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Habitat Provision Differs Across Subtidal Reefs Varying in Location Within the Estuarine Landscape

Alyssa Outhwaite¹ · Benoit Lebreton² · Terence A. Palmer¹ · Jennifer Beseres Pollack¹

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Abstract

Although position within the estuarine landscape is known to influence structural characteristics and ecological functioning of many habitats, the influence of position on subtidal oyster reef characteristics and functioning is relatively understudied. This study assessed habitat provision by oysters and benthic macrofauna on subtidal bar and patch oyster reefs within the northwestern Gulf of Mexico estuary. Bar reefs had greater and more variable oyster density, biomass, and volume, as well as dead shell material, compared to patch reefs. Benthic macrofaunal community composition differed between reef types, with bar reefs hosting 11× and 30× higher biomass of Porcellanidae and Ampithoidae crustaceans, and patch reefs supporting 34× and 47× higher biomass of Eunicidae annelids and Leptocheliidae crustaceans. The environmental variables most highly correlated with macrofaunal communities on both bar and patch reefs were sediment chlorophyll-*a*, volume of dead oyster shells, and depth. Despite differences in structural characteristics and position within the estuarine landscape, subtidal oyster reefs are often managed as a single habitat type. Our findings emphasize the importance of considering location in oyster reef conservation and restoration efforts to better predict and optimize faunal provision outcomes.

Keywords Conservation · *Crassostrea virginica* · Macrofauna · Habitat · Management · Restoration · Texas · USA

Introduction

The distribution and abundance of ecological functions within ecosystems often correlate with the location and position of biogenic habitats within the landscape (Boström et al. 2011; Pulliam and Danielson 1991). In terrestrial systems, advances in understanding the influence of habitat location within the broader landscape have helped inform conservation strategies (Liu and Taylor 2002). However, these principles have not been applied extensively to coastal ecosystems, and studies of how habitat position within the estuarine landscape affects faunal communities have focused

primarily on seagrass and salt marsh (Micheli and Peterson 1999; Boström et al. 2018). An increased awareness of large historic loss of estuarine habitats has expanded the number of conservation and restoration efforts seeking to stimulate recovery (Lotze et al. 2006; Elliott et al. 2007; Lotze 2010; Mazor et al. 2021). Although substantial advances have been made toward identifying the stressors responsible for degradation of coastal habitats, additional work is needed to define and predict successful ecological conditions to be achieved after management actions (Palmer 2009). An improved understanding of how ecosystem functions differ by location within the diverse estuarine landscape can help inform ecosystem-based management and restoration strategies.

Oysters are foundational species that support myriad ecosystem functions in estuaries. Structurally complex oyster reefs increase habitat heterogeneity (Humphries et al. 2011; Karp et al. 2018), provide complex substrate for refugia (Soniati et al. 2004), increase local biodiversity (Godbold et al. 2011; Blomberg et al. 2018a; De Santiago et al. 2019), and alter water flows and delivery of suspended organic matter to the sediments (Lenihan 1999; Grabowski and Powers 2004). Extensive losses of oyster reefs driven

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✉ Jennifer Beseres Pollack
Jennifer.Pollack@tamucc.edu

- ¹ Harte Research Institute for Gulf of Mexico Studies, Texas A&M University-Corpus Christi, 6300 Ocean Drive, Corpus Christi, TX 78412, USA
- ² UMR Littoral, Environnement et Sociétés, CNRS - University of La Rochelle, Institut du Littoral et de l'Environnement, La Rochelle 17000, France

by both human activities and a changing climate over the past century (Kirby 2004; Jackson 2008; Zu Ermgassen et al. 2012) have stimulated conservation efforts (Blomberg et al. 2018b; Duarte et al. 2020) and legislative protections (*Council Directive 92/43/EEC1992*; *31 Tex. Admin. Code § 58.211996*; European Commission, Directorate-General for Environment 2019; MD Annotated Code 4§-1009.1 2023) to conserve enduring reef habitats and rebuild lost ecosystem benefits.

Ecological processes and functions on oyster reefs can be influenced both directly and indirectly by location within the estuarine landscape, through effects on physical structure, orientation, and prevailing local conditions (Bahr and Lanier 1981; Hosack et al. 2006; Byers et al. 2015; Smyth et al. 2015). Current understanding of the influence of landscape setting on ecosystem service provision comes predominantly from studies of intertidal oyster reefs (Grabowski et al. 2005; Harwell et al. 2011; Ziegler et al. 2017), and it is not clear whether similar landscape-based effects apply to subtidal reef systems. To improve predictions of how subtidal reef fauna may respond to management actions, direct in situ measurements are needed to evaluate differences at reefs located in different positions across the estuarine landscape. The findings of such measurements can improve the ability of resource managers to define success criteria for habitat provision following management intervention and increase

return on investment from restoration efforts (Simenstad et al. 2006).

This study investigated whether habitat provision and biodiversity of resident macrofauna vary by position within the estuarine landscape for natural subtidal *Crassostrea virginica* oyster reefs. We conducted measurements of (1) oyster population (e.g., oyster density, biomass) and (2) resident macrofauna (e.g., density, biomass, community composition) on subtidal oyster reefs that differ in shape, hydrology, and proximity to the nearby shore. Given the economic and political challenges associated with natural resource management decisions, determining how differences in ecological functioning of oyster reefs may vary by position within the estuarine landscape can provide an important data basis to support future conservation and restoration actions.

Materials and Methods

Study Area

This study was conducted in the eastern arm of Matagorda Bay, a large (1013 km²), shallow (~2 m) bay within the Lavaca-Colorado Estuary, Texas, USA, in the northwestern Gulf of Mexico (Fig. 1; Armstrong 1987). Oyster reefs sampled in this study comprise two common subtidal reef

