

The influence of habitat characteristics on intertidal oyster *Crassostrea virginica* populations

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ABSTRACT: Habitat heterogeneity is increased in natural systems via habitat loss and fragmentation, which decreases the patch size and alters the amount of edge relative to interior. However, our understanding of how increased habitat heterogeneity influences population dynamics, particularly set within a large scale marine landscape, is relatively incomplete. Eastern oyster *Crassostrea virginica* populations have drastically declined resulting in fragmentation within and among reefs, thus altering reef size and distances from edge to interior. Over 2 yr (2011 to 2012), we evaluated oyster populations relative to varying distances from the reef edge to interior locations, habitat patch size, and reef type on naturally occurring intertidal fringing and patch reefs in southeastern North Carolina. Additionally, the influences of distance from edge to interior locations and habitat patch size were examined for oyster populations on 3 size classes of created intertidal reefs at 2 locations. The habitat characteristics examined significantly influenced oyster populations, with increased densities towards interior locations on a reef, a trend of overall higher densities on intermediate sized reefs, significantly greater densities on natural patch reefs compared to natural fringing reefs. Density and recruitment patterns suggested differences between edge and interior locations. However, other population characteristics, such as oyster condition and shell height, indicated there may be ecological trade-offs among the habitat characteristics examined. These results suggest intertidal reefs cannot be considered a uniform whole and may have substantially different habitat characteristics, which should be taken into account when further examining habitat fragmentation and restoration success.

KEY WORDS: Landscape · Habitat heterogeneity · Patch size · Edge effect · Eastern oyster · *Crassostrea virginica* · Habitat fragmentation · Habitat restoration

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INTRODUCTION

As ecosystems become increasingly altered due to anthropogenic impacts, assessing and understanding how populations respond to increasing habitat heterogeneity is a key aspect of efforts to maintain biodiversity and prevent further species loss (Fahrig 2003, Laurance 2008). Habitat heterogeneity can be exacerbated via habitat loss and fragmentation, causing patches to become smaller and increasingly dominated by edge, while the interior, and its unique

characteristics, are lost (Ries & Sisk 2004). The response of a population to a heterogeneous landscape, in terms of size and shape of habitat patches, is vital to understand because the arrangement, and potential alteration, of habitat patches can strongly influence abundance and distribution (Bender et al. 1998, Holyoak 2000). For example, dynamics of a habitat patch can be altered by highly mobile species with the ability to survive disturbances and to rapidly colonize disturbed habitat patches (Thomas 2000). This response can be particularly important for species

that are periodically sedentary, such as the eastern oyster *Crassostrea virginica*, whose life history characteristics prevent movement between habitat patches after larval settlement. Therefore, understanding how habitat patch characteristics such as patch type, patch size, and distance from the edge to interior influence a sedentary species with larval dispersal can be particularly important for understanding the population's response to a changing landscape.

The understanding of patch structure, patch connectivity, and the ecological consequences of patch alteration is well understood in many terrestrial habitat types (e.g. Bender et al. 1998, Kosydar et al. 2014). Within marine systems, studies of the consequences of an altered landscape have historically been limited to the context of seagrass and saltmarsh systems (Boström et al. 2011), with only a recent focus on oyster reefs (e.g. Harwell et al. 2011, Smyth et al. 2015). Seagrass and marsh habitats are naturally patchy habitats that have experienced increased fragmentation from natural and anthropogenic forces, which has caused a drastic alteration in the seascape and, subsequently, decreased primary production and increased plant mortality (Craft et al. 1999, Bologna & Heck 2002). These changes can subsequently alter the composition of macroinvertebrate assemblages and produce a pronounced difference in species abundances (Minello & Rozas 2002, Smith et al. 2008, Macreadie et al. 2010). Restoration efforts to mitigate for the loss of these habitat types have created habitat patches with varied edge-to-interior distances (Rozas & Minello 2007, Smith et al. 2010). Consequently, the varied sizes of natural and restored habitat patches for marsh and seagrass systems can impact both physical and biological processes (Peterson & Turner 1994, Reed & Hovel 2006), yet many of these processes remain largely unknown for altered oyster reef habitats (Boström et al. 2011, Smyth et al. 2015).

The eastern oyster is an ecologically and economically important species that creates 3-dimensional structure and habitat for fauna and epifauna on areas that would otherwise be unstructured bottom (Peterson et al. 2003, Grabowski 2004, Coen et al. 2007). Intertidal oyster reefs, which are the dominant form along the southeastern Atlantic coast of the United States, are subjected to tidal fluctuations, which influence faunal encounter patterns within the reefs, connectivity among reefs, and available feeding time for organisms on the reefs (Dame & Patten 1981, Fodrie et al. 2014, Byers et al. 2015). With an incoming tide, the reef edge is almost a 2-dimensional environment at the point of contact and tidal influx

and ebb makes the edge particularly important as a transitional zone affecting water flow, sedimentation, predator encounter, and utilization by mobile fauna (Lenihan 1999, Whitman & Reidenbach 2012). With increased habitat loss and fragmentation, the proportion of the reef edge that is in first contact with the tide will increase and the relative amount of interior habitat will decline, which can subsequently alter hydrodynamics and species interactions. Oyster reefs in the intertidal zone can exist as patch reefs, which are completely surrounded by open bottom habitat or fringing reefs which border *Spartina alterniflora* marsh or upland areas (McCormick-Ray 2005, van de Koppel et al. 2015). Within an intertidal system, these reefs differ, since fringing reefs have a single encounter edge for an incoming tide, while patch reefs have multiple access points. While both patch and fringing intertidal reefs are common within the southeastern United States (Byers et al. 2015), the functional differences between these 2 intertidal reef types, in terms of oyster population dynamics, remain unclear.

Oyster populations have drastically declined within the last century due to overfishing, eutrophication, disease, disturbances, deposition of sediments and other pollutants (Lenihan & Peterson 1998, Coen & Luckenbach 2000, Beck et al. 2011). The decline in oyster abundances has increased reef fragmentation, causing the reefs to shift from expansive reefs to smaller, more isolated, patches and fringes. Some consequences of fragmentation have been evaluated for organisms utilizing smaller reefs on the scale of 1 to 10 m² (Eggleston et al. 1998, 1999, Harwell et al. 2011). However, the impact of fragmentation on oyster population dynamics has not been fully evaluated, especially as it relates to change in habitat type for larger sized reefs, which dominate most intertidal areas along the southeastern coast of the United States. As oyster populations and subsequently the sizes of oyster reef patches have declined, the amount of interior on the reef has decreased relative to the reef edge. The response to a changing landscape, specifically for altered distances from edge to interior habitats, can vary with life history traits, with some species being more sensitive to the increase of edge habitat than others (Ewers & Didham 2006). The distribution of several organisms inhabiting intertidal oyster reefs differs between the edge and interior (Harwell et al. 2011), but the response of intertidal oyster populations to differences in patch type, patch size, and edge versus interior patch size has been given little attention (McCormick-Ray 2005, Powers et al. 2009).

Substantial efforts have been made to restore the lost ecosystem services that oysters provide by artificially creating reefs (Coen et al. 2007). Artificially created oyster reefs (henceforth: created reefs) are used to increase shellfish resources, increase habitat for reef-associated organisms, and provide other services such as shoreline stabilization and water filtration (Meyer et al. 1997, Coen & Luckenbach 2000). Initially, created reefs are functionally different because they lack the greater 3-dimensional structure created by adult oysters in established or natural systems (Bartol et al. 1999, Meyer & Townsend 2000). Created reefs may quickly (~8 mo) trend towards oyster densities on natural reefs (Meyer & Townsend 2000), yet this varies with location and it can take multiple years before densities approach those on natural reefs (Powers et al. 2009, Schulte et al. 2009, Lipcius et al. 2015). Despite the increasing number of oyster reef restoration projects, and the successful establishment of oyster populations, many questions still remain regarding the dynamics on created reefs that may influence restoration design. These questions include issues related to the design of created reefs over a large spatial scale, such as the determination of optimal patch size and, consequently, the relative amount of edge versus interior habitat (Eggleston et al. 1998, Coen & Luckenbach 2000, Harwell et al. 2011).

