Vol. 590: 35–51, 2018
https://doi.org/10.3354/meps12470

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 12

Faunal communities on restored oyster reefs: effects of habitat complexity and environmental conditions

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ABSTRACT: Wild oyster populations have suffered >85% global loss, and in Chesapeake Bay, only 1% of the historic oyster population remains. In response, efforts to restore oysters and the services they provide, such as water filtration and habitat, have increased. A critical step towards restoring these services is understanding the role of restored reefs in marine ecosystems and determining the factors that affect how species utilize them. In a field survey, we embedded benthic settling trays into restored reefs that varied in structural complexity in 4 rivers in Chesapeake Bay. We retrieved trays after 7 wk to estimate species diversity, density, and biomass of macrofauna; these metrics were then related to structural indices and environmental conditions at each reef. A total of 66 macrofaunal species inhabited restored oyster reefs across all the samples, and reefs supported on average 75.6 g AFDW m^{-2} and 6356 ind. m^{-2}. Species composition differed significantly among the rivers, and salinity best explained the differences. Salinity and rugosity were significantly and positively related to macrofaunal diversity, while negatively related to fish density. Salinity was also significantly and negatively related to macrofaunal density and biomass, whereas live oyster volume was significantly and positively related to total macrofaunal biomass and density, as well as densities of specific taxa (fish, polychaete, mud crab, mussel). Restored oyster reefs can be productive habitats with this potential varying with both salinity and habitat complexity. Our results suggest that habitat quality and utilization of reefs will be enhanced when habitat complexity of restored oyster reefs is high.

KEY WORDS: *Crassostrea virginica* · Oyster reefs · Macrofauna · Habitat complexity · Salinity · Restoration · Ecosystem services · Species–environment relationships

INTRODUCTION

Many marine benthic habitats are defined by the presence of either a single or a few habitat-modifying species that provide structural habitat for other species (Bruno et al. 2003). Examples of these habitat-forming species include corals, seagrass, saltmarsh plants, mangroves, and oysters (Jones et al. 1994, Bruno et al. 2003). The structural complexity and habitat architecture provided by these species have profound effects on the abundance and diversity of organisms (Alvarez-Filip et al. 2011). Unfortunately, many of these biogenic habitats have been declining worldwide. In the last 15 yr, oyster reefs have been recognized as an important biogenetic habitat, but similar to other biogenic habitats, oyster reefs have suffered global declines and are currently one of the most rapidly deteriorating habitats, with an estimated 85% global loss since the 1880s (Beck et al. 2011). This dramatic decline, resulting from a combination of stressors experienced by the oyster population including harvesting, declining water quality

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(Rothschild et al. 1994), and increased prevalence of diseases (such as MSX and Dermo) (Carnegie & Burreson 2011), has had negative economic and ecological impacts worldwide.

The need to restore oyster reef habitats is recognized globally, and several small-to-medium scale restoration efforts have been carried out during the last several decades. However, these efforts have had limited success in spite of substantial investments by state and federal agencies (Brumbaugh et al. 2010, Beck et al. 2011). The main focus of early restoration efforts was to increase oyster biomass to maintain oyster fisheries, and success was typically measured by the density of market-sized (>76 mm shell height [SH]) oysters (Luckenbach et al. 2005, Beck et al. 2011). Recently, oyster reefs have been recognized as providing a suite of ecosystem services, or 'benefits to humans' beyond their direct economic value as a harvested resource. These services include water filtration (Grizzle et al. 2008), sequestration of carbon (Peterson & Lipcius 2003), stabilization of intertidal and benthic habitats, de-nitrification (Kellogg et al. 2013), provision of habitat and foraging grounds for benthic invertebrates and fish, and enhanced benthic–pelagic coupling through facilitation of energy from the benthos to higher trophic levels (Dame 1979, Harding & Mann 2001, Peterson et al. 2003, Plunket & La Peyre 2005, Rodney & Paynter 2006). In recognition of these benefits, recent management objectives have shifted to managing and restoring oyster reefs for their ecosystem services, and particularly, for their value as productive estuarine and coastal habitats (Brumbaugh et al. 2010, Beck et al. 2011). Many of these services, particularly the provision of habitat and foraging grounds, have not been adequately quantified. Quantitative assessments to highlight the role of restored oyster reefs as habitat for benthic invertebrates and fish, and identification of the factors that influence the utilization of restored reefs as habitat, are crucial to the development of successful restoration strategies.

Two factors that may influence the success of restoration efforts are reef architecture (complexity) and environmental conditions (Dame 1979, Bruno et al. 2003, Peterson et al. 2003, Quan et al. 2012). Salinity is a key environmental factor governing the community structure and distribution of aquatic fauna (Wells 1961, Vernberg & Vernberg 1972). As salinity declines, marine species that cannot physiologically tolerate lower salinities are absent, thus, there is a notable decline in species diversity until the freshwater environment is encountered. The relationship between salinity and species diversity has implications for selection of oyster restoration sites because oysters and their associated fauna may respond differently along a salinity gradient. Despite the importance of salinity in shaping faunal communities, the effect of salinity on oyster reef communities has received limited attention (e.g. Wells 1961, Tolley et al. 2005, 2006, Bergquist et al. 2006, Quan et al. 2012).

Habitat complexity, which encompasses the amount, density, and configuration of structural elements in a habitat, is another factor that influences the abundance, diversity, and distribution of organisms (Tews et al. 2004, Harwell et al. 2011, Hanke et al. 2017b). The 'heterogeneity hypothesis' proposes that complex habitats sustain more diverse and dense macrofaunal communities than simple habitats (Diehl 1992, Tews et al. 2004). The hypothesis originally described diversity in complex terrestrial habitats, but it has also been applied to aquatic habitats such as coral reefs (Alvarez-Filip et al. 2011), freshwater macrophyte communities (Crowder & Cooper 1982), and oyster reef communities (e.g. Cranfield et al. 2004; Hanke et al. 2017b). Oysters are important ecosystem engineers, forming the structural element of the habitat, providing hard 3-dimensional structure and modifying the environment in ways that facilitate their growth and survival, as well as growth and survival of other species (Jones et al. 1994). The topography, morphology, and spatial extent of oyster reefs can affect the recruitment, abundance, and diversity of reef inhabitants (Plunket & La Peyre 2005, Hanke et al. 2017b).