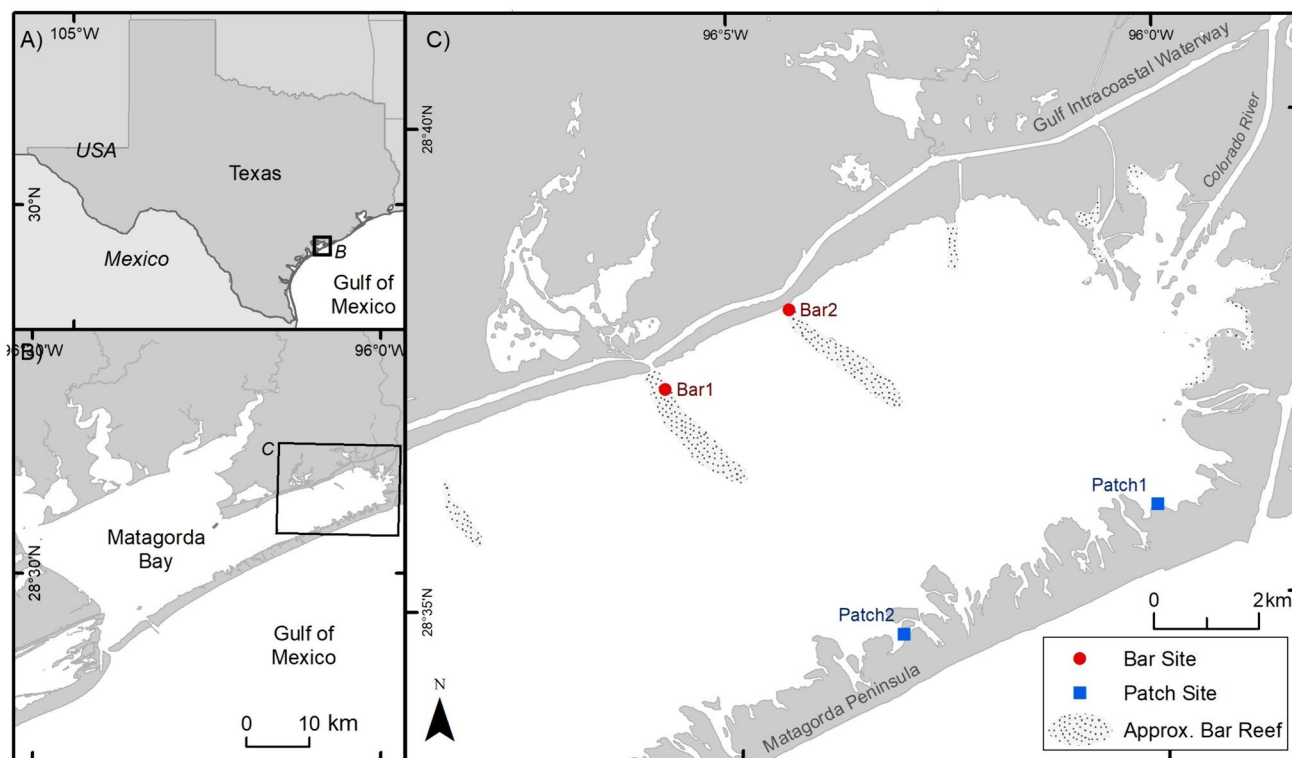


Fig. 1 Map of sampling sites within **A** Texas, USA; **B** the Lavaca-Colorado Estuary; and **C** the eastern arm of Matagorda Bay. Approximate locations of oyster reefs are from NOAA electronic navigation charts (NOAA 2018)

types characterized by their shape and position relative to the nearby shore (Stenzel 1971; Kennedy and Sanford 1999). Bar reefs (also called string reefs) extend perpendicular from shore across the currents into deeper water, with narrow crests of dead shells that may be exposed at low tide and live oysters on the sloping shoulders (Moore 1907; Hedgpeeth 1953; Stenzel 1971; Dellapenna and Simons 2010). Patch reefs run parallel to shorelines and have a flat, compact form that does not extend much above the surrounding bottom and contains limited extensive shell deposits (Moore 1907; Kennedy and Sanford 1999; Online Resource 1).

Sample Collection

Two bar reefs (Bar 1, Bar 2) and two patch reefs (Patch 1, Patch 2) were sampled seasonally in winter (24 January), spring (5 May), summer (17 August), fall (19 November) 2020, and winter (21 January) 2021. Samples were collected from subtidal areas (10–50-cm water depth) along the shoreline edge of each reef that were not subject to harvest. During each sampling event, discrete measurements of water temperature (°C), salinity, and dissolved oxygen (DO) concentration (mg l^{-1}) were collected approximately 0.1 m above the sediment surface at each reef using a YSI ProDSS multiparameter Instrument (YSI ProDSS User Manual 2014). Bottom water was collected from above each reef using replicate 1-L amber bottles for measurement of water chlorophyll *a* (Chl *a*). Sediments were collected from each reef using replicate benthic cores (2 cm deep, 38.5 cm² area) for measurement of sediment Chl *a*. Live oysters and dead oyster shells (> 25 mm) were collected by hand from three replicate 0.25 or 0.07 m² quadrats (depending on oyster densities) on the surface of each reef. Within each replicate sample, shell heights (mm) of all live oysters were measured, all live oysters and dead oyster shells were counted, and the volume of live oysters and dead oyster shells was quantified by water displacement (L). Resident macrofauna were collected by hand from three replicate 0.25 or 0.07 m² quadrats excavated to a depth of 0.1 m and thoroughly rinsed over a 500- μm mesh. Water, sediment, and live oyster samples were placed on ice in coolers, and macrofauna were placed into jars with 10% buffered formalin, and transported to the laboratory for further processing.

Laboratory Procedures

In the laboratory, water samples were sieved on a 250- μm mesh screen to remove large zooplankton and detritus and filtered through pre-combusted (4 h, 450 °C) glass fiber filters (Whatman GF/F, 0.7 μm porosity), and then, the filters were freeze-dried for 24 h (Labconco Freezone). Sediment was sieved over 500- μm mesh screen to eliminate macrofauna, large detrital particles, and shell hash,

then freeze-dried for 24–72 h, and ground using a mortar and pestle. Chl *a* was extracted from filters and sediments overnight using a non-acidification technique and measured using a Turner Trilogy fluorometer ($\mu\text{g l}^{-1}$; Turner Designs, Sunnyvale, USA) (Welschmeyer 1994; EPA method 445.0).

Dry weight biomass measurements of oyster soft tissues were obtained after drying at 60 °C for 24 h. Resident macrofauna were identified to the lowest practical taxonomic level using a stereo microscope and enumerated. Dry weight biomass measurements of resident macrofauna were obtained after drying for 24 h at 60 °C. Mollusk shells were removed with 1 mol L⁻¹ HCl prior to drying and weighing.

Statistical Analysis

Two-way analysis of variance (ANOVA) tests were used to test for the effects of date and reef on live oyster density, size (shell height), biomass, and volume; dead oyster shell density and volume; and macrofaunal density, biomass, and diversity (Hill's N1 per 0.25 m² area). Levene and Shapiro-Wilk tests were used to test for homoscedasticity and normality of the data. Data were log_e- (live and dead oyster density, macrofauna density, and biomass), or fourth root- (live oyster biomass and volume, live: dead oyster density and volume) transformed to improve ANOVA normality assumptions. When assumptions of normality could not be met, the non-parametric Scheirer-Ray Hare test was used. Statistically significant interactions ($\alpha=0.05$) were examined using simple main effects analyses. Post-hoc comparisons were performed using Tukey's HSD test in multcomp package (Hothorn et al. 2008) where applicable. All univariate data management and analyses were performed using R Studio 4.0.0 (R Core Team 2021). Dead oyster shell density and volume and live oyster tissue biomass were mistakenly not measured in winter 2020. A linear relationship between biomass and density for bar and patch reef types ($R^2=0.721$, $R^2=0.839$) was used to estimate live oyster tissue biomass for winter 2020 (Online Resource 2).

