte del año, lo que sugiere diferencias en la calidad del hábitat o, al menos, variación en la disponibilidad de tipos de hábitat, que se sabe que contribuyen a las diferencias en los atributos de diversidad de peces.

Palabras clave: Artes de pesca, estuarios, peces costeros, carnada, hábitat de cría.

INTRODUCTION

Coastal estuaries usually consist of a variety of structured and productive ecosystems such as marshes, mangroves, seagrasses, and reefs (Beck et al. 2001) that act as a habitat for a variety of organisms and create a nursery system for many commercially important fish species all over the coastal world (Hampel et al. 2005; Whitfield 2016; Breaux et al. 2019), many spawning offshore and using these areas as larvae and juveniles (Heck et al. 1997). Economically, these ecosystems are incredibly important locally, regionally, and nationally. In the United States of America (USA), the Texas coast alone brings in about USD 2 billion for recreational fishing, USD 5.4 million from tourism, and USD 250 million for seafood production (Rosen 2013).

Smaller and lower trophic level schooling fishes, known as forage fish, are usually found to be prey items to larger predatory fishes within the estuary. Forage fishes populate these ecosystems playing an important role within the community and trophic web as they make up a large part of the diet of many higher-level predators that use the estuary to feed and grow (Pikitch et al. 2012; Faletti et al. 2019). Many of these forage fishes will stay within the estuary their entire life, whereas others will travel offshore to spawn (Murphy and Taylor 1989; Wilson and Nieland 1994; Brown-Peterson et al. 2002; Faletti et al. 2019).

On the Gulf coast of Texas, which stretches about 644 km, there are about 10,522 km² of estuary habitat and seven major bay systems (Rosen 2013). Along the Texas coast, many of the estuaries have a high presence of seagrass that allows for sediment stabilization, nutrient cycling, protection, and detrital production and export (Heck et al. 2003). The most southern bay system of the Texas Gulf coast is the Laguna Madre. The most southern portion of the Laguna Madre, the Lower Laguna Madre (LLM), has been considered as hypersaline due to little freshwater inputs, few inlets to the Gulf of Mexico (GOM), and high evaporation (Tunnell and Judd 2002; Rosen 2013; Kowalski et al. 2018). The LLM has a high presence of seagrasses mostly including Turtle Grass (*Thalassia testudinum* K. D. Koenig, 1805) and Shoal Grass (*Halodule wrightii* (Ascherson, 1868)), but other species such as Manatee Grass (*Syringodium filiforme* Kützing, 1841), Widgeon Grass (*Ruppia maritima* Linnaeus, 1753), and Clover Grass (*Halophila engelmannii* Ascherson, 1875) can be found (Sheridan and Minello 2003). It is expected to find a higher number of fishes residing in areas of the estuary that have higher densities of seagrasses and other plant structures, which was shown in the LLM by Sheridan and Minello (2003). Though with changing climatic conditions, anthropogenic disturbances, and the increase of cold fronts and storm surges, many organisms are seeing declines, mass mortalities, or displacement (Sheridan and Minello 2003; Kowalski et al. 2018).

Due to the high productivity within these ecosystems, a high diversity of species (fishes and invertebrates) is usually found (Beck et al. 2001) which leads to interactions among different species using the same resources (Whitfield 2016). This creates biotic interactions that may affect local species distributions and abundances. An ecosystem's productivity is largely attributed to the area's biodiversity, making biodiversity a crucial metric for conservation and management (Pawluk et al. 2021). Fish diversity within the marine environment is constantly changing and will continue to fluctuate with changing environmental conditions. Habitat heterogeneity, basin area, physicochemistry of the water, primary productivity, resources availability and historical factors are known drivers of fishes diversity (Tonn 1990; Ricklefs and Schluter 1993; Gelwick et al. 2001; Ricklefs 2004; Auber et al. 2017; Thompson et al. 2020). As Pawluk et al.

(2021) pointed out, it is important to assess the patterns in fish abundances and species richness within marine systems in order to better understand community dynamics given changing temperatures and environmental conditions and point out what potential vulnerabilities there are. Given the importance of biodiversity and their connection with productivity and conservation, it is crucial to characterize these low-studied areas (as is the case in the southernmost Texas coast) and understand the dynamics of the forage fish community that can have a major impact on the local and state economies.

This study is derived from a broader one (to be published elsewhere) focusing on the age, growth, diet, and trophic web reconstruction of *Sciaenops ocellatus* and looks at forage fishes' diversity to better understand if there are any changes due to shifting environmental factors that are continually increased by climate change. Objectives of this study were: (1) compare forage fishes' biodiversity between two sites within the LLM, a bay and a lagoon, and (2) identify variations within a single year as a driver of any changes in forage fishes biodiversity by using netting to capture and record species along the shoreline of both sites. Because of differences in basin area (the lagoon site being smaller as detailed in methods), connection to the GOM, and seagrass coverage, it is hypothesized that the bay system will have greater fishes diversity than the lagoon system. Furthermore, fishes biodiversity is expected to fluctuate throughout the year due to a combination of factors including fishes migration cycles (e.g. Livingston et al. 1976; Timmerman et al. 2021), spawning and recruitment, juveniles survivorship (Livingston et al. 1976; Morin et al. 1985; Meffe and Berra 1988; Yoklavich et al. 1991), movement and dispersal of fishes that might be affected by home ranges, and degree of connectivity as well as physical barriers (Livingston et al. 1976; Yoklavich et al. 1991; Gelwick et al. 2001).