Previous studies have compared the abundance and diversity of organisms from structured oyster reef habitats and non-structured environments (e.g. Plunket & La Peyre 2005, Tolley & Volety 2005); however, the manner in which organisms respond to changes in habitat complexity within oyster reef habitats is inconsistent among locations and oyster species, and may depend on how habitat complexity is quantified. In Mobile Bay, Alabama, more organisms are found on low-relief reefs than high-relief reefs, with reef relief serving as a measurement of reef complexity, and diversity remains the same between the 2 relief heights (Gregalis et al. 2009). In contrast, species diversity and abundance increase with increasing reef height and surface rugosity on oyster reefs in New Zealand (Cranfield et al. 2004). These studies highlight how the manner in which organisms respond to changes in structural complexity may differ by location and the community or structural metric of interest.

Our study aims to increase the understanding of the habitat value of restored oyster reefs and their community response to habitat complexity and envi-

ronmental conditions (especially salinity) by (1) quantifying species diversity, density, and biomass on restored oyster reefs, and (2) determining the relationship between the physical aspects of the habitat (structural complexity and salinity) and 3 biological metrics (macrofaunal density, biomass, and species composition). We hypothesized that (1) macrofaunal communities on restored reefs vary among locations, (2) diversity on restored reefs increases with increasing salinity, and (3) habitat complexity of restored reefs positively affects macrofaunal diversity, density, and biomass.

MATERIALS AND METHODS

Sampling locations

Field sampling occurred during summer 2014, 2015, and 2016 on previously restored oyster reefs in 4 rivers in lower Chesapeake Bay — the Great Wicomico, Piankatank, Lafayette, and Lynnhaven Rivers (Fig. 1). Chesapeake Bay has suffered some of the greatest declines in oyster populations in the world, and has been classified as being in 'poor condition' (Beck et al. 2011), with only 1% of its historic population remaining. Large-scale oyster restoration projects have been carried out in Chesapeake Bay since the mid-1990s, making this an ideal system in which to study restored oyster reef communities. Due to logistical constraints, not all rivers were sampled in each year. In 2014, the Lynnhaven and Great Wicomico Rivers were sampled, in 2015 the Lynnhaven, Piankatank, and Lafayette Rivers were sampled, and in 2016 the Lafayette and Great Wicomico Rivers were sampled.

In each river, 4 previously restored subtidal reefs were selected using Army Corps of Engineers (ACOE) and Virginia Marine Resource Commission (VMRC) maps of the reefs. These maps provided information on relief (categorized as high or low) of the reefs and oyster abundance, which was used to ensure that the sampled reefs represented the variability in architecture of the reefs in each river. As we did not measure reef relief during our field sampling, the information from the maps was only used for reef selection and was not used in further analyses. Sampled reefs were part of previous large-scale restoration efforts carried out by ACOE and VMRC, and varied in age and size, although all had been restored at least 5 yr prior to the time of sampling. Reefs were initially constructed in the Piankatank River from 1993–1995, Lafayette River from 1998–2009, Great Wicomico River from 2003–2004, and Lynnhaven River from 2008–2009, with periodic shell planting since construction. After 1 to 3 yr post-construction, oysters and their associated macrofaunal communities on reefs in North Carolina were

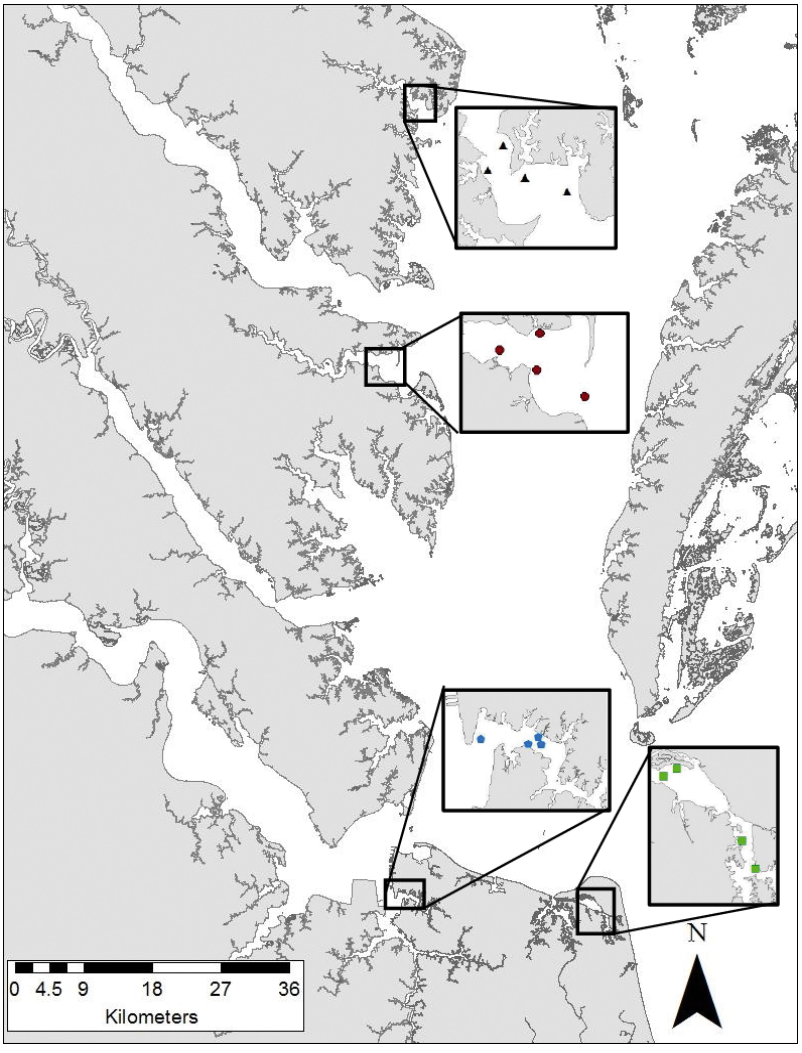

Fig. 1. Lower Chesapeake Bay and locations of the reefs sampled in each of the 4 rivers. Inserts (from top to bottom): Great Wicomico (37.82708° N, 76.2989° W), Piankatank (37.51137° N, 76.3327° W), Lafayette (36.90546° N, 76.3191° W), Lynnhaven (36.90469° N, 76.0413° W). Points indicate locations of each reef sampled; GPS coordinates are for the reef closest to the mouth of each river

well established and similar to natural reefs (Meyer & Townsend 2000, Hadley et al. 2010, Humphries et al. 2011b). Sampled subtidal reefs were relatively large ranging in size from 1.62 to 4.86 ha, and surrounded by sand or mud bottoms (Schulte et al. 2009, Lipcius et al. 2015, Theuerkauf & Lipcius 2016).

