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A COMPARISON OF *CRASSOSTREA VIRGINICA* AND *C. ARIAKENSIS* IN CHESAPEAKE BAY: DOES OYSTER SPECIES AFFECT HABITAT FUNCTION?

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ABSTRACT We examined the possibility that a nonnative oyster species would provide an ecologically functional equivalent of the native oyster species if introduced into the Chesapeake Bay. Habitat complexity and associated benthic communities of experimental triploid *Crassostrea virginica* and *Crassostrea ariakensis* reefs were investigated at 4 sites of varying salinity, tidal regime, water depth, predation intensity, and disease pressure in the Chesapeake Bay region (Maryland and Virginia). Four experimental treatments were established at each site: *C. virginica, C. ariakensis*, 50:50 of *C. virginica and C. ariakensis*, and shell only. Abundance, biomass, species richness, evenness, dominance, and diversity of reef-associated fauna were evaluated in relation to habitat location and oyster species. Although habitat complexity varied with location, no differences among complexity were associated with oyster species. Similarly, differences in faunal assemblages were more pronounced between sites than within sites. Our results show functional equivalency between oyster species with respect to habitat at the intertidal site and the low-salinity subtidal location. At subtidal sites of higher salinity, however, the numbers of organisms associated with *C. virginica* reefs per unit of oyster biomass were significantly greater than the numbers of organisms associated with *C. ariakensis* reefs. Multivariate analyses of data from subtidal high-salinity sites revealed unique communities associated with *C. virginica* treatments, whereas mixed-oyster species assemblages were functionally equivalent to monospecific *C. ariakensis* experimental treatments. Our study represents the first effort to quantify the potential habitat function of *C. ariakensis*, which has been proposed for an intentional introduction into Chesapeake Bay, and provides evidence of species-specific similarities and differences in reef-associated communities.

KEY WORDS: oyster, *Crassostrea ariakensis*, *Crassostrea virginica*, reef-associated fauna, habitat complexity

INTRODUCTION

Biogenic reefs constructed by the Eastern oyster, *Crassostrea virginica*, provide complex, three-dimensional structural habitats in soft-sediment marine systems analogous to those provided by coral reefs (e.g., Genin et al. 1986), seagrass beds (e.g., Heck & Orth 1980), salt marshes (e.g., Kneib 1984), kelp beds (e.g., Estes & Duggins 1995), foliose algae (e.g., Kelaher & Rouse 2003), reef-building polychaetes (e.g., Schwindt & Iribarne 2000), and mussel beds (e.g., Seed 1996). The physical structure of these biogenic habitats, including their size, location, and architectural complexity, may influence ecological function (Bell et al. 1991). For example, the morphology, structural heterogeneity, and vertical complexity of oyster reefs often control the recruitment, persistence, and diversity of their inhabitants (e.g., Lenihan & Peterson 1998). Furthermore, macroinvertebrate densities and species richness are generally positively correlated with habitat structural complexity (Crowder & Cooper 1982, Diehl 1992, Posey et al. in preparation), which often allows for the coexistence of competitors while providing refuge for prey species (Hixon & Menge 1991).

Dramatic declines in the abundance of *C. virginica* populations in Chesapeake Bay and other localities along the U.S. eastern seaboard have been observed during the past 50 y as a result of the combined stresses of disease (*Haplosporidium nelsoni* [MSX] and *Perkinsus marinus* [Dermo]; Fisher 1996, Ford & Tripp 1996, Lenihan et al. 1999, Mann 2000), overfishing (Gross & Smyth 1946, Rothschild et al. 1994), deterioration in water quality (Lenihan & Peterson 1998), and reef degradation (Hargis & Havin 1988, Coen 1995, Lenihan & Peterson 1998, Mann 2000). In addition to the loss of a once valuable oyster fishery, these declines have reduced many of the ecological functions once provided by this species.

The native Eastern oyster, *C. virginica*, provides several critical ecosystem services, including reduction of water turbidity through active filtration (Newell 1988, Nelson et al. 2004) and decreased water flow (Dame et al. 1984), stabilization of substrate, erosion amelioration (Meyer et al. 1997), habitat provision for many other marine organisms (Coen et al. 1999), and enhanced benthic–pelagic coupling through the transfer of nutrients from the water column to the benthos (Dame 1999, Dame et al. 2001, Porter et al. 2004) and the facilitation of the transfer of energy from the benthos to higher trophic levels (Peterson et al. 2003). As a result of the three-dimensional

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structure provided by *C. virginica* that supports a diverse assemblage of organisms generally not found in surrounding soft-bottom habitats (Dame 1979, Zimmerman et al. 1989, Coen et al. 1999, Posey et al. 1999), oyster reefs are now broadly recognized as ecosystem engineers (Luckenbach et al. 1999, Gutiérrez et al. 2003, ASMFC 2007).

Substantial efforts to restore both the fishery resource and habitat value of oyster reefs in many Atlantic coast estuaries (Ortega & Sutherland 1992, Luckenbach et al. 1996, Coen et al. 1997, Mann & Powell 2007) have often been limited in their success. As a result of the continued decline of *C. virginica* in Chesapeake Bay, the introduction of a nonindigenous oyster species (the Suminoe oyster, *Crassostrea ariakensis*) that is resistant to known diseases of the native oyster has been under consideration by the states of Maryland and Virginia for most of the past decade (e.g., Rickards & Ticco 2002).

Proposals of deliberate introductions of exotic species raise many concerns. In this case, for example, issues of controversy included possible competitive interactions with the native species for food and space, the possible cointroduction of other nonnative species, including pathogens, and the general lack of information on the biology and ecology of the Suminoe oyster, *C. ariakensis*, in its native environment. Although an introduction has been tabled at present, the proposal was far from novel, and we expect similar proposals to arise in the future. The premeditated movement of aquatic species for aquaculture and fishery enhancement purposes has occurred for more than 2000 y (Mann et al. 1991), with oysters being perhaps the most pervasive example (Ruesink et al. 2005). Thus, despite the current abandonment of the proposal in Chesapeake Bay, results of research investigating this proposed introduction may be far-reaching.

Given the accepted habitat value of *C. virginica* reefs, the functional equivalency of *C. ariakensis* reefs should be of concern, particularly given that the growth forms and reef-forming capabilities of *C. ariakensis* remain in question (Zhou & Allen 2003). Functional equivalency, often used as a predictor of restoration success in marine systems (Lockwood & Pimm 2001, Peterson & Lipcius 2003, Peyre et al. 2007), may be especially important if the introduced species were to outcompete the native species in some areas, leaving only the nonnative species with ecologically relevant population sizes. As a result of morphological and genetic uncertainties surrounding species identifications in the genus *Crassostrea*, there is a general lack of information on the basic biology and ecology of *C. ariakensis* within its native habitat, making the prediction of the ecological impacts of an introduction of *C. ariakensis* within Chesapeake Bay more difficult. Short-term laboratory trials have also raised doubts over the ability of *C. ariakensis* to form the dense aggregations observed in *C. virginica* (Luckenbach, unpublished data); however, long-term trials have yet to be conducted because of quarantine system constraints.

Previous studies of *C. virginica* have shown that certain aspects of reef morphology (e.g., shape, size, and vertical complexity) may influence the degree to which reefs are used as habitat by other species (Posey et al. in preparation). If *C. virginica* and *C. ariakensis* differ in their reef-forming capabilities, this could have dramatic effects on the reef-associated fauna of Chesapeake Bay if *C. ariakensis* were to be introduced.

Although there have been several previous field studies investigating the survival and growth of *C. ariakensis* in Virginia and North Carolina waters, (e.g., Calvo et al. 2001, Grabowski et al. 2005), these trials provide little information on the growth form and reef-building potential of *C. ariakensis*, or the potential competitive interactions between the 2 *Crassostrea* species. Although several recent studies using diploid *C. ariakensis* and *C. virginica* in quarantined systems (Kingsley-Smith & Luckenbach 2008, Newell et al. unpublished data, Allen et al. unpublished data.) have addressed some of these issues, they do not duplicate conditions in natural-bottom habitats and therefore have limitations in their applications.

In a recently completed large-scale field study, Kingsley-Smith et al. (2009) examined the comparative survival, growth, and disease dynamics of *C. virginica* and *C. ariakensis* in bottom environments in the Chesapeake Bay region. This project provided the first opportunity for an on-bottom comparison of reef formation, habitat provision, and habitat function in *C. virginica* and *C. ariakensis*. Given the ecological importance of habitat provision by the native oyster, *C. virginica* (Luckenbach et al. 2005b, Rodney & Paynter 2006), there is an obvious need to evaluate the functional equivalency of a nonnative species prior to an intentional introduction. The objective of the current study was to provide a quantitative comparison of the habitat structure of *C. virginica* and *C. ariakensis* experimental reefs, and of their utilization as habitat by other marine organisms throughout the course of reef development. Our results suggest habitat function may vary between species at some locations within the Chesapeake Bay region. These findings should be included among future considerations of the advantages and concerns surrounding the potential environmental impacts of nonnative species introductions.

MATERIALS AND METHODS

Experimental Design

Details of the experimental design are given in Kingsley-Smith et al. (2009), which compared the survival, growth, and disease dynamics of triploid *C. virginica* and triploid *C. ariakensis* in bottom environments across a range of environmental conditions in the Chesapeake Bay region. Briefly, 4 field sites within the Chesapeake Bay region were selected to encompass a range of tidal environments, predicted salinities, disease pressures, and relative predator abundances (Table 1, Fig. 1).