MATERIALS AND METHODS

Study sites

Study sites are South Bay (SB) and Holly Beach (HB), both located in Cameron County, southern Texas, USA. This area has several knowledge gaps including baseline studies as compared to other geographic locations in the country. Both sites are part of the LLM, which is one of the six largest hypersaline estuarine systems in the world (Tunnell and Judd 2002; Marquez et al. 2017). The climate is categorized as semiarid and subtropical (Tunnell and Judd 2002; Marquez et al. 2017). Estuaries of the LLM are connected to the GOM at the Brazos-Santiago Pass which was created in the 1930's (Tunnell and Judd 2002; Marquez et al. 2017).

South Bay (26° 01′ 20.6″ N-97° 11′ 03.8″ W) is classified as a bay system by name only, as it is an enclosed lagoon which only connects to the Brownsville Ship Channel through a narrow opening (Figure 1). It is located south of the Brazos-Santiago Pass. It is a shallow body of water and connects to the Rio Grande River on the south end. It has an average depth of 0.85 ± 0.15 m with an area of about 14.2 km² (Marquez et al. 2017). Holly Beach (26° 07′ 30.5″ N-97° 17′ 48.4″ W) is classified as a lagoon system and is located north of SB and the Brazos Santiago Pass (Figure 1). It lies between the Laguna Atascosa National Refuge and the LLM with the Laguna Vista Cove on the south end (Murphy et al. 2021). It has an average depth of about 1 m and has a great seagrass bed presence. As HB is part of the LLM aquatic system, for the purposes of this study, an area of ~ 42 km² was estimated using Google Earth (2022). Both study sites are popular bodies of water for fishing and birding as they provide a variety of ecosystem services and a habitat for many fishes of commercial and recreational importance.
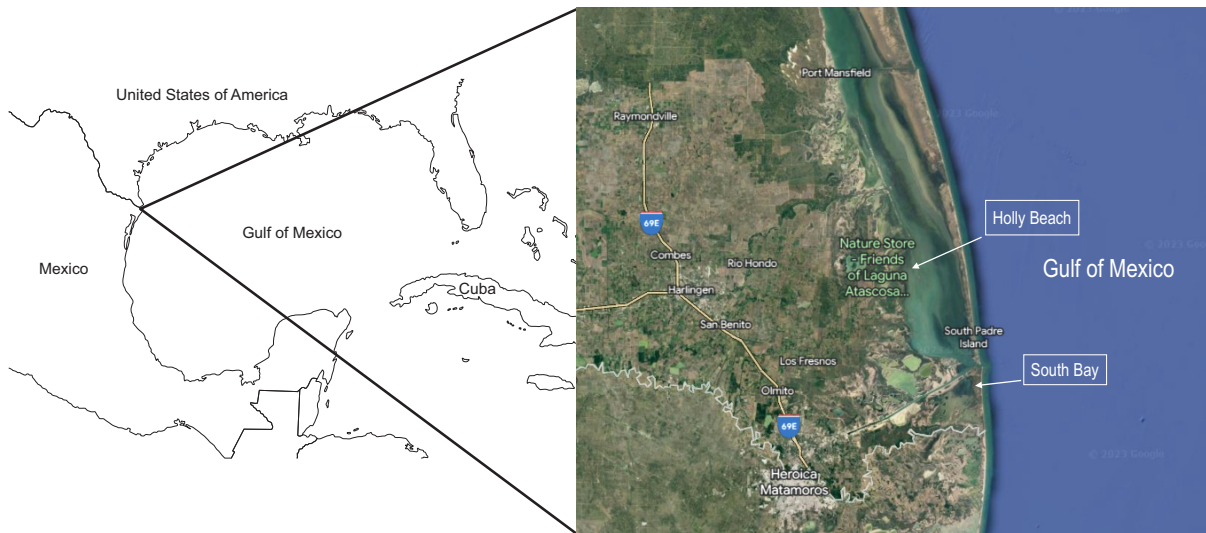
Figure 1. Gulf of Mexico map and study sites Holly Beach and South Bay located within the Lower Laguna Madre, Texas, United States of America. Map modified from Google Earth.

Sampling

Sampling procedure for this study followed the protocol from the Texas Parks and Wildlife Department (TPWD), which uses bag seines as part of their survey efforts. Bag seines utilized were made to replicate those from TPWD, which are 18.3 m long with 1.3 cm stretched nylon # 5 multifilament mesh in the bag, and 1.9 cm stretched nylon # 5 multifilament mesh in the wings and were used along the shore of both sites. Sampling effort goal was five bag seine replicates per site for a total of 20 replicates per quarter (Q), given four overall visits to each site. Due to restricted access to SB by SpaceX during rockets testing, unpredictable weather, and a set limit of 300 individual *S. ocellatus* each Q under the University of Texas Rio Grande Valley, Institutional Animal Care and Use Committee (IACUC, AUP-19-40). Bearing in mind that, in order to comply with the approved protocol under AUP-19-40, no further sampling occurred once the set number of *S. ocellatus* was achieved on each Q (i.e. 300 between both sites); hence, a balanced sampling effort was not achievable. This resulted in vari-

able numbers in replicates per site visit, as well as sample area covered. Nonetheless, the sampling effort goal was exceeded every Q as follows: Q1 21 samples (n), Q2 n = 35, Q3 n = 36, and Q4 n = 30. For future comparison purposes to the TPWD database, sampling was diurnal and occurred during high tides. A total area of about 720 m^2 was covered at both sites. Fishes were counted and identified for each bag seine replicate. All fishes (other than *S. ocellatus*) and their count were noted and then released back into the water. For identification purposes, when needed two voucher specimens of each species were kept and taken back to the laboratory.