Exceptions to the above sampling regime occurred in the Lynnhaven River in 2014, when instead of 4 individual reefs, high- and low-relief sections at each of 2 large reefs were sampled. In 2015, 4 individual reefs were sampled in the Lynnhaven River, 2 of which were the ones that were sampled in 2014. Additionally, the Lafayette River contained only 2 restored reefs, both of which were sampled. In addition to the 2 restored reefs, 2 relict natural reefs in the Lafayette River were also sampled (discovery and mapping of relict reefs: R. Lipcius, D. Schulte, R. Burke, J. Lazar, D. Bruce unpubl. data). We examined whether relict reefs and restored reefs differed in terms of reef characteristics (number of oysters, oyster volume, and rugosity) to determine if all reefs in the Lafayette River could be treated similarly for further analyses.

Field sampling: tray deployment and retrieval

Four locations per reef were randomly selected each year using the numbered grid cells on the ACOE and VMRC maps. To avoid potential edge effects or sampling of non-reef sites, only grids cells that were at least 1 full grid cell (10 × 10 m) from the edge were used for site selection. At each selected location, replicate benthic sampling trays (0.122 m^2 × 0.15 m deep, 1.0 mm mesh liner) were embedded into the reef matrix by divers, who excavated a hole in the reef in which to place the tray flush with the reef. Excavated reef material was placed into the tray, taking care to maintain the orientation and vertical dimensions of the reef matrix. Trays were deployed for a 7 to 9 wk soak period to allow resident macrofauna to occupy the tray. Variability in soak time was due to weather conditions, which prevented retrieval of the trays on specific days. Trays were deployed on 21–23 May 2014, 20–27 May 2015, and 24–25 May 2016. Retrieval of the trays occurred on 8–9 July 2014, 9–16 July 2015, and 22–25 July 2016.

Bottom temperature, salinity, and dissolved oxygen (DO) were measured using a handheld YSI model 85 and depth was measured using a weighted measuring tape during deployment and retrieval of each tray. An index of surface complexity, or rugosity, was measured immediately after each tray was retrieved, and brought back to the boat using the 'chain-link' method (Rodney & Paynter 2006) with a 1 m long chain comprised of 1.5 cm long links. The rugosity index provides information on the configuration of the oyster material in the habitat, and is essentially a measure of the number of wrinkles, creases, and ridges present on the surface of the reef. Two rugosity measurements were made at 90° angles to each other across the middle of each tray by starting at one edge of the tray and, following a straight line, laying the chain over shells and gently forcing the chain down into the spaces between shells to the other side. The chain was then removed, straightened, and measured. The measurement was divided by the length of the tray, and the 2 measurements were averaged to obtain a mean rugosity for each tray. All material in the tray was transferred to sealable bags and placed on ice for transport to the lab where bags were stored in −21.1°C freezers for later processing.

Laboratory processing

Samples were thawed and rinsed over a 1 mm sieve prior to sorting. During sorting, all organisms were removed and stored in vials with 75% ethanol for subsequent identification. Organisms were identified to the lowest taxonomic level practical, usually species. Encrusting algae and bryozoans were not quantified in this study. The oyster material in each sample was sorted into 3 categories: live single oysters, live clumped oysters, and dead shell hash. For this study, live oyster clumps were defined as 2 or more live oysters stuck together. The shell height of each live oyster was measured, and the volume (l) for each category of oyster material was determined using water displacement. Organisms were dried in an oven at 65°C for ≥24 h and then burned in a muffle furnace at 550°C for 6 h to obtain species-specific ash-free dry weight (AFDW). Measures of oyster biomass, live and dead volumes, and density served as additional potential metrics of reef complexity, but note that these oyster metrics were not included in the calculation of total macrofaunal biomass or density.

Statistical analysis

Due to the unbalanced design of our study, each river–year combination was treated as a unique group for purposes of statistical analysis. Univariate macrofauna community metrics, density, Shannon diversity (H'), Pielou's evenness, richness, and biomass,

as well as mean environmental and structural metrics were compared among river–year groups using ANOVA, in R v.3.3.0 statistical software (R Core Team 2016). Prior to analysis, community structure metrics were evaluated for normality and homoscedasticity using the Shapiro-Wilk and Levene's test, respectively. When necessary, abundance and biomass metrics were transformed to remove heteroscedasticity and deviations from normality. Post hoc pairwise comparisons were made using Tukey's HSD test when significant differences among river–year groups were present; this approach adjusts the significance level for each pairwise comparison to ensure an experiment-wise significance level of 0.05. In cases where transformations failed to achieve homoscedasticity, Welch's ANOVA was conducted followed by the Games-Howell post hoc test, which adjusts for unequal variances and sample sizes. For all analyses, α was set at 0.05.

The PRIMER-6 statistical package (Clarke & Gorley 2001) was used to describe multivariate patterns in community composition in terms of abundance and biomass of organisms present. Non-metric multidimensional scaling (nMDS) plots were created from square-root transformed abundance and biomass data using the Bray-Curtis similarity index (Clarke 1993, Clarke & Warwick 2001). ANOSIM was conducted to examine differences among the 7 predetermined river–year groups' community composition (Clarke & Warwick 2001), and to statistically evaluate the grouping pattern observed in the nMDS ordination plots. BioEnv analysis was used to identify the subset of water quality and reef structural parameters that best explained patterns in community composition in terms of abundance and biomass (Clarke & Ainsworth 1993).

