

INFLUENCE OF OYSTER STRUCTURES (OYSTER REEFS AND AQUACULTURE
OPERATIONS) ON ADJACENT INFAUNAL ASSEMBLAGES

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A Thesis Submitted to the
University of North Carolina at Wilmington in Partial Fulfillment
of the Requirements for the Degree of
Master of Science

Center for Marine Science
University of North Carolina at Wilmington
2020

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This thesis has been prepared in the style and format

consistent with the journal

Estuaries and Coasts

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ABSTRACT

Predators' use of structural habitats is often associated with a shift in the abundance and/or composition of infaunal communities in the adjacent soft substrate. This alteration of the infauna is often referred to as a "halo effect". The halo effect is one factor that can be used to evaluate utilization patterns of structural habitats. Shellfish themselves and aquaculture gear used for shellfish grow-out provide structural habitat in otherwise unstructured soft-bottoms areas. Shellfish provide many ecosystem services, influence habitat complexity, provide settlement surface for sessile invertebrates, and attract economically and recreationally important fisheries' species. Few studies have examined habitat utilization of shellfish aquaculture relative to wild or restored oyster reefs. We looked at how various oyster structures (shellfish aquaculture and natural and created oyster reefs) in different locations differed in habitat impacts and whether they displayed halo patterns for infauna in adjacent soft substrates. Comparisons of relative mean abundances of infaunal functional guilds (feeding modes and living positions) and relative mean abundances of dominant taxa based on distances from oyster structures were made. Nekton mean abundances and relative predation was investigated to provide insight on nektons' use of soft-bottoms adjacent to oyster structures and potential impacts on infaunal abundances. Key findings included similar structural habitat effects among different structural habitat types, but strong location impacts on functional guild and taxa patterns. Halo patterns were detected for several infauna taxa (Cirratulidae, Orbiniidae, and juvenile bivalve species). These results showed similarity in function of different types of oyster structures suggesting replacement of soft-bottoms with artificial structures may provide similar habitat utilization patterns as wild oyster reefs. Strong site differences emphasize the need to include various sites in habitat studies.

ACKNOWLEDGEMENTS

I would like to thank my advisor and mentors, Dr. Martin Posey and Troy Alphin, for their guidance, time, and enthusiasm. I am grateful for the experiences, learning opportunities, and room for growth that the Benthic Lab has provided. Thank you for shaping me into the researcher I am today. I would also like to thank my committee members Dr. Chris Finelli, and Dr. Michael Mallin for their comments and insight towards the completion of this project.

Thank you to Jessica Carlton, Scott Adams, Ryan Lowndes, and the entire UNCW Benthic Ecology Lab for their help and support in the field and lab- without their assistance sorting would never have been completed. I would also like to thank Sherry Banner for helping with and teaching me taxonomy identifications and The Hurst Family, Dr. Ami Wilbur and Tim Holbrook for the use of their property and leases as study sites.

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INTRODUCTION

Major habitats that are characteristic to North Carolina estuarine ecosystems are salt marshes, oyster reefs (*Crassostrea virginica*), seagrass meadows, and soft-bottoms (mud flats). Structural habitats contribute to shoreline protection and water quality improvement, and all contribute to the support of economically and recreationally important fisheries species (Coen et al. 2007, Cressman et al. 2003; Grabowski et al. 2005; Hanke et al. 2017). In NC, as elsewhere, there is ongoing development of the coastal areas affecting habitat quantity and quality. In some instances, such as potentially with shellfish aquaculture, this may involve replacement of estuarine soft-bottoms with man-made structures (e.g. shellfish and associated aquaculture gear) that will provide different ecosystem services (Dumbauld et al. 2009; Bricker et al. 2018). The transition of a barren unstructured environment to one dominated by artificial structures can provide settlement surface for sessile invertebrates (O'Beirn et al. 2004; Atilla et al. 2005) and increase habitat complexity attracting other invertebrates (ie. crustaceans) and economically and recreationally important fisheries species (DeAlteris et al. 2004; Tallman and Forrester, 2007).

There have been few studies examining habitat utilization of shellfish aquaculture compared to wild or restored oyster reefs. Oyster structures are known to have influences that occur far beyond the structure itself through a variety of mechanisms such as alteration to flow, organic and nutrient enhancement, sediment stabilization, and attraction of finfish and crustaceans. Oyster filtration removes suspended particulates and nutrients from the water column and the biogenic structure of reefs and shellfish aquaculture operations alter flow dynamics removing additional particulate matter and depositing it on and adjacent to the structure rather than remaining suspended in the water column (Brumbaugh et al. 2000; Nelson et al. 2004; Coen et al. 2007; zu Ermgassen et al. 2013). Finfish and crustaceans are attracted to

gear used for grow-out as it provides an artificial structural habitat in intertidal and subtidal areas. Three-dimensional structural habitats are characterized by having higher densities of macroinvertebrates (infauna and crustaceans) and finfish predators than unstructured soft-bottom habitats (Posey et al. 1999; Meyer and Townsend, 2000; Grabowski et al. 2008). However, natural reefs, created reefs, and shellfish aquaculture operations may differ in several important ways that could affect their utilization relative to unstructured habitats.

Structural habitats' function as a refuge and foraging ground possibly influencing trophic dynamics by weakening top predator foraging (Posey et al. 1995; Luckenbach et al. 1999; Harwell et al. 2011; Hanke et al. 2017). Distributions of infauna around oyster structures can provide important information concerning trophic links between structural and soft-bottom habitats. Predation pressure from reef associated finfish foraging on soft-bottoms adjacent to structures have been shown to reduce the distance to which reef oriented intermediate predators are willing to travel to forage on the adjacent soft-bottoms. This foraging impact creates an area of shifted infauna abundance with proximity to the structure called a halo effect. The halo effect has been observed in soft-bottom communities adjacent to offshore natural (Posey et al. 1992; Posey and Ambrose 1994) and artificial (Davis et al. 1982; Nelson et al., 1988) reefs. Intertidal reefs may also attract predators along their edges with the incoming tide, creating areas of greater predation intensity near the reef's edge. Other studies have observed patterns in shifted fauna abundances but attributed these impacts to physical effects of the structural habitat (Ambrose and Anderson 1990; Posey et al. 1992). There is conflicting evidence regarding the existence of infaunal halos adjacent to structural habitats and little is known about estuarine infaunal distributions relative to distance from structured habitats.

The focus of this study was to investigate infaunal communities' functional guild and faunal abundance patterns in relation to various shellfish structures (natural and created oyster reefs and shellfish aquaculture operations) as well as possible existence of a halo adjacent to these structures. Additionally, this study looked at differential habitat use of structured and non-structure habitats, similarity in function of different structural habitat types, and among-site variability impacts on habitat utilization.

METHODS

Patterns of infaunal distribution adjacent to oyster structures (natural and created oyster reefs and aquaculture operations) were used to evaluate functional group (feeding modes and living positions) distributions and dominant infaunal taxa distributions relative to varying structure type. Dominant infauna taxa also were compared across varying distance from structures. Nekton' use of structural and non-structural habitats was evaluated using seine nets and Breder traps in order to relate potential predator abundance to infaunal patterns. Assessment of the in-situ effects of predation on patterns of abundance at varying distances from a structure was tested using clam outplant experiments.

Study Sites

We selected 4 sites in southern North Carolina estuaries for our study (Figure 1). Sampling occurred adjacent to 3 structural habitat types (natural oyster reefs, created oyster reefs, and shellfish aquaculture operations) and 2 unstructured soft substrate habitat types (intertidal mud flats and subtidal mud flats) distributed across these locations (not all habitat types were found at each site). The UNCW Research Lease site is an embayment next to the mouth of Hewletts Creek and connects to the intracoastal waterway. The habitats at the UNCW Research Lease site

were a natural and created oyster reef and an intertidal mud flat. The CMS site parallels the intracoastal waterway. The habitats at the CMS site were a created oyster reef, shellfish aquaculture operation, and an intertidal and subtidal mud flat. The Masonboro and Topsail sites are located in back bays behind Masonboro Island and Topsail Island, respectively and connect to the intracoastal waterway via marsh channels. The habitats at the Masonboro site were a natural oyster reef, shellfish aquaculture operation, and an intertidal and subtidal mud flat. The habitats at the Topsail site were a natural and created oyster reef, shellfish aquaculture operation, and an intertidal and subtidal mud flat. Table 1 summarizes which habitat types were found within each sampling site and the mean low water (MLW) height of the habitats. Sediment characteristics, as determined by percent silt/clay, were different among all sites and occasionally among habitats within sites (Table 1).

Benthic Sampling

Benthic samples were collected in the spring (May) and fall (October) of 2017. Spring represents a period of greater infaunal recruitment and lower nekton predation whereas fall represents a community that has undergone predation throughout the summer (Posey et al., 1995; Harwell et al., 2011). Benthic cores (10cm diameter and 15cm deep) were collected adjacent to the structural habitats (n=3 for each structural habitat type) at the edge of the structure, 3m, 6m, and 12m from the structure edge (n=16 cores per structured habitat type). Edge of oyster reefs was defined as the area where there was no shell present on the surface or within the first 5cm of surface sediment. Edge of aquaculture operations was defined by the operation's boundaries where there is no direct operational footprint of support or mooring structures interacting with the bottom sediments. Reference intertidal and subtidal mud flat habitats (n= 4 for intertidal mud flats, n=3 for subtidal mud flats) were selected in areas that were at the same tidal height as the

respective structural habitat, oyster reefs and aquaculture operations, and where there was no other structural habitat present within a minimum distance of 25m (n=4 cores per mud flat habitat). Samples were fixed in 10% buffered formalin with Rose Bengal dye for 4 weeks then sieved with a 500 µm mesh and transferred to 70% isopropanol for storage. Identification and counting were done under a dissection microscope, counting only whole individuals or heads present. Identifications to the taxonomic family level were made using Bousfield (1970), Fauchald (1977) and Uebelacker et al. (1984).

Assigning infauna to functional groups

Variations in distribution and relative contributions ecological species, those species that may have similar responses to nektonic predators or changes in local food supply. Individual species may exert similar functional impacts based on their mobility and feeding habits (Rhoads and Young 1970; Woodin 1974; Brenchley 1982; Posey 1987). Four feeding modes were identified for the purposes of this study: 1) Direct deposit feeders are taxa that gulp and ingest sediments. 2) Indirect deposit feeders capture deposited or resuspended particles and can be selective or non-selective of particle size. 3) Suspension feeders obtain their food from particles suspended in the water column. 4) Predator-grazers capture prey on the sediment surface or graze on microbiota and/or plant material. Taxa in the predator-grazer group (e.g. Amphipoda) may be opportunistic in their feeding strategy, utilizing mixed feeding strategies. Five living position modes were identified for the purposes of this study: 1) Deep burrowers are organisms that can be free burrowers and can burrow greater than 3-5cm, thus going deeper than the range of many surface oriented predators. 2) Shallow burrowers are within the first 3cm surface sediments and are easily in range of surface predators. 3) Surface dwellers move through/across the sediment surface and do not form permanent structures to reside in. 4) Tube dwellers construct permanent

tubes connected to the surface. 5) Sedentary infauna are stationary or have low mobility and generally must maintain contact with the surface.

