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Title: Edge effects influence the composition and density of reef residents on subtidal restored oyster reefs

Running Head: Edge effects on restored oyster reefs

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Author Contributions

TMD, JHG, ARH conceived the research questions and designed the study; TMD gathered data and performed analyses; TMD, JHG, ARH led the writing of this manuscript; all authors contributed critically to the drafts and gave final approval for publication.

Abstract

Within estuarine and coastal ecosystems globally, extensive habitat degradation and loss threaten critical ecosystem functions and necessitate widescale restoration efforts. There is abundant evidence that ecological processes and species interactions can vary with habitat characteristics, which has important implications for the design and implementation of restoration efforts aimed at enhancing specific ecosystem functions and services. We conducted an experiment examining how habitat characteristics (presence; edge vs. interior) influence the

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communities of resident fish and mobile invertebrates on restored oyster (*Crassostrea virginica*) reefs. Similar to previous studies, we found that restored reefs altered community composition and augmented total abundance and biomass relative to unstructured sand habitat. Community composition and biomass also differed between the edge and interior of individual reefs as a result of species-specific patterns over small spatial scales. These patterns were only weakly linked to oyster density, suggesting that other factors that vary between edge and interior (e.g., predator access or species interactions) are likely more important for community structure on oyster reefs. Fine-scale information on resident species' use of oyster reefs will help facilitate restoration by allowing decision makers to optimize the amount of edge vs. interior habitat. To improve the prediction of faunal use and benefits from habitat restoration, we recommend investigations into the mechanisms shaping edge and interior preferences on oyster reefs.

Keywords

community composition, edge effects, habitat restoration, habitat structure, landscape, oyster reef, Crassostrea virginica

Implications for Practice

- Restoration to enhance biodiversity should incorporate how the edges and interiors of habitats differ since many species vary in abundance across these zones.
- Given mounting evidence for edge effects on biodiversity, ecosystem functions, and associated services, within-patch variation should be considered in coastal habitat restoration research and practice more generally.

Main text

Introduction

Biogenic habitats such as forests, grasslands, mangroves, seagrasses, and reefs are inhabited by a wide variety of resident organisms (Robinson & Holmes 1982; Morris 2000; Beck et al. 2001). These habitats provide substrate for settlement, decrease predation rates, and promote growth of resident species (Rausher 1979; Hixon 1998; Knutson et al. 2006). Thus, biogenic habitats are important to the life cycles of many species and are critical to maintain biodiversity (Ward et al. 1999; Beck et al. 2001; Wintle et al. 2019).

Human populations continue to grow and modify ecosystems globally, leading to habitat degradation and loss (i.e., reduced aerial extent and complexity of biogenic habitats) and threatening the critical ecosystem functions they provide (Halpern et al. 2015; Waycott et al. 2009; zu Ermgassen et al. 2013). To combat these impacts, restore ecosystem functions, and recover lost ecosystem services, calls for restoring biogenic habitats are increasing (Peterson & Lipcius 2003; Rey Benayas et al. 2009; Suding 2011). Habitats are often restored as patches within a matrix of distinct habitats. Naturally, these habitat patches are not uniform in their characteristics or distribution, and habitat heterogeneity can have profound influences on ecological processes and ecosystem functioning such as vegetation growth, mortality and reproductive rates (Chen et al. 1992), soil formation (Vasconcelos & Luizão 2004), and seed dispersal (Vespa et al. 2014).

One key source of habitat heterogeneity is the differentiation in biological and physical properties (e.g., light availability, nutrient flux, herbivory, and propagule dispersal) among the edge vs. interior of habitat patches, known as edge effects (Murcia 1995; Cadenasso et al. 2003; Ries et al. 2004). Patterns and processes shaping edge effects have been well studied in terrestrial systems, and there are an increasing number of studies demonstrating their importance in coastal

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and estuarine habitats (Tanner 2005; Connolly & Hindell 2006; Boström et al. 2011). Several mechanisms have the potential to create variation in the densities of species associated with edges vs. interiors of estuarine biogenic habitats (Fagan et al. 1999; Ries et al. 2004). For example, the distributions of many organisms are positively correlated with the availability of their resources, which can vary within patches, e.g., pipefish densities follow that of their major prey, small crustaceans, which are denser at seagrass patch edges (Macreadie et al. 2010). Abundances of species that use multiple habitats, such as blue crabs that shelter in seagrass but forage in adjacent mud bottom (Summerson & Peterson 1984), may also differ between habitat edges vs. interiors. Species interactions, such as competition for space or avoidance of a predator, can also mediate habitat partitioning; for example, Meyer (1994) demonstrated habitat partitioning by two species of xanthid crabs on intertidal oyster reefs, most likely to reduce competition. While edge effects occur in a variety of estuarine habitats, few studies have investigated within-patch variation in oyster reef community structure and individual species densities (but see Hanke et al. 2017).

Restoration of subtidal oyster (*Crassostrea virginica*) reefs provides habitat for resident and transient organisms (Lehnert & Allen 2002; Plunket & La Peyre 2005; Shervette & Gelwick 2008); yet, it remains unclear whether there are differences in organism densities from the edge to the interior of subtidal reefs. Because the size and shape of restored reefs remain largely consistent through time, even as other reef characteristics (e.g., structural complexity, vertical relief) vary over time following restoration (Quan et al. 2012; La Peyre et al. 2014; Rodriguez et al. 2014), edge effects could have sustained influence on oyster reef community structure. Thus, understanding edge vs. interior patterns of faunal use will improve our understanding of how patches contribute to ecosystem functions, and as a result, facilitate decision makers ability to

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enhance ecosystem service delivery from future conservation and restoration efforts. To examine the influence of reef presence and edge effects on subtidal restored oyster reef-associated communities, we partnered with the Rhode Island Division of Marine Fisheries and The Nature Conservancy in Rhode Island to examine a set of restored subtidal oyster reefs of the same size and shape in Quonochontaug Pond, RI. We asked the following research questions: 1) How has oyster reef restoration influenced reef resident species densities and biodiversity? 2) How do the densities of reef resident species and biodiversity in general differ between the edge vs. interior of oyster reefs?

Methods

Site selection

Historically, extensive oyster (*Crassostrea virginica*) reefs supported a valuable fishery in Rhode Island that peaked in Narragansett Bay around 1822 (Kirby 2004), though overfishing prompted gear restrictions as early as 1766 (Rice 2006). Over the past two decades, oyster reefs have been the focus of restoration efforts in several of the coastal ponds in southwestern Rhode Island (Rhode Island Shellfish Initiative 2017; Griffin 2016). Quonochontaug Pond, the focal area for this study, is shallow (average depth ~ 6 feet, maximum depth ~ 12 feet; Town of Charlestown, Rhode Island 2018), euhaline (~ 31 PSU; Table S1), and is connected to the Atlantic Ocean via a single breachway first constructed in the early 1900s and deepened and widened for continuous connection in the 1950s. Quonochontaug Pond has been the focus of restoration efforts since 2006 (Griffin 2016).