Multiple linear regression analysis was carried out using the 'lm' procedure in R to determine the effect of salinity and oyster reef habitat complexity on each community metric: macrofaunal density, biomass, and diversity. Organism density (ind. m^{-2}) and biomass (g AFDW m^{-2}) were square-root transformed to meet the assumptions of normality and homogeneity of variance. An initial model was fit that included all habitat complexity parameters (clump volume, live oyster volume [live single oysters + clumped oysters], shell hash volume, number of live oysters, total oyster volume, and rugosity). Tolerance statistics were used to evaluate multicollinearity in this full model; tolerances <0.1 indicated a potential problem. After evaluating tolerances, the final model included 4 predictors: salinity and 3 oyster reef-complexity metrics (total live oyster volume [clump + live volumes], shell hash, and rugosity). These factors have been proposed to impact macrofaunal abundance and diversity, and such measures can be made in the field with minimal amount of destruction to the reef habitat. Additionally, live oyster volume was significantly and positively correlated with live oyster density ($r = 0.60$, $p < 0.05$), and therefore also provided some information on the effect of live oyster density. Furthermore, the 3 reef-complexity measurements represent different aspects of complexity within the oyster reef habitat. This may provide insight regarding aspects of complexity to which organisms are most strongly responding (either the amount of live or dead oyster material, or the configuration of the structural elements in the habitat), and how restoring one aspect of complexity may impact the resultant abundance, biomass, or diversity of organisms utilizing the restored reef.

Additional models were fit to describe the densities of the 4 main taxonomic groups within the reef community: mussels, mud crabs, polychaetes, and fish. In our study, mussels were almost exclusively *Ischadium recurvum*, and therefore only this species was considered in the analysis of mussel density, whereas densities of mud crabs, polychaetes, and fish were summed across multiple species within each taxon.

RESULTS

Environmental and structural parameters

Environmental conditions were significantly different among river–year combinations (Table 1). Mean salinity ranged from 13.7 to 24.7 psu, and significantly increased from north to south towards the mouth of the Chesapeake Bay (Fig. 2). Mean DO, on the other hand, was greater in the 2 northernmost rivers (Great Wicomico and Piankatank) compared with the 2 southern rivers (Lafayette and Lynnhaven); however, conditions were normoxic (>4 mg l^{-1} O_2) in all rivers during the sampling periods (Table 1) and therefore differences in DO were most likely of little biological consequence. Mean temperature differed among the river–year groups (Table 1); however, the greatest difference in mean temperature was 2.6°C, a difference which is most likely not biologically meaningful in this estuarine system where temperature can fluctuate as much as that on a daily basis during the summer months (https://tidesandcurrents.noaa.gov/stations.html?type=Physical%20Oceanography).

Reef characteristics (mean number of oysters, mean oyster volume, and mean rugosity) did not differ sig-

Table 1. Mean environmental and structural variables of reefs sampled in each of 4 rivers over 3 yr. Environmental parameters were calculated as the average of measurements taken during deployment and retrieval of sampling trays using a YSI. Only sites where trays were successfully retrieved were included in the calculation. Different superscript letters indicate significant differences ($p < 0.05$) from post hoc tests. Salinity and temperature were analyzed using Welch's ANOVA and a Games-Howell post hoc test; all others were analyzed with ANOVA and Tukey's HSD. Data for oyster density, market-sized oyster density, live and clump volume were square-root transformed for analysis, but raw averages are presented here. Sample sizes were n = 15 in the Great Wicomico River (GW) during 2014, n = 14 in 2016, n = 11 in the Piankatank River (PR) and Lafayette River (LAF) in 2015, n = 10 in the LAF in 2016 and Lynnhaven River (LYN) in 2014, and n = 8 in the LYN in 2015. Due to a missing rugosity value for one sample in the LYN 2014, n = 79 for this analysis

Variables	Rivers							*F*	df	p
	GW 2014	GW 2016	PR 2015	LAF 2015	LAF 2016	LYN 2014	LYN 2015			
Salinity (psu)	13.76^{a}	16.35^{b}	17.75^{c}	21.44^{d}	19.59^{e}	22.4^{f}	24.69^{g}	921.24	6, 27.7	<0.001
Dissolved oxygen (mg O_2 l^{-1})	7.13^{a}	6.95^{ab}	6.63^{ab}	6.26^{b}	5.25^{c}	5.16^{c}	6.26^{b}	17.8	6, 73	<0.001
Temperature (°C)	24.75^{abc}	25.27^{a}	24.61^{b}	25.68^{a}	23.72^{c}	25.69^{a}	26.28^{abc}	30.92	6, 29.5	<0.001
Depth (m)	3.14^{ab}	3.52^{a}	2.19^{c}	2.32^{bc}	2.29^{bc}	2.50^{bc}	2.38^{bc}	6.03	6, 73	<0.001
Rugosity	1.34^{ad}	1.68^{bc}	1.60^{abc}	1.39^{abd}	1.81^{c}	1.22^{d}	1.63^{abc}	7.67	6, 72	<0.001
Oyster density	485.25^{ab}	819.09^{a}	377.79^{abc}	153.50^{c}	324.14^{bc}	231.15^{bc}	225.41^{bc}	6.58	6, 73	<0.001
Market-sized oyster density	80.33	84.31	160.21	76.01	124.44	122.95	88.11	1.28	6, 73	0.276
Oyster shell height	60.25^{ab}	52.65^{a}	82.19^{bc}	68.97^{abc}	63.60^{abc}	84.46^{c}	68.56^{abc}	4.61	6, 73	<0.001
Total oyster volume (l)	4.92^{ab}	5.14^{a}	3.81^{bc}	2.87^{c}	3.12^{c}	4.55^{ab}	3.67^{bc}	8.66	6, 72	<0.001
Dead (shell hash)	2.52^{ab}	3.14^{b}	1.80^{a}	1.75^{a}	1.75^{a}	2.29^{ab}	1.55^{a}	5.95	6, 73	<0.001
Live volume	1.50^{a}	0.989^{abc}	0.854^{abc}	0.477^{b}	0.660^{bc}	1.29^{ac}	0.690^{abc}	4.94	6, 73	0.001
Clump volume	0.786	0.707	0.912	0.43	0.591	0.820	1.15	1.70	6, 73	0.134