Statistical analyses

Fishes' data were analyzed in Primer v7, before any routine a log (abundance + 1) was necessary as determined by a shade plot as per Clarke et al. (2014), which down-weighted contributions by highly abundant species and allow low-and-mid-range species to also influence assemblage similarities calculations (Clarke and Warwick 2006). The following Primer routines

and tests allowed comparisons between fish assemblages from both sites throughout the year on a quarterly basis. Natural groups of fishes at each site for every Q were identified with group-averaged cluster analysis based on Bray-Curtis similarities and non-metric multidimensional scaling (nMDS), only the latter was presented graphically (Figure 2), followed by a similarity profile (SIMPROF) test to identify genuine groups. A similarity percentage (SIMPER) test was performed to determine fishes that contributed to assemblages' dissimilarities among Qs and sites. Because there are only two sites, a one-way ANOSIM was performed on Qs. The DIVERSE routine was utilized to obtain species richness, Shannon-Wiener diversity (H' here-after), and Jaccard evenness (J' hereafter). These metrics as well as the overall abundance (abundance hereafter) per Q at each site were compared with a model 1 two-way analysis of variance (ANOVA) unless otherwise noticed (see below). Fishes' dominance ratios (DRs) were estimated by locality for each Q and were compared graphically using descriptive statistics (mean ± stan-

dard deviations), as no further statistical analyses were deemed appropriate because of the effect of highly abundant taxa in a given Q, which skewed the fishes' dominance ratio distributions.

Prior to performing any ANOVA, fish species richness, abundance, H', and J's at each site were subjected to Q-Q plots and Kolmogorov-Smirnov tests to verify normality, while homoscedasticity was evaluated with Levene's test (Zar 1996). Fishes' abundance violated both assumptions and were subjected to a $\log_{10} + 1$ transformation (Zar 1996). Species richness was not normally distributed, but the ANOVA was deemed robust enough for such violation (Underwood 1997) and was performed on non-transformed values. Diversity was heteroscedastic and the $\log_{10} + 1$ transformation made data even less homoscedastic but as the variances difference was < 3 times, the ANOVA was deemed robust for this violation and was performed on non-transformed values. Evenness was not complaint to either assumption (i.e. normality or homoscedasticity) and $\log_{10} + 1$ transformation made it worst. In this case, the ANOVA could have been still performed as ANOVA is based on
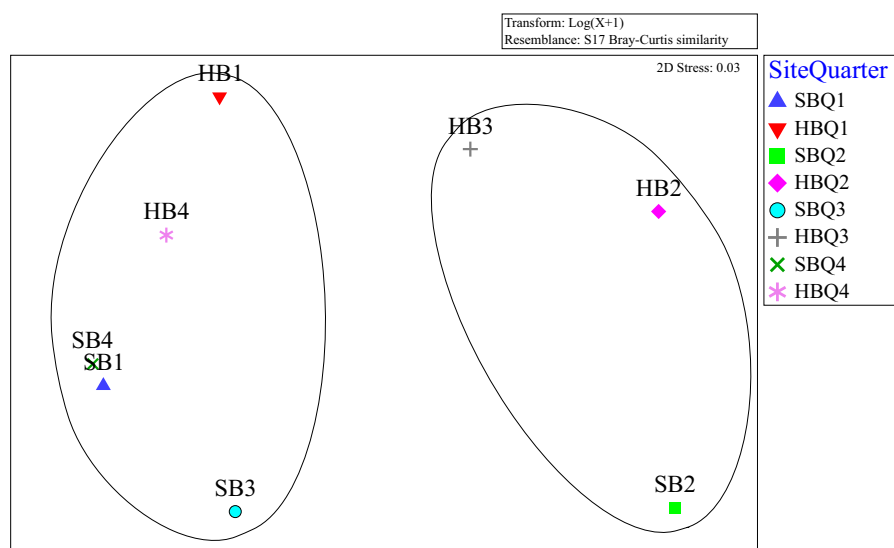

Figure 2. Non-metric multidimensional scaling plot of fishes' assemblages similarities. Ovals indicate 50% resemblance levels. Holly Beach = HB, South Bay = SB, quarter = Q. Q1 = October-December 2020; Q2 = January-March 2021; Q3 = April-June 2021; Q4 = July-September 2021.

means which conforms to the Central Limit Theorem making the assumption of normality not too critical, and the same reasoning used for H' might have been applied to the J' lack of homoscedasticity compliance. Hence, the non-parametric option (i.e. Kruskal-Wallis) was performed as an academic exercise only, because it is sensitive to departures from homoscedasticity (Underwood 1997). Noteworthy, Kruskal-Wallis runs only as a one-way therefore two tests were performed one for Qs and the second one for sites. A Tukey Honest Significant Difference (Tukey hereafter) test was performed when ANOVA indicated significant differences to identify the Qs responsible for them (Zar 1996). Note as there are only two sites the software does not perform this test for that variable and issues a warning, but the difference indicated by the ANOVA remains and therefore can be determined from the mean values. All parametric statistics were performed with SPSS v27.