Nekton sampling

Seine nets and Breder traps were used to sample the nekton community in the summer (July, August and September 2017) at the Research Lease, CMS, and Masonboro sites (Topsail was excluded for logistics purposes). Seine nets were used to target larger nekton foraging near reefs and adjacent mudflats. Seines were pulled during a mid-flood tide (water depth ~1m) for all habitat types. At structured habitats a 10m seine net was towed for 20m parallel to the structure in the direction of the incoming tide. At reference mud flat habitats the seine was towed for 20m perpendicular to shore in the direction of the incoming tide. The seine was collected by bringing the poles together creating an enclosure and picking up the lead line. The second gear type, Breder traps, were used to target epibenthic and bottom-oriented fish and crustaceans. Breder traps were deployed at a low flood tide and allowed to fish for 2 hours once submerged (Breder 1960). At structured habitats three traps were placed (1m apart) at the habitat edge then 3m, 6m, and 12m distances from the habitat. At reference mud flat habitats three traps were placed (1m apart). Trap orientation was so the center trap opening was oriented towards the structure (or perpendicular to shore for mud flat habitats), the remaining two traps were oriented so the openings were opposite from one another at a 90° rotation away from the center trap. All organisms captured were identified to the species level, measured, and released.

Clam outplant experiment

To evaluate the influence of predator foraging on benthic communities at varying distances from a structure, a clam outplant experiment was used to investigate relative predation at the Research

Lease and Masonboro sites in July 2017. Clams were used because they are a common infauna prey item with limited mobility. Juvenile hard clams *Mercenaria mercenaria* (8-15mm in length) were used because they represent the size class of clams found in the surface sediments that could be preyed upon by predators attracted to the reef; larger clams would be deeper in the sediment (not accessible) and/or be too large to consume for many predators. There were 2 treatments: 1) uncaged outplants and 2) caged outplants (cages constructed of hardware cloth with a mesh size of 5mm). Twenty *M. mercenaria*, were placed in containers (0.20cm x 0.20cm x 0.10m) and allowed to burrow for 24h. At oyster reefs and aquaculture operations three uncaged and three caged clam containers were placed (1m apart) at the structures' edge then 3m, 6m, and 12m distances from the structures. At reference mud flat habitats three uncaged and three caged clam containers were also deployed. Clam containers were buried (flush with the sediment horizon) at low tide (water depth ~0.1m at intertidal habitats) and deployed for 6h, following flood tide. Upon retrieval clams were categorized as: 1) present (live-shell intact) or 2) absent (fragments of shell or no evidence of organism).

Statistical Analysis

We compared functional group mean relative abundance, functional group mean abundance, dominant taxa mean relative abundance, and mean taxa richness. Relative abundance is the proportional representation of each functional guild or taxa within the community. Relative abundance was used because it indicates the relative contribution of each guild or taxa whereas mean abundances indicates which guild or taxa is most common. All data- functional group mean relative abundance, functional group mean abundance, dominant taxa mean relative abundance, and mean taxa richness - were tested for homogeneity of variances. Only the direct deposit feeder functional group did not conform to test assumptions. A square root

transformation was used on direct deposit feeders but did not yield different results to that of untransformed data so the untransformed data was used for comparison purposes. A 4-way analysis of variance (ANOVA) with season, site, habitat and distance was initially used to compare functional group patterns on mean relative abundances and mean abundance, dominant taxa mean relative abundance, and mean taxa richness. This indicated significant interaction with season for all data leading to a by season 3-way ANOVA follow up analyses.

Mean abundances of nekton catches in seine net and Breder trap conformed to test assumptions for homogeneity of variances. Seine net catches were compared using a 3-way ANOVA with month, site and habitat. Breder trap catches were compared using a 4-way ANOVA with month, site, habitat and distance. For the outplant experiment mean proportional survivorship (arc-sine (square root) transformed) was calculated as number of clams returned/number of clams deployed. A 4-way ANOVA with cage type, site, habitat, and distance was used. This indicated significant interaction with cage type and site leading to a follow up analysis by cage type and by site 2-way ANOVA with habitat and distance.

Table 1 Habitat types located at each sampling site. For subtidal habitats water depths (in meters) at low tide is indicated in parentheses. Intertidal habitats were completely exposed at low tide.

	Aquaculture operations	Created oyster reef	Natural oyster reef	Intertidal mud flat (IMF)	Subtidal mud flat (SMF)
UNCW Research Lease (RL)	----	27%	43%	28%	----
CMS	39% (.6m)	40%	----	41%	33% (.6m)
Masonboro (MI)	24% (.4m)	----	48%	50%	63% (.4m)
Topsail (TS)	25% (.2m)	54%	69%	68%	27% (.4m)



Fig 1 Location of study sites near Wilmington (left) and Topsail (right) North Carolina.

RESULTS

Infauna community composition

There were 84 infauna groups (family level or higher) observed and assigned to functional guilds for feeding mode (direct deposit, indirect deposit, predator-grazer, and suspension feeder) and living position (deep burrower, shallow burrower, surface, tube dweller, and sedentary). There was one group, unidentified amphipod species that was not assigned to functional guilds because it could not be reliably identified as having a dominant guild pattern. Dominant taxa (those comprising >1% of the total sample) were represented by 22 families or a higher taxonomic group (Table 2).

Mean taxa richness differed among all sites ((Topsail > Research Lease > CMS > Masonboro) ($F= 87.31$; $p < .0001$)) and showed a temporal pattern of mean richness being greater in the spring than fall (Figure 2). At the Masonboro site in the spring, oyster structures (aquaculture and natural reef) had greater mean richness than non-structured mud flat habitats (Figure 2). At the Topsail site in the spring, subtidal habitats (aquaculture and subtidal mud flats) had greater mean richness than intertidal habitats (oyster reefs and intertidal mud flat); while in the fall the created oyster reef had greater mean richness than the other habitat types (Figure 2). Mean richness did not differ among habitat types at the Research Lease or CMS sites.

Functional Guild Patterns

Relative and mean abundances of feeding modes and living positions did not indicate a detectable halo effect. There is greater relative representation in the spring than fall for suspension feeders, direct deposit feeders, deep burrowers, shallow burrowers, and sedentary infauna (Figure 3). Mean abundances also showed this pattern with the addition of predator-

grazers and tube dwellers. The results indicated strong site interactions that could possibly have obscured detectable distance effects on functional groups.

Feeding Mode Patterns

For feeding modes, relative and mean abundances, there were season-site interactions for all groups. Group differences in proportional representation among sites in the spring showed greatest relative abundances for suspension feeders and predator-grazers at Topsail, direct deposit feeders at the Research Lease and indirect deposit feeders at Masonboro (Table 3). For mean abundances the observed pattern was different for indirect deposit feeders which had greatest mean abundance at CMS (Table 4). Group differences in proportional representation among sites in the fall showed greatest relative abundances for indirect deposit feeders at CMS, predator-grazers at the Research Lease, and suspension and direct deposit feeders at Topsail (Table 3). For mean abundances the observed pattern was different for suspension feeders and direct deposit feeders which had greatest mean abundances at the Research Lease (Table 4).

Feeding mode relative abundances showed a site-habitat interaction for suspension feeders and predator-grazers in the spring and for suspension feeders, predator-grazers and indirect deposit feeders in the fall. Mean abundances showed the same pattern with the addition of direct deposit and indirect deposit feeders in the spring and direct deposit feeders in the fall. Actual mean abundances (rather than relative numbers) indicated the same difference among sites (Table 5). For example, suspension feeders, which had overall low abundances, were at least 2-fold greater at the Topsail site than the other sites (Table 5). At Masonboro direct deposit feeders were in notably lower abundances compared to other sites but the site had similar abundances of predator-grazers and indirect deposit feeders as the CMS and Research Lease sites (Table 5; Fig 4). Suspension feeders were proportionally dominant at subtidal habitats

(aquaculture and subtidal mud flats) at CMS and Topsail (Fig 4). Other groups were proportional dominant at select habitats within a site.

Habitat effects were detected on for both relative representation and mean abundances of suspension feeders which were more common at subtidal habitats (aquaculture and subtidal mud flats) in the spring. Proportionally dominant groups were indirect deposit feeders at non-structured habitats (intertidal mudflats and subtidal mud flats) and natural oyster reefs in the spring and direct deposit feeders had greater representation at structured habitats (aquaculture and created reefs) in the fall. Mean abundance results also suggest direct deposit feeders were more common at structured habitats (created and natural oyster reefs and aquaculture) and intertidal mud flats in the spring (Table 3, Table 4).

Living Position Patterns

For living position, relative and mean abundances, there were season-site interactions for all groups. In the spring there were differences in group proportional representation among sites with greatest relative abundances for deep burrowers, surface dwellers, and sedentary infauna at Topsail site, shallow burrowers at the Research Lease site, and tube dwellers at Masonboro site (Table 6). For mean abundances the pattern was different for tube dwellers which had greatest mean abundance at CMS (Table 7). Group differences in proportional representation among sites in the fall showed greatest relative abundances for tube dwellers at CMS, shallow burrowers at the Research Lease, surface dwellers at Masonboro, sedentary infauna at Topsail, and no site differences for deep burrowers (Table 6). Mean abundances differed from relative abundances for sedentary and deep burrower group which had greatest mean abundances at the Research Lease and surface dwellers which had the greatest mean abundance at Topsail (Table 7).

Living position relative abundances showed a site-habitat interaction for almost all groups except surface dwellers in the spring and deep burrowers in the fall. For mean abundances site-habitat interactions were observed in the spring and fall for all living position groups. Actual mean abundances of infauna also indicated differences among sites. For example, at Masonboro deep burrowers in the spring were 3-fold less compared to the other sites (Table 5). Sedentary infauna, which overall had low abundances at all sites, were in particularly low abundance at Masonboro compared to other sites (Table 5). Differences in relative representation among habitat types within a site are shown in Fig. 5. Sedentary infauna were proportionally dominant at subtidal habitats (aquaculture and subtidal mud flats) and CMS and Topsail. While shallow burrowers and surface dwellers showed differences in proportional representation among habitat types at some sites.