nificantly between relict and restored reefs in the Lafayette River (Table 2). Therefore, observations from all reefs in the Lafayette River were treated similarly for further analysis. Mean oyster density was significantly greater in the Great Wicomico River (2014 and 2016) compared with the Lafayette River in 2015, and in the Great Wicomico River in 2016 compared with the Lafayette River in 2016, and the Lynnhaven River in 2014 and 2015 (Table 1). Mean oyster density in the Piankatank River was not significantly different from the other river-year groups. Mean total oyster volume was also greater in the Great Wicomico River (2014 and 2016) compared with the Lafayette River in 2015 and 2016, and in the Great Wicomico River in 2016 compared with the Piankatank River in 2015 and Lynnhaven River in 2015 (Table 1). In contrast, the mean volume of dead shell hash was significantly greater in the Great Wicomico River in 2016 compared with the Piankatank River in 2015, Lafayette River (2015 and 2016), and Lynnhaven River in 2015 (Table 1). The mean volume of live single oysters was significantly greater in the Great Wicomico River in 2014 compared with the Lafayette River (both years), and in the Lynnhaven River in 2014 compared with the Lafayette River in 2015. Although the mean density of market-sized oysters (>76 mm SH) did not differ significantly among the

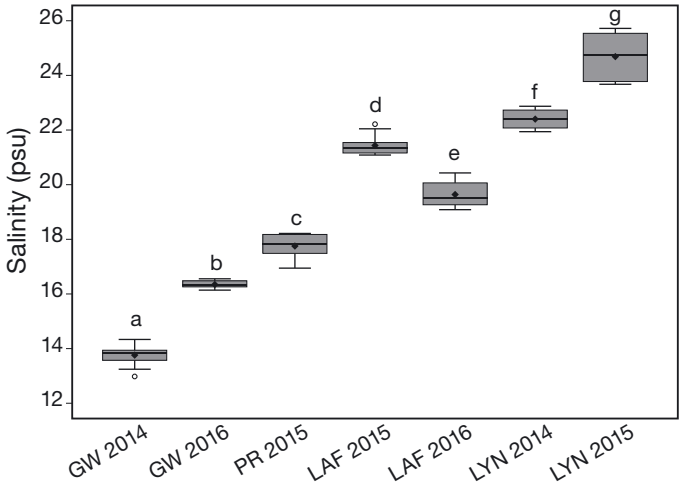

Fig. 2. Salinity by river–year group. Horizontal bar: median salinity; black diamond: mean salinity in each river–year group. See Table 1 for site abbreviations. Different letters indicate significant differences at $\alpha = 0.05$

Table 2. Reef structural characteristics and 1-way ANOVA results for restored and relict reefs in the Lafayette river. Values are the average of restored or relict reefs across both sampling years (2015 and 2016). Sample sizes: restored reefs, n = 11; relict reefs, n = 10

Variables	Restored reefs	Relict reefs	*F*	df	p
Rugosity	1.63	1.56	0.159	1, 20	0.694
Oyster density	245.22	231.15	0.182	1, 20	0.835
Total oyster volume (l)	3.09	2.88	0.252	1, 20	0.621

river–year groups, average oyster shell height did (Table 1). On average, oysters were significantly larger in the Piankatank and Lynnhaven Rivers in 2014 compared with the Great Wicomico River in 2016, and in the Lynnhaven River in 2014 compared with the Great Wicomico River in 2014. Mean rugosity also varied among river–year groups, but no clear pattern was evident in this variation (Table 1). Mean clump volume was not significantly different among the river–year groups.

Species and community composition

In total, 62 035 organisms representing 66 macrobenthic species were collected from 80 benthic settling trays retrieved from the 4 rivers during 3 yr (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m590p035_supp.pdf). The most abundant taxa were Polychaeta (primarily *Alitta succinea*), accounting for 45.9% of the total number of organisms collected, followed by amphipods accounting for 13.72% of total abundance, and gastropods accounting for 9.83% of total abundance. Of the 66 species collected, 20 occurred in all rivers (Table S1). Six taxa (*Marphysa sanguinea*, *Terebellid* sp., *Arabella iricolor*, *Glycera dibranchiata*, *Lepidametria commensalis*, and *Anomia simplex*) were unique to the 2 southernmost rivers (Lynnhaven and Lafayette), 3 taxa (*Leitoscopolos* sp., *Tritia obsoleta*, and *Idotea baltica*) were found only in the Lynnhaven River, and 2 species (*Astyris rosacea* and *Costoanachis avara*) were unique to the Lafayette River. Two species (*Arcuatula papyria* and *Palaemonetes pugio*) were unique to the 2 northernmost rivers (Great Wicomico and Piankatank), and the 2 species (*Tagelus plebeius* and *Anguilla rostrata*) were unique to the Great Wicomico River.

Twenty-five dominant species (>1% in at least 1 river) accounted for >95% of the total abundance in any river–year group (Fig. 3A). Differences in the relative proportions of dominant species occurred among the rivers (Fig. 3A). In the Great Wicomico and Piankatank Rivers, the polychaete *A. succinea* accounted for 52 to 64% of total abundance. In the Lafayette and Lynnhaven Rivers, that same proportion of total abundance was accounted for by the 3 most abundant species, which differed across the 2 rivers and years: *A. succinea* (both rivers and years), *Molgula manhattensis* (Lafayette 2015 and 2016, Lynnhaven 2014), *Marphysa sanguenia* (Lafayette 2015 and Lynnhaven 2014), *Melita nitida* (Lynnhaven 2014), and *Palaemonetes vulgaris* (Lynnhaven 2015).

Nineteen dominant species (>1% in at least 1 river–year group), accounted for >95% of the total biomass in any river–year group (Fig. 3B). Unlike abundance, biomass was largely dominated by crustaceans. For example, the mud crab *Panopeus herbstii* accounted for 20 to 40% of the total biomass in each of the river–year groups (Fig. 3B). Additionally, relative contribution of the various organisms to total biomass appeared more similar among river–year groups than relative contribution in terms of numerical abundance.