Differences in reef structure (i.e., volume and density of live oysters and dead shells) and water quality among reefs were compared using principal component analysis (PCA). Data were log-transformed and standardized prior to analysis (Clarke and Gorley 2014). Differences in biomass-based community composition of reef macrofauna were described using non-metric multidimensional scaling (nMDS; Clarke and Warwick 1994) plots superimposed with groupings from group-average cluster analysis. Both nMDS and cluster analysis used log_e-transformed biomass data in a Bray-Curtis similarity matrix. Significant clusters ($\alpha=0.05$) were determined using similarity profile analysis (SIMPROF). Species with the greatest contributions to dissimilarity between clusters were determined using similarity percentage analysis (SIMPER). The biotic-environmental

(BIO-ENV) procedure was used to correlate macrofaunal community composition with combinations of abiotic (water quality and reef structure) variables using weighted Spearman rank correlations (Clarke and Ainsworth 1993; Clarke et al. 2008). All multivariate analyses were conducted using PRIMER v7.0 (Clarke and Gorley 2014).

Results

Water and Sediment Characteristics

Water temperature, salinity, and dissolved oxygen displayed expected seasonal fluctuations and were similar among reefs (Online Resource 3). Temperature and salinity ranged from 16.4 ± 0.8 °C and 17.3 ± 3.4 (mean \pm standard deviation) in winter 2020 to 30.4 ± 0.9 °C and 24.7 ± 3.0 , respectively, in summer 2020. Dissolved oxygen concentrations were inversely related to temperature, ranging from 6.2 ± 1.2 mg L⁻¹ in summer 2020 to 11.2 ± 2.4 mg L⁻¹ in winter 2020. Concentration of water chlorophyll *a* (water chl *a*) and sediment chlorophyll *a* (sediment chl *a*) also varied seasonally at all reefs, with water chl *a* ranging from 6.8 ± 3.3 µg L⁻¹ in winter 2020 to 21.3 ± 11.3 µg L⁻¹ in spring 2020, and sediment chl *a* ranging from 42.8 ± 38.9 mg m⁻² in fall 2020 to 121.0 ± 82.9 mg m⁻² in winter 2020.

The first and second principal components (PC1 and PC2) for water quality metrics accounted for 47.8% and 25.4% of the variability within the data set (73.2% total, Fig. 2). Positive PC1 scores corresponded with high depth, temperature, and salinity values, while negative PC1 scores corresponded with high sediment chl *a* and dissolved oxygen concentrations. Most reefs had positive PC1 and PC2 values in spring and summer 2020. The water and sediment quality of patch reefs was more similar to each other than to that of the bar reefs in all sampling seasons except for in winter 2021. However, differences in water quality among seasons were greater than differences among sites.

Oyster Characteristics

Differences in live oyster density were observed among reefs ($p < 0.001$) and among seasons ($p = 0.009$) (Table 1). Oyster densities were higher at Bar 2 reef (245 ± 153 ind. m⁻²) than Bar 1 (31 ± 29 ind. m⁻²), Patch 1 (26 ± 31 ind. m⁻²), and Patch 2 reef (19 ± 16 ind. m⁻²) (Fig. 3).

There were no consistent differences in live oyster height among reefs or among seasons (Season \times Reef interaction $p = 0.047$, Table 1). However, differences among reef-season combinations occurred. Oyster heights were lower in fall 2020 at Bar 1 reef (38.5 ± 12.3 mm) than at Bar 2 reef in winter 2020 (87.0 ± 22.9 mm), spring 2020

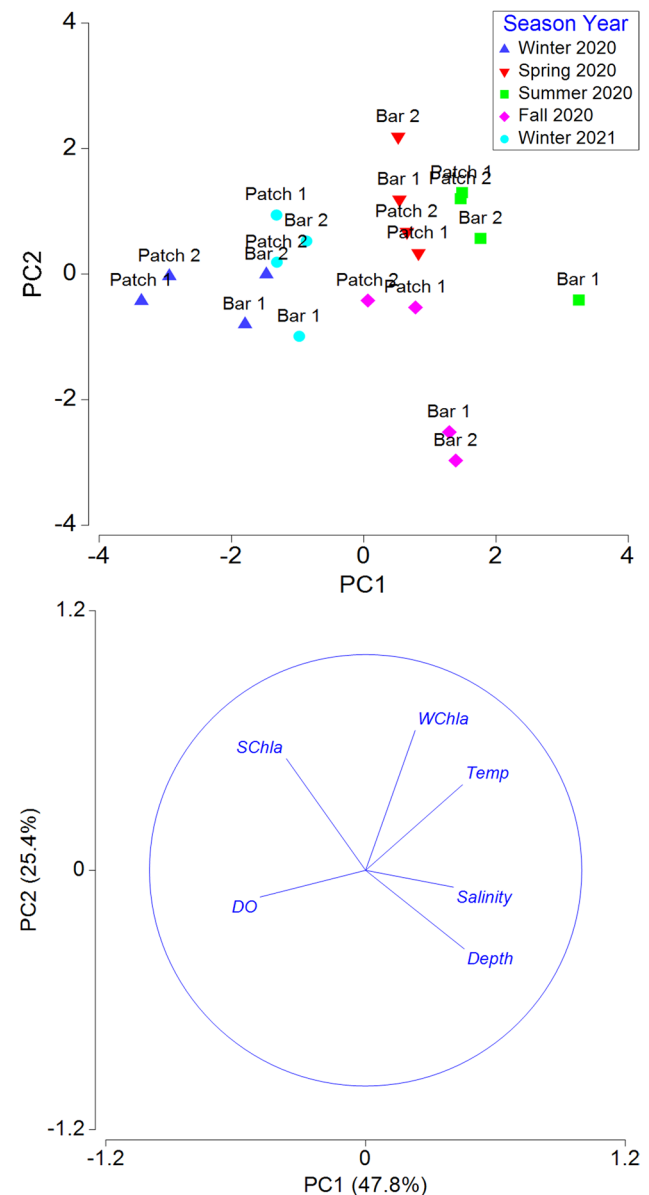


Fig. 2 Principal component analysis of water quality variables for bar and patch reefs sampled. PCA vectors include sediment chlorophyll *a* (SCHla), water chlorophyll *a* (WChla), temperature (Temp), salinity, depth, and dissolved oxygen (DO)

(92.5 ± 23.7 mm), and summer 2020 (82.1 ± 23.7 mm), but not winter 2021 (72.1 ± 25.8 mm) (Fig. 3).

Live oyster biomass differed among reefs ($p < 0.001$) and among seasons ($p = 0.009$) (Table 1). Live oyster biomass was higher at Bar 2 reef (296.4 ± 235.3 g m⁻²) than at Bar 1 (21.2 ± 25.5 g DW m⁻²), Patch 1 (44.2 ± 54.4 g m⁻²), and Patch 2 reefs (35.4 ± 31.6 g m⁻²) (Fig. 3).