Habitat effects were detected for both relative representation and mean abundances of shallow burrowers and sedentary infauna in the spring. Shallow burrowers were more common at intertidal habitats (created and natural oyster reefs and intertidal mud flats) and sedentary infauna were most common at subtidal habitats (aquaculture and subtidal mud flats). Tube dwellers in the spring were proportionally least dominant at created oyster reefs, and surface dwellers in the fall had greatest proportional representation at non-structured intertidal mud flat habitats. Mean abundance results also suggest deep burrowers were in greatest abundance at structured habitats (aquaculture and created reefs) in the spring (Table 6, Table 7).

Dominant taxa patterns

Proportional representation of dominant taxa (defined by those comprising >1% of the total sample) was strongly influenced by site with 17 of the 22 dominant taxa having a site-habitat interaction (those that did not show an interaction were Ampeliscidae, Nassariidae, Oligochaeta,

Orbiniidae, and Veneridae) (Table 7 supplemental). A change in proportional representation with distance from a structure was detected for Cirratulidae (direct deposit/shallow burrower) with greater relative abundances at the edge and 3m distances and lower relative abundances at the 6m and 12m distances ($F=3.98$; $p<0.0086$).

When dominant taxa were analyzed by season and only structured habitats were considered (oyster reefs and aquaculture operations) distance effects were detected for 3 taxa (Cirratulidae, Orbiniidae, and juvenile bivalve species) (Table 2). The distance pattern previously detected for Cirratulidae (direct deposit feeder/shallow burrower) was only significant in the spring. In the fall Orbiniidae (direct deposit/shallow burrower) and juvenile bivalve species (suspension feeder/sedentary) were in greatest relative abundance furthest from structures at 6m and 12m and at lowest representation at the edge of oyster structures (Table 2).

Proportional representation of dominant taxa showed effects with habitat type. At natural oyster reefs dominant taxa were Arbellidae, Cirratulidae, Nereididae, Veneridae. At aquaculture operations bivalves Astartidae and Tellinidae were dominant. Aquaculture operations and created oyster reef habitats had similar effects on Capitellidae, Maldanidae, Paraonidae, Syllidae, Tornatinidae and juvenile bivalve species.

Nekton community habitat utilization

There were 33 taxa observed in seine nets and 21 taxa observed in Breder traps (species level or higher). Dominant taxa (those comprising >3% of the total sample) that were benthic predators were represented by 8 taxa: pinfish (*Lagodon rhomboides*), spot (*Leiostomus xanthurus*), mud minnow (*Fundulus heteroclitus*, captured in Breder traps only), spotfin mojarra (*Eucinostomus argenteus*), blue crab (*Callinectes* species, predominantly *C. sapidus*), Penaeidae spp., and grass

shrimp, *Palaemonetes vulgaris* and *Palaemonetes pugio* (Table 7 supplemental). For both seine net and Breder trap catches there was a site-habitat interaction. The CMS site had greater mean abundances of benthic predators than the Masonboro and Research Lease sites. There were habitat effects for both gear types with greater mean abundances at structured habitats (created oyster reefs) (Table 8). Breder traps catches did not show differences in mean abundances with distance from a structure.

Clam outplant experiment

Caged treatments did function as an exclusion treatment with greater clam survivorship in caged treatments than uncaged treatments ($F=128.46$; $p<.0001$). For uncaged treatments there was a difference in relative predation among sites. The Masonboro site had greater relative predation than the Research Lease ($F= 22.65$; $p <.0001$). There were no detectable patterns comparing mean percent survivorship among habitats within a site or with distance from oyster structures (Table 9). In uncaged treatments the Masonboro site shows a trend towards 40-60% mean clam survivorship while the Research Lease shows mean clam survivorship at 80-95%.

Table 2 Results for mean relative abundance of dominant infauna at structured habitats using a by season 3-way ANOVA by site, habitat, and distance. Shown are F-values and (p-values) with significant differences (p<0.05) indicated by an asterisk. SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values.

Taxa		Spring	Fall
Ampeliscidae	Site	2.95 (0.0906)	6.61 (0.0119)*
<i>Predator-grazer</i>			Topsail ^A , Masonboro ^{AB} , Research Lease ^B , CMS ^B
<i>Tube Dweller</i>	Habitat	3.06 (0.0970)	2.89 (0.1076)
	Distance	1.31 (0.3306)	3.37 (0.0682)
	Site*habitat	3.48 (0.0637)	3.86 (0.0499)*
	Site*distance	1.01 (0.4950)	1.27 (0.3647)
	Habitat*distance	1.14 (0.4145)	0.92 (0.5316)
Arabellidae	Site	11.57 (0.0019)**	2.03 (0.1798)
<i>Direct deposit feeder</i>		Topsail ^A , Masonboro ^B , Cam Lease ^B , CMS ^B	
<i>Deep burrower</i>	Habitat	11.56 (0.0033)**	1.13 (0.3658)
		Natural ^A , Created ^B Aquaculture ^B	
	Distance	0.84 (0.5071)	1.02 (0.4298)
	Site*habitat	11.53 (0.0019)**	0.45 (0.7232)
	Site*distance	0.59 (0.7755)	0.34 (0.9370)
	Habitat*distance	1.25 (0.3661)	1.24 (0.3716)
Astartidae	Site	39.91 (<.0001)****	2.52 (0.1233)
<i>Suspension feeder</i>		Topsail ^A , Research Lease ^B , CMS ^B , Masonboro ^B	
<i>Sedentary</i>	Habitat	56.74 (<.0001)****	1.36 (0.3047)
		Aquaculture ^A , Created ^B Natural ^B	
	Distance	1.70 (0.2364)	1.36 (0.3170)
	Site*habitat	51.91 (<.0001)****	1.83 (0.2114)
	Site*distance	1.13 (0.4307)	0.92 (0.5466)
	Habitat*distance	2.09 (0.1537)	1.13 (0.4188)
Capitellidae	Site	9.93 (0.0033)**	8.14 (0.0062)**
<i>Direct deposit feeder</i>		CMS ^A , Research Lease ^A , Topsail ^A , Masonboro ^B	Research Lease ^A , CMS ^A , Maosnboro ^A , Topsail ^B
<i>Deep burrower</i>	Habitat	22.36 (0.0003)***	6.48 (0.0180)*
		Aquaculture ^A , Created ^A , Natural ^B	Aquaculture ^A Created ^{AB} Natural ^B
	Distance	0.42 (0.7452)	0.57 (0.6508)
	Site*habitat	8.06 (0.0064)**	4.68 (0.0310)*
	Site*distance	0.63 (0.7509)	1.78 (0.2026)
	Habitat*distance	0.77 (0.6100)	1.71 (0.2246)

Table 2 cont. Results for mean relative abundance of dominant infauna at structured habitats using a by season 3-way ANOVA by site, habitat, and distance. Shown are F-values and (p-values) with significant differences (p<0.05) indicated by an asterisk. SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values.

Taxa		Spring	Fall
<i>Cirratulidae</i> <i>Direct deposit feeder</i> <i>Shallow burrower</i>	Site	106.11 (<.0001)**** Research Lease ^A , Topsail ^B Masonboro ^B CMS ^B	1.14 (0.3836)
	Habitat	11.18 (0.0036)** Natural ^A Created ^B Aquaculture ^C	0.10 (0.9074)
	Distance	4.44 (0.0355)* 3m ^A E ^A 12m ^{AB} 6m ^B	0.24 (0.8697)
	Site*habitat	11.26 (0.0021)**	0.94 (0.4593)
	Site*distance	1.03 (0.4818)	0.45 (0.8758)
	Habitat*distance	0.76 (0.6197)	0.38 (0.8717)
	Site	1.74 (0.2279)	6.07 (0.0152)*
	Habitat	2.77 (0.1154)	4.63 (0.0415)*
<i>Corophiidae</i> <i>Predator-grazer</i> <i>Tube dweller</i>	Distance	0.42 (0.7410)	0.27 (0.8457)
	Site*habitat	2.54 (0.1216)	4.94 (0.0268)*
	Site*distance	0.67 (0.7225)	0.8 (0.6241)
	Habitat*distance	0.95 (0.5042)	1.20 (0.3875)
	Site	2.30 (0.1463)	1.90 (0.2004)
	Habitat	0.72 (0.5150)	3.40 (0.0797)
<i>Gammaridae</i> <i>Predator-grazer</i> <i>Surface dweller</i>	Distance	0.87 (0.4907)	0.14 (0.9304)
	Site*habitat	3.2 (0.0763)	2.19 (0.1586)
	Site*distance	1.59 (0.2499)	0.72 (0.6825)
	Habitat*distance	1.65 (0.2384)	0.60 (0.7258)
	Site	6.64 (0.0117)* Topsail ^A Research Lease ^{AB} CMS ^{AB}	20.65 (0.0002)*** Topsail ^A , Research Lease ^B , Masonboro ^C , CMS ^C
	Habitat	7.26 (0.0132)*	10.81 (0.0041)** Created ^A , Aquaculture ^A , Natural ^B
<i>Juvenile</i> <i>Bivalve spp.</i> <i>Suspension feeder</i> <i>Sedentary</i>	Distance	0.57 (0.6504)	4.31 (0.0383)* 12m ^A , 6m ^B , E ^B , 3m ^B
	Site*habitat	3.16 (0.0786)	11.30 (0.0021)**
	Site*distance	0.65 (0.7347)	1.09 (0.4483)
	Habitat*distance	0.68 (0.6685)	1.77 (0.2124)

Table 2 cont. Results for mean relative abundance of dominant infauna at structured habitats using a by season 3-way ANOVA by site, habitat, and distance. Shown are F-values and (p-values) with significant differences ($p < 0.05$) indicated by an asterisk. SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values.