This lack of knowledge of how habitat characteristics can influence oyster populations on created oyster reefs may have ecological implications for oyster populations and the organisms that utilize them, as well as hindering management decisions. To examine how habitat characteristics influenced intertidal oyster populations, in this study natural and created intertidal oyster reefs were used to evaluate how different reef types, reef sizes, and distances from reef edge to reef center influenced oyster density, reef characteristics, oyster size, condition, recruitment, and growth.

MATERIALS AND METHODS

In order to provide a comprehensive understanding of the 2 oyster habitat types, i.e. natural and created reefs, this research utilized a large-scale observational study of naturally occurring reefs and an independent large-scale experimental study, in which varying sized loose shell reefs were constructed. This approach provided an opportunity to independently observe and analyze spatial patterns for oyster populations on the various sizes of naturally occurring and

experimentally manipulated reefs, and to compare oyster densities on created reefs to those on a local reference reef. Thus, the main emphasis of this study was to observe spatial patterns independently for naturally occurring and created intertidal reefs. The observational study was conducted on a suite of naturally occurring fringing and patch intertidal oyster reefs (Table 1), and sought to examine how habitat characteristics of reef type, reef size, and edge-to-interior distances influenced oyster populations on these reefs. The large-scale experimental study utilized 3 replicate sets of 3 different sized created reefs from 2 different locations in southeastern North Carolina to evaluate how varying edge-to-center distances and reef sizes impacted intertidal oyster populations for these created reefs.

Study sites

Natural reefs

Naturally occurring oyster reefs (n = 22) were selected from the coastal tidal estuaries of Hewletts Creek, Howe Creek, and Masonboro Sound in Wilmington, NC, USA (Fig. 1A). The tidal creeks utilized in this study all have semidiurnal tides with a 1.1 m range (Dame et al. 2000) and mesohaline waters in the middle reaches of the creek. Salinity increases to close to that of 'full strength' seawater close to the Intracoastal Waterway (ICW) (Mallin et al. 2007). These tidal creeks have mainly sandy bottom habitats without submerged aquatic vegetation (SAV) (Cressman et al. 2003). Predator abundances are similar in all the creeks (Hanke 2014). Further, none of the reefs are subjected to legal harvest because they are in areas closed to shellfish harvest.

The fringing reefs selected for this study were chosen to have similar shape, adjacent habitat bordering a *Spartina alterniflora* marsh, a well-defined transition between reef and open bottom (no vegetation or other structured habitat), and similar tidal height (Fig. 2A). The patch reefs were all completely sur-

Table 1. Natural reefs in southeastern North Carolina (n = 22) used to study the influence of habitat characteristics on the intertidal oyster *Crassostrea virginica*, by reef type and size

Reef size	Reef type	
	Fringing	Patch
Small	4	3
Medium	4	5
Large	3	3

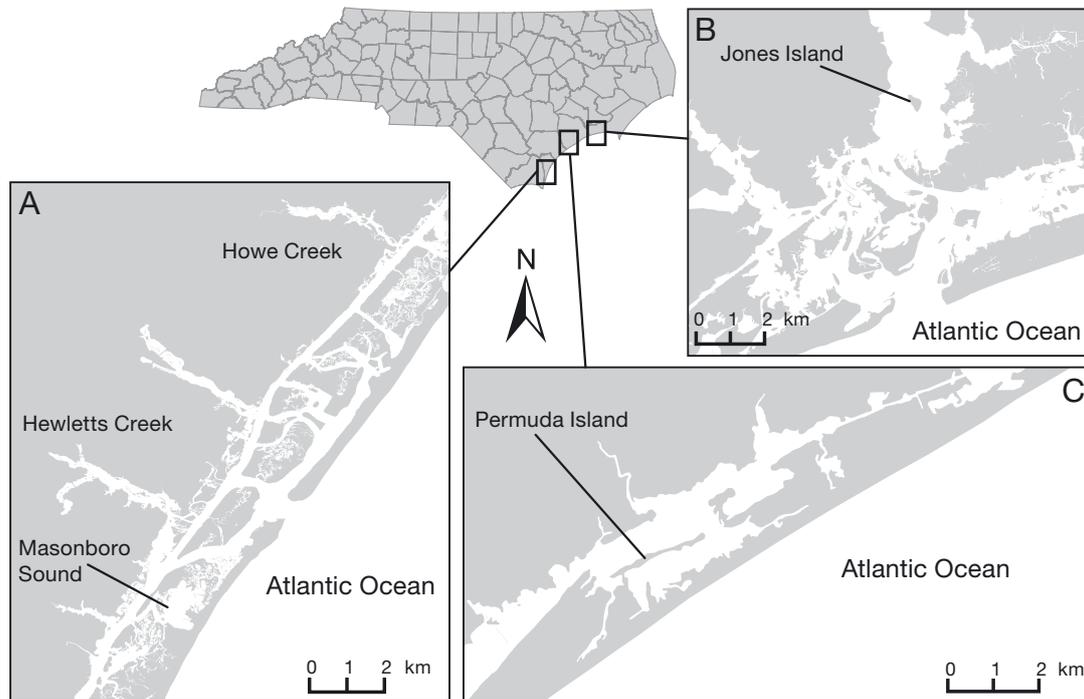
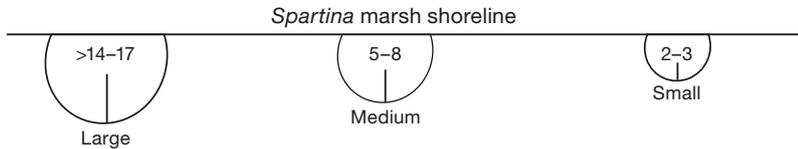
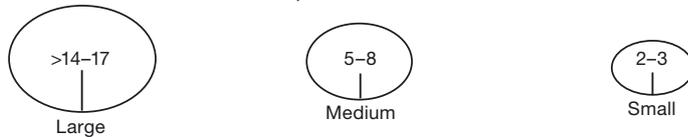


Fig. 1. Locations in southeastern North Carolina used to study the influence of habitat characteristics on the intertidal oyster *Crassostrea virginica*: (A) tidal creeks with naturally occurring intertidal reefs; sites of created reefs at (B) Jones Island and (C) Permuda Island

A) General schematic of natural fringing reefs



B) General schematic of natural patch reefs



C) General schematic of created reefs

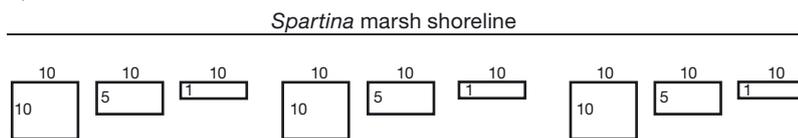


Fig. 2. Conceptual diagrams of natural and created reefs in southeastern North Carolina inhabited by the intertidal oyster *Crassostrea virginica*. The shapes of natural (A) fringing and (B) patch reefs are generalizations of the natural reef shapes, which were used in the sampling design. Sizes are shown as distance (m) from the reef edge to the interior of the reef. (C) The created reefs at Jones and Permuda Islands followed the same conceptual design, with 3 replicate sets of reefs measuring 10 × 10, 5 × 10, and 1 × 10 m (not shown to scale). All reefs at Permuda Island were constructed as shown in the diagram. At Jones Island, 2 sets of reefs were constructed as shown; in the third set, reefs were constructed in the order of 5 × 10, 1 × 10, and 10 × 10 m, due to field site constraints

rounded by open bottom habitat (no vegetation or other structured habitat), had a regular circular or oblong shape, and were also of similar tidal height (Fig. 2B). Further, for inclusion in this study, all reefs selected had a relatively similar tidal height at the reef interior, as many reefs in North Carolina tend to be flat (Byers et al. 2015). For both reef types, 3 size classes of reefs were selected based on the distance from the edge to interior of the reef: small (2–3 m distance to center), medium (5–8 m) and large (>14–17 m distance to center) (Table 1). These distances from edge to interior were selected because they represented the small, medium, and large sizes of oyster reefs naturally found within the tidal creeks of southeastern North Carolina, based on initial surveys. All reefs were measured along the longest axis of the reef in the geometric middle along the channel side, or the side of the reef that the tide will cover first (Fig. 2AB).