Live oyster volume differed among reefs ($p < 0.001$) but not among seasons ($p = 0.09$) (Table 1). Live oyster volume was higher at Bar 2 reef (21.9 ± 14.7 L m⁻²) than at Bar 1

Table 1 Results of two-way ANOVA tests of differences in live oyster density, height, and biomass among seasons and reefs. When an interaction was present, a simple main effects test among Season-

Reef combinations was conducted. The type of transformation used is noted and *p* values < 0.05 are shown in bold

	Oyster density			Oyster height			Oyster biomass			Oyster volume		
	DF	<i>F</i> value	<i>p</i> value	DF	<i>F</i> value	<i>p</i> value	DF	<i>F</i> value	<i>p</i> value	DF	<i>F</i> value	<i>p</i> value
Season	4	3.88	0.009	4	14.15	< 0.001	4	3.9	0.009	4	2.17	0.09
Reef	3	15.32	< 0.001	3	13.07	< 0.001	3	17.54	< 0.001	3	16.04	< 0.001
Season × Reef	12	0.87	0.58	12	1.79	0.047	12	1.36	0.23	12	0.99	0.47
Season-Reef				19	6.18	< 0.001						
Transformation	Log _e			None			4th root			4th root		

(1.5 ± 2.0 L m⁻²), Patch 1 (3.4 ± 4.3 L m⁻²), and Patch 2 reefs (2.4 ± 2.1 L m⁻²) (Fig. 3). There was greater variability in live oyster density, biomass, and volume at Bar 2 reef than at all other reefs.

There were no consistent differences in dead oyster shell density among reefs or among seasons (Season × Reef interaction *p* < 0.0001) (Table 2). Dead oyster shell density was higher in summer 2020 at Bar 2 reef (2024 ± 1352 ind. m⁻²) than Patch 1 and Patch 2 in summer 2020 (173 ± 9 ind. m⁻², 239 ± 48 ind. m⁻²), fall 2020 (111 ± 60 ind. m⁻², 127 ± 91 ind. m⁻²), and winter 2021 (153 ± 85 ind. m⁻², 108 ± 63 ind.

m⁻²), respectively (Fig. 4). Dead oyster shell volume differed among reefs (*p* < 0.001) and among seasons (*p* = 0.03). Dead shell volume was smaller in fall 2020 (6.8 ± 6.2 L m⁻²) than in spring 2020 (12.0 ± 9.2 L m⁻²), summer 2020 (12.0 ± 15.3 L m⁻²), and winter 2021 (10.3 ± 11.4 L m⁻²), although no differences among seasons were detected using Tukey’s post-hoc comparisons tests.

The ratio of live:dead oyster shell density differed among reefs (*p* = 0.005) and among seasons (*p* < 0.001) (Table 2). Live:dead oyster shell density was highest at Bar 2 reef (0.3 ± 0.2) compared to Bar 1 (0.04 ± 0.06),

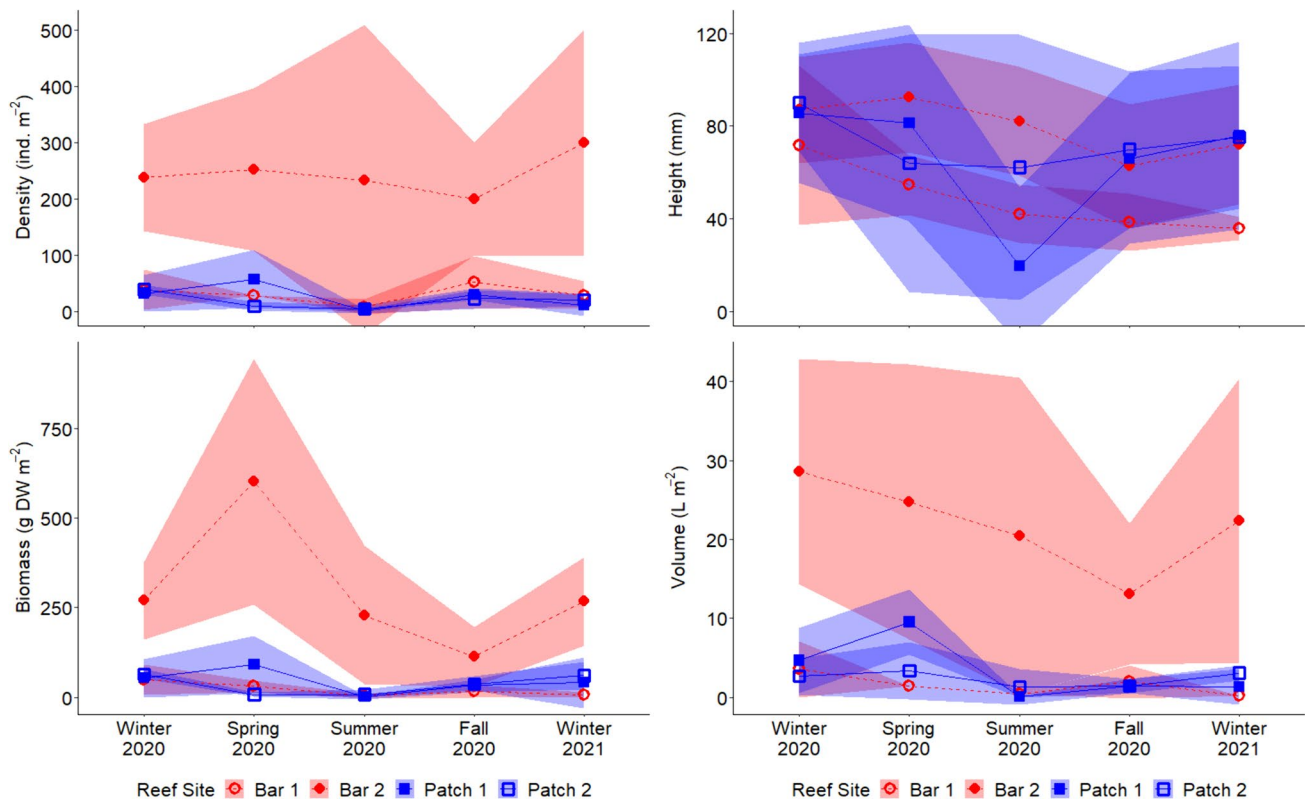


Fig. 3 Oyster density, height, biomass, and volume (mean ± standard deviations) of live oysters at bar and patch reefs in Matagorda Bay. Biomass data were estimated for winter 2020

Table 2 Results of two-way ANOVA tests of differences in dead oyster shell density and volume, and live:dead oyster shell density and volume ratios among seasons and reefs. When an interaction was pre-

sent, a simple main effects test among Season-Reef combinations was conducted. The type of transformation used is noted and *p* values < 0.05 are shown in bold

	Dead shell density			Dead shell volume			Live:dead density			Live:dead volume		
	DF	<i>F</i> value	<i>p</i> value	DF	<i>F</i> value	<i>p</i> value	DF	<i>F</i> value	<i>p</i> value	DF	<i>F</i> value	<i>p</i> value
Season	3	8.86	< 0.001	3	3.51	0.03	3	7.73	< 0.001	3	3.43	0.03
Reef	3	26.11	< 0.001	3	24.56	< 0.001	3	5.16	0.005	3	3.99	0.016
Season × Reef	9	3.06	< 0.001	9	1.93	0.08	9	1.6	0.16	9	2.23	0.046
Season-Reef	15	3.56	0.001							15	1.48	0.17
Transformation	Log _e			Log _e			4th root			4th root		

Patch 1 (0.2 ± 0.2), and Patch 2 reefs (0.2 ± 0.2) (Fig. 4). Live:dead oyster shell volume was not consistently different among reefs or among seasons (Season × Reef interaction $p < 0.046$).