Taxa		Spring	
<i>Lumbrineridae</i> <i>Direct deposit feeder</i> <i>Deep burrower</i>	Site	13.94 (0.0010)** Topsail ^A Masoboro ^B Research Lease ^B CMS ^B	7.87 (0.0069)* Topsail ^A , Masonboro ^B , Research Lease ^B , CMS ^B
	Habitat	9.08 (0.0069)** Natural ^A Created ^B Aquaculture ^B	2.34 (0.1523)
	Distance	1.17 (0.3740)	0.12 (0.9436)
	Site*habitat	6.06 (0.0153)*	4.90 (0.0276)
	Site*distance	1.01 (0.4947)	0.54 (0.8127)
	Habitat*distance	0.98 (0.4926)	1.11 (0.4278)
<i>Maldanidae</i> <i>Direct deposit feeder</i> <i>Tube dweller</i>	Site	19.95 (0.0003)*** Topsail ^A , CMS ^B , Research Lease ^B , Maosnboro ^B	2.01 (0.1834)
	Habitat	10.09 (0.0050)** Aquaculture ^A , Created ^A , Natural ^B	0.35 (0.7167)
	Distance	0.39 (0.7603)	1.27 (0.343)
	Site*habitat	6.85 (0.0106)	2.65 (0.1124)
	Site*distance	0.59 (0.7773)	0.61 (0.7626)
	Habitat*distance	1.15 (0.4093)	1.16 (0.4022)
<i>Melitidae</i> <i>Predator-grazer</i> <i>Surface dweller</i>	Site	4.28 (0.0390)*	0.89 (0.4822)
	Habitat	6.42 (0.0185)* Created ^A , Aquaculture ^B , Natural ^B	1.35 (0.3076)
	Distance	0.45 (0.7205)	1.88 (0.2042)
	Site*habitat	6.42 (0.0129)*	1.67 (0.2417)
	Site*distance	0.67 (0.7223)	0.47 (0.8621)
	Habitat*distance	1.00 (0.4799)	0.49 (0.7982)
<i>Nassariidae</i> <i>Predator-grazer</i> <i>Surface dweller</i>	Site	2.50 (0.1256)	3.65 (0.0570)
	Habitat	1.41 (0.2924)	2.36 (0.1496)
	Distance	1.32 (0.3263)	1.71 (0.2335)
	Site*habitat	2.21 (0.1566)	1.08 (0.4051)
	Site*distance	0.93 (0.5404)	1.21 (0.3907)
	Habitat*distance	0.72 (0.6416)	1.53 (0.2706)

Table 2 cont. Results for mean relative abundance of dominant infauna at structured habitats using a by season 3-way ANOVA by site, habitat, and distance. Shown are F-values and (p-values) with significant differences (p<0.05) indicated by an asterisk. SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values.

Taxa		Spring	Fall
<i>Nereididae</i> <i>Predator-grazer</i> <i>Shallow burrower</i>	Site	9.03 (0.0045)** Masonboro ^A Research Lease ^A Topsail ^B CMS ^C	29.58 (<.0001)**** Research Lease ^A Topsail ^B Maosnboro ^B CMS ^B
	Habitat	5.23 (0.0312)* Natural ^A Aquaculture ^B Created ^B	4.01 (0.0568)
	Distance	0.87 (0.4900)	1.56 (0.2647)
	Site*habitat	11.02 (0.0023)**	3.72 (0.0547)
	Site*distance	1.68 (0.2268)	2.01 (0.1563)
	Habitat*distance	0.86 (0.5556)	0.47 (0.8145)
<i>Oligochaete</i> <i>Direct deposit feeder</i> <i>Deep burrower</i>	Site	2.61 (0.1157)	1.73 (0.2310)
	Habitat	3.47 (0.0766)	0.42 (0.6723)
	Distance	0.50 (0.6920)	0.08 (0.9668)
	Site*habitat	1.19 (0.3684)	0.55 (0.6616)
	Site*distance	0.90 (0.5601)	0.49 (0.8515)
	Habitat*distance	0.58 (0.7400)	1.56 (0.2629)
<i>Orbiniidae</i> <i>Direct deposit feeder</i> <i>Shallow burrower</i>	Site	32.77 (<.0001)**** CMS ^A Masonboro ^B Topsail ^B Research Lease ^C	5.65 (0.00187)* Topsail ^A Research Lease ^{AB} CMS ^{AB} Masonboro ^B
	Habitat	13.64 (0.0019)** Natural ^A Created ^A Aquaculture ^A	4.29 (0.0491)* Natural ^A Aquaculture ^A Created ^A
	Distance	2.00 (0.1842)	3.93 (0.0480)* 6m ^A 12m ^B 3m ^B E ^B
	Site*habitat	8.60 (0.0052)**	2.96 (0.0901)
	Site*distance	1.51 (0.2755)	1.97 (0.1627)
	Habitat*distance	1.03 (0.4623)	1.96 (0.1742)
<i>Paraonidae</i> <i>Direct deposit feeder</i> <i>Shallow burrower</i>	Site	5.33 (0.0219)*	36.85 (<.0001)**** Topsail ^A Research Lease ^B Maosnboro ^{BC} CMS ^C
	Habitat	10.22 (0.0048)** Created ^A Aquaculture ^B Natural ^B	32.08 (<.0001)**** Created ^A Aquaculture ^A Natural ^B
	Distance	0.19 (0.8976)	0.48 (0.7041)
	Site*habitat	6.02 (0.0156)*	7.49 (0.0081)**
	Site*distance	0.54 (0.8174)	0.86 (0.5875)
	Habitat*distance	0.64 (0.6995)	1.18 (0.3968)

Table 2 cont. Results for mean relative abundance of dominant infauna at structured habitats using a by season 3-way ANOVA by site, habitat, and distance. Shown are F-values and (p-values) with significant differences (p<0.05) indicated by an asterisk. SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values.

Taxa		Spring	Fall
<i>Phyllodoceidae</i> <i>Predator-grazer</i> <i>Shallow burrower</i>	Site	14.66 (0.0008)*** CMS ^A Masonboro ^B Topsail ^B Research Lease ^B	7.48 (0.0081)** CMS ^A Topsail ^{AB} Research Lease ^B Masonboro ^B
	Habitat	6.68 (0.0166)*	3.26 (0.0860)
	Distance	2.73 (0.1062)	3.61 (0.0584)
	Site*habitat	7.09 (0.0096)**	1.75 (0.2255)
	Site*distance	2.32 (0.1131)	1.72 (0.2150)
	Habitat*distance	0.71 (0.6516)	2.5 (0.1051)
	<i>Spionidae</i> <i>Indirect deposit feeder</i> <i>Tube dweller</i>	Site	94.66 (<.0001)**** Masonboro ^A CMS ^B Topsail ^C Research Lease ^C
Habitat		5.45 (0.0281)* Aquaculture ^A Natural ^A Created ^B	18.21 (0.0007)***
Distance		2.00 (0.1847)	0.34 (0.7944)
Site*habitat		1.02 (0.4292)	10.14 (0.0030)**
Site*distance		1.58 (0.2529)	1.57 (0.2552)
Habitat*distance		0.48 (0.8078)	1.04 (0.4612)
<i>Syllidae</i> <i>Predator-grazer</i> <i>Shallow burrower</i>		Site	4.29 (0.0387)* Research Lease ^A Topsail ^B Maosnboro ^B CMS ^B
	Habitat	0.52 (0.6130)	7.71 (0.0112)* Created ^A Aquaculture ^A Natural ^B
	Distance	0.02 (0.9951)	0.5 (0.6915)
	Site*habitat	3.86 (0.0500)*	1.81 (0.2149)
	Site*distance	0.16 (0.9936)	0.61 (0.76)
	Habitat*distance	0.22 (0.9602)	0.90 (0.5344)
	<i>Tellinidae</i> <i>Suspension feeder</i> <i>Sedentary</i>	Site	22.17 (0.0002)*** Topsail ^A CMS ^B Masonboro ^B Research Lease ^B
Habitat		28.84 (0.0001)*** Aquaculture ^A Created ^B Natural ^B	2.90 (0.1068)
Distance		0.23 (0.8766)	0.15 (0.9293)
Site*habitat		12.95 (0.0013)**	1.61 (0.2536)
Site*distance		1.03 (0.4846)	0.69 (0.7046)
Habitat*distance		0.98 (0.4917)	0.31 (0.9170)

Table 2 cont. Results for mean relative abundance of dominant infauna at structured habitats using a by season 3-way ANOVA by site, habitat, and distance. Shown are F-values and (p-values) with significant differences ($p < 0.05$) indicated by an asterisk. SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values.

Taxa		Spring	Fall	
Tonatinidae <i>Predator-grazer</i> <i>Surface dweller</i>	Site	58.12 (<.0001)**** Topsail ^A Research Lease ^B CMS ^B Masonboro ^B	18.33 (0.0004)*** Topsail ^A Research Lease ^B Masonboro ^B CMS ^B	
	Habitat	33.34 (<.0001)**** Aquaculture ^A Created ^B Natural ^B	8.66 (0.0080)** Aquaculture ^A Created ^A Natural ^B	
	Distance	1.96 (0.1901)	0.10 (0.9572)	
	Site*habitat	31.90 (<.0001)****	5.21 (0.0234)	
	Site*distance	2.06 (0.1486)	0.21 (0.9842)	
	Habitat*distance	1.42 (0.3063)	1.53 (0.2719)	
	Veneridae <i>Suspension feeder</i> <i>Sedentary</i>	Site	7.48 (0.0081)** Research Lease ^A Topsail ^B CMS ^B Masonboro ^B	12.77 (0.0014)** Research Lease ^A Topsail ^B Masonboro ^B CMS ^B
	Habitat	11.16 (0.0037)** Natural ^A Created ^B Natural ^B	0.38 (0.6916)	
Distance	2.34 (0.1414)	2.67 (0.1112)		
Site*habitat	2.75 (0.1043)	0.74 (0.5521)		
Site*distance	1.42 (0.3060)	2.21 (0.1261)		
Habitat*distance	1.63 (0.2442)	0.73 (0.6409)		