RESULTS

A total of 32 fishes (Table 1) yielded 15,880 individuals collected during the year of sampling, 74.3% of them captured at HB. *Anchoa mitchilli*, *Cyprinodon variegatus*, *Lagodon rhomboides*, and *Micropogonias undulatus* were present year-round at both sites (Table 1). Fishes' richness in HB was 29 with ten species only present there, while SB had 22 species, three occurring only at SB (Table 1). Species richness varied also by Q ranging from 12-16 fishes at HB with 12 species occurring in a single Q, while the range for SB was 8-14 fishes with also 12 species occurring in a single Q (Table 1).

Similarity of fishes yielded two major clusters separating at 40.2%, one cluster included Q2 from both sites as well as Q3 at HB, all other similarities occurred in the second cluster (figure not shown); however, both clusters were not significantly different from one another. Quarters were

not significantly different from one another as per ANOSIM (R = 0.417, p = 0.114) supporting the SIMPROF test. Separation of Q2 was also depicted by the nMDS, with Q3 at HB in between the remaining groups (Figure 2). Similarity among samples ranged from 24.4 to 77.4%, with Qs 1 and 4 at SB being the more similar to one another; and Qs 2 and 4 at SB being more dissimilar from each other. Overall, seven or 12 fishes were needed to explain > 90% of the similarities: *L. rhomboides*, *A. mitchilli*, *M. undulatus*, *S. ocellatus*, *Eucinostomus gula*, *Lutjanus griseus*, and *Brevoortia patronus* explained the similarities between Qs 1 and 4 at SB, while *L. rhomboides*, *A. mitchilli*, *C. variegatus*, *B. patronus*, *Hippocampus* sp., *Mugil cephalus*, *Lutjanus griseus*, *Bairdiella chrysoura*, *Opsanus beta*, *Synodus foetens*, *Hemiramphus brasiliensis*, and *Fundulus grandis* explained similarities between Qs 2 and 4 at SB.

Mean ± standard deviation fishes' richness at HB ranged from 3.27 ± 1.94 to 6.75 ± 1.81, while at SB the range was from 2.75 ± 1.04 to 3.47 ± 1.46. There were significant differences between sites ($F_{0.05 (1,121)} = 60.66$, $p < 0.001$) with HB having greater richness than SB, and among Qs ($F_{0.05 (3,121)} = 6.47$, $p < 0.001$) (Figure 3 A). The Tukey test indicated Q4 at HB was significantly lower than the other 3 Qs, which were not different from one another; while at SB Q4 was significantly larger than all other Qs, which were not significantly different among (Figure 3 A). However, but as expected, the interaction effect was also significant ($F_{0.05 (3,121)} = 8.86$, $p < 0.001$).

Fishes' abundances (mean ± standard deviation) ranged from 84.73 ± 95.24 to 268.00 ± 248.33 at HB, and from 29.00 ± 25.80 to 93.80 ± 38.26 at SB (Figure 3 B). Holly Beach had a significantly larger number of individuals (log_{10} transformed) than SB ($F_{0.05 (1,121)} = 19.25$, $p < 0.001$), significant differences also occurred among Qs ($F_{0.05 (3,121)} = 5.79$, $p = 0.001$), and the interaction between sites and Qs ($F_{0.05 (3,121)} = 14.00$, $p < 0.001$). At both sites, Qs 1, 2, and 4 were not significantly different from one another,

Table 1. Fishes' richness by site and quarter (Q) presented in alphabetical order. Holly Beach = HB; South Bay = SB; Q1 = October-December 2020; Q2 = January-March 2021; Q3 = April-June 2021; Q4 = July-September 2021; Freshw. = freshwater.