The nMDS ordination plot provided further evidence that species composition varied among the rivers, with samples separating into 2 groups that correspond with salinity regime; the first group comprised the Great Wicomico and Piankatank Rivers, and the second comprised the Lafayette and Lynnhaven Rivers (Fig. 4). The greatest differences in community structure in terms of abundance were between either river of the low-salinity group (Great Wicomico and Piankatank) and either river of the high-salinity group (Lafayette and Lynnhaven), with only a moderate degree of separation between rivers within the same group (ANOSIM; Table 3). Salinity best explained the observed separation pattern in community composition (BioEnv; $r = 0.664$, $p < 0.05$).

Ordination of macrofaunal composition in terms of biomass showed a similar pattern as the one observed for abundance (Fig. 4B). As observed for abundance data, the greatest separation was between either of the low-salinity rivers (Great Wicomico and Piankatank) and either of the high-salinity rivers (Lafayette and Lynnhaven); however, the degree of separation between the groups was lower than that observed for species composition in terms of abundance (ANOSIM; Table 3). Similar to the community composition in terms of abundance, salinity best explained the variation in community composition in terms of biomass among rivers (BioEnv; $r = 0.341$, $p < 0.05$) (Fig. 4B).

Macrofaunal density, biomass, and diversity

On average, 6356 ind. m^{-2} and 75.6 g AFDW m^{-2} were supported on restored or relict reefs, however, mean density and biomass differed significantly among rivers ($F_{6,73} = 7.39$, $p < 0.05$, and $F_{6,73} = 3.52$, $p < 0.05$ respectively; Fig. 5). Consistent with the results of the ANOSIM analysis, we observed greater differences among rivers in terms of mean total macrofaunal density compared with biomass (Fig. 5). Mean macrofaunal density was significantly greater in the Pianka-

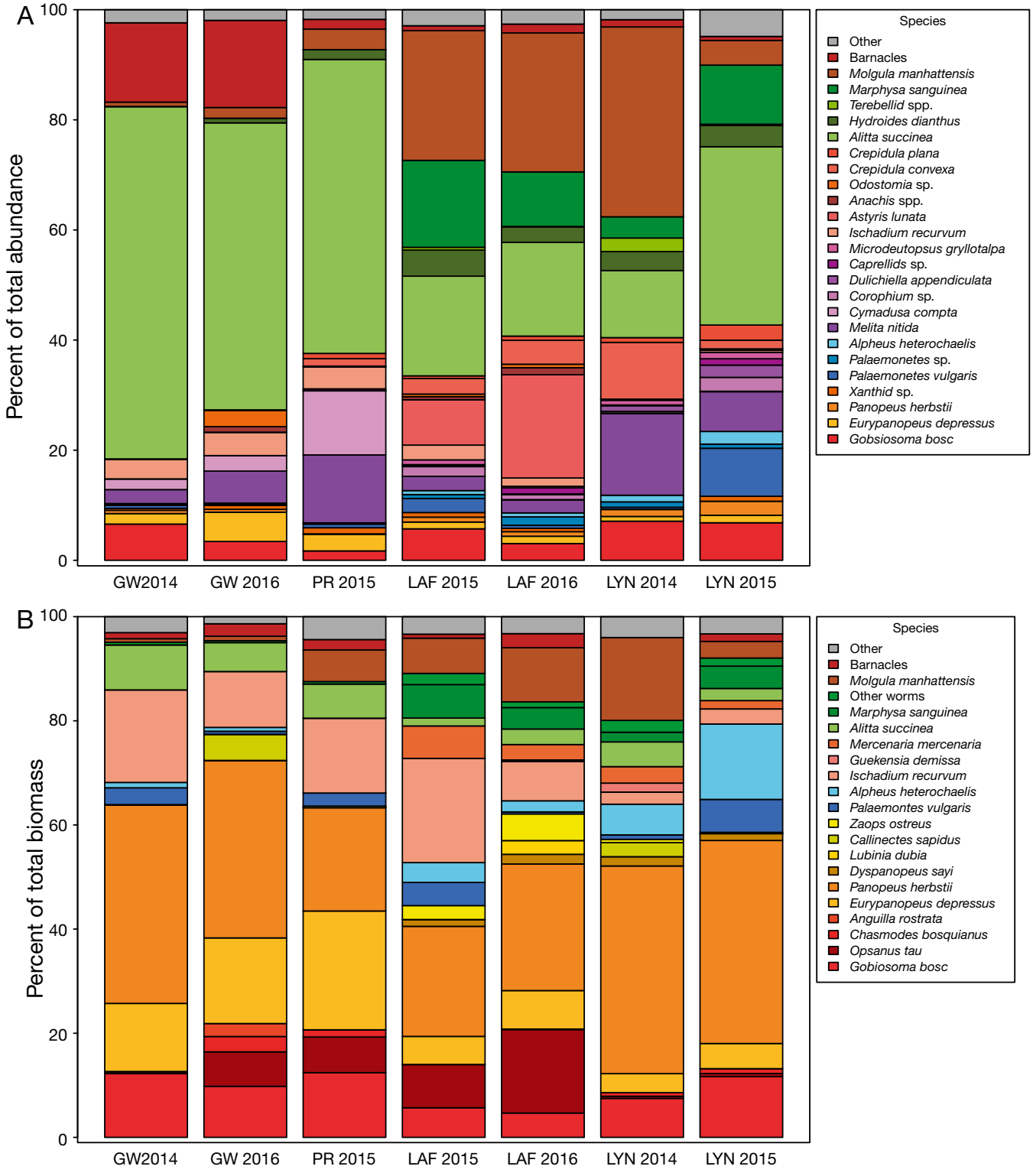

Fig. 3. Proportion of average total (A) abundance and (B) biomass of macrofauna in each river–year group attributed to the numerically or biomass-dominant species, ordered by similar taxa. Dominant organisms were those that accounted for on average at least 1% or more of total abundance or biomass in at least one of the river–year groups. 'Other' represents the remaining organisms not listed in the legend. The organisms are listed by taxonomic group and in the same order in both (A) and (B) from bottom to top of legend. Red and maroon: fish; orange and yellow: crabs; blue: shrimp; purple: amphipods; peach and light brown: molluscs; green: polychaetes; dark brown: barnacles and tunicates; grey: 'other'. See Table 1 for site abbreviations