We conducted this study on oyster reefs restored in Quonochontaug Pond in May 2017 (Fig. 1). Nine reefs were constructed with 10.2 m³ each of steam-shucked Atlantic surf clam

Spisula solidissima) and oyster shell that was exposed to the sun for at least 6 months prior to use in restoration. Restored reefs were ~22 m² in area, ~5.3 m in diameter, 0.5 – 0.8 m in height, and they remain submerged by at least 0.3 m at mean low water. Within one week of construction, reefs were seeded with a veneer of remote-set oyster spat on shell (clean shell with settled larvae that were set and raised in a hatchery) from parent oysters sourced from either a local commercial hatchery or natural reefs in one of two local tributaries to Narragansett Bay. Restored reefs were arranged in a blocked experimental design, with three reefs and a control plot in each block, randomly arranged at equal distances from the shoreline (Fig. 1). Control plots were designated on soft sediment (mud or sand) at least 40 m from a reef (Fig. 1). Block 1, on the southwestern side of Quonochontaug Pond, is characterized by fine muddy sediment, whereas blocks 2 and 3 are located in the northeastern corner of Quonochontaug Pond on sandy sediment and near frequent large boulders (Block 3). By the time of sampling in July 2018, the oyster shell from the top of most reefs had shifted towards the edges of the reef; as a result, reef centers consisted of surf clam shell with low oyster densities, whereas reef edges had high oyster densities (Fig. S1).

Reef depth and relief were measured by divers, and salinity (PSU) was quantified during each sampling period (Table S1). Bottom water temperatures were measured during deployment using one Onset Tidbit v2 HOB0 temperature logger per block in summer 2018 and one logger at both the edge and interior of 3 reefs (one per block) in fall 2018 (Fig. S2).

Sampling fish and invertebrate communities

To compare reef-associated community colonization among oyster reef and sand habitats, we deployed experimental sampling trays assigned to four experimental treatments. Sampling

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trays (plastic bakery trays, 0.66 m L x 0.56 m W x 0.14 m H) were lined with fiberglass window screen (1-mm mesh opening). For the reef edge, reef interior, and shell treatments, trays were filled with five gallons of clean, articulated oyster shell from a shell recycling program run by The Nature Conservancy. For the sand treatment, the sampling trays were lined as before but filled with ten gallons of locally-sourced sand that was sieved to remove live organisms. Reef edge treatments of a single tray filled with shell were placed abutting each reef at a position randomized by cardinal direction (Fig. S3). Reef interior treatments of a single tray filled with shell were placed at the innermost point on each reef (Fig. S3). Shell and sand treatments of a single tray filled with shell or sand, respectively, were placed in each control plot (Fig. S3). Trays were deployed by divers on SCUBA on July 10, 2018 (summer) and September 7, 2018 (fall) and were leveled with surrounding substrate by carefully excavating the surrounding reef material (interior treatment) or sediment (edge, shell, and sand treatments).

After 28 - 29 days, divers collected the trays by carefully lifting them off the substrate and noting any organisms that escaped during retrieval. Divers brought the trays to the boat where fish were removed and euthanized in a eugenol/seawater solution before they were bagged and placed in coolers. All remaining tray contents were placed in separate 3-mm mesh bags, stored in coolers, and returned to the lab for processing. Tray contents were rinsed and sieved at the lab, and all individuals were removed by hand and stored in 10% isopropyl alcohol. Individuals were enumerated and identified to the lowest possible taxonomic group, measured, and weighed (wet weight in grams) in the lab (See Supplement S1 for additional details). Trays were rinsed and allowed to dry fully between deployments. Two trays were upturned during the fall deployment (block 1 reef interior; block 3 reef interior), leading to 24 trays sampled in summer and 22 trays in fall.

To quantify the observed pattern of higher oyster density around the edges of reefs, we surveyed oyster density and reef relief the following spring (May 2019). Divers haphazardly placed 0.25 m² quadrats on each oyster reef and excavated all live and recently dead oysters (N = 3-5 quadrats per reef on each of edge and interior). Live and recently dead oysters were counted, and shell heights measured to the nearest 1 mm in the field before returning them to the reef in the same location where they were collected. Top valves were removed from recently dead oysters (open oysters with both valves present, but no live tissue) to confirm dead before replacing. Divers also measured water depth with a meter stick at each quadrat, at the highest point on each reef, and at unstructured bottom adjacent to each reef. Reef relief and quadrat relief were calculated by subtracting water depth at each quadrat (quadrat relief) or the highest point on the reef (reef relief) from water depth on adjacent unstructured bottom.

Data Analysis

Community colonization of oyster reef vs. sand habitats

We first assessed how the species composition of communities colonizing the trays varied across oyster reef and sand habitats by comparing three experimental treatments: reef interior, sand control, and shell control (Table S2). The reef interior treatment was used in the reef-control contrast. To detect differences in community composition by treatment and season, we performed permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis dissimilarity calculated from square root transformed species densities. Experimental treatment (reef interior, sand control or shell control), season (summer or fall), the interaction between season and treatment, and experimental block were included as fixed effect predictor variables. If treatment effects (but not interactions) were significant ($P < 0.05$), we performed

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further PERMANOVAs of independent planned contrasts among reef interior and the sand or shell control treatments. We adjusted p-values for these non-orthogonal contrasts using a sequential Bonferroni correction (Holm 1979). After each PERMANOVA, we performed a permutation test to assess the assumption of equal multivariate dispersion among treatment types and noted where this permutation test was significant ($P < 0.05$). Relationships between community composition and experimental treatments, seasons, and/or experimental blocks were visualized using non-metric multidimensional scaling (nMDS). We then performed a similarity percentages (SIMPER) analysis to determine which variables (species) contributed the most to differences in community composition among the treatments. All analyses were conducted in R (version 3.6.1; R Core Team 2019). Multivariate analyses were conducted using the vegan package (version 2.5-6; Oksanen et al. 2019).

To determine how whole communities and individual species differed across treatments and seasons, we examined the total density and biomass per tray, and the density of the most abundant species (≥ 25 individuals total). We performed linear mixed effect model analyses on each of these response variables by treatment and season. Our predictor variables were experimental treatment (reef interior, sand control, or shell control), season (summer or fall), and the interaction between season and treatment as fixed effects, and experimental block as a random intercept. When mixed models converged on a singular fit due to a near-zero variance estimate for the random effect of block, we ran a general linear model with the same predictor variables, but experimental block as a fixed effect. When the treatment and season interaction was significant, we performed planned contrasts between reef interior and either control treatment (sand or shell) separately for each season and adjusted p-values from these non-orthogonal contrasts using a sequential Bonferroni correction (Holm 1979). When treatment

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effects were significant but not the interaction between treatment and season, we performed planned contrasts to determine which controls (sand or shell) differed from reef interiors. Shapiro-Wilk tests were performed on the residuals for normality, and visually inspected them for potential violations of homoscedasticity. When necessary, we transformed the response variables to satisfy these assumptions and did not conduct analyses for response variables when both untransformed and transformed data violated these assumptions. We performed all linear mixed model analysis in R using the lme4 package (Bates et al. 2015).

For those species represented by ≥ 10 individuals per tray and with non-zero densities at all habitats and seasons, we examined how body size differed across reef interior, sand, and shell experimental treatments. For each of these species, we conducted linear mixed effect model analyses to assess the effects of experimental treatment, season, and the interaction between treatment and season as fixed predictor variables on organism size with tray nested within block as a random variable. Mixed models with a singular fit due to a near-zero variance estimate for the random effect of block were replaced with fixed effect models as above.

Reef-associated community colonization of reef edges vs. interiors

To assess how reef treatment (i.e., edge vs. interior) affects colonization on reef habitats (Table S2), we first examined the relationships between community composition, experimental treatment, and season. We performed PERMANOVA as above, though with reef edge or interior experimental treatments. The relationships were visualized with nMDS, and SIMPER analysis was conducted as above with reef interior and edge as the experimental treatments.