Created reefs

For the experimental study, oyster reefs were created in southeastern North Carolina from loose oyster shell at Jones (Fig. 1B) and Permuda (Fig. 1C) Islands during summer 2010. At each location, 3 replicate sets of oyster reefs were constructed by placing the loose oyster shell approximately 0.2 m deep on sandy substrate in areas without any SAV. Each replicate set of reefs consisted of 3 reefs, measuring 10 × 10, 5 × 10, and 1 × 10 m, with the long axis parallel to the shore, giving a total of 9 reefs constructed at each location (Fig. 2C). All reefs were set approximately 2 m from the shoreline, with a minimum of 3 m between each reef, and were representative of natural patches in the general area. The reefs were created to be fringing reefs and to help prevent marsh erosion; however, they were not directly adjacent to the marsh and all of the reefs function as discrete patches of habitat (Fig. 2C). At both locations, a nearby reference reef similar to the intermediate sized reefs (5 × 10 m) was selected to provide a comparison (Baggett et al. 2014). These reference reefs at Jones (34° 41' 23.43" N, 77° 5' 39.81" W) and Permuda (34° 28' 46.31" N, 77° 29' 22.88" W) were both <2.5 km from the constructed reefs. However, due to failure of the reference reef at Permuda Island, a new reference reef was selected for the second year of the study and only data from the second year were included in the analysis.

Sampling methods

Demography and reef characteristics

The natural and created reefs were sampled bi-annually in spring (May to June) and fall (October to December) for 2 yr (2011 to 2012). All of the natural oyster reefs were sampled at 1 and 3 m from the edge; the 3 m distance was selected because changes in edge effects have been observed at this distance for other marine habitats (e.g. Peterson & Turner 1994, Minello & Rozas 2002, Smith et al. 2008). The medium and large sized reefs were also sampled at the center location on the reef (5–8 m for medium and 14–17 m for large). At Jones and Permuda Islands, the 1 × 10 m plots were sampled with triplicate quadrates along the reef, whereas the 10 × 10 m, 5 × 10 m plots, and reference reef were sampled with triplicate quadrats along the lower edge (i.e. 2.5 m from edge), the center of the reef (i.e. 5 m from edge),

and the upper (shoreward) edge. At each sampling location, oyster density and size were recorded. Densities were initially sampled with a 0.25 m² quadrat: the shell height (SH, mm) of 20 haphazardly selected oysters was measured and the remaining oysters were enumerated. However, due to the amount of time and effort spent for this size quadrat during the first sampling period (May to June 2011), the quadrat size was decreased to 0.04 m² and replicated twice at each location on the reef, with all oysters being measured (SH, mm) and enumerated. Based on previous work (T. Alphin and M. Posey unpubl. data) and concurrent estimates from both quadrat sizes, the methods did not differ in their overall density estimates. For reef metrics, percent shell cover and percent live oyster cover was measured using a 0.25 m² quadrat with 16 evenly spaced points in a 4 × 4 pattern that was placed on the reef. Percent cover of shell on the reef was measured by determining if live oysters, shell hash, or open bottom was present underneath each point in the quadrat. The percentage of live oysters for each quadrat was then determined by the number of points with live oysters divided by the total number of points where shell was recorded, either live or shell hash. Reef rugosity, which is a measurement of topographical heterogeneity and is an indicator of reef complexity, was quantified by laying a 1 m chain (12.8 mm link size) parallel to the quadrat location and then measuring the chain distance after conformation with the reef. These reef metrics were collected at each sampling event for the natural reefs (spring 2011 to fall 2012), but were started during the fall 2011 for the created reefs.

Condition

Oyster condition index (CI), a metric that provides a relative indication of oyster health, was calculated by determining the amount of tissue within an oyster in relation to the available volume inside the shell (Lawrence & Scott 1982, Abbe & Albright 2003):

$$CI = \frac{\text{Dry meat weight (g)}}{\text{Internal shell cavity volume (cm}^3\text{)}} \times 100 \quad (1)$$

The internal shell cavity volume was determined as the differential weight between the whole oyster and the weight of the dried empty shell (Abbe & Albright 2003, Mercado-Silva 2005). On all the naturally occurring reefs, twenty 50–70 mm SH oysters were collected at each distance from the reef edge (i.e. 1 and 3 m for all reefs, and additionally as the

center for medium and large reefs), with collections temporally coinciding with sampling for oyster density and size. This size class of oysters was used because smaller oysters (<50 mm SH) tend to show an inflated CI (T. Alphin and M. Posey unpubl. data). On the created reefs, sampling of oysters to determine CI was not possible until fall 2011, when the oysters recruited into the 50–70 mm SH size class. Due to the limited recruitment of oysters into this size class, CI was sampled on one set at both Jones and Permuda Islands. From the reefs, 20 oysters were collected along the 1 × 10 m plot and along the lower edge and center of the 5 × 10 m and 10 × 10 m reefs.

Recruitment

Oyster recruitment, which included larval and immediate post-settlement processes, was sampled by deploying 0.04 m² caged trays onto the reefs. Each tray was constructed from 1 × 1 cm hardware cloth and filled with 20 pieces of similar sized cultch (50–70 mm), to provide similar area among cages. Duplicate caged trays were deployed in June 2011 at 1 and 3 m from the reef edge on all naturally occurring oyster reefs, approximately 2 m apart, and at the reef center for medium and large reefs. On all created reefs, the duplicate caged trays were deployed on lower edge of the reefs and the center of the reefs for the 5 × 10 m and 10 × 10 m plots. All trays were retrieved in October 2011. For the 2012 sampling season, the trays were deployed in May and retrieved in October, as results of the ongoing Oyster Spat Monitoring Project (<http://ncoystermonitoring.org>) indicated an earlier start (i.e. May instead of June) to the recruitment period. During the 2012 sampling, in addition to the caged trays, partially caged trays were also deployed to observe predation effects on oyster spat in relation to habitat characteristics. Partially caged trays had 5 cm width of hardware cloth attached to the top in an L-shaped pattern, which allowed predator access to the spat that settled but partially imparted water flow similar to caged trays. All 2012 trays were deployed using the same methods as in 2011, except that partially caged trays were deployed within 0.5 m from the caged trays, with an alternation between caged and uncaged trays at each location on the reef. When the trays were retrieved from all the reefs, only one caged and partially caged tray was processed for each distance, with all spat in each tray being processed and counted.

Growth

Oysters between 30–40 mm SH were hand-collected from natural intertidal reefs not utilized in this study and located within the University of North Carolina Wilmington research lease, near the mouth of Hewletts Creek (34° 10' 30" N, 77° 50' 39" W). The collected oysters were returned to the lab and maintained in a flow-through sea water system. A unique identification tag was applied to each oyster and then initial SH (36.98 ± 0.10 mm, mean ± SE) was recorded. Five oysters were placed in 0.04 m² hardware cloth trays with 3 × 3 mm openings. Half the of the hardware cloth trays were enclosed with the same hardware cloth material attached to the top to ensure there was no predation on the oysters, while half of the cages were left completely open to allow effects of predation. In July 2013, 2 caged trays and 2 uncaged trays were deployed at 1 and 3 m on all sizes of naturally occurring oyster reefs and at the center of medium and large reefs. The tray order of position placement alternated between caged and uncaged trays for each location on the reef, each approximately 1 m apart from one another. Trays were retrieved in September 2013 and the final SH was recorded for all surviving oysters. The change in SH (final SH minus initial SH) served as a proxy for the influence of the habitat characteristics on oyster growth.

Statistical analysis

Data for the natural and created reefs were analyzed separately using SAS Version 9.2 software. Prior to running analysis of variance (ANOVA) with the proc GLM procedure with random effects, all data were tested for homogeneity of variance (Levene's tests). If the variance tests failed, the data were transformed ($\log(x + 1)$) prior to analysis. All significant ANOVA results ($p < 0.05$) were analyzed with Student Newman-Keuls (SNK) post hoc tests.

Density and reef characteristics

Potential differences for oyster densities on the natural reefs for time (spring 2011, fall 2011, spring 2012, and fall 2012), reef type, reef size, and location from reef edge to interior were analysed using a 4-way ANOVA on log-transformed data. An analysis of covariance (ANCOVA) was used on log-transformed densities for the medium and large naturally occur-

ring reefs to determine if oyster density varied by reef type and reef size with the actual distance from the reef edge as a covariate. For oyster densities on the created reefs, data were transformed and then differences were examined with a 3-way ANOVA using time, reef size, and edge versus interior as the main effects for each location. Additional 3-way ANOVAs compared the 5 × 10 m created reefs with the nearby reference reefs for habitat factors.