In late October to early November 2005, 4 experimental treatments were established at each of the 4 sites. Each site included 2 blocks with 1 treatment replicated per block. Experimental triploid oyster treatments were as follows: *C. virginica* only, *C. ariakensis* only, and a 50:50 mixture of the 2 oyster species. A tray control with no live oysters was also included, comprised of clean *C. virginica* shell. In-depth descriptions of triploid oyster production, setting, and biosecurity precautions can be found in Kingsley-Smith et al. (2009).

Treatment replicates (henceforth referred to as reefs) were established as 5 × 5 arrays of plastic oyster grow-out trays. Each tray (58.4 cm in width × 58.4 cm in length × 7.3 cm in height) was evenly ventilated with 0.6-cm-diameter holes. Prior to the start of experiments, all trays were lined with 2-mm Fiberglas window screen and filled with a base layer of clean *C. virginica* shell. For live oyster treatments, juvenile oysters were added to achieve a target density of ~400 oysters/m^2 (136 animals/tray). The tray control received oyster shell but no live oysters. Realized

TABLE 1.

Field site characteristics, predicted disease pressures, and relative predator abundances.

Site	Tidal Regime	Depth (m)	Salinity (psu) (average; range)	Predicted Disease Pressure*	Predicted Relative Predator Abundance†
Severn	Subtidal	3–4	Low (9.6; 3–14)	No Dermo, no MSX	Low
Patuxent	Subtidal	3–4	Mid (11.6,8–16)	Low Dermo, no MSX	Moderate
York	Subtidal	1–2	High (16.5; 8–22)	High Dermo, high MSX	High
Machipongo	Intertidal	0–2	High (25.8; 3–34)	High Dermo, high MSX	Highest

* Supporting citation for *a priori* prediction of disease patters across sites: Calvo et al. (1999).
† Supporting citation for *a priori* prediction of predation patterns across sites: White and Wilson (1996).

initial densities differed slightly across sites and between treatments (Virginia sites: *C. virginica* = 358.1 oysters/m^2, *C. ariakensis* = 325.9 oysters/m^2, mixed-species treatments = 342.0 oysters/m^2; Maryland sites: all treatments = 353.1 oysters/m^2). Mean shell heights of *C. virginica* and *C. ariakensis* at deployment were 12.80 mm ($n = 1{,}362$, SD = 5.68) and 13.85 mm ($n = 1{,}272$, SD = 5.45), respectively.

Because 2 of our treatments contained nonnative oysters, it was necessary to enclose all our experimental reefs in cages as a biosecurity measure to protect against disturbances, redistributions, and losses of oysters from the experimental plots by extreme weather events and anthropogenic activities. Each array of 25 trays was surrounded by a large metal cage constructed from 3.8-cm-diameter galvanized steel pipe and chain-link fence with 5-cm openings. Cages were placed on the seabed at least 1 m apart. The 5-cm mesh prevented disturbances by large epibenthic predators, such as cownose rays, while permitting access to the oysters by small benthic predators such as gobies, blennies, and xanthid crabs.

Sampling occurred 1 mo postdeployment and again in spring, summer, and fall of the following 2 y (2006 and 2007). Using the risk–averse sampling design described by Kingsley-Smith et al. (2009), 3 trays were removed from each cage at each site during each sampling event and were replaced with trays filled with clean shell to maintain the spatial integrity of each experimental reef. All 24 trays (3 trays per cage × 4 treatments × 2 blocks) from a site were sampled on a single day and transported to the laboratory for processing. As a result of unforeseen complications, discussed at length in Kingsley-Smith et al. (2009), July 2006 was the last sampling period for which all treatment replicates were intact across all sites, and results from that sampling event are reported here. Temporal comparisons of habitat complexity and faunal communities will be reported elsewhere (Harwell et al. in preparation).

Habitat Complexity

Upon returning to the laboratory, each tray was photographed from the side, maintaining a predetermined, consistent distance between the camera and each tray. The software program Image-J (National Institutes of Health, Bethesda, MD, version 1.41) was used to quantify habitat complexity by obtaining measurements of maximum vertical reef height, average reef height, and surface rugosity from each digital image. Maximum vertical height was defined as the greatest distance between the top of the tray and the growing margin of an oyster protruding upward from the tray. In addition to the maximum vertical height, measurements were taken for the next 9 oyster-growing margins judged to be at the greatest perpendicular distance from the upper level of the tray. Average reef height was calculated as the means of these sets of 10 measurements. A unitless surface rugosity measurement was obtained from digital images of each tray by calculating the ratio of a contoured outline of the oysters within a tray to the linear length of the tray. This was a modified adaptation of the "chain-link" method, widely used to assess surface topography of coral reefs (Rogers et al. 1983, Aronson & Precht 1995), in which rugosity (R) was calculated as $R = 1 - d/l$, where d is the horizontal distance covered by the chain when conformed to the substratum and l is the length of the chain when fully extended (Aronson & Precht 1995).

Associated Fauna

After the removal of experimental oyster clumps and all *C. virginica* shell material, the remaining contents of each tray were rinsed on a 1-mm mesh sieve, then fixed in 10% buffered formalin for a minimum of 48 h prior to sorting, identification, and enumeration of organisms at the lowest practical taxonomic

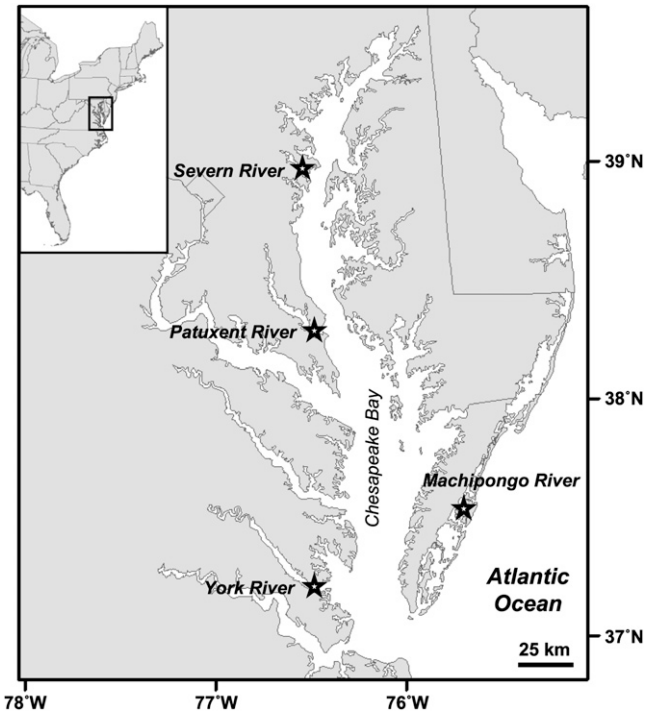

Figure 1. Study site locations throughout the Chesapeake Bay region.

level. Organisms were then preserved in 70% ethanol prior to drying, weighing, and combustion to determine ash-free dry weights. In addition to abundance and biomass data, species richness, Pielou's evenness, and Shannon-Weiner diversity were calculated for each sample using the PRIMER software package.

Statistical Analyses

Prior to analyses, all data from July 2006 were log-transformed to meet the assumptions of normality (Shapiro-Wilk) and homogeneity of variance (F-max test). Three-way, fixed-factor analysis of variance (ANOVA) models, with site, treatment, and block (nested with site) as factors, were used to analyze data for each index of habitat complexity (maximum reef height, average reef height, and surface rugosity) and each of the community metrics (total number of individuals per sample, species richness, Pielou's evenness, and Shannon-Weiner diversity). As a result of the high prevalence of significant site–treatment interactions, a series of 2-way, fixed-factor ANOVAs for each main effect (site, treatment) were run within appropriate subsets of the data. In 2-way ANOVA models, block effects were generally not significant (block effects were rare), so we removed block from the model and ran 1-way ANOVA models. Pairwise comparisons were made using Tukey's tests when ANOVA indicated a significant site or treatment effect.

A similar series of tests (3-way, fixed-factor ANOVA models followed by reduced 2-way and 1-way models) were run on the total abundance and biomass of all reef-associated fauna, as well as for individual dominant species. Species comprising at least 1% of the total abundance or biomass of associated fauna at a site were considered dominant. All abundance and biomass data for live oyster treatments were standardized by oyster biomass prior to further analyses and met assumptions of normality (Shapiro-Wilk) and homogeneity of variance (F-max test). When block was not significant, the fixed-factor ANOVA model was reduced and Tukey's test was used to conduct pairwise comparisons among sites and treatments if ANOVA indicated a significant effect of a main factor.

To evaluate further the variations in community structure between treatments, multivariate approaches in the PRIMER statistical software package (Plymouth Marine Laboratory, Plymouth, UK, version 5) were also used. Similarity matrices were calculated using nontransformed abundance and biomass data standardized by oyster biomass. These similarity matrices were used to create nonmetric multidimensional scaling plots of each sample at a given site. Analysis of similarity, which takes both species composition and abundance into account, was then performed on the similarity matrices to determine whether treatment differences were present.