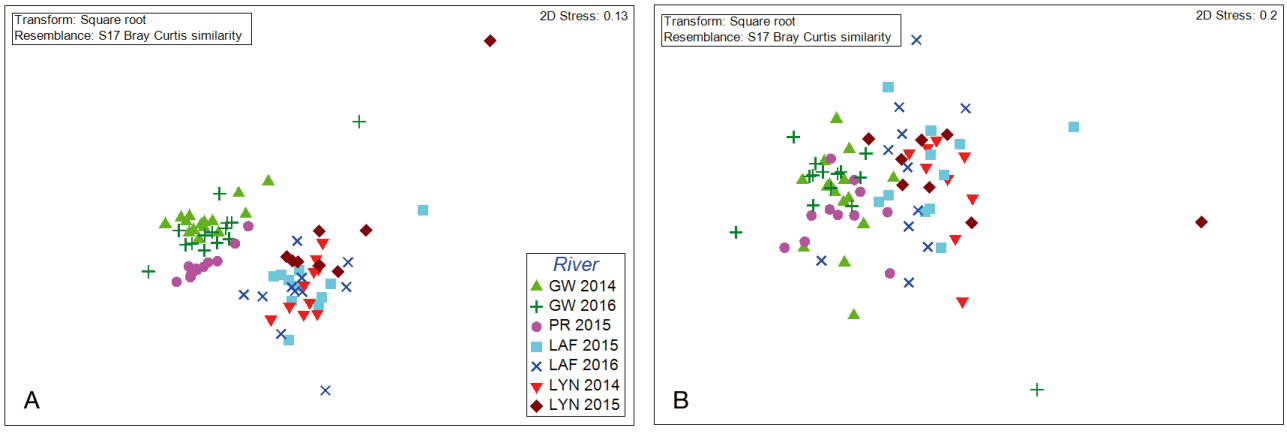

Fig. 4. Non-metric multidimensional scaling plot (A) abundance and (B) biomass of associated fauna in the 7 river–year groups. Plots were created using a Bray-Curtis similarity matrix on square-root transformed data. See Table 1 for site abbreviations

tank River compared with both years in the Lafayette and Lynnhaven Rivers, in the Great Wicomico (2014 and 2016) compared with the Lynnhaven River in 2015, and in the Great Wicomico in 2014 compared with the Lafayette River in 2015 (Fig. 5). In contrast, mean macrofaunal biomass was significantly greater only in the Great Wicomico in 2016 compared with both years in the Lynnhaven River.

Table 3. ANOSIM analysis for differences in community composition in terms of biomass and density in each of the river–year groups. See Table 1 for site abbreviations

		Biomass		Density	
		R	Sig. p (%)	R	Sig. p (%)
Global R		0.418	0.1	0.64	0.1
Pairwise Tests					
GW 2014	LYN 2014	0.687	0.1	0.993	0.1
	LAF 2015	0.636	0.1	0.919	0.1
	LYN 2015	0.589	0.1	0.886	0.1
	PR 2015	0.288	0.1	0.547	0.1
	GW 2016	0.146	0.2	0.235	0.1
	LAF 2016	0.637	0.1	0.91	0.1
LYN 2014	LAF 2015	0.242	0.5	0.366	0.1
	LYN 2015	0.085	8.5	0.425	0.1
	PR 2015	0.681	0.1	0.996	0.1
	GW 2016	0.626	0.1	0.829	0.1
	LAF 2016	0.225	1.1	0.298	0.6
LAF 2015	LYN 2015	0.188	1.2	0.350	0.3
	PR 2015	0.539	0.1	0.855	0.1
	GW 2016	0.575	0.1	0.748	0.1
	LAF 2016	0.027	25.4	0.019	12.2
LYN 2015	PR 2015	0.534	0.1	0.829	0.1
	GW 2016	0.548	0.1	0.705	0.1
	LAF 2016	0.205	1.9	0.340	0.1
PR 2015	GW 2016	0.179	0.5	0.439	0.1
	LAF 2016	0.442	0.1	0.823	0.1
GW 2016	LAF 2016	0.474	0.1	0.709	0.1

Mean H' and Pielou's evenness indices also differed significantly among the river–year groups ($F_{6,73}$ = 12.99, p < 0.05, and $F_{6,73}$ = 11.24 respectively, p < 0.05; Fig. 6). In contrast to the pattern observed for mean biomass and density, mean H' and Pielou's evenness were greater in the high-salinity rivers (Lafayette and Lynnhaven) compared with the lower-salinity rivers (Great Wicomico and Piankatank; Fig. 6). Mean species richness also differed significantly among rivers ($F_{6,72}$ = 5.88, p < 0.05), and was generally greater in the higher-salinity rivers compared with the lower-salinity rivers; however, it was only significantly greater in the Lafayette River in 2015 compared with the Great Wicomico River (both years) and Piankatank River in 2015, and the Lafayette River in 2016 compared with the Great Wicomico River in 2014 (Fig. 6).

Habitat complexity and salinity

Several predictors were significant in the multiple linear regression models describing relationships between macrofaunal community metrics and reef or environmental characteristics (Table 4). Total live oyster volume was a positive and significant predictor of mean macrofaunal density and biomass (Fig. 7) and all taxon-specific densities (Table 4). Salinity was a negative and significant predictor of mean macrofaunal density and biomass, and all taxon-specific densities; salinity was a positive and significant predictor of mean diversity (Table 4). Rugosity was a significant positive predictor of mean diversity and mean mud