The first and second principal components (PC1 and PC2) of the reef structure PCA accounted for 70.6% and 25.9% (96.4% total) of the variability within the data set (Fig. 5). Reef structure at Bar 2 was characterized by high live oyster density, biomass, and volume (high PC1 scores). Oysters on patch reefs usually had larger oyster heights (high PC2 scores).

Resident Macrofauna Characteristics

A total of 76 different reef-associated macrofaunal taxa (excluding oysters) were identified over the course of the

study (Online Resource 4). Thirty-nine and 37 taxa occurred at Bar 1 and 2 reef sites, while 48 and 53 taxa occurred at Patch 1 and 2 reef sites. The most abundant taxa at both Bar 1 and Bar 2 reefs were Amphithoidae (Amphipoda, 883 ± 915 ind. m^{-2} and 1016 ± 965 ind. m^{-2}) and Oligochaeta (548 ± 900 ind. m^{-2} and 1054 ± 1537 ind. m^{-2}). At the most abundant taxa at the Patch 1 and Patch 2 sites were Corophiidae (Amphipoda, 6246 ± 8254 ind. m^{-2} and 761 ± 686 ind. m^{-2}) and Leptocheliidae (Tanaidacea, 2243 ± 1567 ind. m^{-2} and 1237 ± 1212 ind. m^{-2}).

Macrofaunal density differed among reef sites ($p < 0.001$) and among seasons ($p = 0.001$) (Table 3). Macrofaunal density was higher at Patch 1 ($10,217 \pm 10,044$ ind. m^{-2}) than at Patch 2 (3610 ± 1705 ind. m^{-2}), Bar 1 (3015 ± 2259 ind. m^{-2}), and Bar 2 sites (4423 ± 4336 ind. m^{-2}) (Fig. 6). Macrofaunal densities were lower in fall 2020 (2186 ± 1648 ind.

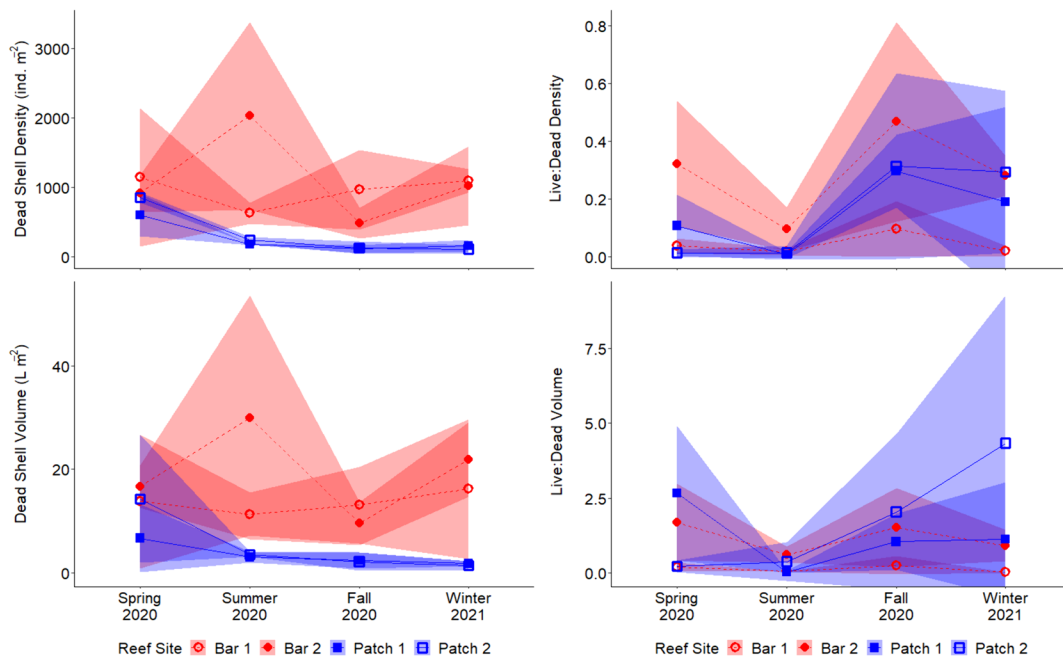


Fig. 4 Density and volume (mean ± standard deviations) of dead oyster shell and Live: Dead ratios at bar and patch reefs in Matagorda Bay. Data are unavailable for winter 2020

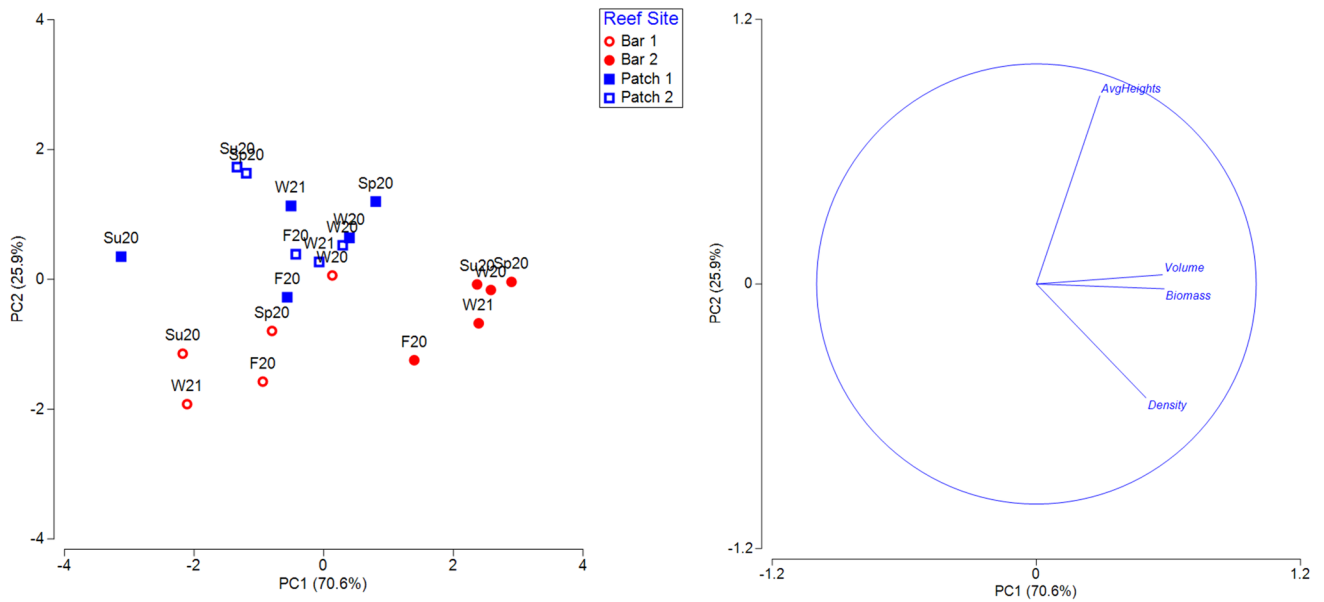


Fig. 5 Principal component analysis of live oyster characteristics for bar and patch reefs sampled in winter 2020 (W20), spring 2020 (Sp20), summer 2020 (Su20), fall 2020 (F20), and winter 2021 (W21)

m^{-2}) than in spring 2020 ($7345 \pm 7045 \text{ ind. } m^{-2}$) and summer 2020 ($7742 \pm 9543 \text{ ind. } m^{-2}$).