We also examined how whole communities and individual species differed across reef treatments (edge and interior) and seasons using linear mixed effect models as above, with total density, biomass, and species richness per tray, and the density of the most abundant species (\geq

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25 individuals) as response variables. When the edge and interior treatments differed, we used linear mixed effects models to examine the potential role of oyster density and reef depth as drivers of differences in density or biomass. Oyster cluster production has been used as a proxy for structural complexity and potential refuge availability (Meyer and Townsend 2000), and reef depth / tidal elevation can drive community structure on oyster reefs (Menendez 1987) and in soft sediment communities (Peterson 1991). Because all reefs were constructed with the same volume of dead shell, we used living oyster density as a metric for habitat quality. Linear mixed effect models examined the influence of oyster density (as orthogonal linear and quadratic terms) and reef depth at the base as fixed effects and experimental block as a random effect on the density, biomass and richness of reef-associated species on oyster reefs (edge and interior treatments). Mixed models with a singular fit due to a near-zero variance estimate for the random effect of block were replaced with fixed effect models as above. For response variables with significant interactions between treatment and season, we modeled seasons separately. When there was a relationship between oyster density and species densities, we examined the t-tests for each coefficient to determine whether linear or quadratic slopes were significantly different from zero. We were unable to include treatment as a predictor variable in these regression models because oyster density and reef depth did not overlap across treatments (i.e., oyster density was consistently lower and reef relief was higher at reef interiors than edges; Fig. S1). In addition, we did not include season as a predictor, as oyster densities were quantified across reef edges and interiors once (in May 2019). Finally, we did not include quadrat relief in the models, because it was correlated with oyster density (Fig. S1).

Finally, we examined whether there were differences in the size of individuals of each species between reef edges and interiors. We examined if the size of species with ≥ 25

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individuals total and with non-zero densities in all habitats and seasons differed across reef interior and edge treatments. We used linear mixed effect models with experimental treatment (reef edge or interior), season (summer or fall), and the interaction between season and treatment as fixed effects, and sampling tray nested within block as a random intercept. Where sizes differed across reef edge and interior treatments, we examined the potential role of oyster density and reef depth as drivers of these differences using linear mixed effects models. These models contained oyster density (as orthogonal linear and quadratic terms) and reef depth at the base as fixed effects and tray nested within block as the random effect. Where oyster density effects on body size were significant, we examined the t-tests for each coefficient to determine whether linear or quadratic slopes were significantly different from zero.

Results

We collected a total of 4,597 individuals (including 4,052 decapod crustaceans and 349 fishes) representing thirty-five species. Eight of these species were represented by at least 25 individuals total (Table S3).

Community colonization of oyster reef vs. sand habitats

Twenty-six species colonized reef interior, sand and/or shell treatments (Table S3). SIMPER analysis identified five species that contributed to 76% of the differences among the reef interior and sand treatments, and to 72% of the differences between reef interior and shell treatments (Table S4). The centroid of community composition for reefs (teal) was closer to that for shell treatments (gray) than sand (tan) (Fig. 2), whereas variability (shown as the size of the 95% confidence interval) was higher in sand treatments, with eight species only found there (Table S3).

Community composition was different among treatments (reef interior, sand, and shell) ($F_{2,20} = 13.42$, $p = 0.0001$; Fig. 2; Table S5), but treatments were overdispersed ($F_{2,25} = 14.93$, $p = 0.001$; Fig. S4). Community composition also differed among blocks ($F_{2,20} = 4.27$, $p < 0.001$; Fig. 2; Table S5). Planned contrasts showed different community composition between reef interior and shell ($F_{1,16} = 3.71$, $p = 0.02$; Table S5) and reef interior and sand ($F_{1,16} = 23.72$, $p = 0.0002$; Table S5), though reef interior and sand treatments were overdispersed ($F_{1,20} = 36.61$, $p = 0.001$).

Total density of organisms colonizing the trays was higher at interior than sand treatments (Treatment $F_{2,20} = 77.47$, $p < 0.0001$; Season $F_{1,20} = 7.62$, $p = 0.01$; Table S6; mean difference \pm SE of Sand – Interior = -0.71 ± 0.10 , $Z = -7.17$, $p < 0.001$, Fig. 3a), and lower in fall (Fig. S5). Interior reef trays had higher biomass than sand trays (Treatment $F_{2,20} = 77.47$, $p < 0.0001$; Season $F_{1,20} = 7.62$, $p = 0.01$; Table S6; Sand - Interior = -3.50 ± 1.04 , $Z = -3.38$, $p = 0.001$; Fig. 3b), whereas shell trays had higher biomass than interior trays (Shell - Interior 2.43 ± 1.04 ; $Z = 2.34$, $p = 0.02$; Fig. 3b), and biomass was higher in fall than summer (Fig. S5).

One of few species present at all three experimental treatments was *Dyspanopeus sayi* (Say's mud crab), with higher densities at reef interior than sand treatments (Treatment $F_{2,20} = 94.10$, $p < 0.0001$; Sand – Interior = -1.16 ± 0.13 , $Z = -8.94$, $p < 0.0001$, Fig. 4a, Table S7). *Eurypanopeus depressus* (flatback mud crab) was present at reef interiors but absent at sand treatments (Treatment $F_{2,20} = 9.82$, $p = 0.004$; Sand – Interior = -9.04 ± 0.30 , $Z = -3.03$, $p = 0.005$; Shell – Interior = -9.04 ± 0.30 , $Z = -3.03$, $p = 0.005$; Fig. 4b). *Palaemonetes vulgaris* (grass shrimp) densities were higher at reef interior than both sand and shell treatments (Treatment $F_2 = 6.06$, $p = 0.009$; Sand – Interior -5.64 ± 0.22 , $Z = -2.62$, $p = 0.03$; Shell – Interior = -5.64 ± 0.22 , $Z = -2.68$, $p = 0.03$, Fig 4c). Densities of *Opsanus tau* (oyster toadfish) differed

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across treatments ($F_{2,20} = 7.01$, $p = 0.005$; Fig. 4d), though interior densities did not differ from either control (Fig. 4d). There were more oyster toadfish in fall (Season $F_{1,20} = 5.35$, $p = 0.03$; Fig. S6, Table S7). *Gobiosoma ginsburgi* (seaboard goby) densities differed among treatments and seasons (Treatment x Season $F_2 = 3.70$, $p = 0.04$; Fig. 4e; Table S7), with higher densities at interior than sand treatments in both summer (Sand – Interior = -0.84 ± 0.19 , $Z = -4.42$, $p = 0.004$; Fig. 4e) and fall (Sand – Interior = -0.66 ± 0.20 , $Z = -3.36$, $p = 0.03$; Fig. 4e).

Say's mud crabs ($F_{2,22} = 9.29$, $p = 0.001$; Table S8) were smaller at sand compared to reef interiors in summer (Sand – Interior = -0.91 ± 0.13 , $Z = -6.76$, $p = 0.004$, Fig. S8). Low densities in some treatments precluded analysis of organism sizes for all other species (Table S3).

Reef-associated community colonization of reef edges vs. interiors

Twenty-six species colonized edge and/or interior reef treatments (Table S3). Five species contributed 70% of the differences between the reef interior and edge treatments (Table S9). The 95% confidence intervals around the centroids for community composition overlap across reef edge and interior treatments in summer and fall, while confidence intervals for interior trays were smaller than at edges, indicating more variation in community structure at reef edges (Fig. 5). Community composition tended to differ among combinations of treatment and season with a marginally significant ($0.05 \leq p < 0.1$) interaction (Treatment x Season $F_{1,28} = 2.25$, $p = 0.07$; Fig. 5; Table S10), and community composition varied by block ($F_{2,28} = 10.37$, $p < 0.001$; Table S10). Blocks were over-dispersed ($F_{2,31} = 6.34$, $p = 0.009$; Fig. S9), whereas habitat and season were not.