RESULTS

Habitat Complexity

Maximum reef heights for *C. ariakensis* treatments were lowest at the intertidal, high-salinity site (Machipongo River, VA), averaging 2.42 cm above the top of the trays ($F = 16.79$, $P < 0.0001$; Fig. 2). Nonnative oysters grown at the subtidal sites exhibited a positive relationship between maximum reef height and salinity, with averages of 3.75 cm, 5.15 cm, and 5.97 cm at the low- (Severn River, MD), mid- (Patuxent River, MD), and high-salinity (York River, VA) subtidal sites, respectively. Statistically, values at the Severn were lower than those at the York, whereas the intermediate heights observed at the Patuxent were similar to the other 2 subtidal sites. *C. virginica* maximum heights were also lowest at the intertidal site (mean, 2.19 cm). At subtidal locations, the native species (*C. virginica*) displayed similar maximum reef heights, regardless of salinity ($F = 11.64$, $P = 0.0001$), with average values of 3.78 cm (Severn), 4.74 cm (Patuxent), and 3.47 cm (York). Site effects on maximum reef height for mixed-oyster species treatments were similar to those of *C. ariakensis*, with lowest values at the

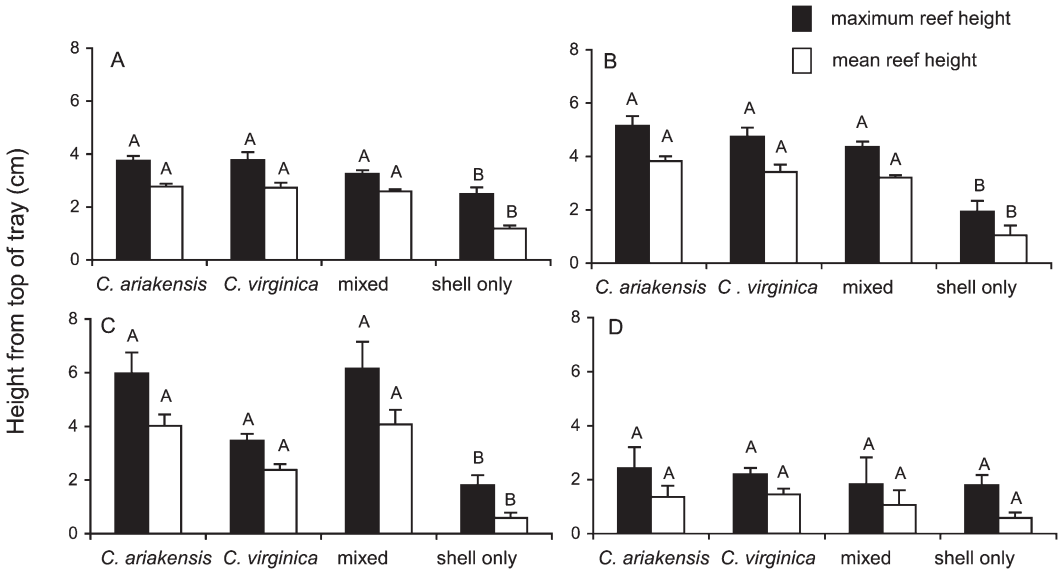

Figure 2. Mean maximum (black bars) and average (white bars) "reef" heights of experimental treatments at each site in July 2006. (A) Severn. (B) Patuxent. (C) York. (D) Machipongo. Data are expressed as mean reef height (in centimeters) as measured from the top of each tray. Error bars represent the SEM, and different letters over bars indicate significantly different values ($P < 0.05$, Tukey's test).

intertidal site (1.83 cm) and increasing heights with increasing salinity at subtidal locations (F = 25.51, $P < 0.0001$). Similar heights were observed at all 4 sites for shell-only treatments.

Site effects were also observed for average reef height, where, once again, intertidal reefs were shorter than all subtidal reefs, irrespective of oyster treatment (F = 47.87, $P < 0.0001$). *C. ariakensis* and mixed-species treatments displayed a pattern similar to that observed for maximum height, in that greater average heights were observed at the high-salinity subtidal site than at the low-salinity site (F = 40.07, $P < 0.0001$ and F = 31.68, $P < 0.0001$). *C. virginica* reefs, however, achieved higher average heights at the mid-salinity subtidal site (Patuxent) than at the high-salinity subtidal site (York), with intermediate, overlapping heights found at the low-salinity site (Severn; F = 19.61, $P < 0.0001$). Average heights of shell-only treatments were similar across all sites.

Site effects were not found for mean surface rugosity of shell-only treatments, nor for native oyster treatments (Fig. 3). In the cases of *C. ariakensis* and mixed reefs, however, at both the York and Severn River sites, higher rugosity values were found than at the Machipongo River site (F = 8.30, $P < 0.001$ and F = 16.4, $P < 0.0001$, respectively), with intermediate, overlapping (i.e., nonsignificant) values at the Patuxent River site.

Habitat complexity indices differed between live oyster treatments and controls, but did not differ among the 3 live oyster treatments. With the exception of maximum reef height at the Machipongo River, values from live oyster treatments were significantly higher than those without live oysters (Table 2) for all 3 habitat complexity indices (maximum reef height, average reef height, and surface rugosity) at all 4 sites. Significant differences between live oyster treatments were not observed for any of the habitat complexity indices used in this study, regardless of location in the Chesapeake Bay region.

Associated Fauna: Community Metrics

Of the community metrics tested in this study, significant treatment effects were rare, but site effects were common. The total number of organisms collected and identified from the July 2006 samples was 94,434 individuals, with a total biomass of reef-associated fauna in all samples reaching 983.9 g ash-free dry weight (Table 3). The greatest abundances of organisms were found at the 2 higher salinity subtidal sites, the York (n = 40,695) and Patuxent (n = 32,419) rivers. Intermediate numbers were found at the Severn River (n = 17,009), with lowest overall abundances occurring at the Machipongo (n = 4,311; F = 180, $P < 0.0001$). This trend of increased total abundances with increased salinity in subtidal sites was seen across all experimental treatments. Without taking oyster biomass into account, the total number of reef-associated organisms was significantly higher in the live oyster treatments than in the shell-only treatment (F = 6.00, P = 0.0011), but similar across oyster treatments, regardless of oyster species.

For *C. ariakensis* reefs, species richness was highest (33.5 species) at the York River (F = 24.78, $P < 0.0001$), with similar values found at the remaining sites (Severn, 11.2 species; Patuxent, 15.0 species; Machipongo, 16.7 species). Species richness for *C. virginica* reefs was also highest at the York (37.8), with intermediate values in the Patuxent (16.5) and Machipongo (15.5), and lowest values at the Severn (10.7) site (F = 114.21, $P < 0.0001$). Mixed-oyster species reefs exhibited a trend similar to that of the *C. ariakensis* oyster reefs, with highest species richness at the York (33.5) and similar values for the remaining sites (Severn, 11.8; Patuxent, 16.3; Machipongo, 15.5; F = 17.86, $P < 0.0001$). The numbers of species found in the shell-only treatment were highest in the York (34.8), lowest in the Severn (12.8) and Machipongo (12.5), and intermediate in the Patuxent (18.2; F = 73.02, $P < 0.0001$).

Pielou's species evenness for *C. ariakensis* treatments was similar across the Machipongo, Severn, and York River sites, with lowest values at the Patuxent site (F = 9.36, P = 0.0005; Table 4). Lowest species evenness was also observed at the Patuxent site for all other treatments ($P < 0.0001$ in all cases). Species evenness for *C. virginica* reefs was higher at the Machipongo than at the York (F = 14.46, $P < 0.0001$), with

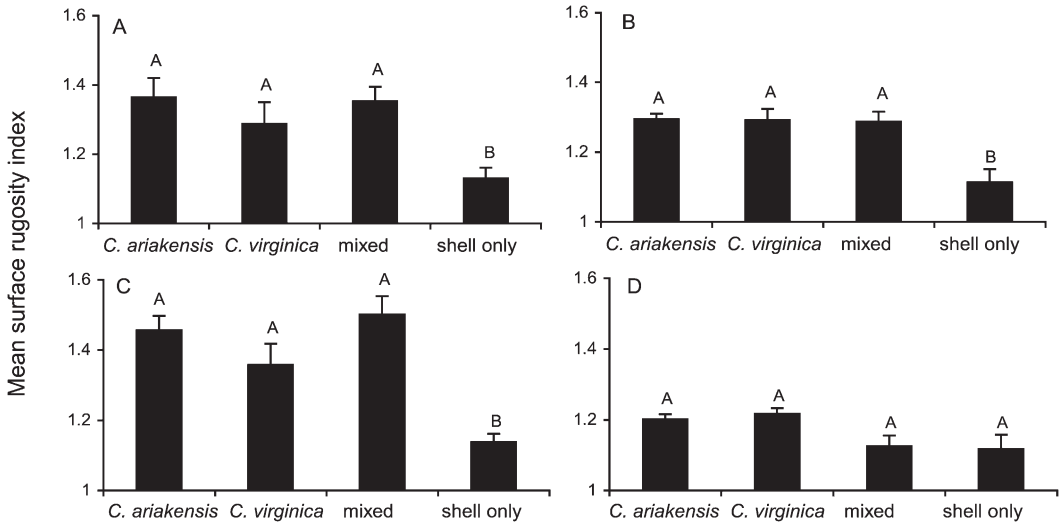

Figure 3. Mean surface rugosity index values of experimental treatments at each site in July 2006. (A) Severn. (B) Patuxent. (C) York. (D) Machipongo. Unitless surface rugosity measurements were obtained from digital images by calculating the ratio of a contoured outline of the oysters within a tray to the linear length of the tray. Error bars represent the SEM, and different letters over bars indicate significantly different values ($P < 0.05$, Tukey's test).

TABLE 2.

Mean (and SD) of habitat complexity indices (maximum reef height, average reef height, surface rugosity) for each treatment by site.