For oyster reef characteristics, the values for percent cover, percent live, and rugosity for the natural reefs and both created sites were arcsine square root transformed on the proportional data prior to analysis. On the natural reefs, 4-way ANOVAs tested how percent reef cover, percent live oyster, and rugosity varied with time, reef type, reef size, and distance from edge. Percent reef cover, percent live oyster, and rugosity for the created reefs were analyzed with a 3-way ANOVA with time, reef size, and edge versus interior as the main effects.

Shell height

For oyster SH on natural reefs, only the interaction reef type × reef size was significant ($F_{2,172} = 8.18$, $p < 0.0005$) when originally tested with a 4-way ANOVA (time, reef type, reef size, and distance from edge as main effects). Therefore, we carried out separate 1-way ANOVAs to test to how oyster SH varied for reef size by reef type. For the created reefs, Oyster SH was analyzed on transformed data for Jones and Permuda Islands using a 3-way ANOVA with time, reef size, and edge versus interior as main effects.

Condition

Oyster CI on the natural reefs met assumptions of homogeneity and a 4-way ANOVA tested variation by time, reef size, reef type, and distance from edge as the main factors. The created reefs met homogeneity of variance, and 3-way ANOVAs for both Jones Island and Permuda Island tested variance among time, reef size, and edge versus interior.

Recruitment

All recruitment data, for both natural and created reefs, were transformed prior to analysis. In 2011, differences in recruitment on the naturally occurring reefs were tested by reef type, reef size, and distance

from the edge with 3-way ANOVA. In 2012, 4-way ANOVA tested for variation in oyster recruitment by tray type (caged versus partially caged), reef type, distance from the edge, and reef size. For the created reefs, the 2011 recruitment data was analyzed with 3-way ANOVA using site (Jones Island or Permuda Island), reef size, and edge versus interior as main factors. In 2012, recruitment was analyzed with 4-way ANOVA, which added tray type to the main effects in the analysis.

Growth

Change in oyster SH (final SH minus initial SH) was log transformed and analyzed with a 4-way ANOVA to determine the effects of reef type, reef size, distance from the edge, and tray type on oyster growth.

RESULTS

Natural reefs

Density

Overall, there was a significant edge-to-interior pattern for oyster densities ($p < 0.001$); however, there was a significant interaction of time and distance from reef edge ($p = 0.01$; Table 2A) because there was no significant difference ($F_{2,56} = 2.40$, $p = 0.09$) in densities between edge and interior locations during fall 2011. Oyster densities demonstrated reef type specific patterns for the distances from edge to interior (reef type × distance from edge to interior: $p = 0.02$; Table 2A). Densities were significantly lower along the reef edge on fringing reefs ($F_{2,113} = 10.80$, $p < 0.0001$; Fig. 3A), whereas densities on the patch significantly increased from edge to interior ($F_{2,117} = 27.55$, $p < 0.0001$; Fig. 3B). Reef size significantly ($p = 0.01$; Table 2A) influenced oyster densities, with significantly greater densities on medium sized reefs compared to large reefs (Fig. 3C). While there was a significant interaction for reef type and size (Table 2A), the interaction was only of magnitude, and data from both reef types were combined to highlight the spatial patterns (Fig. 3C).

With the inclusion of the actual distance from the reef edge (covariate) for the analysis (ANCOVA) for medium and large natural reefs only, there was an interactive effect of reef type and reef size ($p = 0.01$;

Table 2. Four-way ANOVA showing effects of time (spring 2011, S11; fall 2011, F11; spring 2012, S12; fall 2012, F12), reef type (patch, P; fringing, F), reef size (small, S; medium, M; large, L), and distance from reef edge (1 m, 1; 3 m, 3; and center, C) for naturally occurring intertidal oyster reefs in southeastern North Carolina (n = 22). Student Newman-Keuls (SNK) results are presented for significant main effects ($p < 0.05$, shown in **bold**) with different superscript letters representing different means (superscript, in parentheses)

Effect	df	F	p	SNK
A. Oyster density				
Time	3,172	2.57	0.06	
Reef type	1,172	2.57	0.11	
Reef size	2,172	0.02	0.02	S ^{AB(690)} M ^{A(807)} L ^{B(656)}
Distance from edge	2,172	36.97	<0.0001	1 ^{C(1925)} 3 ^{B(2225)} C ^{A(2325)}
Time × Type	3,172	0.26	0.85	
Time × Size	6,172	0.62	0.71	
Time × Distance	6,172	2.78	0.01	
Type × Distance	2,172	3.96	0.02	
Type × Size	2,172	4.06	0.02	
Size × Distance	3,172	0.59	0.62	
Time × Type × Size	6,172	0.50	0.81	
Time × Type × Distance	6,172	0.30	0.96	
Time × Size × Distance	9,172	0.28	0.97	
Type × Size × Distance	3,172	2.46	0.06	
Time × Type × Size × Distance	9,172	0.97	0.46	
B. Percent cover				
Time	3,172	0.60	0.61	
Reef type	1,172	0.78	0.37	
Reef size	2,172	2.35	0.09	
Distance from edge	2,172	27.06	<0.0001	1 ^{B(77.6)} 3 ^{A(89.9)} C ^{A(93.1)}
Time × Type	3,172	0.01	0.99	
Time × Size	6,172	0.76	0.59	
Time × Distance	6,172	1.20	0.30	
Type × Distance	2,172	1.29	0.27	
Type × Size	2,172	6.56	0.0018	
Size × Distance	3,172	3.50	0.01	
Time × Type × Size	6,172	0.17	0.98	
Time × Type × Distance	6,172	0.29	0.93	
Time × Size × Distance	9,172	0.41	0.92	
Type × Size × Distance	3,172	0.89	0.44	
Time × Type × Size × Distance	9,172	0.58	0.81	
C. Percent live				
Time	3,172	1.24	0.29	
Reef type	1,172	2.00	0.15	
Reef size	2,172	1.95	0.14	
Distance from edge	2,172	2.01	0.13	
Time × Type	3,172	1.83	0.14	
Time × Size	6,172	0.06	0.99	
Time × Distance	6,172	0.35	0.91	
Type × Distance	2,172	0.25	0.77	
Type × Size	2,172	9.34	<0.0001	
Size × Distance	3,172	1.42	0.23	
Time × Type × Size	6,172	0.45	0.84	
Time × Type × Distance	6,172	0.61	0.72	
Time × Size × Distance	9,172	0.83	0.58	
Type × Size × Distance	3,172	0.63	0.59	
Time × Type × Size × Distance	9,172	0.21	0.99	
D. Rugosity				
Time	3,172	7.94	<0.0001	S11 ^{C(0.62)} F11 ^{A(0.72)} S12 ^{BC(0.62)} F12 ^{AB(0.66)}
Reef type	1,172	0.04	0.84	
Reef size	2,172	1.61	0.20	
Distance from edge	2,172	7.29	0.0009	1 ^{B(0.30)} 3 ^{A(0.32)} C ^{A(0.34)}
Time × Type	3,172	0.44	0.84	

Table 2 (continued)

Effect	df	F	p	SNK
Time × Size	6,172	1.59	0.15	
Time × Distance	6,172	1.70	0.12	
Type × Distance	2,172	0.35	0.70	
Type × Size	2,172	2.01	0.13	
Size × Distance	3,172	0.26	0.85	
Time × Type × Size	6,172	2.12	0.05	
Time × Type × Distance	6,172	0.34	0.91	
Time × Size × Distance	9,172	0.63	0.76	
Type × Size × Distance	3,172	0.10	0.96	
Time × Type × Size × Distance	9,172	0.19	0.99	
E. Condition index				
Time	3,172	1.83	0.14	
Reef type	1,172	3.47	0.06	
Reef size	2,172	6.47	0.002	S ^A (6.8) M ^{AB} (6.5) L ^B (6.25)
Distance from edge	2,172	0.84	0.43	
Time × Type	3,172	0.34	0.79	
Time × Size	6,172	0.55	0.76	
Time × Distance	6,172	0.44	0.85	
Type × Distance	2,172	0.22	0.80	
Type × Size	2,172	0.92	0.40	
Size × Distance	3,172	0.36	0.78	
Time × Type × Size	6,172	0.50	0.80	
Time × Type × Distance	6,172	0.73	0.62	
Time × Size × Distance	9,172	0.50	0.87	
Type × Size × Distance	3,172	0.92	0.43	
Time × Type × Size × Distance	9,172	0.94	0.49	

Table 3) and there was also an interactive effect of reef size and covariate of actual distance from reef edge on oyster density ($p = 0.0007$; Table 3). Oyster densities were significantly greater ($F_{1,80} = 11.90$, $p = 0.0009$) at the center of medium fringing reefs compared to large reefs; a similar trend was evident on patch reefs, although the pattern was not significant ($F_{1,92} = 1.95$, $p = 0.16$).