There were inconsistent differences in macrofaunal biomass and diversity among sites and seasons for macrofaunal

biomass and N1 diversity (both Season \times Reef interaction $p < 0.001$) (Table 3). Macrofaunal biomass was higher at Bar 2 in winter 2020 ($467.2 \pm 143.7 \text{ g } m^{-2}$) and spring 2020 ($351.0 \pm 186.1 \text{ g } m^{-2}$) than at Bar 1, Patch 1, and Patch 2 in

Fig. 6 Density, biomass and diversity of reef macrofauna (mean \pm standard deviation; excluding oysters) at bar and patch reefs in Matagorda Bay

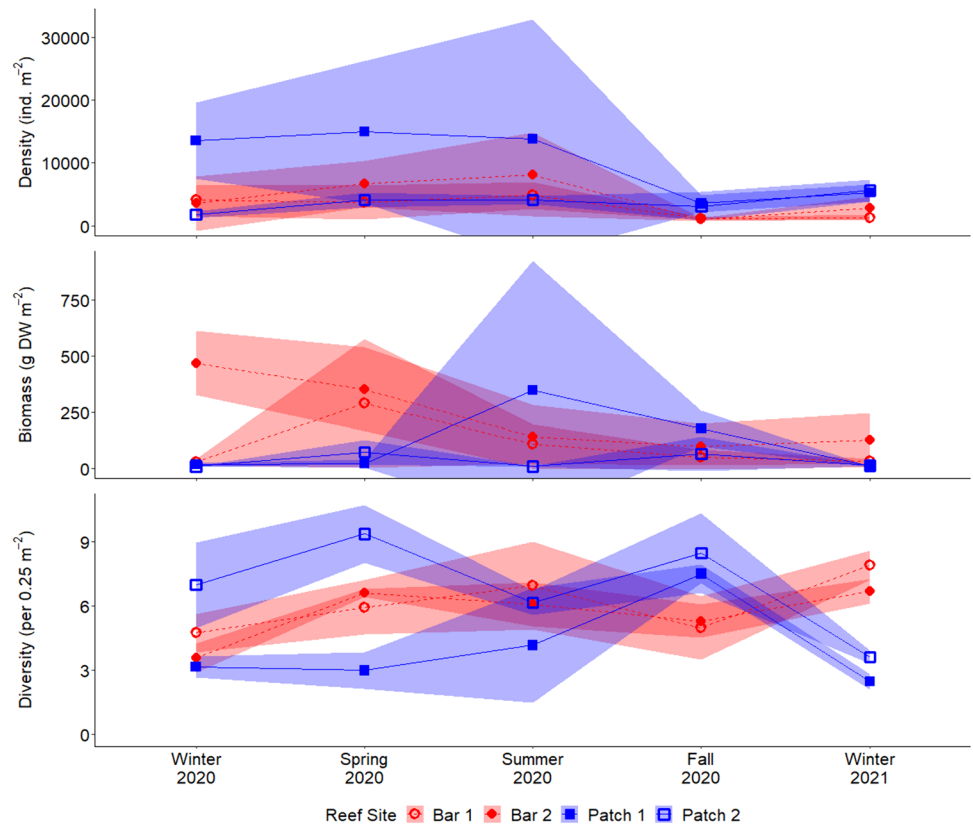


Table 3 Outputs from two-way ANOVA for differences in macrofauna density, biomass, and diversity by season, reef, and season:reef interaction. When an interaction was present, simple main effects

(season_reef) analysis was used. Type of transformation used is noted and significant values (<0.05) are shown in bold

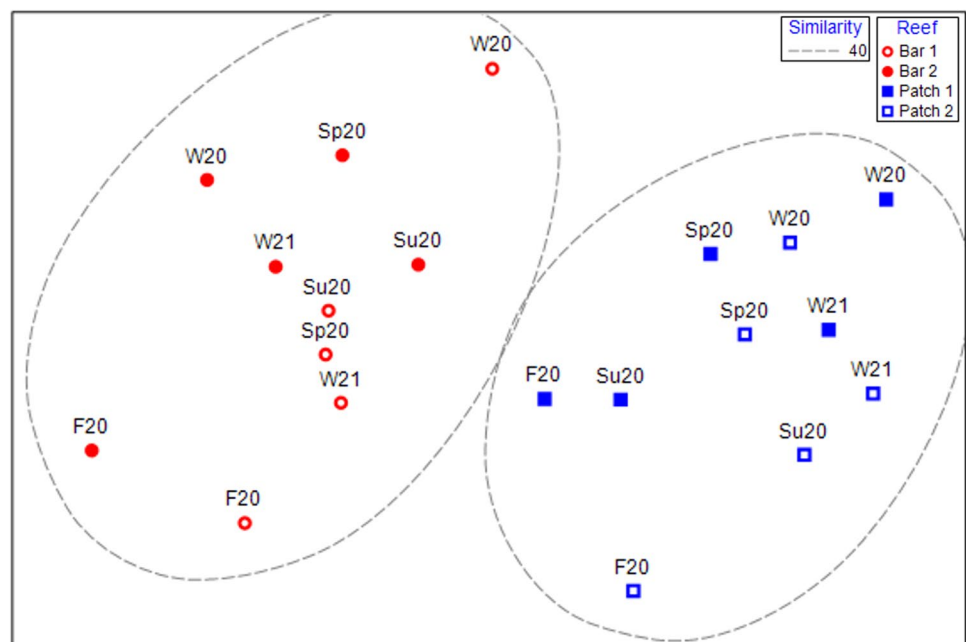
	Fauna density			Fauna biomass			Fauna diversity		
	DF	<i>F</i> value	<i>p</i> value	DF	<i>F</i> value	<i>p</i> value	DF	<i>F</i> value	<i>p</i> value
Season	4	5.51	0.001	4	2.27	0.08	4	4.62	0.004
Reef	3	6.97	<0.001	3	12.27	<0.001	3	15.64	<0.001
Season × Reef	12	1.15	0.35	12	2.33	0.02	12	6.08	<0.001
Season-Reef				19	3.89	<0.001	19	7.28	<0.001
Transformation	Log			Log			None		