The total density of organisms colonizing the trays differed among combinations of treatment and season with a marginal ($0.05 \leq p < 0.1$) interaction (Treatment x Season $F_{1,28} =$

3.45, $p = 0.07$; Fig. 6a; Table S11). Mean density decreased from summer to fall at reef interiors but did not differ between summer and fall at reef edges (Fig. 6a). Mean biomass was higher at reef edges than interiors (Treatment $F_{1,28} = 4.71$, $p = 0.04$; Table S11, Fig. 6b), and higher in fall than summer ($F_{1,28} = 27.6$, $p < 0.0001$; Table S11, Fig. 6b). Species richness did not differ across treatments, seasons, or their interaction (Table S11). Total density in summer decreased with reef depth at the base ($F_1 = 6.88$, $p = 0.02$, Table S12, Fig. S10).

Densities of several species varied across reef treatments (Fig. 7; Table S13). Flatback mud crabs ($F_{1,28} = 14.73$, $p < 0.001$; Fig. 7a, Table S13) and grass shrimp ($F_{1,28} = 9.71$, $p = 0.004$; Fig. 7c, Table S13) had higher densities at reef interiors. Say's mud crabs had higher densities at reef edges in fall, but not summer (Treatment x Season $F_{1,28} = 7.49$; $p = 0.01$, Fig. 7b). Seaboard goby densities different among treatment and season with a marginally significant interaction ($0.05 \leq p < 0.1$); there was a trend toward higher densities at reef interiors than edges in the summer, and lower at reef interiors than edges in the fall (Treatment x Season $F_{1,28} = 3.94$, $p = 0.06$; Fig. 7d, Table S13). *Alitta succinea* (clam worm) densities were higher at reef edges ($F_{1,28} = 11.54$, $p = 0.002$; Fig. 7e, Table S13) and in summer ($F_{1,28} = 4.62$, $p = 0.05$; Fig. S11, Table S13). Oyster toadfish densities were higher in the fall than summer ($F_{1,28} = 5.95$, $p = 0.02$; Fig. S11, Table S13).

Densities of flatback mud crabs ($F_{2,28} = 6.17$, $p = 0.006$, $R^2 = 0.12$, Fig. S13a, Table S14) and grass shrimp ($F_2 = 4.13$, $p = 0.03$, $R^2 = 0.15$; Fig. S13b, Table S14) decreased as oyster density increased. In summer, seaboard goby densities were lowest at intermediate oyster densities, ($F_2 = 11.74$, $p = 0.001$, $R^2 = 0.02$; Fig. S13, Table S14). The density of clam worms increased with oyster density ($F_{2,29} = 4.49$, $p = 0.02$, $R^2 = 0.09$; Fig. S13). The densities of flatback mud crabs ($F_{1,29} = 4.39$, $p = 0.04$, $R^2 = 0.05$) and grass shrimp ($F_1 = 4.40$, $p = 0.05$, $R^2 =$

0.10) decreased with reef depth (Fig. S14, Table S14). The total variation explained by these relationships was low ($R^2 \leq 0.15$).

Flatback mud crabs were larger in the interior than the edge (Habitat: $F_{1,15} = 7.74$ $p = 0.01$; Season: $F_{1,16} = 18.59$, $p < 0.001$, Fig. *a, Fig. 8a, Table S15), whereas naked gobies were larger at the edge than the interior ($F_{1,22} = 17.54$, $p < 0.001$; Fig. 8b). Sizes of flatback mud crabs ($F_{1,16} = 18.59$, $p < 0.001$), naked gobies ($F_{1,22} = 5.01$, $p = 0.04$), seaboard gobies ($F_{1,176} = 89.33$, $p < 0.0001$), and Say's mud crabs ($F_{1,26} = 95.65$, $p < 0.001$) were all larger in the fall than the summer (Fig. S15, Table S15). None of the observed differences in body size between the edge and interior were significantly correlated with oyster density or reef depth at the base (Table S16).

Discussion

Our analyses confirmed that both structural complexity (reef vs sand) and the surrounding landscape (reef vs shell) influence reef-associated communities, and they suggest these influences differ in their relative importance. With eight species unique to sand treatments, differences in multivariate dispersion likely reflect distinct communities found on sand compared to those at reef interiors (Anderson et al. 2006). Further, the shell and reef communities were also distinct, and the reef community was more similar to the shell community than the sand community. Thus, the addition of physical structure, as small amounts of shell, shifted communities in our study system, and the addition of three-dimensional reefs with living oysters further altered community structure. Shell treatments harbor similar fish and crustacean densities and biomass to reefs, yet, they do not appear to support the full suite of species found on reefs. While we may have underestimated diversity in sand and shell habitats due to a reduced

total area sampled (MacArthur & Wilson 1967; Connor & McCoy 1979), unique species among the treatments suggest biodiversity is best enhanced by including three-dimensional reefs in our system.

Community composition, biomass, and individual species' densities differed between reef edges and interiors. Several non-mutually exclusive mechanisms can contribute to such edge effects (Ries et al. 2004). Foraging species may more frequently access the edges of habitat patches if they use complementary resources from multiple, spatially separated habitats (Ries et al. 2004). Say's mud crabs tended to be more abundant along reef edges in our experiment in the fall, though their densities were high across reefs in summer. In a substrate preference study of three xanthid species (flatback, Say's, and black-fingered mud crabs, *Panopeus herbstii*), Say's mud crabs were very active (Day & Lawton 1988). Say's mud crabs changed substrates approximately 3 to 5 times more frequently than flatback mud crabs, particularly at dawn and dusk (Day & Lawton 1988). Similarly, blue crab densities are higher at salt marsh edges than interiors (Minello & Rozas 2002), and they forage in adjacent oyster and mud bottom (Summerson & Peterson 1984; Micheli & Peterson 1999; Hines 2003). As we observed Say's mud crabs at all habitats and more frequently at edge habitats, they may also be frequently changing habitats in our study, seeking complimentary resources, leading to higher frequencies at reef edges. Additional studies examining foraging patterns among reef edges and adjacent habitats would help determine if and how landscape processes structure variation in oyster reef resident communities.

We found only weak evidence that the densities of reef-associated organisms were elevated by live oyster density; however, experiments that manipulate oyster density would provide a stronger test of whether it potentially drives variation in the distributions and

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abundances of reef associated species (Ries et al. 2004). In contrast, there were several indications that species interactions contributed to the observed edge effects. For example, two species of xanthid crabs were differentially distributed between the reef zones, with Say's mud crabs more abundant along reef edges in the fall, and flatback mud crabs at higher densities on reef interiors. Studies of diet and experimental substrate preferences among juvenile mud crabs (McDonald 1982, Day and Lawton 1988), along with documented dominance hierarchies (Brown et al. 2005) and disjunct reef distributions (Meyer 1994) among related crab species, suggest that this pattern may result from habitat partitioning to avoid competition for shared resources. In addition, higher densities of grass shrimp at reef interiors may reflect differential refuge value between edges and interiors, with higher predator-prey encounter rates expected at reef edges (Humphries et al. 2011). In seagrass patches, prey species are more common in seagrass interiors and predation higher at outer seagrass patches (Smith et al. 2011). Thus, species interactions may complicate the ability to infer changes in community composition from reef edge to interior based on individual species' preferences alone. We recommend experimentally examining how species interactions, such as competition, predation, and mutualism, mediate edge effects and influence community composition within restored oyster reefs.