Complexity Index	Treatment				F Value	*P* Value
	C. ariakensis	*C. virginica*	Mixed Species	Shell Only		
Maximum reef height, cm						
Severn	3.75 (0.42)^{A}	3.78 (0.73)^{A}	3.25 (0.34)^{A}	2.49 (0.62)^{B}	8.04	0.0010
Patuxent	5.15 (0.87)^{A}	4.74 (0.84)^{A}	4.37 (0.47)^{A}	1.94 (0.90)^{B}	17.24	<0.0001
York	5.97 (1.90)^{A}	3.47 (0.61)^{A}	6.15 (2.46)^{A}	1.81 (0.92)^{B}	11.74	0.0001
Machipongo	2.42 (0.52)^{A}	2.19 (0.45)^{A}	1.83 (0.30)^{A}	1.79 (0.61)^{B}	2.29	0.1112
Average reef height, cm						
Severn	2.77 (0.28)^{A}	2.72 (0.15)^{A}	2.59 (0.18)^{A}	1.19 (0.29)^{B}	43.87	<0.0001
Patuxent	3.82 (0.46)^{A}	3.42 (0.68)^{A}	3.20 (0.22)^{A}	1.05 (0.82)^{B}	23.65	<0.0001
York	4.03 (1.01)^{A}	2.38 (0.54)^{A}	4.07 (1.33)^{A}	0.59 (0.48)^{B}	30.72	<0.0001
Machipongo	1.36 (0.19)^{A}	1.45 (0.16)^{A}	1.07 (0.25)^{A}	0.59 (0.33)^{B}	14.88	<0.0001
Surface rugosity index						
Severn	1.36 (0.14)^{A}	1.29 (0.15)^{A}	1.35 (0.10)^{A}	1.13 (0.15)^{B}	4.98	0.0096
Patuxent	1.30 (0.04)^{A}	1.29 (0.08)^{A}	1.29 (0.07)^{A}	1.11 (0.09)^{B}	8.50	0.0090
York	1.46 (0.10)^{A}	1.36 (0.15)^{A}	1.50 (0.13)^{A}	1.13 (0.06)^{B}	13.09	<0.0001
Machipongo	1.20 (0.03)^{A}	1.22 (0.04)^{A}	1.13 (0.07)^{A}	1.12 (0.10)^{B}	3.35	0.0408

F and *P* values from reduced-model 1-way ANOVAs on the effect of treatment with site. Different letters within a row indicate significantly different values ($P < 0.05$, Tukey's test).

intermediate, overlapping values at the Severn. Mixed-species reefs had highest species evenness at the Machipongo River site ($F = 18.23$, $P < 0.0001$) and intermediate values at the York and Severn, whereas the shell-only treatment had the highest species evenness at both the Machipongo and the Severn sites, with intermediate values occurring at the York.

For both single oyster species treatments (*C. virginica* only and *C. ariakensis* only), dominance differed significantly among sites, with the highest values at the York, followed in decreasing order by the Machipongo, the Patuxent, and finally the Severn ($P < 0.0001$ in all cases). In the mixed treatment, where both oyster species coexisted, a similar trend was observed, with highest values recorded at the York ($F = 28.76$, $P < 0.0001$), although dominance at the Patuxent overlapped values seen at both the Machipongo and Severn River sites. In the absence of live oysters (i.e., shell-only treatment), dominance was significantly higher at the York River site ($F = 45.16$, $P < 0.0001$) than at all other sites.

Site effects on Shannon-Weiner diversity, which takes species richness, dominance, and evenness into account, were similar across all live oyster treatments, with the highest species diversity found at the sites of higher salinities: the York and Machipongo ($P < 0.0001$ in all cases). Similarly, lower values of diversity were observed at the Severn and the Patuxent across live oyster treatments. The shell-only treatment had lower Shannon-Weiner diversity at the Patuxent River site than at all other sites ($F = 12.48$, $P < 0.0001$).

Of the community metrics tested in this study, significant treatment effects were rare and were only observed at the low-salinity site (Table 4). At the Severn River site, dominance was higher in the shell-only treatment than in the reefs comprised of only the native oyster, *C. virginica* ($F = 4.47$, $P = 0.0148$). Nonnative (*C. ariakensis*) and mixed-oyster species reefs exhibited intermediate, overlapping values for dominance. The only other treatment effect on a community metric was higher Shannon-Weiner diversity at the Severn River site in the shell-only treatment compared with *C. ariakensis* reefs ($F = 4.10$, $P = 0.0202$).

Associated Fauna: Total Standardized Abundance and Biomass

Oyster survival and growth differed significantly between sites (see Kingsley-Smith et al. 2009 for details). To compare the effects of oyster species more accurately, not oyster survival, on reef-associated communities across sites, the total abundances and ash-free dry weights of reef-associated organisms per sample were standardized by the oyster biomass present (methods described in Kingsley-Smith et al. 2009). ANOVAs for log-transformed data revealed site and treatment effects that differed from the ANOVA results for raw abundance data. Correcting for oyster biomass removed all site effects on the total abundance and biomass of reef-associated fauna. Oyster species did not affect the total number of reef-associated organisms at either the Machipongo River or the Severn River site (Table 5). At the Patuxent and York River sites, however, the average standardized number of organisms associated with

TABLE 3.

Summary of associated fauna found across all sites in July 2006.

	Severn	Patuxent	York	Machipongo
Number of species	22	35	63	48
Number of individuals	17,009	32,419	40,695	4,311
Biomass of associated fauna, g	167.95	571.05	213.2	31.71
Biomass of oysters, g	456.11	781.05	1,371.05	22.59
Biomass index for associated fauna*	0.37	0.73	0.16	1.4

* Ash-free dry weight of associated fauna/ash-free dry weight of oysters.

TABLE 4.

Mean (and SD) of community metrics (species richness, Pielou's evenness, Shannon-Weiner diversity, dominance) for each treatment by site.

Community Metric	Treatment				F Value	*P* Value
	C. ariakensis	*C. virginica*	Mixed Species	Shell Only		
Species Richness (S)						
Severn	11.2 (1.0)	10.7 (1.2)	11.8 (1.2)	12.8 (1.8)	2.91	0.0597
Patuxent	15.0 (3.6)	16.5 (1.5)	16.3 (2.9)	18.2 (1.5)	1.50	0.2444
York	33.5 (6.3)	37.8 (1.9)	33.5 (3.3)	34.8 (6.5)	1.03	0.3995
Machipongo	16.7 (4.9)	15.5 (3.1)	15.5 (6.5)	12.5 (1.6)	0.77	0.5246
Pielou's evenness (J′)						
Severn	0.60 (0.90)	0.63 (0.12)	0.61 (0.11)	0.73 (0.05)	2.26	0.1123
Patuxent	0.45 (0.11)	0.42 (0.08)	0.45 (0.08)	0.47 (0.10)	0.22	0.8784
York	0.58 (0.05)	0.58 (0.07)	0.64 (0.05)	0.59 (0.05)	1.58	0.2263
Machipongo	0.72 (0.09)	0.73 (0.06)	0.78 (0.07)	0.76 (0.03)	1.24	0.3230
Shannon-Weiner diversity (H′)						
Severn	1.44 (0.18)^{B}	1.50 (0.28)^{AB}	1.50 (0.24)^{AB}	1.85 (0.15)^{A}	4.10	0.0202
Patuxent	1.21 (0.39)	1.18 (0.21)	1.26 (0.29)	1.36 (0.32)	0.36	0.7813
York	2.04 (0.12)	2.08 (0.25)	2.24 (0.19)	2.10 (0.25)	1.20	0.3346
Machipongo	1.98 (0.25)	1.99 (0.11)	2.06 (0.31)	1.90 (0.16)	0.44	0.7245
Dominance						
Severn	1.56 (0.11)^{AB}	1.47 (0.21)^{B}	1.62 (0.21)^{AB}	1.91 (0.28)^{A}	4.47	0.0148
Patuxent	1.92 (0.52)	2.13 (0.18)	2.14 (0.41)	2.48 (0.31)	2.14	0.1276
York	4.32 (0.73)	4.84 (0.31)	4.51 (0.43)	4.66 (0.75)	0.90	0.4569
Machipongo	2.97 (0.65)	2.70 (0.46)	3.04 (0.99)	2.44 (0.28)	0.98	0.4227

F and *P* values from reduced-model 1-way ANOVAs on the effect of treatment within site. Different letters within a row indicate significantly different values ($P < 0.05$, Tukey's test).

C. virginica reefs was significantly greater than the number associated with *C. ariakensis* reefs (Patuxent: F = 7.77, $P = 0.0048$; York: F = 8.42, $P = 0.0025$, Fig. 4). When oyster species coexisted in mixed assemblages, standardized abundances at the Patuxent River were similar to those found in *C. virginica* reefs, whereas those in the York River were similar to *C. ariakensis* reefs.

Standardized total ash-free dry weights of reef-associated fauna also showed treatment effects at the Patuxent and the York River sites, but not at the Machipongo or the Severn River sites (Fig. 5). Once again, values were higher for *C. virginica* reefs than for *C. ariakensis* reefs (Patuxent: F = 4.23, $P = 0.0350$; York: F = 5.43, $P = 0.0169$). Mixed-oyster species reefs had values that were intermediate, yet overlapping.

Associated Fauna: Species Composition

A total of 78 different species were found throughout this study, including polychaete worms (28 species), bivalves (11 species), amphipods (10 species), crabs (7 species), fishes (6 species), shrimps (2 species), cnidarians (1 species), and isopods (1 species). A complete list of all species and the sites at which they occurred is presented in Table 6. Standardized abundance and biomass data was used to determine which species dominated samples from each site (Table 7).

Dominant species (defined as those comprising at least 1% of the total abundance of organisms) found at the subtidal site of lowest salinity (Severn) in July 2006 included an errant polychaete (*Neanthes succinea)*, 3 amphipods (*Apocorophium lacustre, Apocorophium simile*, and *Melita nitida*), the white-fingered mud crab (*Rhithropanopeus harrisii)*, unidentified juvenile xanthid crabs (all with a carapace width [CW] < 5 mm), and the naked goby, *Gobiosoma bosc*. At this site, standardized abundances of all dominant species, with the exception of the juvenile xanthids, were similar across live oyster treatments. Once standardized by total oyster biomass, *C. virginica* reefs supported higher numbers of the juvenile xanthids than their nonnative counterparts (*C. ariakensis*), with intermediate, overlapping values found on reefs of mixed oyster species (F = 5.45, $P = 0.0166$).