winter 2020 ($28.1 \pm 14.3 \text{ g m}^{-2}$, $16.7 \pm 5.6 \text{ g m}^{-2}$, $7.9 \pm 2.1 \text{ g m}^{-2}$) and winter 2021 ($32.1 \pm 11.0 \text{ g m}^{-2}$, $8.3 \pm 1.0 \text{ g m}^{-2}$, $11.7 \pm 1.5 \text{ g m}^{-2}$), respectively (Fig. 6). Mean macrofaunal N1 diversity was $6.1 \pm 1.7 \text{ ind. } 0.25 \text{ m}^{-2}$ in Bar 1 reef samples, $5.7 \pm 1.3 \text{ ind. } 0.25 \text{ m}^{-2}$ at Bar 2, $4.1 \pm 2.2 \text{ ind. } 0.25 \text{ m}^{-2}$ at Patch 1 and $7.2 \pm 2.3 \text{ ind. } 0.25 \text{ m}^{-2}$ at Patch 2. N1 diversity at patch reefs was more variable between reefs in winter 2020 and spring 2020, while diversity at bar reefs was similar among reefs and seasons.

Panopeidae (Decapoda) dominated macrofaunal biomass at both bar (80% of total biomass, 267.5 g m^{-2}) and patch (67% of total biomass, 100.4 g m^{-2}) reefs. Biomass-based macrofaunal communities were different between bar and patch reefs; however, all site-season combinations were 59% similar within bar reefs and 60% similar within patch reefs (Fig. 7). Differences in macrofaunal community composition

between reefs were largely attributed to higher biomass of Porcellanidae (Decapoda) and Amphithoidae (Amphipoda) in bar reefs ($13.98 \pm 23.88 \text{ g m}^{-2}$, $0.90 \pm 1.06 \text{ g m}^{-2}$) than in patch reefs ($1.25 \pm 4.56 \text{ g m}^{-2}$, $0.03 \pm 0.08 \text{ g m}^{-2}$) and higher biomass of Corophiidae (Amphipoda) and Leptocheliidae (Tanaidacea) in patch reefs ($1.93 \pm 3.27 \text{ g m}^{-2}$, $0.93 \pm 0.94 \text{ g m}^{-2}$) than bar reefs ($0.08 \pm 0.218 \text{ g m}^{-2}$, $0.02 \pm 0.05 \text{ g m}^{-2}$). The structural and abiotic variables most highly correlated with macrofaunal community composition are the combinations of sediment chl *a*, water chl *a*, and dead shell volume ($r=0.430$, Online Resource 5). The single abiotic variables most highly correlated with macrofaunal community composition are sediment chl *a* ($r=0.326$), followed by dead shell volume ($r=0.177$). Sediment chl *a* and dead shell volume are both in the 10 combinations of variables that are most highly correlated with community composition.

Fig. 7 Non-metric multidimensional scaling analysis with a Bray-Curtis similarity matrix of reef macrofauna biomass data from bar and patch reefs sampled in winter 2020 (W20), spring 2020 (Sp20), summer 2020 (Su20), fall 2020 (F20), and winter 2021 (W21)



Discussion

The current understanding of differences in habitat provision for macrofauna as a function of oyster reef location within the estuarine landscape has predominantly been built from a limited set of reef types. For example, most field studies on the influence of habitat position within the estuarine landscape on macrofaunal assemblages of natural or restored oyster reefs have been conducted on intertidal reefs, or in regions dominated by intertidal reef habitats (Grabowski et al. 2005; Carroll et al. 2015; Ziegler et al. 2017; Bost et al. 2021). In this current study, we evaluated habitat provision by oysters and macrofauna on subtidal bar and patch oyster reefs. Bar reefs had higher quantities and greater variability in oyster density, biomass, and volume, as well as the amount of shell material compared to patch reefs. Macrofaunal community composition was different between reef types, with bar reefs characterized by having more motile nekton, and patch reefs being characterized by having more infauna. The presence of salt marsh and more sheltered conditions corresponded with an increased the amount of fresh organic matter (as measured by sediment Chl *a*) available to oysters and macrofauna on patch reefs. These findings indicate that the effects of reef restoration on habitat provision by oysters and macrofauna may be modified by the position in the estuarine landscape in which the reefs are restored. While this study focused only on the macrofauna of natural reefs, results indicate that it might be possible to better anticipate or even enhance habitat provision benefits of restored subtidal oyster reefs through optimized site selection within the estuarine landscape.

For oyster larvae that depend on currents to reach suitable recruitment areas, effects of reef orientation on water flow can have a substantial impact through effects on hydrodynamics and particle deposition (Lenihan 1999; Kim et al. 2010; Haase et al. 2012; Puckett et al. 2014; Colden et al. 2016). Bar reefs, including those within the eastern arm of Matagorda Bay, extend perpendicularly away from the shoreline in areas with strong currents, whereas patch reefs are located in areas with low water flow (Grave 1903; Moore 1907; Gunter 1945; Hedgepeth 1953; Kennedy and Sanford 1999). Within the eastern arm of Matagorda Bay, long-term net average circulation is in the counterclockwise direction (Opdyke et al. 2024). Physical transport of larvae via prevailing water currents may have promoted high density and biomass of live oysters on Bar 2 reef (7 to 14× greater, respectively) compared to other reefs. High densities of oysters may further influence larval settlement through changes to local currents or boundary layer flows that facilitate settlement onto the reef (Butman 1987), or by increasing chemical cues to larval conspecifics (Crisp 1967; Tamburri et al. 2008).

Proximity to marsh habitat may have influenced reef-associated macrofaunal assemblages via differences in resource subsidies (Micheli and Peterson 1999; Cloern 2007; Conway-Cranos et al. 2015). Terrestrial inputs from salt marsh can enhance the availability of organic matter (Colijn and Dijkema 1981; Dias et al. 2016) and promote secondary production in adjacent habitats (Chanton and Lewis 2002; Dias et al. 2014). Patch reefs in this study, located adjacent (< 30 m) to *Spartina alterniflora*-dominated salt marsh, were characterized by high sediment chlorophyll *a* concentrations, a proxy for fresh organic matter availability (Kromkamp et al. 2006; McTigue et al. 2015). Community composition on patch reefs was characterized by infaunal organisms, which supports previous work demonstrating the importance of sediment organic content on the distribution and abundance of infaunal organisms (Maninno and Montagna 1997; Ysebaert and Herman 2002). Oyster reef connections to nearby marshes have been shown to structure the abundance and diversity of macroinvertebrate communities on oyster reefs (Micheli and Peterson 1999; Gain et al. 2016), and may have contributed to the high densities of macrofauna on Patch reef 1. Bioturbation by infauna, including Corophiidae found in elevated numbers at patch reefs, can further promote sediment organic matter and benthic microalgal biomass (Weerman et al. 2011; Zhang and Wirtz 2017; Fleeger et al. 2022) in a positive feedback process.