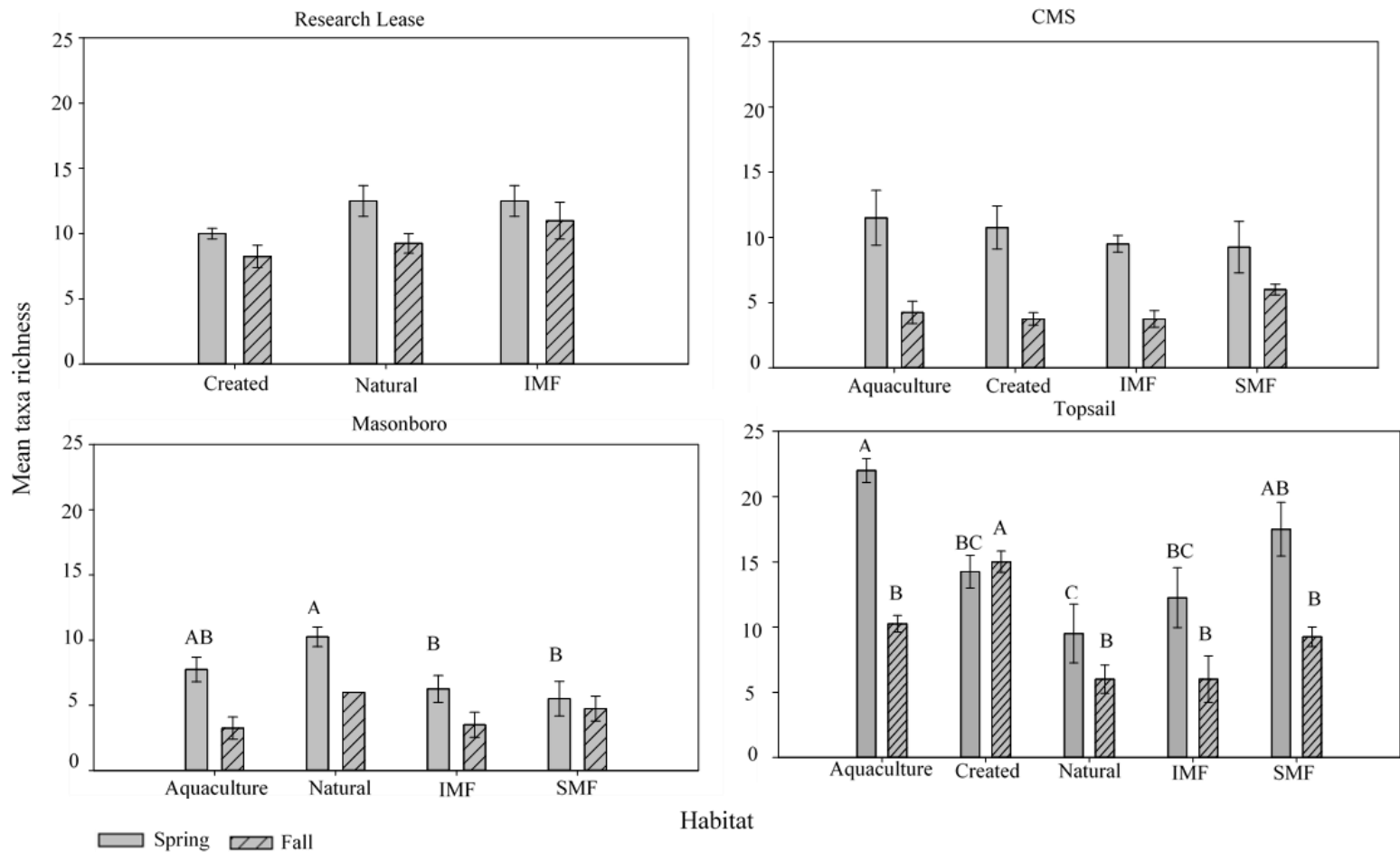


Fig 2 Mean taxa richness (+/- SE) at the edge distance of each habitat type at the Research Lease, CMS, Masonboro Island, and Topsail sites during the spring and fall seasons. Richness had a temporal effect being greater in the spring than fall at all sites ($F=155.35$; $p<.0001$). Sites were significantly different from one another with $\text{Topsail} > \text{Research Lease} > \text{CMS} > \text{Masonboro}$ ($F=87.3$; $p<.0001$). Richness was significantly different among habitats within sites at Masonboro in the spring ($F=4.11$; $p=0.0302$) and at Topsail in the spring ($F=6.90$; $p=0.0023$) and fall ($F=11.58$; $p=0.0002$).

Table 3 Results for mean relative abundance of feeding modes using a by season 3-way ANOVA with site, habitat, and distance. Shown are F-values and (p-values) with significant differences (p<0.05) indicated by an asterisk. SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values. RL=Research Lease, MI=Masonboro Island, and TS=Topsail.

Season		Direct deposit	Indirect deposit	Predator-grazer	Suspension
Spring	Site	43.45 (<.0001)**** RL ^A TS ^B CMS ^C MI ^D	105.99 (<.0001)**** MI ^A CMS ^B TS ^C RL ^C	7.78 (<.001)**** TS ^A MI ^B RL ^B CMS ^B	36.52 (<.0001)**** TS ^A RL ^B CMS ^B MI ^C
	Habitat	1.53 (0.2195)	6.92 (0.0014)** SMF ^A IMF ^A Aquaculture ^A Natural ^A Created ^B	0.93 (0.3977)	43.51 (<.0001)**** Aquaculture ^A SMF ^A Created ^B Natural ^{BC} IMF ^C
	Distance	2.21 (0.0900)	1.08 (0.3607)	0.75 (0.5271)	1.22 (0.3046)
	Site*habitat	1.46 (0.2272)	1.44 (0.2329)	5.24 (0.0019)**	18.40 (<.0001)****
	Site*distance	0.89 (0.5367)	2.23 (0.0240)*	1.70 (0.0951)	1.53 (0.1429)
	Habitat*distance	0.81 (0.5647)	0.51 (0.8004)	1.76 (0.1131)	1.42 (0.2118)
	Site*habitat*distance	0.88 (0.5466)	0.68 (0.7292)	1.13 (0.3457)	0.82 (0.6010)
	Fall	Site	12.60 (<.0001)**** TS ^A RL ^{AB} MI ^B CMS ^C	44.04 (<.0001)**** CMS ^A MI ^B RL ^C TS ^C	18.15 (<.0001)**** RL ^A TS ^A MI ^B CMS ^C
Habitat		5.35 (0.0005)** Aquaculture ^A Created ^{AB} SMF ^{AB} Natural ^{AB} IMF ^B	13.83 (<.0001)**** IMF ^A Natural ^A SMF ^A Created ^A Aquaculture ^A	2.86 (0.0610)	2.84 (0.0620)
Distance		0.69 (0.5568)	0.67 (0.5699)	0.33 (0.8001)	0.67 (0.5706)
Site*habitat		1.58 (0.1370)	6.37 (0.0005)**	4.74 (0.0036)**	3.92 (0.0103)*
Site*distance		1.42 (0.1876)	1.85 (0.0650)	1.54 (0.1420)	0.89 (0.5358)
Habitat*distance		0.99 (0.4350)	0.69 (0.6612)	1.19 (0.3167)	1.73 (0.1188)
Site*habitat*distance		1.05 (0.4054)	0.68 (0.7243)	0.86 (0.5591)	0.74 (0.6711)

Table 4 Results for mean abundance of feeding modes using a by season 3-way ANOVA with site, habitat, and distance. Shown are F-values and (p-values) with significant differences (p<0.05) indicated by an asterisk. SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values. RL=Research Lease, MI=Masonboro Island, TS=Topsail, ISF=intertidal mud flat, and SMF=subtidal mud flat.

Season		Direct deposit	Indirect deposit	Predator-grazer	Suspension feeder
Spring	Site	47.41 (<.0001)**** RL ^A TS ^B CMS ^C MI ^D	36.10 (<.0001)**** CMS ^A MI ^B RL ^C TS ^C	5.79 (0.0010)*** TS ^A RL ^B CMS ^B MI ^B	46.36 (<.0001)**** TS ^A RL ^B CMS ^B MI ^C
	Habitat	7.82 (0.0006)*** IMF ^A Created ^A Aquaculture ^A Natural ^A SMF ^B	4.20 (0.0171)	3.83 (0.0242)* Created ^A Aquaculture ^A SMF ^A Natural ^A IMF ^A	73.24 (<.0001)**** Aquaculture ^A SMF ^B Created ^C Natural ^C IMF ^C
	Distance	0.51 (0.6761)	1.24 (0.2987)	1.22 (0.3052)	0.78 (0.5056)
	Site*habitat	16.79 (<.0001)****	9.63 (<.0001)****	10.84 (<.0001)****	47.80 (<.0001)****
	Site*distance	1.16 (0.3253)	1.72 (0.0899)	1.53 (0.1433)	0.99 (0.4510)
	Habitat*distance	0.75 (0.6074)	1.03 (0.4112)	2.71 (0.0164)*	2.78 (0.0142)*
	Site*habitat*distance	1.78 (0.0780)	0.70 (0.7105)	2.92 (0.0035)**	2.93 (0.0034)**
	Fall	Site	11.83 (<.0001)**** RL ^A TS ^A CMS ^B MI ^B	37.64 (<.0001)**** CMS ^A RL ^B MI ^C TS ^C	34.77 (<.0001)**** RL ^A TA ^B CMS ^B MI ^C
Habitat		2.89 (0.0592)	4.64 (0.0113)*	8.62 (0.0003)*** Natural ^A SMF ^A Created ^A Aquaculture ^A IMF ^A	2.48 (0.0878)
Distance		0.78 (0.5089)	0.91 (0.4371)	1.02 (0.3881)	2.58 (0.0563)
Site*habitat		12.84 (<.0001)****	3.13 (0.0281)*	15.99 (<.0001)****	6.57 (0.0004)***
Site*distance		1.43 (0.1816)	1.63 (0.1129)	1.27 (0.2617)	1.16 (0.3248)
Habitat*distance		1.79 (0.1054)	0.81 (0.5617)	0.51 (0.8018)	0.90 (0.4992)
Site*habitat*distance		0.45 (0.9039)	0.90 (0.5301)	0.46 (0.8958)	0.33 (0.9647)

Table 5 Mean abundance of each feeding mode and living position by season and site.