Species diversity and composition varies across tidal elevation in a wide range of marine and estuarine habitats (Connell 1972; Peterson 1991; Fodrie et al. 2014), suggesting that elevation has the potential to produce edge effects on three-dimensional habitats in marine systems. On domed oyster reefs, like those in our study, reef interiors have a higher elevation than reef edges due to their geometry, and these elevational differences could contribute to the edge effects that we observed. For example, flatback mud crab megalopae use pressure

sensitivity to orient themselves to suitable settlement habitats (Sulkin et al. 1983), which may help them choose the tidal elevations at which they settle. In addition, these crabs are typically more abundant at higher relief reefs (Gregalis et al. 2009), though the presence of more interior habitat could be driving this pattern, rather than reef relief per se. We were unable to decouple the effects of tidal elevation from other edge vs. interior differences such as oyster density in our study, yet we suggest that it deserves explicit consideration in future experiments to understand the factors driving the distribution and abundance of species within oyster reefs.

The differences in oyster reef communities along the edges and interior of reefs in our study highlight that the provision of ecosystem services (i.e., enhancement of fisheries, excess nitrogen removal) may vary within individual oyster reefs, challenging a common simplifying assumption of habitat restoration scaling for nekton (NOAA 1997; Peterson & Lipcius 2003; zu Ermgassen et al. 2016). The total area of restored habitat needed to account for losses of natural resources due to an environmental impact is often determined through the process of restoration scaling, which uses production estimates (e.g., grams of biomass per area per unit time) to determine how much habitat area is needed to reach a baseline density of a target species. If a species' estimated abundance and/or production is not consistent across an entire habitat, then simply using total restored area to estimate enhancement may not effectively achieve restoration goals for that species. Our study suggests that estimations of expected abundance and/or productivity from restored habitats would benefit from partitioning the effects of edge and interior habitats on associated species that are the target of restoration.

Restoration efforts often aim to preserve biodiversity and provide ecosystem services (Peterson & Lipcius 2003). Our study offers guidance on effective strategies for preserving biodiversity in this system. First, unique species were found on reefs and at sand habitats,

suggesting that each habitat is important in supporting biodiversity. Given higher densities of reef-associated species on reefs, our study agrees with previous investigations highlighting the importance of oyster reef habitat for biodiversity conservation. Second, our results demonstrate the need to consider how the edges and interiors of reefs differ in order to enhance biodiversity, since many species have distinct preferences for each reef zone. Reefs of different sizes will vary in their relative amounts of edge vs. interior habitat, so varying reef size (i.e., distance to center) will affect the densities and production of reef-associated organisms per unit area restored. Calls are increasing for consideration of habitat heterogeneity at a variety of spatial scales when restoring coastal ecosystems (Bell et al. 1997; Boström et al. 2011; Suding 2011) and quantification of habitat restoration benefits to associated fauna (Coen & Luckenbach 2000; Peterson & Lipcius 2003; Hollweg et al. 2020). With the mounting evidence for edge effects on biodiversity, ecosystem functions, and associated services, within-patch variation should be incorporated into coastal habitat restoration planning and practice more generally.

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Figures

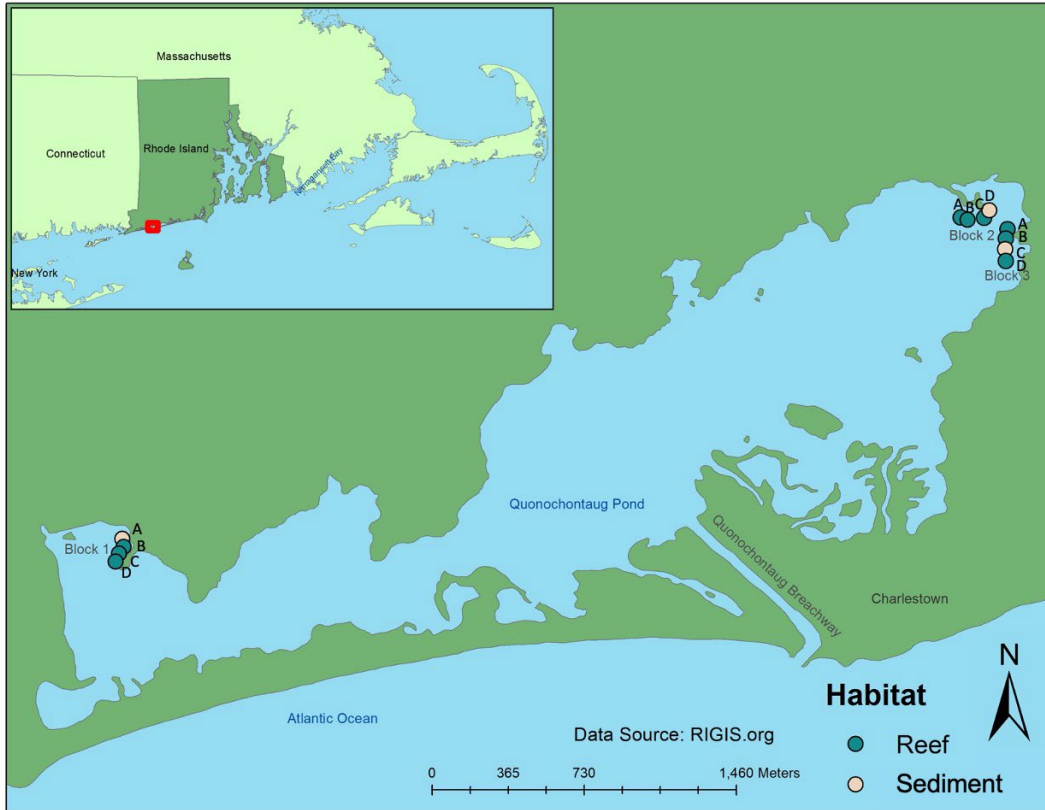


Figure 1. Map of reef and sediment habitats within experimental blocks in Quonochontaug Pond, RI, USA. Colored dots represent the habitats (reef or sediment) in which experimental treatments (trays filled with shell or sand) were deployed. Reef habitats are the restored oyster reefs, to which one reef edge and one reef interior treatment were deployed per season. Sediment habitats are the designated control plots for monitoring that consist of soft sediment (mud or sand). One sand treatment and one shell treatment were deployed in each control plot per season.

Figure 2. Community composition of reef interior and controls (sand or shell). NMDS was conducted using Bray-Curtis dissimilarity with each colonization tray represented by a single point. Density data are square root transformed. Colors represent the habitat treatments (reef interior, sand, or shell) and shapes represent the sampling event seasons. Ellipses depict 95% CI around treatment centroids. PERMANOVA results are included for a model comparing community composition among the habitat treatments and seasons, including a treatment x season interaction and block effects. Multivariate overdispersion is present among habitat treatments.