Species	HB	SB	Environment[1]
Anchoa mitchilli (Valenciennes, 1848)	Q1, Q2, Q3, Q4	Q1, Q2, Q3, Q4	Euryhaline
Archosargus probatocephalus (Walbaum, 1792)	Q3, Q4		Marine/brackish
Bairdiella chrysoura (Lacepède, 1802)		Q1	Marine/brackish
Brevoortia patronus Goode, 1878	Q3	Q4	Euryhaline
Chaetodipterus faber (Broussonet, 1782)	Q3		Marine/brackish
Cynoscion nebulosus (Cuvier, 1830)	Q1, Q4		Marine/brackish
Cyprinodon variegatus Lacepède, 1803	Q1, Q2, Q3, Q4	Q2, Q3, Q4	Euryhaline
Elops saurus Linnaeus, 1766	Q2		Marine/brackish
Eucinostomus gula (Quoy and Gaimard, 1824)	Q1, Q4	Q1, Q4	Euryhaline
Fundulus grandis Baird and Girard, 1853	Q1, Q2, Q3, Q4	Q2, Q4	Freshw./brackish
Fundulus majalis (Walbaum, 1792)	Q2, Q3	Q2	Marine/brackish
Hemiramphus brasiliensis (Linnaeus, 1758)	Q1	Q4	Marine
Hippocampus sp.	Q1	Q1, Q2	
Kathetostoma albigutta Bean, 1892	Q3	Q4	Marine
Lagodon rhomboides (Linnaeus, 1766)	Q1, Q2, Q3, Q4	Q1, Q2, Q3, Q4	Euryhaline
Lucania parva (Baird and Girard, 1855)		Q3	Marine/brackish
Lutjanus griseus (Linnaeus, 1758)	Q1, Q4	Q1, Q4	Euryhaline*
Micropogonias undulatus (Linnaeus, 1766)	Q1, Q2, Q3, Q4	Q1, Q2, Q3, Q4	Marine/brackish
Mugil cephalus Linnaeus, 1758	Q1, Q2, Q3, Q4	Q2, Q3, Q4	Euryhaline*
Mugil curema Valenciennes, 1836	Q3	Q4	Euryhaline*
Oligoplites saurus (Bloch and Schneider, 1801)	Q1		Euryhaline*
Opsanus beta (Goode and Bean, 1880)	Q1, Q2, Q3, Q4	Q1, Q3	Marine
Orthopristis chrysoptera (Linnaeus, 1766)		Q4	Marine/brackish
Paralichthys lethostigma Jordan and Gilbert, 1884	Q1, Q2, Q3	Q3	Euryhaline*
Pogonias cromis (Linnaeus, 1766)	Q3, Q4		Marine/brackish
Sciaenops ocellatus (Linnaeus, 1766)	Q2, Q3	Q2	Marine/brackish
Scomberomorus maculatus (Mitchill, 1815)	Q4		Marine
Strongylura marina (Walbaum, 1792)	Q1, Q3, Q4		Euryhaline
Syngnathus louisianae Günther, 1870	Q2, Q3		Marine
Syngnathus sp.	Q1		
Synodus foetens (Linnaeus, 1766)	Q3	Q1	Euryhaline
Trachurus trachurus (Linnaeus, 1758)	Q4	Q4	Marine

[1]From Froese and Pauly (2022).

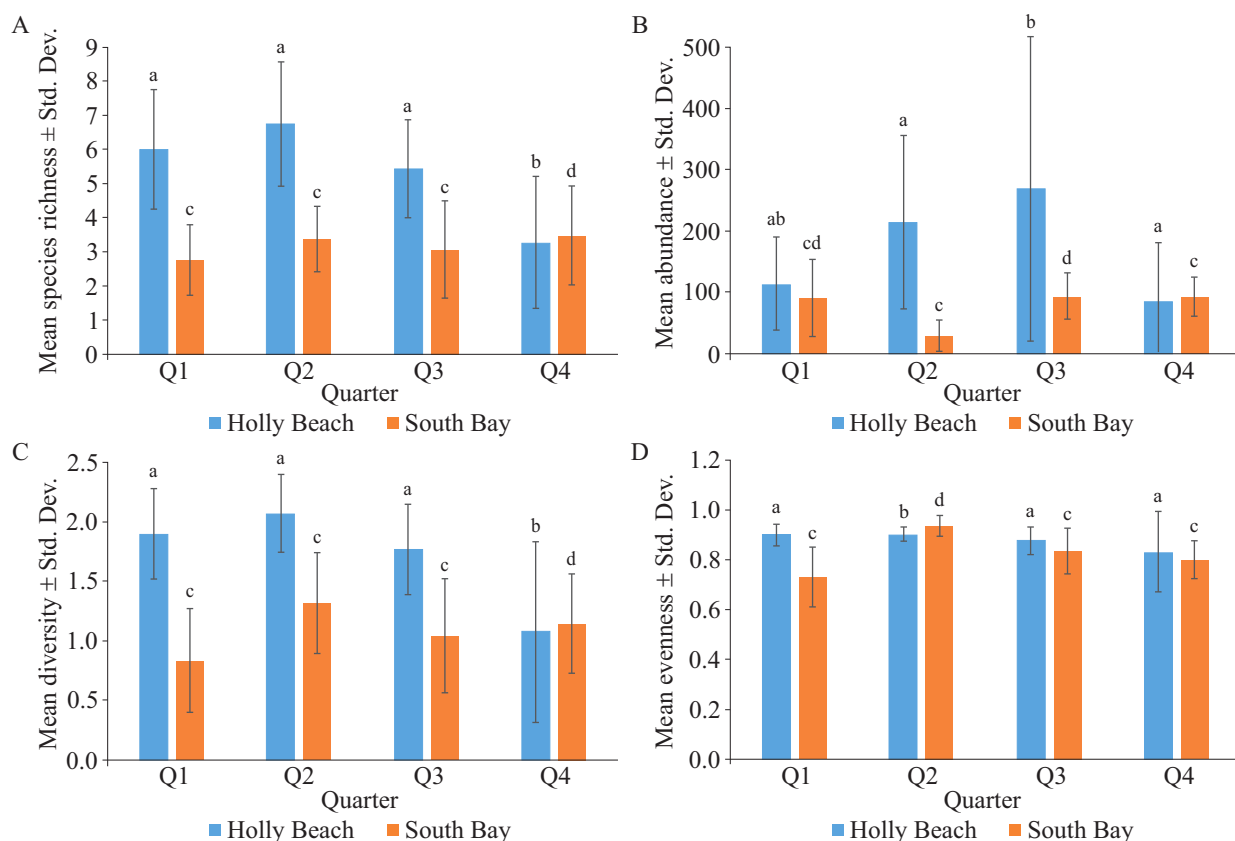*Reported as occasional in freshwater or penetrating rivers, and thus considered euryhaline.