Functional group	<u>Research Lease</u>		<u>CMS</u>		<u>Masonboro Island</u>		<u>Topsail</u>	
	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
<u>Feeding Mode</u>								
Direct deposit	50.69 (2.89)	16.08 (1.58)	26.98 (1.90)	7.73 (1.23)	9.00 (0.95)	5.15 (1.01)	37.53 (3.37)	13.38 (1.74)
Indirect deposit	10.22 (1.08)	18.36 (2.13)	28.25 (2.77)	30.93 (2.13)	19.80 (2.18)	11.05 (1.47)	9.53 (1.12)	8.71 (1.01)
Predator-grazer	8.69 (1.02)	11.03 (1.41)	5.85 (0.74)	1.80 (0.30)	4.15 (0.56)	1.60 (0.36)	16.58 (3.50)	5.45 (0.63)
Suspension feeder	3.28 (0.37)	2.75 (0.54)	2.38 (0.39)	0.58 (0.18)	0.28 (0.08)	0.23 (0.08)	7.96 (1.27)	1.73 (0.25)
<u>Living Position</u>								
Deep burrower	17.31 (1.33)	9.75 (1.32)	18.00 (1.59)	6.03 (0.95)	4.58 (0.66)	3.53 (0.84)	23.95 (2.86)	6.04 (1.05)
Shallow burrower	40.78 (2.71)	15.69 (1.62)	11.73 (0.94)	2.68 (0.51)	7.20 (0.71)	1.98 (0.33)	16.32 (1.59)	8.59 (0.90)
Surface dweller	0.50 (0.14)	0.78 (0.18)	2.33 (0.52)	0.58 (0.20)	1.10 (0.23)	0.98 (0.36)	7.44 (1.57)	2.29 (0.39)
Tube dweller	11.08 (1.11)	19.25 (2.38)	29.08 (2.77)	31.18 (2.16)	20.08 (2.20)	11.35 (1.51)	16.07 (2.99)	10.70 (1.09)
Sedentary	3.22 (0.37)	2.75 (0.54)	2.33 (0.38)	0.58 (0.18)	0.28 (0.08)	0.20 (0.08)	7.82 (1.26)	1.66 (0.25)

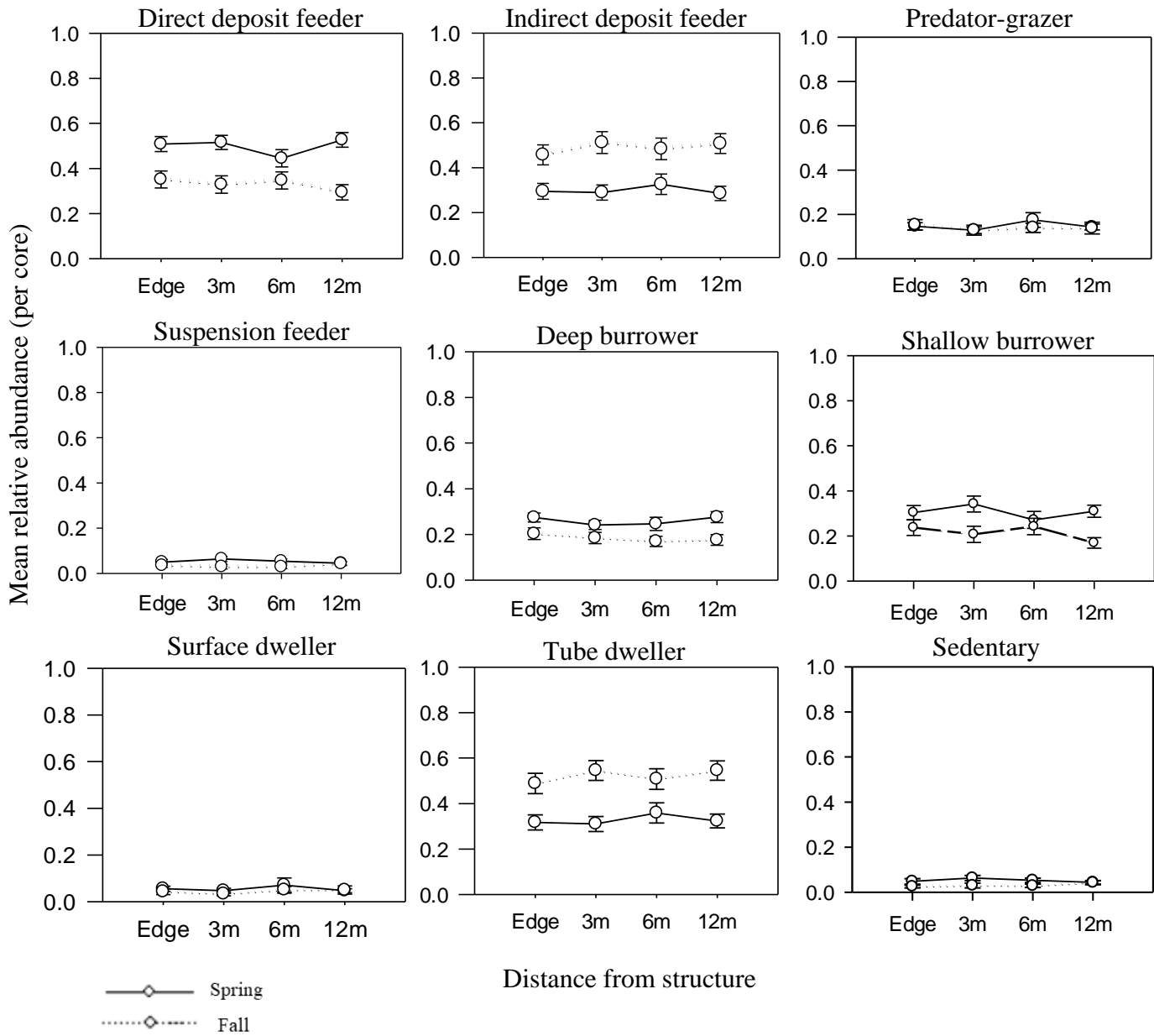


Fig 3 Mean relative abundance by season of feeding modes and living positions with distance (edge, 3m, 6m, and 12m) from oyster structures. Means (+/- SE) are combining aquaculture, created oyster reef, and natural oyster reef habitats.

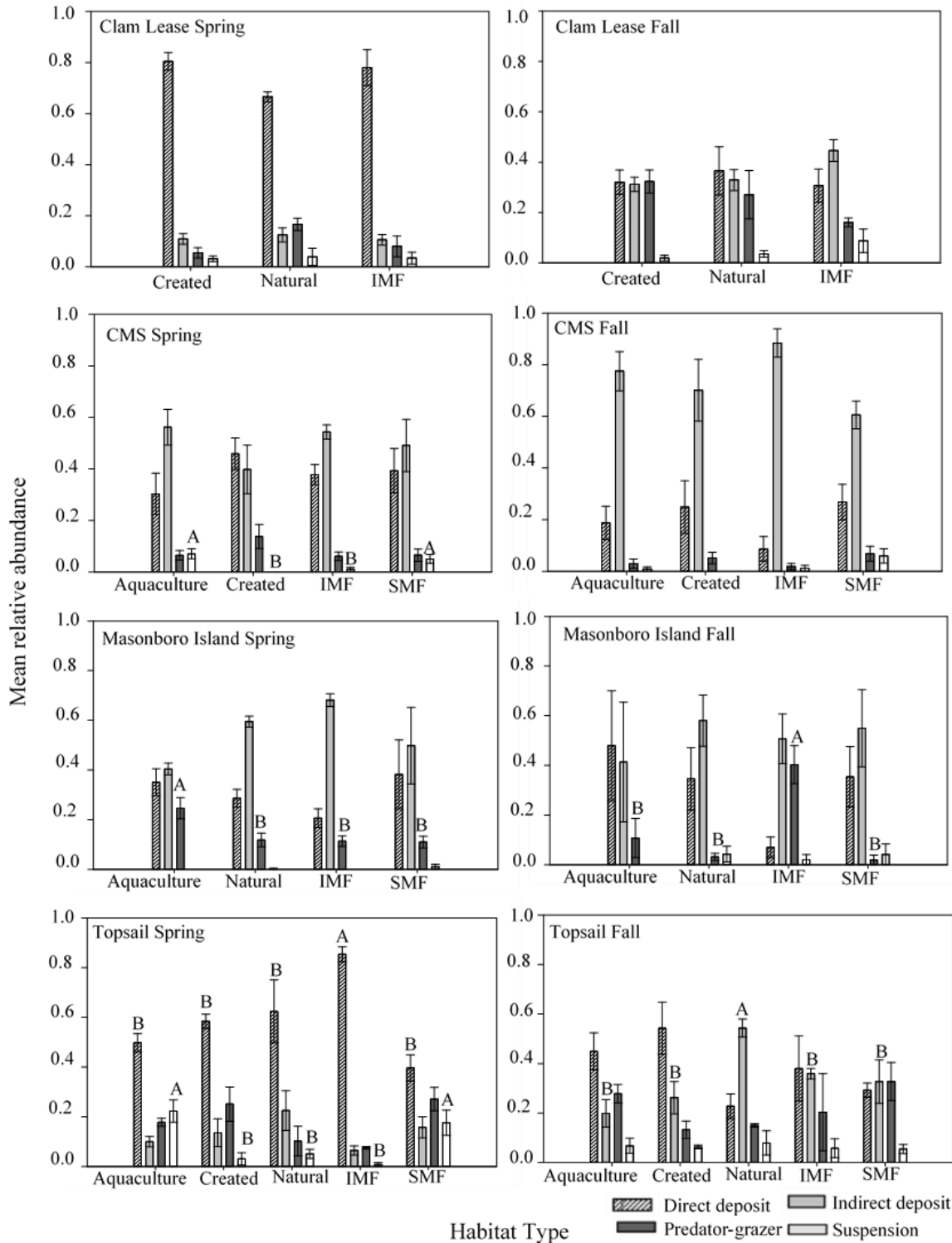


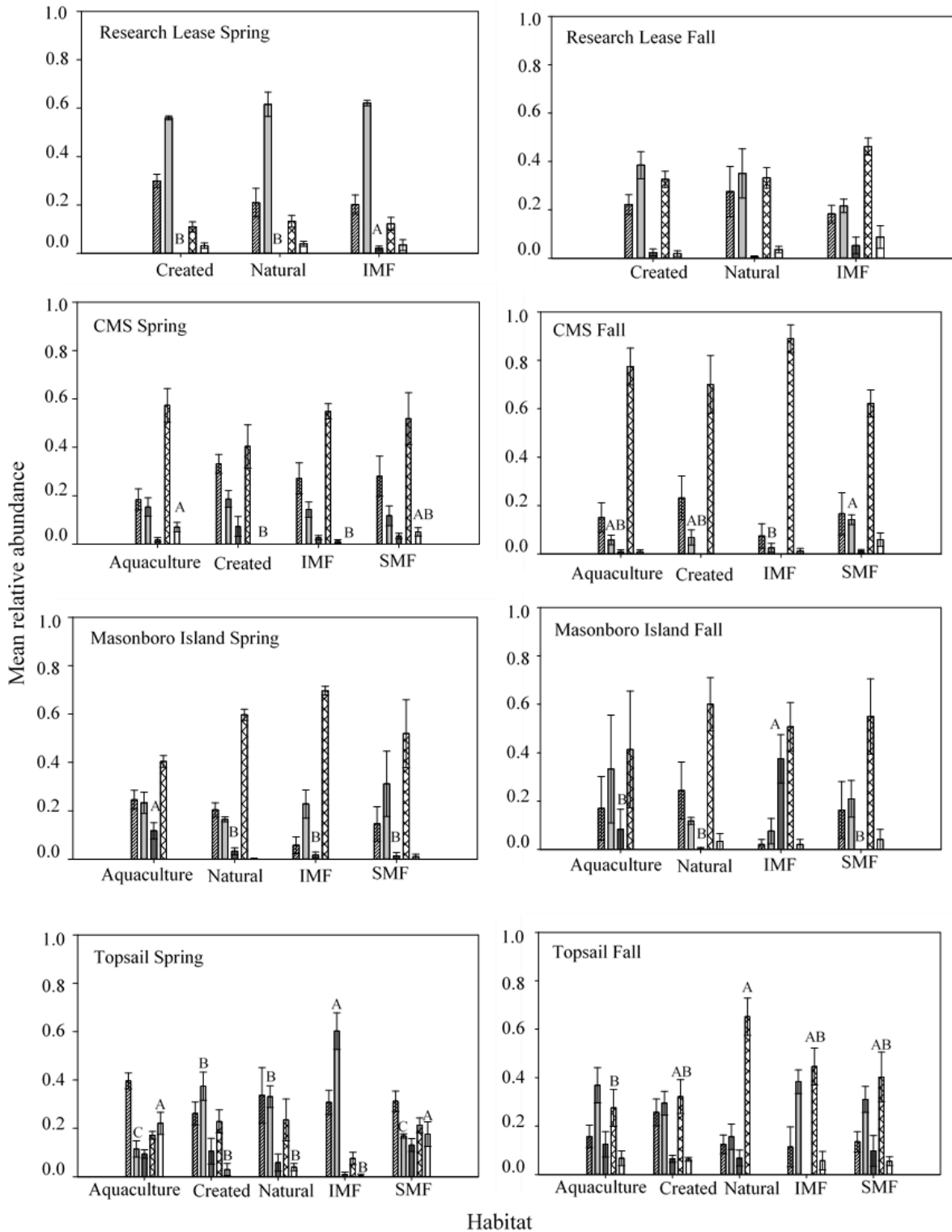
Fig 4 Mean relative abundance (+/- SE) by season and site of each feeding mode with respective habitats (only edge distances considered for oyster structures). Letters indicate when modes were significantly different by habitat type and indicate rank of habitat. ISF=inter-tidal mud flat and SMF=sub-tidal mud flat