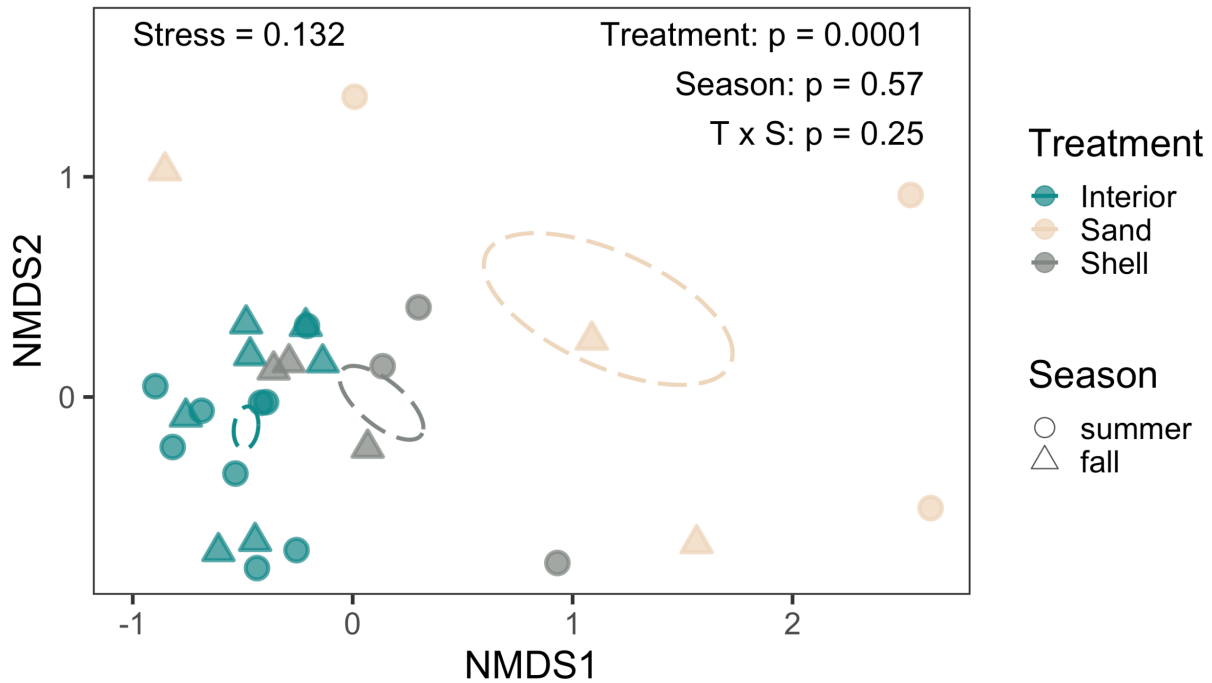


Figure 3. Total density and biomass of resident communities at reef interior and controls (sand or shell). Violin plots indicate the distribution of a) tray density (individuals / 0.37 m^2) and b) tray biomass ($\text{g} / 0.37 \text{ m}^2$), among treatments. Black points represent the total density or biomass in each colonization tray (sampling unit). Colors represent the treatments (reef interior, sand, or shell). Treatment means $\pm 1 \text{ SE}$ for each reef habitat are the colored dots adjacent to the violin plots. Linear modeling analysis demonstrated a significant effect of treatment in models comparing total density (log transformed) or biomass (log transformed) by treatment, season, their interaction and a random block effect. Results of pairwise contrasts among treatments are indicated by the bars with p-values for the habitat contrast indicated above the bars. Non-significant contrasts are labeled “ns”.

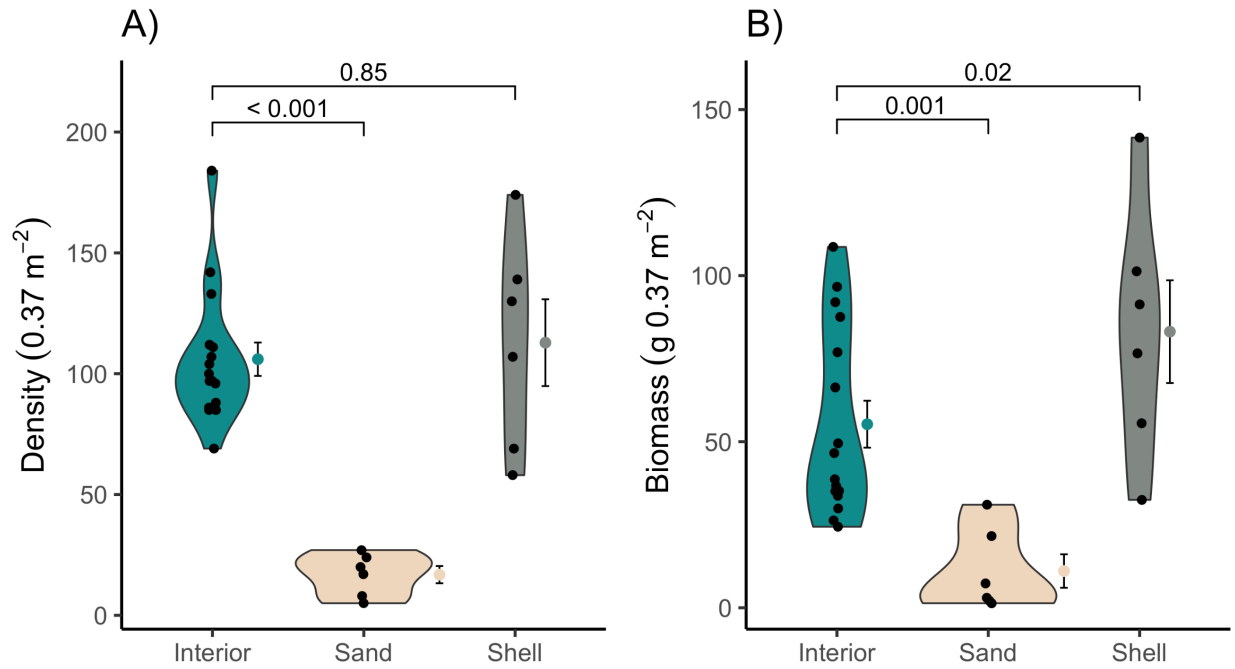


Figure 4. Density of individual resident species at reef interior and controls (sand or shell). Violin plots indicate the distribution of species that demonstrate significant treatment (or treatment x season interaction) effects in linear mixed model analyses of species' densities by treatment, season, their interaction, and a random block effect. Four species' densities differ by treatment: a) *Dyspanopeus sayi* (log), b) *Eurypanopeus depressus* (log + 1), c) *Palaemonetes vulgaris* (log + 1), and d) *Opsanus tau* (log + 1). One species' density differs across treatment and season (summer and fall 2018): e) *Gobiosoma ginsburgi* (log + 1). Black points represent the density of each species on a single colonization tray. Colors represent the habitat treatments (reef interior, sand, or shell). Treatment means ± 1 SE are the colored dots adjacent to the violin plots. Results of pairwise contrasts are indicated by P-values above treatment pairs that share a bar. Non-significant contrasts are labeled "ns".