Figure 3. Mean ± standard deviation (Std. Dev., bars) metrics for each quarter (Q) in the study sites. A) Species richness, B) abundance, C) diversity, and D) evenness. Holly Beach = HB, South Bay = SB. Sample size (n) as follows: HBQ1 n = 13, SBQ1 n = 8, HBQ2 n = 16, SBQ2 n = 19; HBQ3 n = 21; SBQ3 n = 15; HBQ4 n = 15; SBQ4 n = 15. Q1 = October-December 2020; Q2 = January-March 2021; Q3 = April-June 2021; Q4 = July-September 2021.

but Q3 was significantly different than Qs 2 and 4 (Figure 3 B) as per Tukey's test.

Fishes' H' (mean ± standard deviation) at HB ranged from 0.88 ± 0.62 to 1.70 ± 0.27, while in SB ranged from 0.68 ± 0.36 to 1.09 ± 0.35 (Figure 3 C). As for the previous two metrics, there were significant differences in H' between sites ($F_{0.05 (1,121)} = 46.55$, $p < 0.001$), among Qs ($F_{0.05 (3,121)} = 8.32$, $p < 0.001$), and their interaction ($F_{0.05 (3,121)} = 7.40$, $p < 0.001$) (Figure 3 C). Holly Beach once more had higher values than SB for most Qs, while the Tukey test indicated Q4 was significantly different from the other Qs, which were not different from one another at both study sites (Figure 3 C).

Mean ± standard deviation fishes' J' range at HB was 0.83 ± 0.16 to 0.90 ± 0.03, and at SB 0.73 ± 0.12 to 0.94 ± 0.04 (Figure 3 D). Fishes' J' was significantly larger at HB than at SB ($H_{0.05 (1)} = 4.08$, $p = 0.043$), and among Qs ($H_{0.05 (3)} = 24.28$, $p < 0.001$) (Figure 3 D). Regarding J' Q2 was significantly different than the others, which were not different from one another at both sites (Figure 3 D) as per the pairwise comparisons.

Lagodon rhomboides were overwhelmingly the more abundant fish in SB during Qs 1, 3, and 4 DR = 0.93, 0.90, and 0.93, respectively); while Q2 in SB was dominated by *M. undulatus* (DR = 0.37). In HB, the same two species were also dominant during the same Qs with *L. rhomboides*

DR = 0.69, 0.76, and 0.85 in Qs 1, 3, and 4, respectively; the DR in Q2 for *M. undulatus* was 0.39. The second highest DR (0.03) in SB for Q1 was for *E. gula* followed by *A. mitchilli* (DR = 0.02); for Q2 *A. mitchilli* had the 2nd highest DR (0.32), and *S. ocellatus* occupied the 3rd position with a DR of 0.16. *Anchoa mitchilli* had the 2nd highest DR (0.06) during Q3 in SB followed by *C. variegatus* (DR = 0.02), while the 2nd and 3rd place in the last Q were occupied by *E. gula* and *C. variegatus*, respectively. *Eucinostomus gula* also occupied the 2nd highest position with a DR of 0.14 in HB during Q1 followed by *F. grandis* (DR = 0.08); 2nd and 3rd place during Q2 were occupied by *F. grandis* (DR = 0.29) and *L. rhomboides* (DR = 0.13). Dominance was 2nd highest for *Mugil cephalus* (0.13) in HB for Q3 while *A. mitchilli* occupied 3rd place (DR = 0.007), and for the last Q *E. gula* had the 2nd highest DR (0.06) and *M. cephalus* the 3rd one (DR = 0.05). Quarter 2 was the more evenly divided in terms of fishes' dominance as the highest abundances of *L. rhomboides* resulted in high mean dominance ratio values for the other three Qs, particularly in SB (Figure 4).

DISCUSSION

In general, HB showed greater species richness, relative abundances, and H' than SB for Qs 1-3; while in Q4 SB had greater values than HB. This opposite result is likely one cause for the significant interaction effect for relative abundances and H'. As SB and HB have different habitat characteristics (e.g. basin area, connection to the GOM, seagrasses coverage, among others), the observed significant differences between sites are not surprising as HB was expected to host a greater number of fishes than SB.

Another cause for the interaction effect between sites and Qs is the expected changes in fishes' presences throughout the year, which also helps explain the significant differences observed in time. Twelve species were present only during one Q at each site. Such differences are explained by a combination of factors, e.g. fishes migration cycles (Livingston et al. 1976; Timmerman et al. 2021), spawning, recruitment, and juvenile survivorship (Livingston et al. 1976; Morin et al.
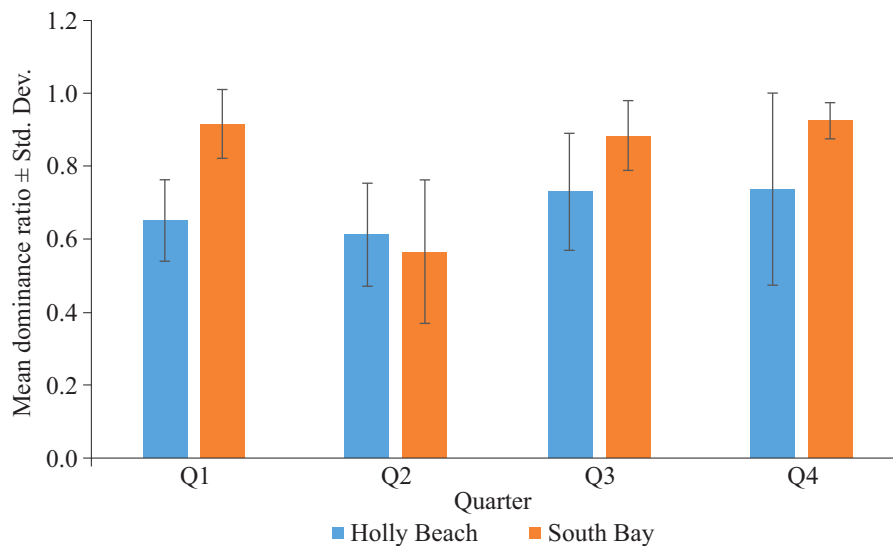