Table 6 Results for mean relative abundance of living positions using a by season 3-way ANOVA with site, habitat, and distance. Shown are F-values and (p-values) with significant differences (p<0.05) indicated by an asterisk. SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values. RL=Research Lease, MI=Masonboro Island, TS=Topsail, IMF=intertidal mud flat, and SMF=subtidal mud flat.

Season		Deep burrower	Shallow burrower	Surface dweller	Tube dweller	Sedentary
Spring	Site	22.12 (<.0001)**** TS ^A CMS ^{AB} RL ^B MI ^C	46.09 (<.0001)**** RL ^A TS ^B MI ^C CMS ^C	5.22 (0.0020)** TS ^A CMS ^B MI ^B RL ^B	85.85 (<.0001)**** MI ^A CMS ^B TS ^C RL ^D	35.25 (<.0001)**** TS ^A RL ^B CMS ^B MI ^C
	Habitat	6.57 (0.0019)** Aquaculture ^A Created ^A SMF ^A Natural ^A IMF ^A	12.56 (<.0001)**** IMF ^A Created ^A Natural ^A SMF ^B Aquaculture ^B	0.31 (0.7325)	2.92 (0.0577) SMF ^A Aquaculture ^A IMF ^A Natural ^A Created ^B	43.19 (<.0001)**** Aquaculture ^A SMF ^A Created ^B Natural ^{BC} IMF ^C
	Distance	0.98 (0.4066)	2.32 (0.0785)	0.38(0.7657)	1.17 (0.3247)	1.26 (0.2904)
	Site*habitat	13.56 (<.0001)****	14.30 (<.0001)****	0.16(0.9198)	2.70 (0.0485)*	18.77 (<.0001)****
	Site*distance	1.47 (0.1671)	1.16(0.3240)	1.65 (0.1074)	2.00 (0.0444)*	1.40 (0.1925)
	Habitat*distance	0.95 (0.4610)	0.48(0.8231)	0.93 (0.4734)	0.38 (0.8922)	1.25 (0.2867)
	Site*habitat*distance	1.51 (0.1503)	0.58 (0.8107)	0.65 (0.7525)	0.59 (0.8019)	0.79 (0.6264)
	Fall	Site	1.64 (0.1835)	28.64 (<.0001)**** RL ^A TS ^A MI ^B CMS ^C	11.859(<.0001)**** MI ^A TS ^A RL ^B CMS ^B	32.18 (<.0001)**** CMS ^A MI ^B TS ^C RL ^C
Habitat		0.55 (0.5800)	6.29 (0.0025)** Created ^A SMF ^A Natural ^A Aquaculture ^A IMF ^A	1.73 (0.1818) IMF ^A Created ^B Aquaculture ^B SMF ^B Natural ^B	9.20 (0.0002)*** IMF ^A Natural ^A SMF ^A Aquaculture ^A Created ^A	5.21 (0.0067)** SMF ^A IMF ^A Aquaculture ^A Created ^A Natural ^A
Distance		0.47 (0.7068)	1.68 (0.1736)	0.42 (0.7359)	0.77 (0.5101)	1.02 (0.3851)
Site*habitat		1.53 (0.2091)	3.43 (0.0191)*	3.16 (0.0271)*	5.00 (0.0026)**	6.59 (0.0004)***
Site*distance		1.38 (0.2049)	0.95 (0.4820)	0.82 (0.6012)	1.54 (0.1394)	0.65 (0.7487)
Habitat*distance		1.91 (0.0836)	1.24 (0.2884)	1.64 (0.1411)	0.64 (0.6962)	0.98 (0.4390)
Site*habitat*distance		1.22 (0.2863)	0.84 (0.5777)	1.54 (0.1420)	0.60 (0.7928)	0.68 (0.7290)

Table 7 Results for mean abundance of living positions using a by season 3-way ANOVA with site, habitat, and distance. Shown are F-values and (p-values) with significant differences (p<0.05) indicated by an asterisk. SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values. RL=Research Lease, MI=Masonboro Island, TS=Topsail, ISF=intertidal mud flat, and SMF=subtidal mud flat.

Season		Deep burrower	Shallow burrower	Surface dweller	Tube dweller	Sedentary
Spring	Site	21.90 (<.0001)**** TS ^A CMS ^B RL ^B MI ^C	83.94 (<.0001)**** RL ^A TS ^B CMS ^C MI ^D	7.55 (0.0001)*** TS ^A CMS ^B MI ^B RL ^B	11.96 (<.0001)**** CMS ^A MI ^B TS ^{BC} RL ^C	46.52 (<.0001)**** TS ^A RL ^B CMS ^B MI ^C
	Habitat	22.14 (<.0001)**** Aquaculture ^A Created ^{AB} IMF ^{AB} SMF ^B Natural ^B	4.33 (0.0151)* IMF ^A Natural ^A Created ^A Aquaculture ^B SMF ^B	6.05 (0.0031)** Created ^A Aquaculture ^A SMF ^A IMF ^A Natural ^A	0.75 (0.4722) Aquaculture ^A SMF ^B Created ^C Natural ^C IMF ^C	74.62 (<.0001)**** Aquaculture ^A SMF ^B Created ^C Natural ^C IMF ^C
	Distance	0.73 (0.5356)	0.66 (0.5775)	0.48 (0.6937)	0.81 (0.4880)	0.82 (0.4847)
	Site*habitat	22.70 (<.0001)****	28.93 (<.0001)****	5.72 (0.0001)***	9.19 (<.0001)****	49.23 (<.0001)****
	Site*distance	0.81 (0.6104)	1.78 (0.0771)	1.16 (0.3282)	1.19 (0.3062)	0.98 (0.4621)
	Habitat*distance	0.85 (0.5319)	0.35 (0.9083)	1.86 (0.0932)	0.94 (0.4716)	2.68 (0.0174)*
	Site*habitat*distance	1.53 (0.1441)	1.81 (0.0725)	2.02 (0.0416)*	1.18 (0.3161)	2.80 (0.0049)**
	Fall	Site	5.17 (0.0021)** RL ^A TS ^B CMS ^B MI ^B	52.07 (<.0001)**** RL ^A TS ^B CMS ^C MI ^C	6.54 (0.0004)*** TS ^A MI ^B RL ^B CMS ^B	30.83 (<.0001)**** CMS ^A RL ^B MI ^C TS ^C
Habitat		0.89 (0.4121)	7.47 (0.0009)*** Natural ^A Created ^A Aquaculture ^A SMF ^A IMF ^A	2.71 (0.0706)	3.70 (0.0273)* IMF ^A Created ^A Aquaculture ^A Natural ^A SMF ^A	2.95 (0.0560)
Distance		1.05 (0.3715)	1.71 (0.1690)	0.48 (0.6989)	1.25 (0.2933)	2.79 (0.0431)* 12m ^A IMF ^A SMF ^A Edge ^A 6m ^A 3m ^A
Site*habitat		6.95 (0.0002)***	25.15 (<.0001)****	4.1 (0.0081)**	3.63 (0.0148)*	7.62 (<.0001)****
Site*distance		1.26 (0.2675)	1.62 (0.1161)	0.74 (0.6692)	1.63 (0.1145)	1.00 (0.4430)
Habitat*distance		1.77 (0.1112)	1.09 (0.3721)	0.27 (0.9486)	0.86 (0.5250)	0.91 (0.4935)
Site*habitat*distance		0.68 (0.7277)	0.55 (0.8324)	0.45 (0.9026)	1.02 (0.4251)	0.33 (0.9650)



Deep Burrower
 Shallow Burrower
 Surface Dweller
 Tube Dweller
 Sedentary

Fig 5 Mean relative abundance (+/-SE) by season and site of each living position with respective habitats (only edge distances considered for oyster structures). Letters indicate when positions were significantly different by habitat type and indicate rank of habitat. ISF=intertidal mud flat and SMF=subtidal mud flat.

Table 8 Results for mean nekton abundances in seine nets using a 3-way ANOVA and Breder trap using a 4-way ANOVA. Shown are F-values and (p-values) with significant differences ($p < .05$) indicated by an asterisk. SNK rankings are shown in decreasing order, with different superscripts indicating statistically different values. Seine nets do not have a distance. ISF= intertidal mud flat, SMF=subtidal mud flat.