Dominant species at the Patuxent River site included *N. succinea*, the mud crab *Eurypanopeus depressus*, the amphipods *Gammarus palustris* and *M. nitida*, and the bivalves *Ischadium recurvum, Macoma balthica*, and *Mya arenaria*. Here, 4 of the 7 dominants displayed significant treatment effects. Standardized abundances of *N. succinea*, *E. depressus*, *G. palustris*, and *M. arenaria* were all higher in *C. virginica* cages than in *C. ariakensis* cages ($P < 0.0196$ in all cases). Mixed-oyster species cages also contained significantly lower numbers of *N. succinea*, *E. depressus*, and *G. palustris* compared with *C. virginica* cages, although numbers of *M. arenaria* did not differ from the other live oyster treatments.

At the York River site, dominant species included polychaete worms (*Demonax microphthalmus, Heteromastus filiformis, Loimia medusa*, and *N. succinea*), amphipods (*Caprella penantis, A. lacustre, Elasmopus levis*, and *M. nitida*), the mud crab *E. depressus*, unidentified juvenile xanthid crabs (all <5 mm CW), the naked goby (*G. bosc*), and the gastropod *Crepidula fornicata*. *C. virginica* reefs at this site supported greater numbers of all dominant species per gram of oyster biomass than *C. ariakensis* reefs ($P \leq 0.015$ in all cases). With 1 exception (*C. fornicata*), when oyster species coexisted, those reefs also

TABLE 5.

Mean (and SD) of total abundance and biomass of associated fauna for each treatment by site.

Associated Fauna	Treatment			F Value	*P* Value
	C. ariakensis	*C. virginica*	Mixed Species		
Standardized Total Abundance					
Severn	23.8 (8.0)	38.9 (12.9)	34.6 (15.1)	2.37	0.1273
Patuxent	22.6 (8.3)^{B}	99.0 (59.3)^{A}	38.3 (13.4)^{A}	7.77	0.0048
York	16.8 (5.8)^{B}	154.1 (116.2)^{A}	15.7 (3.23)^{B}	8.42	0.0035
Machipongo	2,296 (3,250.0)	191.8 (148.5)	418.0 (546.0)	2.21	0.1447
Standardized Total Biomass					
Severn	0.31 (0.11)	0.35 (01.6)	0.31 (0.12)	0.17	0.8491
Patuxent	0.35 (0.29)^{B}	1.40 (1.04)^{A}	0.57 (0.37)^{AB}	4.23	0.0350
York	0.09 (0.04)^{B}	0.48 (0.36)^{A}	0.15 (0.11)^{AB}	5.43	0.0169
Machipongo	21.6 (32.2)	2.58 (3.14)	3.15 (3.98)	1.97	0.1733

F and *P* values from reduced-model 1-way ANOVAs on the effect of treatment within site. Data for each oyster treatment were standardized by oyster biomass. Different letters within a row indicate significantly different values ($P < 0.05$, Tukey's test).

supported lower numbers of dominant species per gram of oyster biomass than reefs comprised only of *C. virginica*.

Using standardized abundance data at the high-salinity, intertidal Machipongo River site, 16 dominant species were identified. These included polychaetes (*Leitoscoloplos fragilis*, *Mediomastus ambiseta*, *N. succinea*, *Streblospio benedicti*, and *Tharyx acutus*), the amphipod *M. nitida*, the isopod *Cyathura burbancki*, gastropods (*Boonea impressa, Nassarius vibex*), crabs (*E. depressus*, *Panopeus herbstii*), unidentified juvenile xanthid crabs (all <5 mm CW), and *Uca* spp. (all <5 mm CW), nemerteans, and 2 insect species. At this site, similar standardized abundances were seen across treatments for all dominant species.

The species comprising at least 1% of the standardized total biomass at each site were different than dominants calculated using abundance data (Table 8). At the Severn River site, dominant species for standardized biomass data included 3 fishes, 4 crabs, 1 polychaete, and 1 bivalve (see Table 7 for the species list). At the Patuxent River site, 17 species dominated ash-free dry weights: 6 bivalves, 2 crabs, 2 fishes, 4 amphipods, 1 polychaete, 1 gastropod, and 1 cnidarian. Biomass dominants at the York site included 13 different species: 5 fishes, 3 crabs, 4 polychaetes, and 1 bivalve. At the intertidal site, only 5 species dominated the biomass of reef-associated fauna: 3 crabs and 2 gastropods.

Standardized ash-free dry weights of biomass dominants were all similar across live oyster treatments at the Severn, Patuxent, and Machipongo sites. At the York River location, 3 species exhibited treatment effects: the polychaete *D. microphthalmus*, the mud crab *E. depressus*, and the skillet fish *Gobiesox strumosus*. As previously observed for dominant species by abundance, *C. virginica* reefs supported a higher biomass of these species than did either *C. ariakensis* or mixed-oyster species reefs ($P \leq 0.007$).

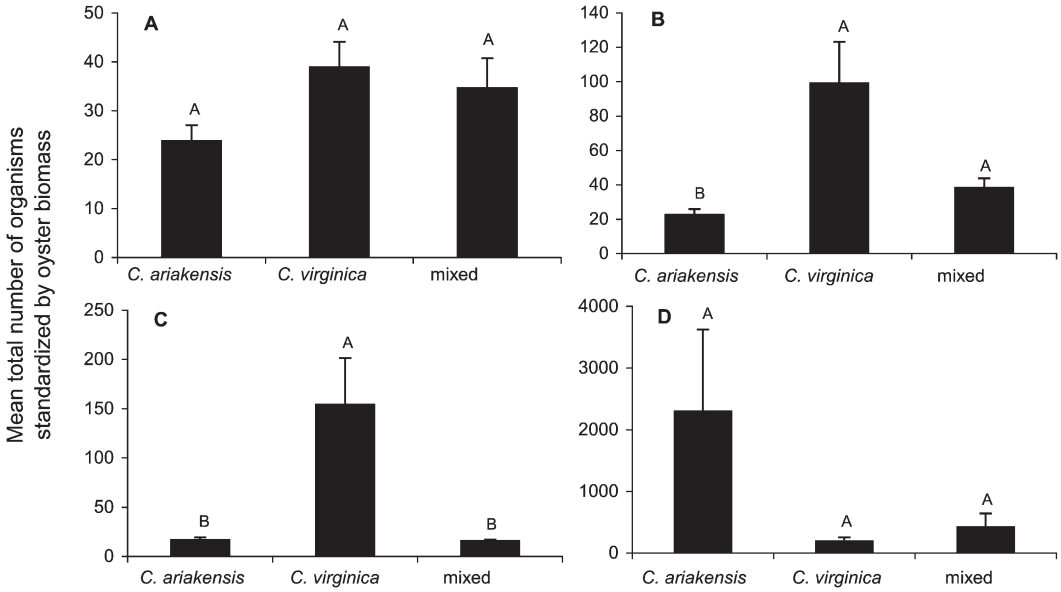

Figure 4. Mean total abundance of associated fauna per sample standardized by oyster biomass for all treatments containing live oysters across all sites. (A) Severn. (B) Patuxent. (C) York. (D) Machipongo. Significant within-site treatment effects are indicated by different letters above the SE bars.

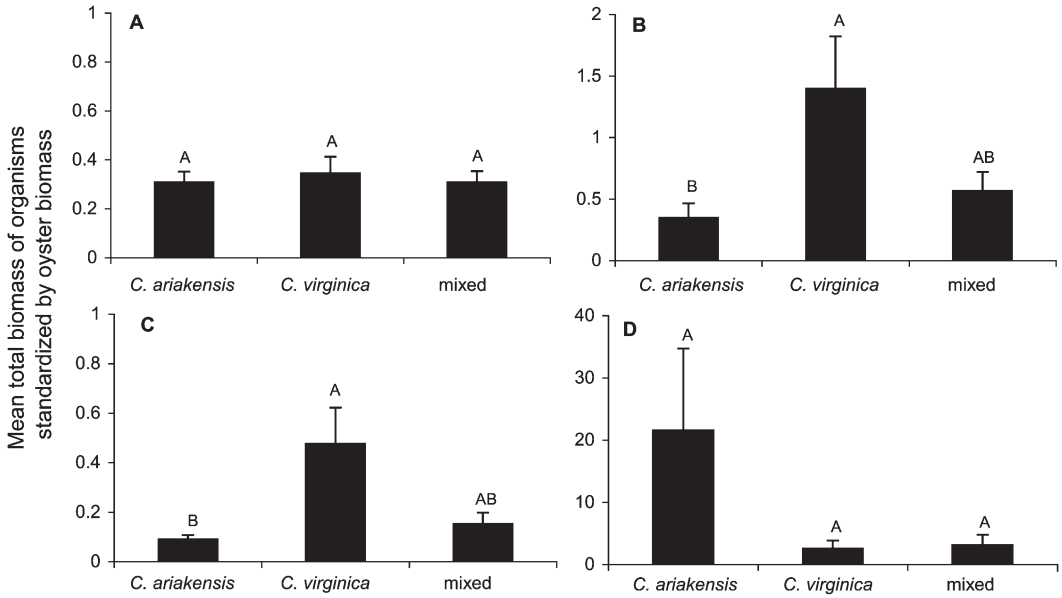

Figure 5. Mean total biomass of associated fauna per sample standardized by oyster biomass for all treatments containing live oysters across all sites. (A) Severn. (B) Patuxent. (C) York. (D) Machipongo. Significant treatment effects are indicated by different letters above the SE bars.