Reef characteristics

Reef cover varied significantly by reef type and size ($p < 0.0001$; Table 2B), as coverage on patch reefs increased with decreased reef size ($F_{2,117} = 2.93$, $p = 0.05$), with no significant difference on fringing reefs ($F_{2,113} = 2.18$, $p = 0.11$). Percent cover also varied significantly by reef size and distance from the reef edge ($p = 0.01$; Table 2B). Percent reef cover increased ($F_{2,69} = 20.91$, $p < 0.0001$) from edge to interior locations on large reefs; by contrast, reef cover was significantly lower at the 1 m location on both the medium ($F_{2,105} = 8.39$, $p = 0.0004$) and small ($F_{1,54} = 6.06$, $p = 0.01$) reefs. Both reef type and size (reef type × size: $p < 0.0001$; Table 2C) significantly influenced percent live oysters, with lower values on

large patch reefs compared to medium or small reefs ($F_{2,117} = 8.15$, $p = 0.0005$), but there was no significant effect on fringing reefs ($F_{2,113} = 2.79$, $p = 0.06$). Reef rugosity varied significantly over time ($p < 0.0001$), as it tended to increase during the fall samplings (Table 2D). Rugosity was also significantly lower ($p < 0.001$) along the reef edge (1 m) compared to the interior locations (Table 2D).

Shell height

On the natural fringing reefs, oyster SH was significantly lower on the medium sized reefs ($F_{2,113} = 5.65$, $p = 0.004$), whereas the large patch reefs had significantly lower oyster SH ($F_{2,117} = 5.40$, $p = 0.005$).

Condition index

For the habitat characteristics examined in this study, reef type ($p = 0.06$; Table 2E) and distance from edge ($p > 0.05$; Fig. 4A) had no significant effect on CI, but reef size influenced CI ($p = 0.001$), as CI increased with decreased reef size (Table 2E, Fig. 4B).

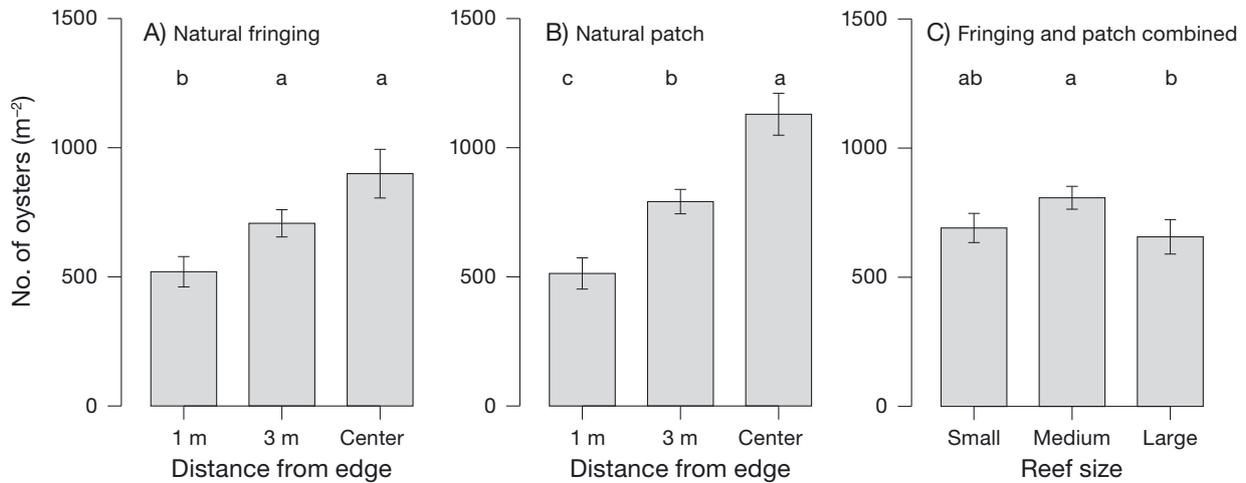


Fig. 3. Oyster density (m^{-2}) from edge to interior locations on (A) natural fringing reefs and (B) natural patch reefs, and (C) on different sized reefs. Samples were taken at 1 and 3 m from the edge of the reef and at the center of the reef. The interactive effects of patch and fringing reefs on oyster density were only in magnitude and data were combined to show effects of size on density in (C). Values are mean \pm SE. Different lowercase letters represent significantly different results ($p < 0.05$) from Student Newman-Keuls post-hoc tests

Table 3. Two-way ANCOVA for oyster density on the medium and large natural reefs, using $\log(x + 1)$ -transformed data with the actual distance from the reef edge as the covariate. Significant effects ($p < 0.05$) are shown in **bold**

Effect	Covariate	df	F	p
Reef size		1	0.06	0.81
Reef type		1	3.32	0.07
Size \times Type		1	6.14	0.01
	Distance	1	51.74	<0.0001
Reef size	Distance	1	11.91	0.0007
Reef type	Distance	1	2.22	0.13
Type \times Size	Distance	1	2.48	0.11

Recruitment

In 2011, recruitment to the natural reefs was only influenced by reef type ($F_{1,52} = 6.88$, $p = 0.01$), with significantly greater recruitment on patch reefs compared to fringing reefs. In 2012, total recruitment on the natural reefs was significantly reduced ($F_{1,99} = 17.14$, $p < 0.0001$) in the partially caged trays compared to the caged trays (Fig. 5). Recruitment in the caged trays on the patch reefs demonstrated increased recruitment from edge to interior locations ($F_{2,24} = 3.43$, $p = 0.04$; Fig. 5C), but there was no edge-to-interior gradient in the uncaged trays ($F_{2,22} = 1.15$, $p = 0.21$; Fig. 5C). While not significant ($F_{2,37} = 2.23$, $p = 0.12$), recruitment for both caged and partially caged trays to the fringing reefs tended to be greatest at 3 m from the edge (Fig. 5A). Reef type and size significantly (reef type \times reef size: $F_{2,99} = 6.8$, $p = 0.0002$) influenced recruitment, as recruitment to fringing

reefs was significantly greater on medium sized reefs compared to small or medium reefs ($F_{2,37} = 7.02$, $p = 0.003$; Fig. 5B); however, there was no significant difference ($F_{2,40} = 0.31$, $p = 0.73$) in recruitment for the different sized patch reefs. (Fig. 5D).

Growth

On the naturally occurring reefs, growth did not significantly differ for oysters in the caged versus uncaged trays ($F_{1,631} = 0.19$, $p = 0.66$), but the retention of oysters in the uncaged trays was low (33.9%). Oyster mortality was 12% in the caged trays and 18% in the uncaged trays. Of the 18% that experienced mortality in the uncaged trays, 22% had obvious signs of predation, but the actual numbers were too low to determine habitat characteristic patterns for mortality-related predation. There was a significant reef size effect on oyster growth, as the change in shell height was significantly lower ($F_{2,631} = 6.77$, $p = 0.001$) on the large (3.26 ± 0.15 mm, mean \pm SE) reefs compared to the small (4.30 ± 0.24 mm) and medium sized reefs (4.58 ± 0.17 mm).