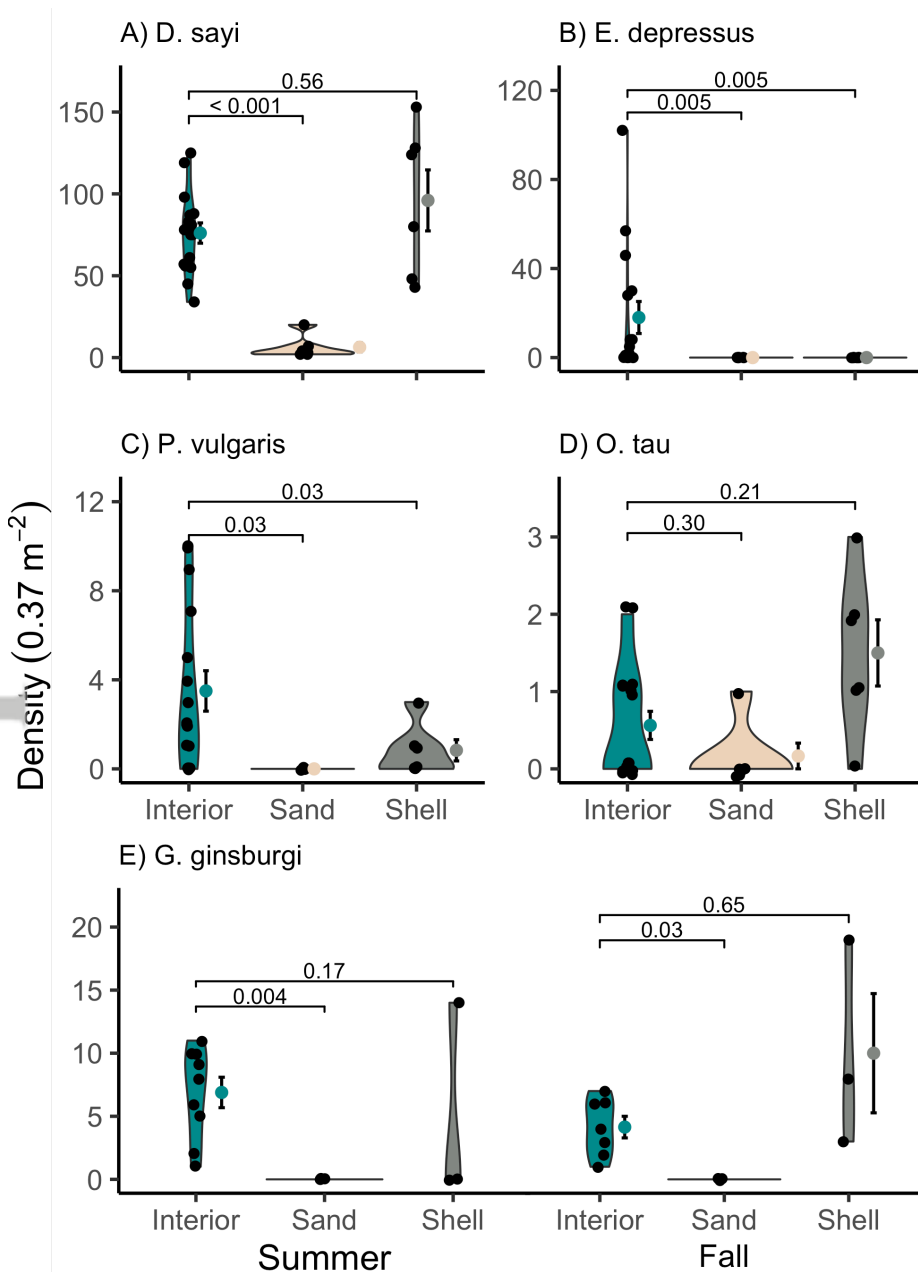


Figure 5. Community composition of restored reef edge and interior. NMDS was conducted using Bray-Curtis dissimilarity with each colonization tray represented by a single point. Density data are square root transformed. Colors represent the reef treatments (reef edge and interior) and shapes represent the sampling event seasons. Species scores are drawn in gray text. Ellipses depict 95% CI around treatment / season combination centroids. PERMANOVA results are included for a model comparing community composition between the treatments and seasons, including a treatment x season interaction and block effects, for square root transformed community composition. P - values for the main effects and interaction are included.

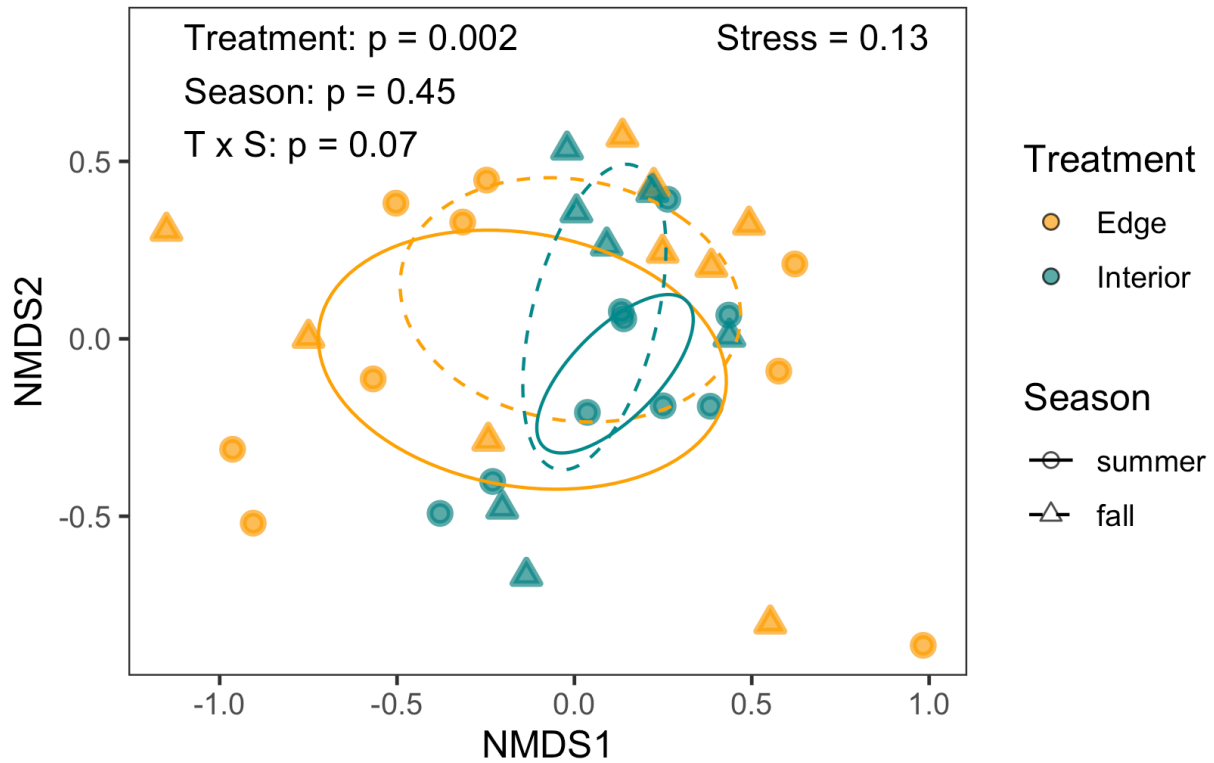


Figure 6. Total density and biomass of resident communities at reef edge and interior. Violin plots indicate the distribution of a) tray density (individuals / 0.37 m^2) and b) tray biomass ($\text{g} / 0.37 \text{ m}^2$), among reef treatments. Black points represent the total density or biomass in each colonization tray (sampling unit). Colors represent the reef treatments (reef edge and interior). Treatment means $\pm 1 \text{ SE}$ for each treatment and season are the colored dots adjacent to the violin plots. The results of linear mixed model analyses are included for a model comparing a) density (log transformed) or b) biomass (log transformed) by treatment, season, their interaction (T x S) and a random block effect. P - values for the main effects and interactions are included.