Figure 4. Mean ± standard deviation (Std. Dev., bars) fishes dominance ratio for each quarter (Q) in the study sites. Abbreviations and sample sizes as in Figure 3.

1985; Meffe and Berra 1988; Yoklavich et al. 1991), movement and dispersal of fishes which might be affected by physical barriers, home ranges, and degree of connectivity (Livingston et al. 1976; Yoklavich et al. 1991; Gelwick et al. 2001).

As HB is not only more open to the GOM but also has a larger area than SB, it is able to support a more diverse ichthyofauna with the following species only occurring there: *Archosargus probatocephalus*, *Chaetodipterus faber*, *Cynoscion nebulosus*, *Elops saurus*, *Oligoplites saurus*, *Pogonias cromis*, *Scomberomorus maculatus*, *Strongylura marina*, *Syngnathus louisianae*, and *Syngnathus* sp. Out of these ten fishes, five were present during a single Q. Three of them were reef-associated species: *Chaetodipterus faber* occurred only during the spring (i.e. Q3) and it is known to be present in estuaries, particularly as juveniles (Froese and Pauly 2022); while *E. saurus* present in winter (i.e. Q2) are known to occur in shallow onshore areas with common occurrence of juveniles in lagoons (Cervigón et al. 1992); in fall (i.e. Q1) *O. saurus* was found, and are known to prefer turbid waters when entering estuaries (Fischer et al. 1995). *Syngnathus* sp. was also present in Q1. Organisms in this genus are associated with aquatic vegetation including seagrasses, noteworthy its congeneric (*S. louisianae*) occurred in the two subsequent Qs and only at HB. For summer (i.e. Q4) the presence of *S. maculatus* was recorded. They are known to be moving along the Mexican coast (which is very nearby the study sites) between August and November (Froese and Pauly 2022).

The three fishes that only occurred at SB were present in a single Q: *Bairdiella chrysoura* (Q1), *Lucania parva* (Q3), and *Orthopristis chrysoptera* (Q4). The former species likely was using the enclosed system as a nursery and/or feeding area, as they are known to move into estuaries during the summer months (Froese and Pauly 2022); while *L. parva* benefitted from the presence of seagrasses, which are denser than at

HB but were not quantified for the purposes of this study. Both species might have been present but not captured in other Qs. This possibility is less likely for *O. chrysoptera* which are mainly nocturnal and apparently avoid low water temperatures as they seasonally migrate to deeper waters during winter (Darcy 1983). While for *B. chrysoura*, the possibility is very feasible as it is known not only to feed but also to mature and reproduce within estuaries, and hence considered an estuarine resident (Grammer et al. 2009). *Lucania parva* is also categorized as an estuarine species, known to prefer areas with high seagrasses canopies that may provide protection from predators and perhaps a larger amount of epibenthic prey items that attach to the seagrasses surface areas (Tomoleoni 2007). Many studies have shown that vegetated habitats tend to rear higher densities of forage fishes and other organisms than those that are non-vegetated sandy or muddy bottoms (Summerson and Peterson 1984; Connolly 1994; Jenkins et al. 1997; Rozas and Minello 1998; Sheridan and Minello 2003), but as the goals of the present study were not to contrast vegetated versus non-vegetated sites neither to estimate seagrasses densities at the studied sites, the subject is not further discussed.

Aside from the aforementioned factors associated with fishes movements (migration, dispersal), ontogenetic (reproduction, growth), survivorship, or diel habits, one other cause for not capturing the eight fishes (five in HB and three in SB) in other Qs could be related to the fishing gear (i.e. bag seine) used. Rozas and Minello (1997) suggested that enclosure devices have a greater catch efficiency of small nekton than towed nets in shallow estuarine habitats. However, see Layman and Smith (2001) for a different perspective. Noteworthy, gear was selected as part of the larger study focused on the age, growth, diet, and trophic web reconstruction of *S. ocellatus* and adopted from the TPWD sampling protocol, which uses bag seines as part of their survey efforts. As the present results will serve as a baseline study to

compare outcomes to TPWD presented else-where, it was necessary to sample with this gear. Nonetheless, even with the inherent bag seine sampling bias and limitations, four species (*A. mitchilli*, *C. variegatus*, *L. rhomboides*, and *M. undulatus*) use both studied sites as their perma-nent home by being present year-round. Three of these fishes are generally euryhaline.