Created reefs

Density

Densities at Jones Island were significantly greater in the fall 2011 compared to spring 2011 ($p = 0.005$; Table 4A), while at Permuda Island densities were

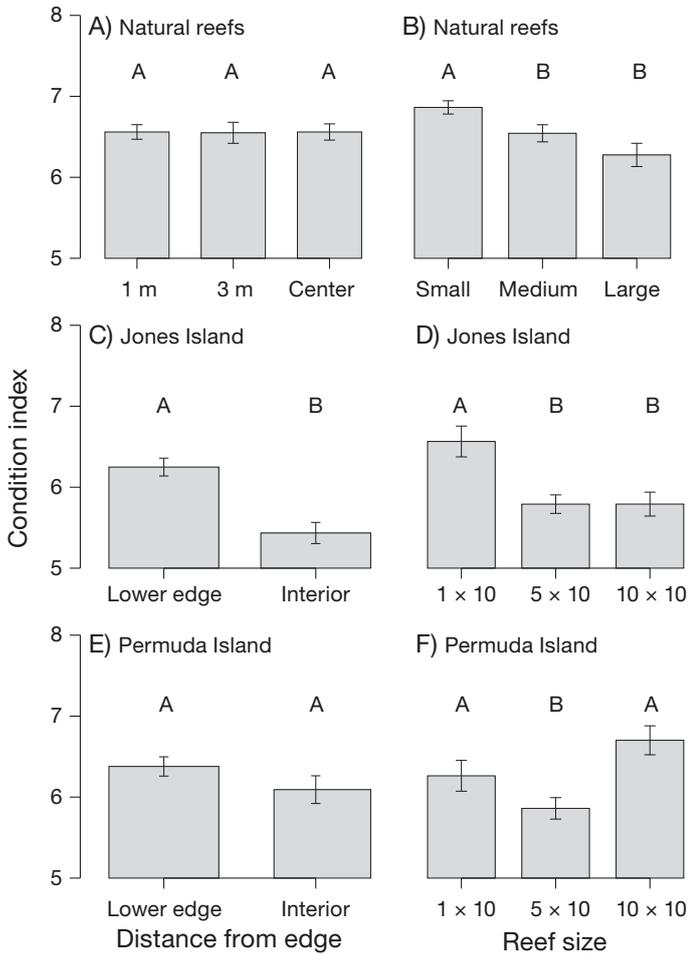


Fig. 4. Oyster condition index (CI) on (A,B) natural reefs and on created reefs at (C,D) Jones Island and (E,F) Permuda Island versus distance from the reef edge (left panels) and reef size (right panels). To assess effects of distance from the edge samples were taken at 1 and 3 m from the edge of the reef on natural reefs and at the lower edge and interior of artificial reefs. For reef sizes see Fig. 2. Values are mean \pm SE. Letters represent results from SNK post-hoc tests and those that do not share a common letter are significantly different ($p < 0.05$). Note that the y-axis was truncated in order to clearly illustrate the patterns.

highest at the beginning of the study (spring 2011), decreased in fall 2011, and leveled off during 2012 ($p < 0.0001$; Table 5A). Oyster density significantly varied between the edge and interior at both Jones Island (Table 4A, Fig. 6A) and Permuda Island (Table 5A, Fig. 6B), with greater densities at interior reef locations compared to the upper and lower edges. The size of created reefs also significantly influenced oyster density at Jones Island (Table 4A, Fig. 6C) and Permuda Island (Table 5A, Fig. 6D), with densities greatest on the 5×10 m reefs and lowest on the 1×10 m reefs.

The intermediate sized (5×10 m) created reefs at Permuda Island supported similar densities as the similar sized naturally occurring reference reef ($330 \pm 28 \text{ m}^{-2}$ and $292 \pm 53 \text{ m}^{-2}$, respectively; $F_{1,66} = 0.61$, $p = 0.43$). Further, there was no significant difference for the edge and interior locations between the created reefs and the reference reef ($F_{1,66} = 0.179$, $p = 0.17$). However, Jones Island supported significantly ($F_{1,147} = 5.38$, $p = 0.02$) greater number of oysters on the created reefs ($2812 \pm 645 \text{ m}^{-2}$) compared to the naturally occurring reference reef ($520 \pm 68 \text{ m}^{-2}$), but no significant edge to interior pattern were evident between the created reefs and the naturally occurring reference ($F_{1,147} = 1.27$, $p = 0.28$).

Reef characteristics

Percent reef cover was greater at interior locations at both Jones ($p = 0.006$; Table 4B) and Permuda Islands ($p = 0.001$; Table 5B) compared to the upper and lower reef edges; however, percent reef cover was not influenced by reef size for either of the created sites (Tables 4B & 5B). Only at Jones Island did the habitat characteristics influence percentage of live oysters (Table 4C), as they were significantly higher ($p = 0.006$) at the interior locations compared to the upper and lower edges. Additionally, small reefs (1×10 m) had lower ($p = 0.01$; Table 4C) percentage of live oysters compared to the other size classes of created reefs. The created reefs at Jones Island were more rugose ($p < 0.0001$; Table 4D) during fall 2011 compared to either sampling period during 2012, but rugosity did not vary by any of the habitat characteristics examined (Table 4D). By contrast, reef rugosity was significantly greater on the 5×10 m and 10×10 m reefs compared to the 1×10 m reefs at Permuda Island ($p < 0.05$; Table 5D).

Shell height

At Jones Island, oyster SH was significantly smaller ($p = 0.0003$) in the spring of 2011 compared to the other 3 sampling times, but no effects based on the habitat characteristics (Table 4E). There were significant ($p < 0.0001$) temporal effects at Permuda Island, with increased oyster SH throughout the study (Table 5E). Further at Permuda Island, oysters along the upper reef edge were found to have a greater SH ($p = 0.001$; Table 5E).

Condition index

Oyster CI did not vary temporally at Permuda Island ($p = 0.39$; Table 5F), but CI increased by time and reef size at Jones Island ($p < 0.0001$; Table 4F). The CI on the 10×10 m reefs was significantly lower during fall 2011 compared to both sampling times in 2012 ($F_{2,209} = 10.31$, $p < 0.0001$). Oyster CI was significantly greater ($p = 0.007$) along the reef edge at Jones Island (Table 4F, Fig. 4C) and a similar ($p = 0.09$) pattern was observed at Permuda Island (Table 4F, Fig. 4E). At Jones Island, oyster CI significantly increased ($p = 0.001$) with decreasing reef size (Table 5F, Fig. 4D). However, at Permuda Island oyster CI was lowest ($p = 0.0003$) on the intermediate sized reefs (Table 5F, Fig. 4F).

Recruitment

In 2011 ($F_{1,20} = 26.31$, $p < 0.0001$) and 2012 ($F_{1,35} = 203.15$, $p < 0.0001$) recruitment was significantly

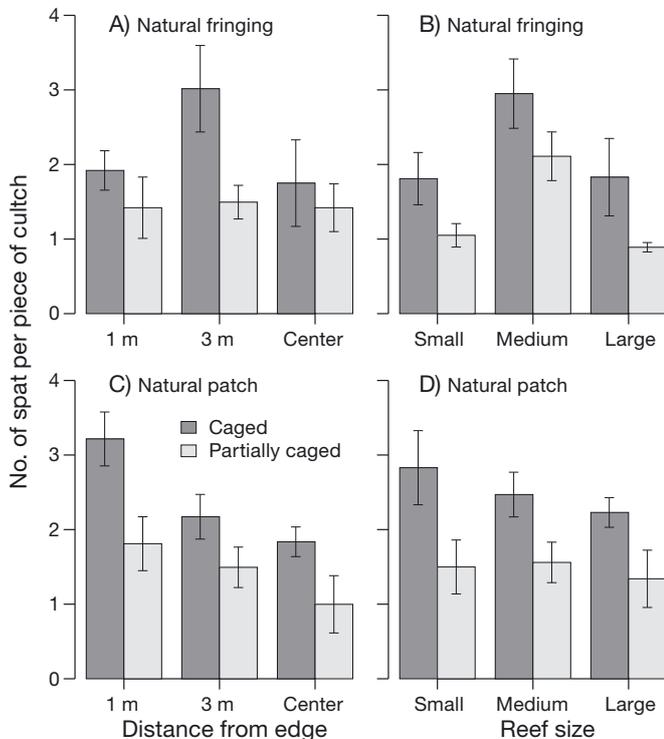


Fig. 5. Oyster recruitment to (A,B) natural fringing and (C,D) natural patched reefs versus distance from the edge and habitat patch size, based on data from 2012 samples. Dark bars: caged trays; light bars: partially caged trays (see 'Materials and methods: Natural reefs' and 'Sampling methods: Recruitment' for more details). Recruitment was calculated as mean number of settled oyster spat (\pm SE) per piece of cultch to standardize for any lost pieces of cultch from partially caged trays

greater at Jones Island compared to Permuda Island, but no habitat characteristics influenced recruitment. In 2012, recruitment was significantly reduced in the partially open trays at Jones Island ($F_{1,18} = 7.07$, $p = 0.01$), but did not differ between treatments at Permuda Island ($F_{1,17} = 0.38$, $p = 0.54$).