Multivariate Analyses

Nonmetric multidimensional scaling plots and analysis of similarity of standardized abundances of associated fauna highlight treatment effects at both the York and Patuxent River sites (Fig. 6). The benthic communities associated with *C. virginica* experimental reefs were different from those associated with both *C. ariakensis* and mixed oyster reefs at both the Patuxent and York River sites. Communities associated with the mixed-species reefs did not differ from the *C. ariakensis* reefs. Reef-associated communities at the Machipongo and Severn River sites did not differ between treatments. Multivariate analyses utilizing the biomass of associated organisms standardized by oyster biomass yielded results similar to those obtained from abundance data, although treatments effects were only observed at the York River site, where once again, *C. virginica* reef communities differed from those supported by *C. ariakensis* and mixed-oyster species reefs (Fig. 7).

DISCUSSION

Although results from short-term laboratory trials and anecdotal observations of *C. ariakensis* in its native range have raised doubt over the species' ability to form the dense aggregations observed in *C. virginica*, a growing body of evidence suggests that the Suminoe oyster is a reef-building *Crassostrea* species. After approximately 8 mo of deployment, comparisons of 3 distinct habitat complexity indices (maximum vertical reef height, average reef height, and surface rugosity) revealed no significant differences between native and nonnative experimental reefs, regardless of location within the Chesapeake Bay region. Despite evidence of negative effects of interspecific competition on the growth of *C. ariakensis* at the low- and mid-salinity subtidal sites (Kingsley-Smith et al. 2009), experimental reefs containing a mixture of both oyster species had similar measures of habitat complexity when compared with monospecific reefs.

Site effects on complexity indices were common, particularly for treatments containing *C. ariakensis*. Because of its relative intolerance of intertidal exposure (Luckenbach et al. 2005a, Kingsley-Smith & Luckenbach 2008, Wang et al. 2008, Yoon et al. 2008), survival of *C. ariakensis* at our intertidal site, the Machipongo River, VA, was markedly low (Kingsley-Smith et al. 2009), negatively affecting all indices of habitat complexity for treatments containing Suminoe oysters at this location. Maximum and average vertical reef heights among native oyster treatments, however, were also significantly lower at this intertidal site. To explore the limits of *C. ariakensis* reef formation, we intentionally placed our experimental reefs near the upper limit of native oyster reefs and acknowledge that this resulted in harsher physical conditions than those occurring on many natural intertidal reefs.

Among subtidal sites, reefs containing *C. ariakensis* (both monospecific and mixed-species assemblages) had significantly higher complexity indices at the higher salinity site (York River). We largely attribute this to the positive relationship between salinity and the growth rate of *C. ariakensis* (Calvo et al. 2001, Grabowski et al. 2004, Hudson et al. 2005, Paynter et al. 2008).

Although qualitative differences in reef morphologies are apparent when visually comparing native and nonnative treatments, particularly those grown at the higher salinity subtidal sites, such observations did not translate to quantitative differences in any of the complexity indices measured in this study. Although treatment effects on maximum and average vertical reef heights were not expected, because there were no discernible visual differences in these characteristics during sampling events, differences in rugosity indices were anticipated. Although the overall amount of interstitial space present within reefs may have been similar among oyster species, the arrangement of that space varied. *C. virginica* reefs contained a tight arrangement of individuals, resulting in a high number of small crevices; *C. ariakensis* reefs grown at high-salinity subtidal

TABLE 6.

Complete list of all species found in July 2006 samples across all sites.

Taxonomic Group	Species	Severn	Patuxent	York	Machipongo
Amphipods					
	Apocorophium lacustre		X	X	X
	Apocorophium simile	X			
	Caprella equilibra			X	
	Caprella penantis			X	X
	Cymadusa compta			X	
	Elasmopus levis	X		X	X
	Gammarus mucronatus		X	X	
	Gammarus palustris		X	X	X
	Melita nitida	X	X	X	X
	Paracaprella tenuis			X	X
Arthropoda					
	Limulus polyphemus			X	
	Unidentified insect				X
	Unidentified insect larva				X
Bivalves					
	Anadora transversa			X	
	Gemma gemma		X	X	X
	Geukensia demissa		X	X	X
	Ischadium recurvum	X	X		
	Macoma balthica	X	X	X	
	Macoma mitchelli		X		
	Macoma tenta			X	
	Mercenaria mercenaria			X	X
	Mulinia lateralis	X	X	X	
	Mya arenaria	X	X	X	
	Mytilus edulis		X		
Cnidarian					
	Unidentified jelly			X	X
Decapod crustaceans					
	Alpheus heterochaelis			X	X
	Callinectes sapidus		X	X	
	Dyspanopeus sayi		X	X	X
	Eurypanopeus depressus	X	X	X	X
	Hexapanopeus angustifrons	X		X	
	Palaemonetes pugio			X	X
	Panopeus herbstii	X	X	X	X
	Rhithropanopeus harrisii	X	X	X	
	Uca spp. unidentified juvenile xanthid	X	X	X	X
Fishes					
	Anguilla rostrata	X		X	
	Chasmodes bosquianus		X	X	
	Gobiesox strumosus	X	X	X	
	Gobiosoma bosc	X	X	X	X
	Hypsoblennius hentz			X	
	Opsanus tau			X	
Gastropods					
	Astyris lunata		X	X	
	Acteocina canaliculata		X	X	
	Boonea bisuturalis		X	X	
	Boonea impressa		X	X	X
	Crepidula convexa			X	
	Crepidula fornicata			X	X
	Crepidula plana			X	
	Nassarius vibex		X	X	X
	Neverita duplicata				X
	Rictaxis punctostriatus	X	X	X	
	Urosalpinx cinerea			X	X

Continued on next page

TABLE 6.

Continued

Taxonomic Group	Species	Severn	Patuxent	York	Machipongo
Isopods					
	Cyathura burbancki				X
Nemerteans				X	X
Polychaetes					
	Capitella capitata				X
	Clymenella torquata			X	
	Cyrtopleura costata			X	
	Demonax microphthalmus			X	
	Edotia triloba		X		
	Eteone heteropoda		X		X
	Glycera dibranchiata		X		
	Hemipodus roseus			X	
	Heteromastus filiformis		X	X	X
	Hobsonia florida				X
	Hydroides dianthus			X	
	Leitoscoloplos fragilis			X	X
	Lepidontus sublevis			X	
	Loimia medusa			X	X
	Lysidice ninetta				X
	Mediomastus ambiseta				X
	Neanthes succinea	X	X	X	X
	Parahesione luteola			X	X
	Pectinaria gouldii		X	X	
	Petriocolaria pholadiformis			X	
	Piromis eruca				X
	Podarke obscura				X
	Polydora websteri				X
	Sabellaria vulgaris			X	
	Scoletoma tenuis				X
	Streblospio benedicti			X	X
	Stylocus sp.	X	X		
	Tharyx acutus				X

sites more frequently had growth trajectories in a more horizontal direction, leading to greater angles between individuals. In retrospect, the "chain-link" method of assessing habitat heterogeneity may not have been the most appropriate choice, given the nature of the visual discrepancies in morphology between oyster treatments. Despite its widespread use and general acceptance as an indicator of habitat complexity in aquatic systems, the rugosity index cannot discriminate between the shape and size of components relative to the scale of the topography under investigation (Roberts & Ormond 1987, Shumway et al. 2007). For example, a complex, small-scale topography would have the same rugosity value as a simple, large-scale topography (Roberts & Ormond 1987). We recommend that future studies of habitat complexity in oyster reefs include more novel approaches to complexity comparisons, such as measuring the distance between individual oysters, or the angles at which individual oysters meet one another.

Although necessary for biosecurity reasons, the cages in which the oysters were deployed may have indirectly affected oyster survival (Kingsley-Smith et al. 2009), because their presence likely reduced predation rates by limiting the access of larger predators such blue crabs (*Callinectes sapidus*) and cownose rays (*Rhinoptera bonasus*). Particularly at small sizes, *C. ariakensis* shells are structurally weaker than those of the native species, allowing for greater susceptibility to predation (Bishop & Peterson 2006, Newell et al. 2007). Therefore, our use of cages in this study may have disproportionately decreased mortality rates of juvenile *C. ariakensis*, which in turn may have affected habitat complexity. It is also possible that observed similarities in habitat complexity may begin to diverge as the reefs mature beyond the age at which they were assessed in the current study. To address this, additional analyses of reef complexity at later time points (e.g., 2007 sampling events described in Kingsley-Smith et al. (2009)) are underway (Harwell et al. in preparation).

As was the case for habitat complexity, differences among reef-associated faunal assemblages were more pronounced between sites than between treatments within sites. Lowest overall abundances were found at the intertidal site, reflecting low oyster survival, growth, and habitat complexity. At subtidal sites, there was a trend of increasing total abundance with increasing salinity across experimental treatments. Similarly, the high-salinity subtidal site (York River) supported higher species richness, dominance, and diversity values. Our observation of a positive relationship between species richness and salinity in oyster reef communities was first suggested by Wells (1961), who documented that a majority of oyster reef inhabitants were limited in their upstream distribution by a reduction in salinity. A more recent study by Tolley et al. (2005) also revealed that several community metrics (organism abundance, biomass, and diversity) increased

TABLE 7.

Reduced-model 1-way ANOVA results for the effect of live oyster treatment on individual species abundances comprising at least 1% of total standardized abundance at each site.