Water velocities in the study area increase as they move north and east, away from the Matagorda Peninsula and into the open bay (Opdyke et al. 2024), which may have positively influenced oyster performance on bar reefs through enhanced filtration rates or changes to fine-scale bottom hydrodynamics (Lenihan 1999). For oysters, increases in initial settlement and subsequent recruitment and decreases in post-settlement mortality have been demonstrated with increasing flow rates (Powers and Grabowski 2023). Perpendicular bar reefs can create conditions that facilitate reef sustainability and oyster performance through increased water flows and enhanced resuspension of reef-deposited sediments (Colden et al. 2016). Although not directly measured in this study, higher waves and current speeds have been measured on windward oyster reefs in nearby estuaries (Lunt et al. 2017). It is notable that oyster density and biomass at Bar 1 reef were not consistently high, as observed at Bar 2 reef, instead being more similar to oyster populations on Patch reefs 1 and 2. Although the direct mechanism for this difference is unknown and warrants additional work, it is plausible that the location of Bar 1 reef—directly adjacent to the channelized outflow from the Gulf Intracoastal Waterway and the Colorado River—produces a different hydrodynamic regime with resulting effects on larval dispersal, retention, and population connectivity (McIntyre et al. 2021).

Water flow may have also contributed to differences in macrofaunal community composition between reef types. Panopeidae and Porcellanidae crabs—dominant on bar reefs—both have a planktonic larval phase with limited swimming capability; physical transport depends upon resuspension and advection through wind-wave action (Garrison 1999; Roman and Boicourt 1999), with higher wind and water velocities aiding in recruitment (Nowell and Jumars 1984). Older life stages of Panopeidae and Porcellanidae that utilize omnivorous and suspension feeding modes may also benefit from reduced energetic costs of foraging facilitated by higher water flow and greater mixing (Trager and Genin 1993). In contrast, sediment deposition is generally higher at oyster reefs experiencing lower flow velocities (Lenihan 1999), including reefs adjacent to salt marsh (Bost et al. 2021), facilitating development of the soft-sediment infaunal communities dominant on patch reefs. Life history traits of many infaunal organisms, e.g., reduced planktonic larval stages, smaller brood size, and higher brood protection (Thrush and Whitlatch 2001; Grantham et al. 2003), help promote small-scale dispersal (Wetzer et al. 1997; Lundquist et al. 2006; Cole et al. 2007) and make these organisms less reliant on hydrodynamics.

Shell material is a critical component of oyster population expansion and reef growth (Waldbusser et al. 2013). Shell volume is naturally added through oyster mortality on the reef, which maintains reef structure (Powell and Klinck 2007). In a positive feedback process, an increase in shell volume encourages settlement of calcifying organisms, whose eventual death increases the rate of shell addition (Kidwell and Jablonski 1983; Solinger et al. 2022). Dead shell density and volume in the current study were consistently high on bar reefs compared to patch reefs. For Bar reef 2, having additional substrate in the form of dead shells may have helped enhance oyster recruitment and encourage population expansion (Mann and Powell 2007; Walles et al. 2015). Although the amount of shell material on Bar reef 1 was also high, a similar enhancement of the oyster population was not observed and warrants additional study. Patch reefs 1 and 2 did not have extensive shell deposits and consisted of scattered patches of clustered oysters lying on soft-mud, similar to previous descriptions of reefs in the Matagorda Bay system (Moore 1907).

Accumulation of shell material on oyster reefs also provides important habitat and foraging grounds for estuarine species (Lehnert and Allen 2002; Shervette and Gelwick 2008) and may have contributed to differences in macrofauna community composition. On bar reefs, where shell material was greatest, the dominant taxa were Panopeidae and Porcellanidae crabs that depend on oyster shell substrates for shelter and refugia (Tolley and Volety 2005; Nevins et al. 2014; George et al. 2015). In contrast, patch reef macrofauna were dominated by infauna that may have benefitted from

lower oyster densities and shell volumes that can yield larger interstitial spaces (O’Beirn et al. 2000) and promote accumulation of soft sediments and organic matter (Castel et al. 1989; Blomberg et al. 2017; Rezek et al. 2017). Macrofauna in Patch 1 reef samples had high densities of Corophiidae, a small amphipod crustacean found in high densities in soft-sediment habitats (Meadows and Reid 1966; Fleeger et al. 2022). Access to soft sediment has been shown to augment survival of errant polychaetes and tanaids—both observed at higher densities in patch reefs—via enhanced feeding and predator refugia (Kneib 1992; Lejart and Hily 2011).

Anthropogenic disturbances were not explicitly measured in this study, yet it is possible that differences exist between reef types that may have contributed to high variability among oyster populations. Although none of the sampling areas in this study were subject to commercial harvest, commercial harvest in Texas is allowed on oyster reefs located > 91 m from shore (*31 Tex. Admin. Code § 58.21* 1996), meaning that portions of bar reefs are accessible for harvest while patch reefs are protected. Resuspension of sediments from nearby dredging, a gear designed to dislodge and excavate invertebrates from the bay bottom, can limit oyster recruitment (Benefield 1976; Powers et al. 2009), and may have contributed to the variability in oyster densities among bar reefs. Spatial differences in boating activity may have also contributed to the observed differences in oyster densities among and between reefs. Because water depths adjacent to bar reefs are deeper (> 1 m) than those near patch reefs (~0.3 m), any effects of boating activity are likely higher on bar reefs. For Bar reef 1, small vessel traffic may be higher due to its location directly adjacent to a cut in the land that allows connection to the Gulf Intracoastal Waterway. Vessel-generated waves disturb and displace sediments, erode shorelines, and increase suspended sediment concentrations (Parnell and Kofoed-Hansen 2001; Houser 2010). Physical disturbances from boat wakes have been shown to disrupt oyster settlement and negatively impact reef growth (Grizzle et al. 2002; Bilkovic et al. 2019), and cause increases in disarticulated oyster shells (Grizzle et al. 2002; Wall et al. 2005), with the latter observed anecdotally on (unsampled) bar reef crests in the current study. On intertidal oyster reefs in Florida, effects of boating activity resulted in half as many shell clusters, a quarter of the number of live oysters, and significantly lower structural complexity compared to reference reefs (Stiner and Walters 2008). In manipulative wave tank experiments, waves as small as 2 cm were able to move individuals and small clusters of oysters and cause measurable increases in sediment erosion (Campbell 2015). Additional research is warranted to understand spatial gradients in disturbance that may have direct or indirect effects on subtidal oyster reefs.

Despite differences in structural characteristics and position within the estuarine landscape, subtidal oyster reefs are

often considered one habitat and managed as such. Our results demonstrate that differences in habitat provision for oysters and macrofauna exist on reefs that differ by position within the estuarine landscape. Findings can be used to efficiently reach conservation and restoration goals by strategically siting reef restoration projects and conservation areas, as well as improve predictions of habitat provision resulting from reefs at different positions in the estuarine landscape. Additional research is warranted to further elucidate the physical and biological influences structuring oyster populations and macrofaunal communities on subtidal reefs.

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Declarations

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