DISCUSSION

Intertidal oyster populations on naturally occurring and created reefs appear to be strongly influenced by the habitat characteristics examined in this study. This study highlights that edge effects do influence the population dynamics of oysters, but the cause of edge effects on these reefs appears to be multifaceted and may be driven by several different processes, which appear to be interactive and complex in nature. The similar edge and interior patterns observed on the natural and created reefs for oyster density and condition indicate that the mechanistic processes for edge effects on established natural reefs are relatively quickly established and can be observed on newly created reefs. Habitat patch size appears to be a deterministic factor for intertidal oyster populations, as intermediate sized natural and created reefs tended to support the greatest densities.

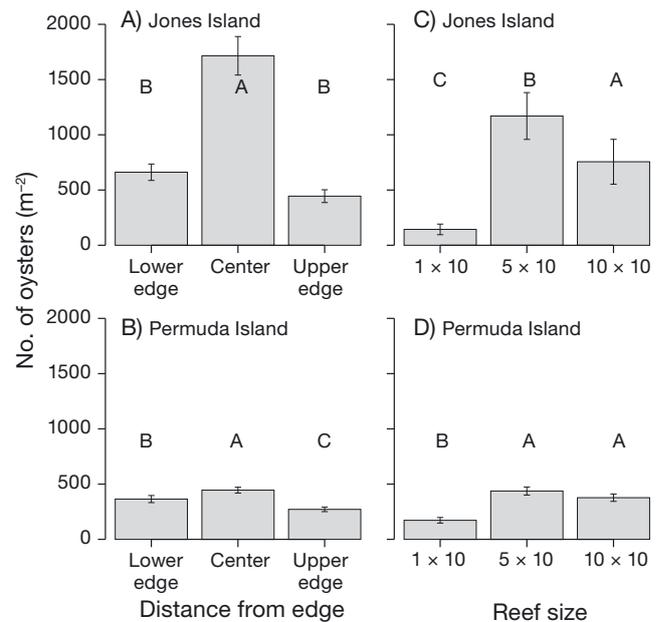


Fig. 6. Oyster density at (A,B) edge and interior locations and (C,D) versus reef size on created reefs at Jones Island (top panels) and Permuda Island (bottom panels). Samples were taken at the lower edge, center and upper edge of the created reefs; for reef sizes see Fig. 2. Values are mean \pm SE. Different letters represent significantly different results ($p < 0.05$) from Student Newman-Keuls post-hoc tests

Table 4. Three-way ANOVAs of time, reef size (1 × 10, 5 × 10, and 10 × 10 m) and distance from reef edge (lower edge, lower; center; and upper edge, upper) for the created intertidal oyster reefs at Jones Island (n = 9). Student Newman-Keuls (SNK) results are presented for significant main effects (p < 0.05, shown in **bold**) with different superscript letters representing different means (superscript, in parentheses). For further abbreviations in the right-hand column, see Table 2 legend

Effect	df	F	p	SNK
A. Oyster density				
Time	3,56	4.71	0.005	S11 ^{B(691)} F11 ^{A(1407)} S12 ^{AB(825)} F12 ^{AB(800)}
Reef size	2,56	10.5	0.0001	1 × 10 ^{C(143)} 5 × 10 ^{A(1170)} 10 × 10 ^{B(750)}
Distance from edge	2,56	4.53	0.01	Center ^{A(1675)} Lower ^{B(625)} Upper ^{B(425)}
Time × Size	6,56	2.33	0.05	
Time × Distance	6,56	0.75	0.61	
Size × Distance	2,56	0.67	0.51	
Time × Size × Distance	6,56	0.64	0.69	
B. Percent cover				
Time	2,42	0.21	0.80	
Reef size	2,42	0.93	0.40	
Distance from edge	2,42	8.97	0.006	Center ^{A(82)} Lower ^{B(63)} Upper ^{B(56)}
Time × Size	4,42	1.52	0.21	
Time × Distance	4,42	1.47	0.22	
Size × Distance	2,42	0.68	0.51	
Time × Size × Distance	4,42	0.31	0.87	
C. Percent live				
Time	2,42	1.17	0.31	
Reef size	2,42	5.04	0.01	1 × 10 ^{B(13)} 5 × 10 ^{A(55)} 10 × 10 ^{A(57)}
Distance from edge	2,42	5.80	0.006	Center ^{A(82)} Lower ^{B(63)} Upper ^{C(56)}
Time × Size	4,42	0.69	0.60	
Time × Distance	4,42	0.89	0.48	
Size × Distance	2,42	1.11	0.33	
Time × Size × Distance	4,42	0.05	0.99	
D. Rugosity				
Time	2,42	20.2	<0.0001	F11 ^{B(0.56)} S12 ^{A(0.83)} F12 ^{A(0.75)}
Reef size	2,42	0.49	0.61	
Distance from edge	2,42	1.05	0.36	
Time × Size	4,42	2.11	0.10	
Time × Distance	4,42	2.02	0.11	
Size × Distance	2,42	1.19	0.31	
Time × Size × Distance	4,42	0.74	0.56	
E. Oyster shell height				
Time	3,55	7.32	0.0003	S11 ^{B(23.6)} F11 ^{A(29.1)} S12 ^{A(32.2)} F12 ^{A(38.9)}
Reef size	2,55	0.69	0.5	
Distance from edge	2,55	0.50	0.60	
Time × Size	6,55	0.70	0.65	
Time × Distance	6,55	0.15	0.98	
Size × Distance	2,55	0.41	0.66	
Time × Size × Distance	6,55	0.17	0.98	
F. Condition index				
Time	2,276	7.7	0.0005	F11 ^{B(5.5)} S12 ^{A(6.1)} F12 ^{A(6.1)}
Reef size	2,276	9.02	0.0002	1 × 10 ^{A(6.6)} 5 × 10 ^{B(5.7)} 10 × 10 ^{B(5.7)}
Distance from edge	1,276	13.5	0.007	Edge ^{A(6.2)} Interior ^{B(5.4)}
Time × Size	4,276	7.99	0.0001	
Time × Distance	2,276	2.36	0.09	
Size × Distance	1,276	5.35	0.02	
Time × Size × Distance	2,276	0.79	0.37	

Table 5. Results of 3-way ANOVAs of time, reef size, and distance from reef edge for the created intertidal oyster reefs at Permoda Island (n = 9). Student Newman-Keuls (SNK) results are presented for significant main effects (p < 0.05, shown in **bold**) with different superscript letters representing different means (superscript, in parentheses). For abbreviations in the right-hand column, see previous table legends (Tables 2 & 4)

Effect	df	F	p	SNK
A. Oyster density				
Time	3,56	16.63	<0.0001	S11 ^{A(555)} F11 ^{B(415)} S12 ^{C(285)} F12 ^{C(235)}
Reef size	2,56	19.90	<0.0001	1 × 10 ^{B(150)} 5 × 10 ^{A(325)} 10 × 10 ^{A(400)}
Distance from edge	2,56	3.24	0.04	Center ^{A(425)} Lower ^{B(350)} Upper ^{C(250)}
Time × Size	6,56	0.89	0.50	
Time × Distance	6,56	0.86	0.52	
Size × Distance	2,56	1.10	0.33	
Time × Size × Distance	6,56	0.38	0.89	
B. Percent cover				
Time	2,42	0.85	0.43	
Reef size	2,42	0.25	0.77	
Distance from edge	2,42	7.94	0.001	Center ^{A(90)} Lower ^{B(67)} Upper ^{B(68)}
Time × Size	4,42	0.67	0.61	
Time × Distance	4,42	0.55	0.70	
Size × Distance	2,42	0.45	0.63	
Time × Size × Distance	4,42			
C. Percent live				
Time	2,42	0.34	0.71	
Reef size	2,42	0.53	0.59	
Distance from edge	2,42	3.21	0.05	
Time × Size	4,42	0.36	0.83	
Time × Distance	4,42	0.62	0.64	
Size × Distance	2,42	0.00	0.99	
Time × Size × Distance	4,42	0.07	0.98	
D. Rugosity				
Time	2,42	1.61	0.21	
Reef size	2,42	3.21	0.04	1 × 10 ^{B(0.85)} 5 × 10 ^{A(0.74)} 10 × 10 ^{A(0.77)}
Distance from edge	2,42	0.76	0.47	
Time × Size	4,42	0.55	0.69	
Time × Distance	4,42	0.22	0.92	
Size × Distance	2,42	0.05	0.95	
Time × Size × Distance	4,42	0.33	0.85	
E. Oyster shell height				
Time	3,56	280.8	<0.0001	F12 ^{A(70.3)} S12 ^{B(66.1)} F11 ^{C(62.0)} S11 ^{D(35.3)}
Reef size	2,56	0.66	0.51	
Distance from edge	2,56	7.07	0.001	Upper ^{A(60.9)} Lower ^{B(57.6)} Center ^{B(55.5)}
Time × Size	6,56	1.42	0.22	
Time × Distance	6,56	0.41	0.86	
Size × Distance	2,56	0.95	0.39	
Time × Size × Distance	6,56	0.08	0.92	
F. Condition index				
Time	2,234	0.92	0.39	
Reef size	2,234	6.98	0.001	1 × 10 ^{A(6.2)} 5 × 10 ^{B(5.7)} 10 × 10 ^{B(6.7)}
Distance from edge	1,234	2.76	0.09	
Time × Size	4,234	1.02	0.39	
Time × Distance	2,234	0.50	0.60	
Size × Distance	1,234	0.07	0.78	
Time × Size × Distance	2,234	0.70	0.49	