Site	Species	F Value	*P* Value	Ranking
Severn				
	Apocorophim lacustre	2.52	0.1140	
	Apocorophium simile	1.66	0.2230	
	Gobiosoma bosc	0.72	0.5033	
	Melita nitida	1.34	0.2908	
	Neanthes succinea	0.35	0.7101	
	Rhithropanopeus harrisii	1.91	0.1823	
	U/I juvenile xanthid	5.45	0.0166	*C. v.*^{A} mixed^{AB} *C. a.*^{B}
Patuxent				
	Eurypanopeus depressus	10.35	0.0015	*C. v.*^{A} mixed^{B} *C. a.*^{B}
	Gammarus palustris	8.61	0.0032	*C. v.*^{A} mixed^{B} *C. a.*^{B}
	Ischadium recurvum	2.64	0.1039	
	Macoma balthica	0.82	0.4583	
	Melita nitida	0.99	0.3951	
	Mya arenaria	5.17	0.0196	*C. v.*^{A} mixed^{AB} *C. a.*^{B}
	Neanthes succinea	13.02	0.0005	*C. v.*^{A} mixed^{B} *C. a.*^{B}
York				
	Apocorophium lacustre	10.30	0.0015	*C. v.*^{A} mixed^{B} *C. a.*^{B}
	Caprella penantis	5.63	0.0150	*C. v.*^{A} mixed^{B} *C. a.*^{B}
	Crepidula fornicata	4.97	0.0221	*C. v.*^{A} mixed^{B} *C. a.*^{B}
	Demonax microphthalmus	28.22	<0.0001	*C. v.*^{A} mixed^{AB} *C. a.*^{B}
	Elasmopus levis	10.30	0.0015	*C. v.*^{A} mixed^{B} *C. a.*^{B}
	Eurypanopeus depressus	18.12	<0.0001	*C. v.*^{A} mixed^{B} *C. a.*^{B}
	Gobiosoma bosc	7.03	0.0070	*C. v.*^{A} mixed^{B} *C. a.*^{B}
	Heteromastus filiformis	19.69	<0.0001	*C. v.*^{A} mixed^{B} *C. a.*^{B}
	Loimia medusa	7.71	0.0050	*C. v.*^{A} mixed^{AB} *C. a.*^{B}
	Melita nitida	22.06	<0.0001	*C. v.*^{A} mixed^{B} *C. a.*^{B}
	Neanthes succinea	37.01	<0.0001	*C. v.*^{A} mixed^{B} *C. a.*^{B}
	Unidentified juvenile xanthid	12.17	0.0007	*C. v.*^{A} mixed^{B} *C. a.*^{B}
Machipongo				
	Boonea impressa	0.02	0.9805	
	Cyathura burbancki	2.76	0.0955	
	Eurypanopeus depressus	0.31	0.7372	
	Leitoscoloplos fragilis	0.35	0.7117	
	Mediomastus ambiseta	1.96	0.1758	
	Melita nitida	0.19	0.8260	
	Nassarius vibex	0.74	0.4946	
	Neanthes succinea	1.63	0.2294	
	Nemertean	0.63	0.5460	
	Panopeus herbstii	1.39	0.2797	
	Streblospio benedicti	1.00	0.3898	
	Tharyx acutus	0.08	0.9260	
	Uca spp.	1.12	0.3510	
	Unidentified insect	2.71	0.0988	
	Unidentified insect larva	2.64	0.1041	
	Unidentified juvenile xanthid	0.51	0.6093	

Treatments are ranked in descending order. Different letters within a row indicate significantly different values (Tukey's test). *C. v.* = *C. virginica; C. a.* = *C. ariakensis*.

downstream in a Florida estuary. Furthermore, they observed that salinity appeared to be more important than abundance of living oysters as a predictor of increased community metrics (Tolley et al. 2005). Similarly, our findings suggest that, at least at the scale addressed here, salinity-driven effects on reef biota are greater than those of the reef-forming species in question.

Significant treatment effects on community metrics were rare, even when comparing live oyster treatments with the shell-only treatment. Although average total abundance per sample was higher for live oyster reefs than for the shell-only treatment, no significant differences in species richness or evenness were detected. At the low-salinity location (Severn River, MD), Shannon-Weiner diversity was actually higher for the treatment without live oysters (shell only). The importance of the biological properties of live bivalves in determining the structure of associated macroinvertebrate assemblages has been assessed by several previous studies, many of which have documented similar colonization of mimics, live, and dead bivalves (Crooks & Khim 1999, Tolley & Volety 2005), although that is not always the case (Boudreaux et al. 2006, Norling & Kautsky 2007). Most dead

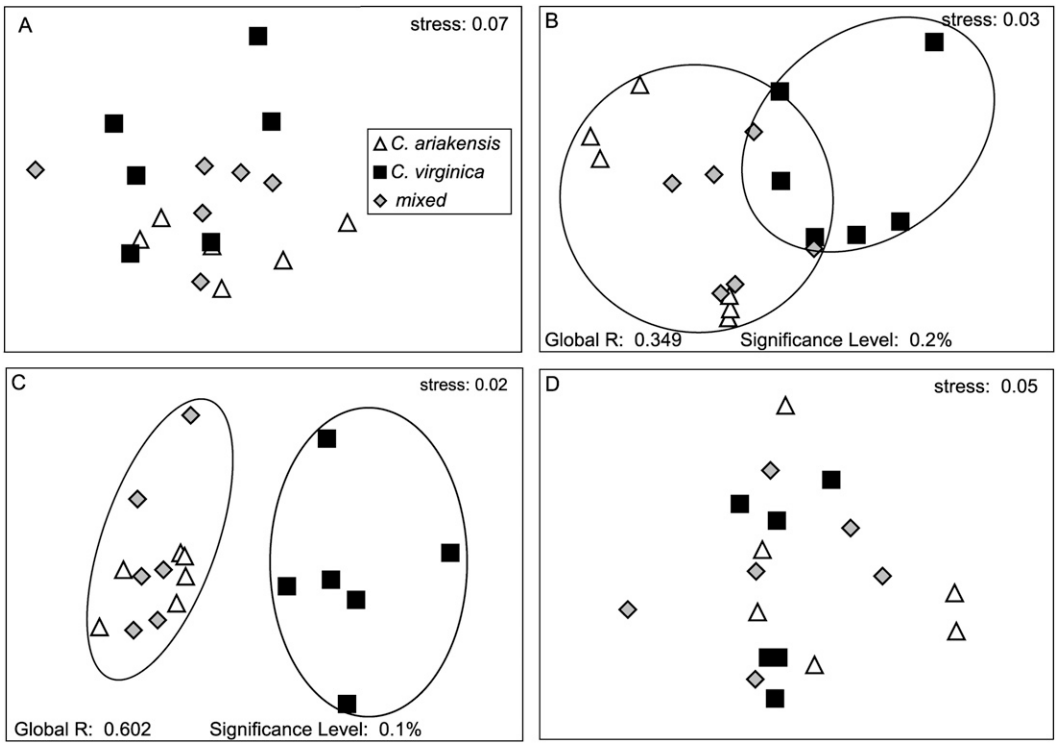

Figure 6. Nonmetric multidimensional scaling plots for standardized abundances of associated fauna at all sites. (A) Severn. (B) Patuxent. (C) York. (D) Machipongo. Significant analysis of similarity results were found only at the Patuxent and York River sites, where the *C. virginica* treatment differed significantly from both the *C. ariakensis*-only and mixed-species treatments.

oysters differ structurally from their live counterparts, however, as the valves of dead oysters typically disarticulate within 12 mo (Ford et al. 2006). This decrease in vertical height compared with live oyster reefs has been thought to lead to a decrease in habitat function. Summerhayes et al. (2009), however, observed that epibiota were generally more abundant in treatments containing half shells than in those with whole oysters, suggesting that the shells offered additional interstitial space and greater surface area for initial colonization. Whether this relationship changes over time is not known. The results of the current study, as well as previous research, indicate that the effects of live oyster presence on community structure remain poorly understood, largely as a result of the coupling of oyster presence with increased habitat complexity.

Without taking oyster biomass into account, the total numbers of reef-associated organisms were similar among live oyster treatments, suggesting habitat functional equivalency of *C. ariakensis* and *C. virginica*. However, both oyster survival and growth varied across and within sites in this study (Kingsley-Smith et al. 2009). This analysis simply compares the habitat function of the *surviving* oysters, not the overall capability of the species. By normalizing abundance and biomass of reef-associated fauna in each sample by the oyster biomass, we were better able to examine the functional equivalency of the 2 oyster species with regard to habitat provision. The results support functional equivalency with respect to habitat between oyster species at the intertidal site, as well as the low-salinity subtidal location. At subtidal sites with higher salinities (York and Patuxent), however, habitat function varied between oyster species after the data were normalized. Here, the mean number and biomass of organisms associated with *C. virginica* reefs was significantly greater than the number associated with *C. ariakensis* reefs. This suggests that, if introduced, the nonnative oyster may have less potential for habitat provision than the native oyster in subtidal high- and mid-salinity regions of the Chesapeake Bay. The decreased habitat potential of *C. ariakensis* in these areas may be reinforced by increased predation as a result of its weaker shell (Bishop & Peterson 2006, Newell et al. 2007), or may be offset by increased growth rates (Calvo et al. 2001, Grabowski et al. 2004, Hudson et al. 2005, Paynter et al. 2008).