In terms of fishes' relative abundances, 11,795 and 4,085 individuals were captured at HB and SB, respectively. Temporally, the greater abun-dances occurred in Q3 at both sites, then changed depending on location with the 2nd largest abun-dances at HB during Q2 and Q4 at SB. Thus, the spring (i.e. Q3) seems to be the more beneficial season at both sites but as this is a single-year study such a statement may not hold when multi-ple years are accounted for. Nonetheless, for the purposes of the results here presented, 47.7% and 34.4% of the fishes' abundances occurred at HB and SB respectively during the spring. *Lagodon rhomboides* was mainly responsible for this pat-tern with 4,271 individuals at HB and 1,267 at SB. Noteworthy, the species was least abundant during Q2 (~ winter), and as mentioned before occurred year-round at both sites. Hence, *L. rhomboides* had higher abundances during spring-summer, which was also reported for the Mad Island estuary in Texas (Akin et al. 2003), and in Tampa Bay, Florida (Chacin et al. 2016).

Lagodon rhomboides post-larvae arrive in the GOM and southeastern USA estuaries during winter as they reproduce offshore (Darcy 1985), hence the higher abundances during spring to fall (i.e. ca. Qs 3, 4, and 1) of one of the most widely distributed and common fishes in the USA (Hoese and Moore 1998), which follows such ontogenetic cycle. This also explains its lesser abundances during winter (Q2). Furthermore, Stoner (1980) indicated *L. rhomboides* as impor-tant mesograzers in the Laguna Madre seagrass beds being abundant from early spring to fall, while Hoss (1974) observed a minimal overwin-tering of the *L. rhomboides* population in North

Carolina's estuarine waters as the majority of the fish migrated offshore upon the onset of colder water temperatures.

Fish assemblages similarities formed two clus-ters (not shown), but there was no significant dif-ference between them. Nonetheless, the group formed in Q2 for both sites with Q3 at HB in the nMDS is likely the result of greater variability in the abundances of taxa, with the two higher abun-dances at HB and the least abundance at SB. This exchange of abundance values among seasons is complementary to the more abundant fishes which might have contributed to the lack of sig-nificant difference found and helps to also explain the interaction effect in abundances and diversity (discussed above) resulting in the gener-ally observed equitability. However, winter con-ditions should not be disregarded and likely allowed some degree of grouping of both sites during Q2.

Although DRs were variable throughout the year and between sites, *L. rhomboides* was over-whelmingly more abundant from spring to fall at both sites, while *M. undulatus* was more domi-nant in winter (Q2) with a DR of 0.37 at SB and 0.39 at HB. As mentioned in the results, the 2nd and 3rd positions based on DRs varied among species and might have resulted from resource partition throughout the year. Likely migration offshore for reproduction purposes, decreasing temperatures, or both factors combined, *L. rhom-boides* (see above) allowed the rise of another year-round resident to become dominant in Q2. Akin et al. (2003) also found seasonal changes in estuarine fishes assemblages in Mad Island Marsh, Matagorda Bay, Texas with *M. undulatus* being more abundant from December-April when temperatures were low, while *L. rhomboides* was abundant during spring and summer. Resource partitioning could also be exemplified by *A. mitchilli* and *L. rhomboides*, regarding the DRs of the former species tended to be the 2nd most abundant in half of the Qs at SB. Although habitat zonation was not the focus of this study, Gelwick

et al. (2001) identified zones based on depth, salinity, and dissolved oxygen gradients also in Matagorda Bay and indicated *A. mitchilli* occupied a different zone than *L. rhomboides*.

Lastly, six of the eight more dominant species are important for fisheries (*A. mitchilli*, *C. variegatus*, *L. rhomboides*, *M. undulatus*, *M. cephalus*, and *S. ocellatus*) and were present year-round highlighting the importance of both study sites as important in their life cycle, although *M. cephalus*, and *S. ocellatus* were not always captured by the bag seines. According to Froese and Pauly (2022) these species as fishery resources have the following uses: 1) major relevance as bait *A. mitchilli*, *C. variegatus* and *L. rhomboides*; 2) considered game fishes *L. rhomboides*, *M. undulatus*, *M. cephalus* and *S. ocellatus*; 3) commercial *M. undulatus* and *M. cephalus*, while *L. rhomboides* and *S. ocellatus* are used in minor extent; 4) aquarium fishes' exploitation *C. variegatus* and *S. ocellatus*; and 5) used in aquaculture *M. undulatus*, *M. cephalus*, and *S. ocellatus*.

Although the present study only encompassed one-year, it was evident that both sites are interconnected as no fishes similarities difference was found, nonetheless their multiple differences (i.e. basin area, seagrasses coverage, connection to the GOM, etc.) resulted in significant differences in fishes richness, abundances, H', and J' suggesting differences in habitat quality, or at the very least variation in the availability of habitat types, which are known to contribute to differences in fish diversity attributes (Meffe and Berra 1988). It also highlights the importance of HB and SB as a permanent residency for several species that were present year-round, including six fishes relevant to fisheries. This calls for further studies in this relatively abandoned area (compared to other USA GOM ones), particularly as global warming and increasing sea-level are expected to impact the coastal areas likely impacting not only resources useful to feed the increasing human population but also affecting forage fishes which should be managed at the very least as a group because of their relevance as an energy source within any marine food web.

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