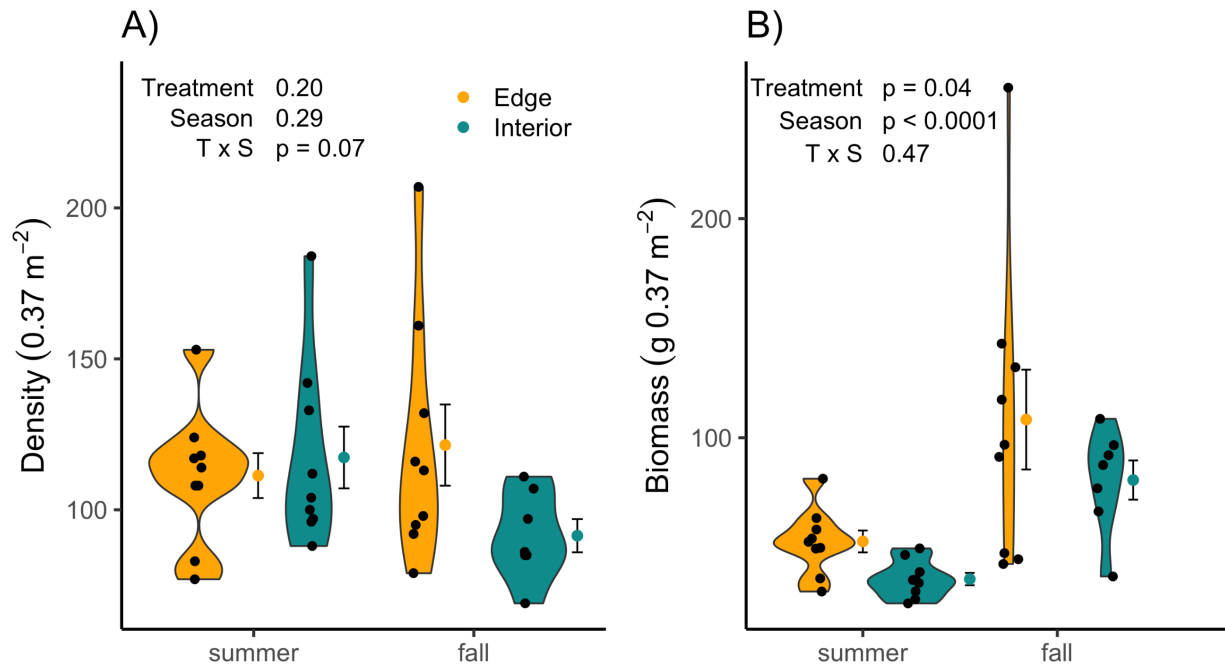


Figure 7. Density of resident species at reef edge and interior treatments. Violin plots indicate the distribution of species densities for those that demonstrate significant treatment (or treatment by season interaction) effects in linear mixed model analyses of species' densities by treatment, season, their interaction, and a random block effect. Three species' densities differ by reef treatment: a) *Eurypanopeus depressus*, c) *Palaemonetes vulgaris*, and e) *Alitta succinea*, and two species' densities differ across reef treatment and season (summer and fall 2018): b) *Dyspanopeus sayi* and d) *Gobiosoma ginsburgi*. Black points represent the density of each species on a single colonization tray. Colors represent the reef treatments (reef edge and interior). Means \pm 1 SE for each treatment and season are adjacent to the violin plots. P - values for the treatment effects (or interactions) are included.

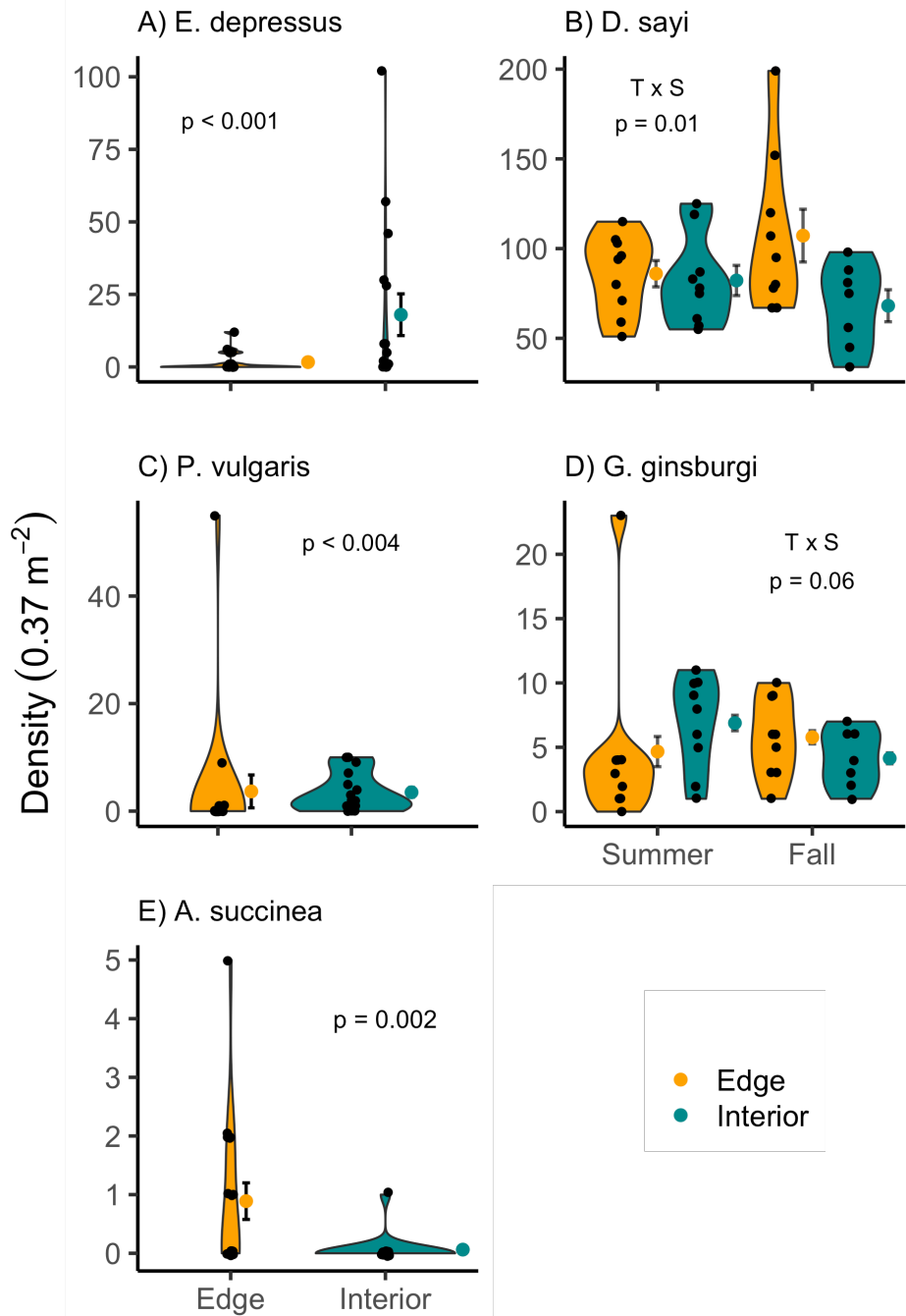


Figure 8. Sizes of resident species at reef edge and interior. Violin plots indicate the distribution of organism sizes by reef treatment for each species that demonstrated differences among treatments. Violin plots indicate the distribution of organism sizes for those that demonstrate significant treatment effects in linear mixed model analyses of organism sizes by treatment, season, their interaction, and random effects of tray nested within block. Two species' sizes differ by reef treatment: a) *Eurypanopeus depressus* carapace width (mm), and b) *Gobiosoma bosc* total length (mm). Black dots represent the sizes of a single individual of each species. Colors represent the reef treatments (reef edge and interior). Means ± 1 SE for each treatment and season are adjacent to the violin plots. P - values for the treatment effects are included.