More than 75 species were identified during the current study, which is the first investigation of benthic community composition on experimental Suminoe oyster (*C. ariakensis*) reefs in the Chesapeake Bay region. Dominant species varied among locations and included amphipods, bivalves, fishes, decapod crustaceans, gastropods, and polychaete worms. The assemblages collected during this study were similar to those previously reported on restored and natural reefs from temperate waters (Coen et al. 1999, Posey et al. 1999, Rodney & Paynter 2006). Similar to results for community metrics, the number of dominant species generally increased with increasing salinity. Patterns of standardized abundances of individual dominant species largely mirrored those observed for overall abundance, in that no differences were seen at the intertidal site between live oyster treatments, and only 1 group (juvenile xanthid crabs) had increased numbers on native reefs compared with nonnative treatments at the low-salinity site. Significant increases in individual species abundances associated with *C. virginica* treatments were seen predominantly at the subtidal site of highest salinity (York), with some occurrences at the upper mesohaline location (Patuxent). We observed increased abundances of all dominant species on native oyster reefs at the York River site and

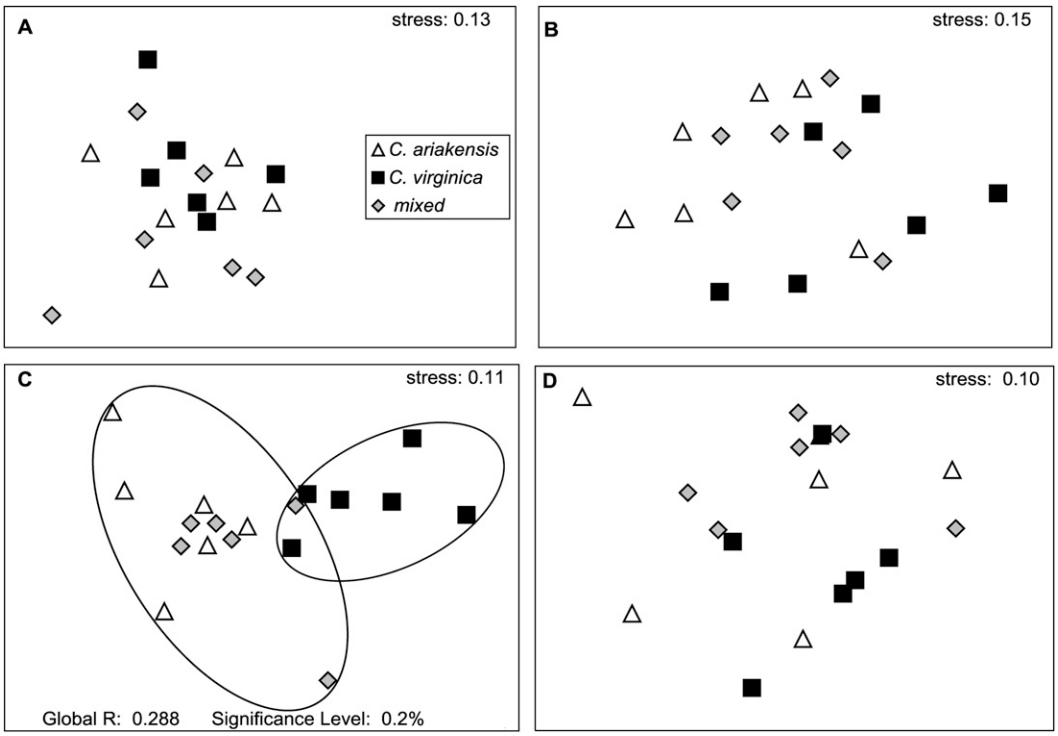

Figure 7. Nonmetric multidimensional scaling plots for standardized biomass of associated fauna at all sites. (A) Severn. (B) Patuxent. (C) York. (D) Machipongo. Significant analysis of similarity results were found only at the York, where the *C. virginica* treatment differed significantly from both the *C. ariakensis*-only and mixed-species treatments.

increased abundances of 50% of dominants at the Patuxent River site, further supporting a greater potential for habitat provision by native oysters in subtidal areas of high salinity.

Unlike standardized abundance data for individual dominant species, standardized biomass data for dominant reef-associated fauna revealed very few treatment effects. We observed increased biomass on native oyster treatments for only 3 dominant species at the high-salinity subtidal site: *D. microphthalmus*, a polychaete worm; *E. depressus*, a xanthid crab; and *G. strumosus*, the skillet fish. In all other cases, standardized biomasses of species comprising at least 1% of the total biomass were similar regardless of oyster species. At the York and Patuxent sites, where differences in habitat complexity were visually observed but not quantitatively detected, oyster species had a greater influence on reef-associated species that were dominant in abundance, rather than biomass. In other words, it was mostly the smaller, more prolific organisms that were significantly affected by oyster species. This suggests that oyster species may have significantly impacted the size of organisms able to use the reefs as habitat. It appears that *C. virginica* reef communities at this location were comprised of a greater number of relatively smaller individuals, and that those found on *C. ariakensis* reefs, although lower in standardized abundances, were larger in size.

Results from multivariate analysis of similarity comparisons, which take into account both species composition and relative abundance, revealed similar patterns to those observed from univariate ANOVA comparisons. Once again, oyster species did not affect community structure at the low-salinity (Severn) or intertidal (Machipongo) site. At both subtidal sites of higher salinity (York and Patuxent), the benthic communities associated with *C. virginica* reefs were unique among live oyster treatments, although the mechanism behind this difference remains unclear. Although community differences may have been related to subtle differences in complexity that we were unable to quantify using the rugosity index, larval recruitment dynamics, chemical cues, or other unknown factors may also have been involved.

Although site and treatment effects of oyster species on reef-associated fauna were observed, we acknowledge the limitation of this study in estimating abundance and biomass of faunal assemblages occurring on natural oyster reefs. Cage presence likely reduced predator–prey interactions through the exclusion of larger predators, such as large blue crabs, cownose rays, striped bass (*Morone saxatilis*), sheepshead (*Archosargus probatocephalus*), and oyster toadfish (*Opsanus tau*). A lack of larger predators may have resulted in increased abundances of prey species. It may have also increased the effectiveness of intermediate predators via trait-mediated effects (Grabowski 2004). Although our results should not be directly compared with other studies estimating tertiary production on oyster reefs, the relative comparisons made between our experimental oyster treatments remain valid.

Should an introduction of *C. ariakensis* occur, it is most likely that the 2 species would co-occur on some reefs. In this regard, our results from the mixed-species treatment are informative. Although significant differences were found between the benthic communities supported by native and nonnative experimental reefs, mixed-oyster species treatments most often displayed patterns similar to those of monospecific *C. ariakensis* reefs. Although the mechanism behind this remains unknown and may be unrelated to reef morphology, more robust measures

TABLE 8.

Reduced-model 1-way ANOVA results for the effect of live oyster treatment on individual species biomass comprising at least 1% of total standardized biomass at each site.

Site	Species	F Value	*P* Value	Ranking
Severn				
	Anguilla rostrata	0.62	0.5513	
	Eurypanopeus depressus	2.37	0.1276	
	Gobiesox strumosus	1.11	0.3563	
	Gobiosoma bosc	0.20	0.8178	
	Mya arenaria	0.80	0.4688	
	Neanthes succinea	0.04	0.9566	
	Panopeus herbstii	0.79	0.4708	
	Rhithropanopeus harrisii	1.95	0.1777	
	Unidentified juvenile xanthid	2.50	0.1154	
Patuxent				
	Apocorophium lacustre	2.52	0.1141	
	Boonea bisuturalis	0.51	0.6090	
	Eurypanopeus depressus	1.81	0.1982	
	Gammarus mucronatus	1.29	0.3039	
	Gammarus palustris	2.14	0.1524	
	Gemma gemma	1.23	0.3190	
	Gobiesox strumosus	1.04	0.3762	
	Gobiosoma bosc	0.91	0.4229	
	Ischadium recurvum	1.23	0.3192	
	Macoma balthica	1.54	0.2457	
	Macoma mitchelli	1.30	0.3021	
	Melita nitida	0.40	0.6756	
	Mulinia lateralis	0.86	0.4423	
	Mya arenaria	2.45	0.1201	
	Neanthes succinea	0.18	0.8339	
	Panopeus herbstii	1.79	0.2005	
	Unidentified cnidarian	1.17	0.3375	
York				
	Anguilla rostrata	0.97	0.4003	
	Callinectes sapidus	1.04	0.3770	
	Chasmodes bosquianus	2.02	0.1666	
	Demonax microphthalmus	10.97	0.0012	*C. v.*[A] mixed[B] *C. a.*[B]
	Eurypanopeus depressus	10.73	0.0013	*C. v.*[A] mixed[B] *C. a.*[B]
	Gobiesox strumosus	6.94	0.0074	*C. v.*[A] mixed[B] *C. a.*[B]
	Gobiosoma bosc	2.14	0.1527	
	Heteromastus filiformis	0.81	0.4642	
	Hypsoblennius hentz	0.68	0.5226	
	Loima medusa	0.99	0.3935	
	Mya arenaria	1.58	0.2394	
	Neanthes succinea	3.51	0.0562	
	Panopeus herbstii	0.59	0.5654	
Machipongo				
	Astyris lunata	1.00	0.3911	
	Boonea impressa	1.09	0.3628	
	Dyspanopeus sayi	0.78	0.4779	
	Eurypanopeus depressus	0.70	0.5117	
	Panopeus herbstii	0.88	0.4370	

Treatments are ranked in descending order. Different letters within a row indicate significantly different values ($P < 0.05$, Tukey's test). *C. v.* = *C. virginica; C. a.* = *C. ariakensis.*

of habitat complexity, such as distance between individual oysters or the angles at which they meet, may aid in the elucidation of this mechanism.

This study indicates that, if introduced to the Chesapeake Bay region, the ability of *C. ariakensis* to serve as a functional equivalent of the native oyster with respect to habitat provision is likely to vary with location. Poor survival of *C. ariakensis* in intertidal areas suggests that *C. virginica* would be a better provider of habitat in such areas, although differences in intertidal reef communities were not detected here. A degree of functional equivalency is more likely in low-salinity subtidal areas, where the growth of the 2 oyster species is most similar. Pronounced differences in benthic community structure are most likely to occur in the lower reaches of Chesapeake Bay.

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