Variable	Seine Net	Breder Traps
Month	4.69 (0.0125)*	0.91 (0.4061)
Site	July ^A August ^A September ^B 21.90 (<.0001)**** CMS ^A Masonboro ^B Research Lease ^B	12.96 (<.0001)**** CMS ^A Masonboro ^B Research Lease ^B
Habitat	22.37 (<.0001)**** Created ^A IMF ^B Natural ^B Aquaculture ^B SMF ^B	17.34 (<.0001)**** Created ^A Natural ^B Aquaculture ^B SMF ^B IMF ^B
Distance	----	2.26 (0.0834)
Month*site	3.03 (0.0234)	0.40 (0.9967)
Month*habitat	1.86 (0.0820)	0.31 (0.8717)
Month*distance	----	0.65 (0.6905)
Site*habitat	10.87 (<.0001)****	12.31 (0.0006)***
Site*distance	----	2.08 (0.0584)
Habitat*distance	----	2.02 (0.0660)
Month*site*habitat	1.44 (0.1953)	0.17 (0.8449)
Month*site*distance	----	0.72 (0.7353)
Month*habitat*distance	----	0.56 (0.8693)
Site*habitat*distance	----	1.93 (0.1270)
Month*site*habitat*distance	----	0.57 (0.7556)

Table 9 Mean percent survivorship (+/- SE) of clams from uncaged and caged treatments at the Research Lease and Masonboro sites Differences in percent survivorship were most pronounced between sites. Percent survivorship was marginal differences among habitats within site.

Habitat type	Distance from structure	Research Lease		Masonboro	
		Uncaged mean percent survivorship	Caged mean percent survivorship	Uncaged mean percent survivorship	Caged mean percent survivorship
Aquaculture operation	Edge	----	----	57.8 (12.3)	98.8 (0.7)
	3m	----	----	52.8 (14.7)	97.2 (1.8)
	6m	----	----	42.8 (16.2)	100 (0)
	12m	----	----	47.8 (11.2)	99.4 (0.5)
Created oyster reef	Edge	83.3 (10.1)	96.6 (1.8)	----	----
	3m	57.8 (14.6)	98.8 (1.1)	----	----
	6m	88.3 (4.0)	98.3 (0.8)	----	----
	12m	75.0 (10.9)	98.3 (0.8)	----	----
Natural oyster reef	Edge	95.0 (2.2)	99.4 (0.5)	41.1 (15.2)	98.8 (0.7)
	3m	94.4 (2.7)	99.4 (0.5)	72.2 (9.2)	100 (0)
	6m	92.8 (2.2)	99.4 (0.5)	46.7 (11.1)	100 (0)
	12m	89.4 (3.9)	99.4 (0.5)	75.0 (7.7)	99.4 (0.5)
Intertidal mud flat	----	87.2 (4.2)	98.8 (1.1)	56.7 (10.7)	99.4 (0.5)
Subtidal mud flat	----	----	----	59.4 (13.4)	96.6 (1.8)

DISCUSSION

This study demonstrated strong site differences in benthic infaunal community assemblages as has been reported elsewhere (Johnson 1970; Hyland et al. 2004). Infaunal functional guild relative representation, actual abundances of infauna, and predator utilization of habitats was influenced by structural (structured vs. non-structured habitats). Strong site-habitat interactions indicated differential use of habitats among sites and occasionally habitat differences were detectable within one site but not in a different site. A halo pattern was seen for several infauna taxa (Cirratulidae, Orbiniidae, and juvenile bivalve species), but effects appeared to be minor relative to by habitat differences, season, and site factors. Benthic infauna are influenced by sediment grain size (Bloom et al. 1972), seasonality (Boesch 1973; Posey et al. 1998), availability of food and space (Posey et al. 2006), and higher trophic level predator foraging (Posey and Hines 1991) all of which have probably contributed to the patterns observed in this study.

In this study, benthic infauna richness, showed strong site and temporal differences. All sites were different in mean richness in the spring. In the fall mean richness was similar among the Research Lease and Topsail sites and the CMS and Masonboro sites. Most functional group interactions were detected in the spring; this aligned with a period when mean infauna abundances were also greater, with increased number of infauna taxa possibly causing more pronounced functional group patterns. Mean richness showed habitat effects within sites. At the Masonboro and Topsail sites mean richness was greatest at oyster structures. There is probably a combination of factors such as differences in sediment grain size, structure associated biogenic processes, and predator foraging influencing benthic infauna community composition between structured and unstructured habitats.

Grain size and environmental effects

The three feeding modes that showed site specific habitat responses may be attributed to differences in sediment grain size among sites and between habitats within sites. At Topsail and CMS suspension feeders were proportionally dominant at aquaculture and subtidal mud flats which had a lower proportion of silt-clay compared to other habitats within the sites. Also, at Topsail direct deposit feeders were most represented at intertidal mud flats and indirect deposit feeders were dominant at the natural reef. Both the intertidal mud flat and natural reef had greater silt-clay ratios compared to other habitats within the Topsail site. Grain size can influence efficacy of feeding modes making different modes advantageous under specific sediment sizes. This could explain the feeding mode patterns observed. Suspension feeders are more common in sandier sediments and direct deposit feeders are more common in finer sediments due to sediment stability (Sanders 1958). The pattern for indirect deposit feeders could have been observed because of fine sediments coupled with reef associated biogenic processes leading to the transport of organic materials to adjacent sediments where it would be available and attainable to the group (Dame 1999). Living position groups also showed a response possibly due to sediment grain size. Aquaculture and subtidal mud flat habitats at the Topsail and CMS site had a lower percentage of silt-clay compared to other habitats within the sites. Sedentary infauna, which were all juvenile bivalves (<10mm) in this study, at Topsail and CMS had greatest proportional dominance at the aquaculture operations and subtidal mud flat habitats.

The observed site differences for feeding modes and living positions could be due to the natural heterogeneity of soft-bottom infauna communities (Johnson 1970; Hyland et al. 2005). Mean abundances for all functional groups were different among sites. For example, sedentary infauna had a greater mean abundance by at least 2-fold at the Topsail site in the spring

compared to any of the other sites. Temporal differences observed in the functional group could also be explained by seasonal variations in food supply, timing and success of recruitment, and greater predator foraging in the summer (Hines et al. 1989; Posey et al. 1998).

Predator foraging effects

The two living positions that showed site specific habitat responses may be due to differences in predator foraging among sites and between habitats within sites. Surface dwellers at the Research Lease and Masonboro were proportionally dominant at the intertidal mud flat compared to oyster structures. Shallow burrowers were proportionally dominant and had greatest mean abundances at intertidal mud flats and natural and created oyster reefs. At Topsail shallow burrowers were most common at intertidal mudflats, had intermediate representation at natural and created oyster reefs and had lowest representation at aquaculture operations and subtidal mudflats. These patterns could be an effect of intermediate predators (ie. *Callinectes* spp., *Palaemonetes* spp., and *Leiostomus xanthurus*) foraging on soft-bottoms adjacent to structural habitats or of attraction of predators to the reef edge with the rising tide. This may reflect higher nekton abundances near structures in intertidal areas as well as continual susceptibility at subtidal habitats (Lehnert and Allen 2002; Meyer and Posey 2009).

Halo impacts

Despite strong site and habitat impacts, halos were still detected for a few taxa. Cirratulidae (direct deposit feeder/shallow burrower) had a detectable distance effect which trended towards greater representation near structures at the edge and 3m distance and lower representation at 6m and 12m distances. When seasons were taken into consideration the previously observed pattern for Cirratulidae only held true in the spring. This is consistent with a halo that relates to a zone of

reduced predation related to interactive effects of off-reef foraging and non-reef foraging (Ambrose and Anderson 1990; Posey and Ambrose 1994). In addition, Orbiniidae (direct deposit feeders/shallow burrower) and juvenile bivalve species (suspension feeders/ sedentary) showed a relationship with distance from structure in the fall having lower proportional dominance near structures and increasing with distance away from structure. This halo is consistent with impact of reef-associated predators or short distance environmental impacts of the reef structure (Ambrose and Anderson 1990; Posey et al.1992). As shown in the clam outplant experiment, predators use of habitats was different among sites but not between habitats within a site. Several taxa showed habitat specific effects, this was perhaps because physical effects of the habitat created a suitable environment. Halos possibly exist in estuarine soft-bottom communities but are limited to a small area and difficult to detect because there are a combination of factors, such as resource and space availability, deposition of nutrients, and intense predation, overwhelming distance effects.

Effects of structural vs. non-structural habitats

Impact of habitat on functional groups showed some general habitat patterns, especially general differences between oyster structures and non-structured (mud flat) habitats. Differences in guild representation were observed for direct and indirect deposit feeders and may be explained by environmental factors. Direct deposit feeders were proportionally dominant and had greater actual mean abundances at structural habitats. Oyster structures cause turbulence in the boundary layer leading to deposition or resuspension of material creating unstable bottom conditions that can be better tolerated by this group (Levinton 1972; Aller and Dodge 1974). Indirect deposit feeders were proportionally dominant at unstructured habitats. Indirect deposit feeders may be more common on barren bottoms outside of the oyster structures because of availability of

surface space with direct contact to the overlaying water (Woodin 1974; Brenchley 1982). Differences in guild representation was also observed for tube dwellers and surface dwellers and can be explained by predators' use of habitat. Surface dwellers had greatest proportional representation at non-structured habitats (intertidal and subtidal mud flats). Tube dwellers were proportionally dominant and deep burrowers had greater actual means at structured habitats (aquaculture and natural reefs). Surface dwellers are susceptible to predation by nekton while tube dwellers and deep burrowers can seek refuge that is out of reach from nekton patrolling the soft-bottoms (Kneib and Stiven 1972; Posey and Hines 1991). Surface dwellers low representation adjacent to structural habitats could be due to off-reef predation by nekton. In this study Breder traps and seine net catches showed greater utilization of structured habitats by finfish and decapods. Particularly by *L. xanthurus*, *Callinectes* spp., *P. vulgaris*, and *Penaeidae* spp. which are known predators of benthic infauna (Virnstein 1977; Nelson 1981).

Conclusion

In this study a halo effect wasn't consistently detected in infaunal communities adjacent to estuarine oyster structures. This could possibly be due to the scaling effect of the habitat since offshore reefs extended several miles while the oyster habitats are on the scale of several meters. However, significant differences in use of structural and non-structural habitat was observed, though patterns of structural habitat use differed among sites. This provides some caution in extrapolation of habitat use patterns from work conducted in a single, local location. We can provide insight on habitat function of shellfish aquaculture compared to wild or restored oyster reefs. Structural habitats, regardless if it is an oyster reef or shellfish aquaculture operation, have similar effects on infauna functional guild representation and habitat use by nekton. Replacement of soft-bottoms with man-made oyster structures will provide similar habitat functions to that of

wild oyster reefs. However, the strong site differences observed in the study suggest the degree to which environmental processes and predator foraging influence infauna communities is site specific. Strong site differences emphasize the need to include various sites in habitat studies as there is differential habitat use among sites.

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