This study highlighted many differences between the fringing and patch reefs for oyster populations in terms of densities, reef characteristics, and larval recruitment. Further, reef type may also influence the magnitude of impact for other habitat characteristics, as medium fringing reefs had significantly greater oyster densities compared to large fringing reefs, but this pattern was not observed on patch reefs. Finally, trade-offs were observed between habitat characteristics and other oyster population characteristics: there was decreased oyster condition at interior locations, decreased oyster size in high oyster density habitats, and increased recruitment along reef edges.

Edge effects were observed on the natural and created reefs in this study, as densities and habitat complexity (shell cover and rugosity) were lower along the reef edge and increased towards the reef interior. Predation is one factor limiting densities for edge habitats (Ries et al. 2004, Gorman et al. 2009) and predation on oysters can subsequently limit habitat complexity (Grabowski 2004). While not quantified as part of this study, the decreased habitat complexity along the reef edge could also be indicative of increased physical disturbances. For example, reef edges can experience higher sedimentation rates (Lenihan 1999), thus causing oyster mortality, and leading to a localized decrease in the shell cover and complexity (rugosity). These factors may limit the physical structure along the reef edge, which may perpetuate low oyster densities in this microhabitat, considering that the decreased shell cover and complexity may limit the available substrate for larval settlement and further increase predation risks. Therefore, spatially independent feedback mechanisms may contribute to oyster survivorship and densities; the increased shell cover and vertical complexity towards interior locations may increase oyster survivorship (Sonnier 2006) and the limited shell cover and complexity (rugosity) along the reef edge may limit survivorship.

Habitat patch size is one of the major factors that influence population dynamics (Hanski 1999) and the results of this study suggest intermediate sized natural and created reefs tended to have higher oyster densities, possibly due to comparative smaller and larger reef size limitations. However, the influence of reef size on oyster densities could be driven by multiple processes and appears to have a complex interaction with other landscape factors, including the distance from the edge and reef type. The smaller reef size limitation may be governed by an Allee effect, which is a phenomenon where population growth rate is negative below a certain population

(Gascoigne & Lipcius 2004, Kramer et al. 2009, Swift & Hannon 2010). Other marine benthic organisms have been suggested to be susceptible to Allee effects (Stoner & Ray-Culp 2000, Gascoigne & Lipcius 2004) and this effect may explain the inability of the smallest sized created reefs to support a single generation of oysters or perpetuate reef structure. Conversely, large habitat patches inherently have more interior area, which has been suggested to be a refuge from predation on oyster reefs (Macreadie et al. 2012); however, the interior of medium reefs supported greater densities. This suggests an upper habitat patch size threshold relative to oyster density at the reef interior and that, beyond a critical distance, density at interior locations begins to decline. This threshold, coupled with decreased growth on large sized reefs, may possibly exist due to limited food sources in the water column when water reaches the reef interior. However, interior oyster density appeared to be confounded with reef type, as the interior of medium sized fringing reefs had greater densities than the large fringing reef, but no differences were seen on patch reefs. This may be a result of the tide flowing along a single edge to reach the interior for fringing reefs and consequent depletion of food resources before reaching the interior of the reef; whereas on patch reefs water moves simultaneously onto the reef from multiple edges.

Recruitment patterns of larvae, throughout many different systems, have been demonstrated to be skewed towards the edge of a habitat (Robertson & Hutto 2006). Recruitment in the caged trays for the natural reefs in 2012 was greater along the edge, which might be expected since the edge of intertidal reefs is encountered first by the flooding tide, assuming sufficient substrate is available. Larval recruitment was also influenced by reef size on the natural fringing reefs, as recruitment was greatest on the intermediate sized reefs. This pattern could be a density-dependent response of the oyster larvae, as larval survivorship is thought to be related to adult density (Gascoigne & Lipcius 2004, Smee et al. 2013) and adult densities were greatest on intermediate sized reefs. Furthermore, larval recruitment may be a contributing factor to density differences between natural fringing and patch reefs, as recruitment during 2011 was significantly greater on patch reefs compared to fringing reefs.

Predation may be one mechanism structuring the landscape of intertidal oyster reefs (Grabowski 2004, Hill & Weissburg 2013, Kimbro et al. 2014), as predation neutralized spatial patterns of increased recruitment along the reef edge. Carroll et al. (2012) de-

monstrated a similar pattern with bay scallops *Argopecten irradians* in seagrass habitats, with increased recruitment along the edge, but with predation effects, survivorship was equal between the edge and the interior. With the presence of an interior habitat, predation by juvenile blue crabs on intertidal oyster reefs has been demonstrated to be limited to the reef edge (Macreadie et al. 2012), which suggests that the effects of predation may negatively correlate with habitat size. This was demonstrated on the natural patch reefs, as oyster recruitment on natural patch reefs increased with decreasing reef size for the predation controlled treatments (caged trays), but was equalized across reef size due to effects of predation, possibly due to the small reefs lacking sufficient interior area and increasing spat predation susceptibility.

As seen in other marine systems (Smith et al. 2010, Carroll et al. 2012), there may be ecological tradeoffs for oysters among habitat characteristics examined in this study. Greater recruitment along the edges increases competition for the limited available substrate but increases predation risk. However, increased predation along the edge decreased post-settlement densities, in turn decreasing intraspecific competition and increasing oyster sizes and condition. Similar tradeoffs were observed for bay scallops *A. irradians* inhabiting seagrass beds, where predation risk was greatest along the edge, but growth rates were also highest along the edge due to increased food availability (Bologna & Heck 1999, Carroll et al. 2012). Further, oysters from the reef interior, which had higher oyster densities, had decreased condition. This suggests decreased predation pressure at the reef interior but greater intraspecific competition for food and space. Mercado-Silva (2005) suggested that oyster condition is not impacted by time of aerial exposure, further indicating intra-specific competition may drive spatial patterns of oyster condition at the reef interior. Finally, intraspecific competition among oyster populations based on reef size may result in ecological tradeoffs. For example, greater densities of oysters were observed on medium fringing reefs, which created greater intraspecific competition for space and food, and as a result, these sizes of reefs had smaller sized oysters.

The population decline of oysters within the last century has created habitat loss and fragmentation (Beck et al. 2011), and this study emphasizes that oyster reefs cannot be considered as uniform wholes, but may differ substantially across various microhabitats. The results of this study indicate that increased reef fragmentation, and the subsequent increase of edge

habitat, would further exacerbate population declines with the loss of a unique interior habitat. The habitat patch-size effect observed in this study suggests that fragmentation may have varied impacts on oyster populations based on reef size. The observation of concordant patterns of increased densities towards interior locations on the natural and created reefs indicates that the processes that structure oyster densities on natural and created reefs are similar and future designs of reefs for oyster restoration would benefit from understanding functions of edge and interior microhabitats. The patterns for oyster density, CI, recruitment, and growth across different habitat characteristics indicated that multiple population characteristics should be taken into account when trying to understand an evolving natural or created landscape. Together these results have implications for future management and restoration efforts, as these efforts may have to include several variations of habitat characteristics within the context of the landscape to maximize the biological output of intertidal oysters and their potential in providing reef habitat.

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