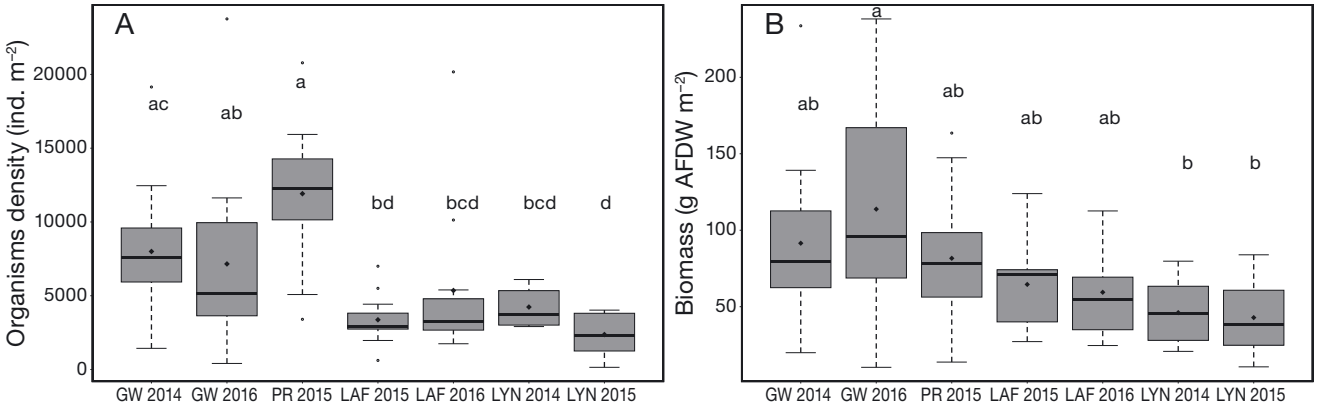

Fig. 5. Distribution of macrofaunal (A) density and (B) biomass by river–year group. Horizontal bar represents the median (A) density or (B) biomass whereas the bolded black diamond represents the mean abundance or biomass in each river–year group. Smaller black dots: outliers. See Table 1 for site abbreviations. Boxplots with different letters above them are significantly different from each other (Tukey's HSD) at $\alpha = 0.05$

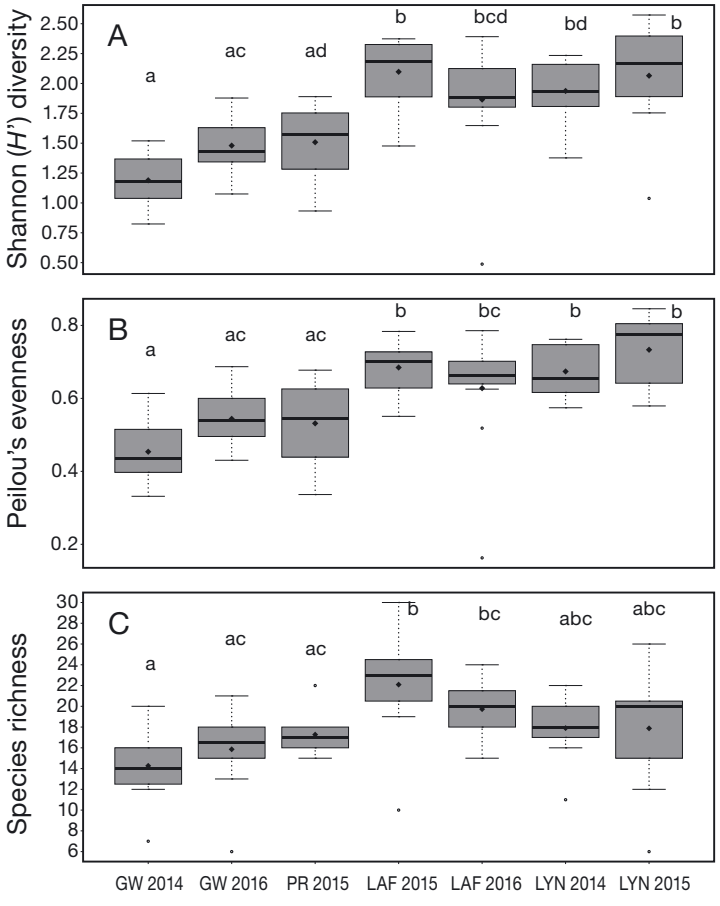

Fig. 6. Community structure metrics by river. (A) Shannon (*H'*) diversity, (B) Pielou's evenness, and (C) species richness. Different letters above boxplots indicate significant differences, based on Tukey's HSD after a 1-way ANOVA. Bolded black diamonds: raw mean; black horizontal bar: median; smaller black dots: outliers. See Table 1 for site abbreviations

crab density, and a significant negative predictor of mean fish density (Table 4). Shell hash was not a significant predictor of any of the macrofaunal metrics.

DISCUSSION

Restored oyster reefs provided habitat that supported an abundant and diverse benthic macrofaunal community. Additionally, restored reef characteristics were similar to those for relict reefs in the Lafayette River, highlighting the ability of restoration efforts to restore reefs to a natural state. Benthic macrofaunal communities differed among years and rivers, and were largely associated with differences in salinity and habitat complexity. Our study provides one of the most comprehensive quantifications of the density, biomass, and diversity of macrofaunal communities associated with restored oyster reefs. Additionally, to our knowledge, this study is one of the most extensive studies of restored oyster reefs with regards to the size of the reefs sampled (e.g. oyster reefs ranged from 1.62 to 4.86 ha) and the geographic range over which reefs were sampled (164 km from north to south).

Macrofaunal communities

A total of 66 macrofaunal species and a mean density of 6356 ind. m^{-2} were observed on the restored oyster reefs sampled in our study. This is

Table 4. Multiple linear regression analysis for macrofaunal density, biomass, and diversity. Densities and biomass were all square-root transformed to meet the assumptions of normality and homogeneity of variance unless otherwise indicated. **Bold** values are significant in the model at $\alpha = 0.05$. *H′*: Shannon diversity. Polychaete density was $\log_{10}$ transformed; mussel density was third-root transformed

Dependent variables	Estimate					*F*	p	Adj. R^2
	Intercept	Total live oyster volume	Shell hash	Rugosity	Salinity			
Macrofaunal density	128.11	**9.34**	−1.92	−1.82	**−3.35**	9.32	<0.05	0.30
Macrofaunal biomass	7.64	**1.02**	0.35	1.61	**−0.23**	12.14	<0.05	0.36
H′ diversity	−0.81	0.0037	0.042	**0.41**	**0.094**	22.84	<0.05	0.53
Fish density	24.79	**1.82**	0.10	**−3.97**	**−0.38**	11.37	<0.05	0.35
Polychaete density	4.24	**0.014**	0.007	0.047	**−0.069**	22.39	<0.05	0.52
Mud crab density	10.83	**1.68**	0.87	**4.99**	**−0.50**	6.63	<0.05	0.22
Mussel density	10.86	**0.91**	−0.056	1.36	**−0.53**	20.25	<0.05	0.50

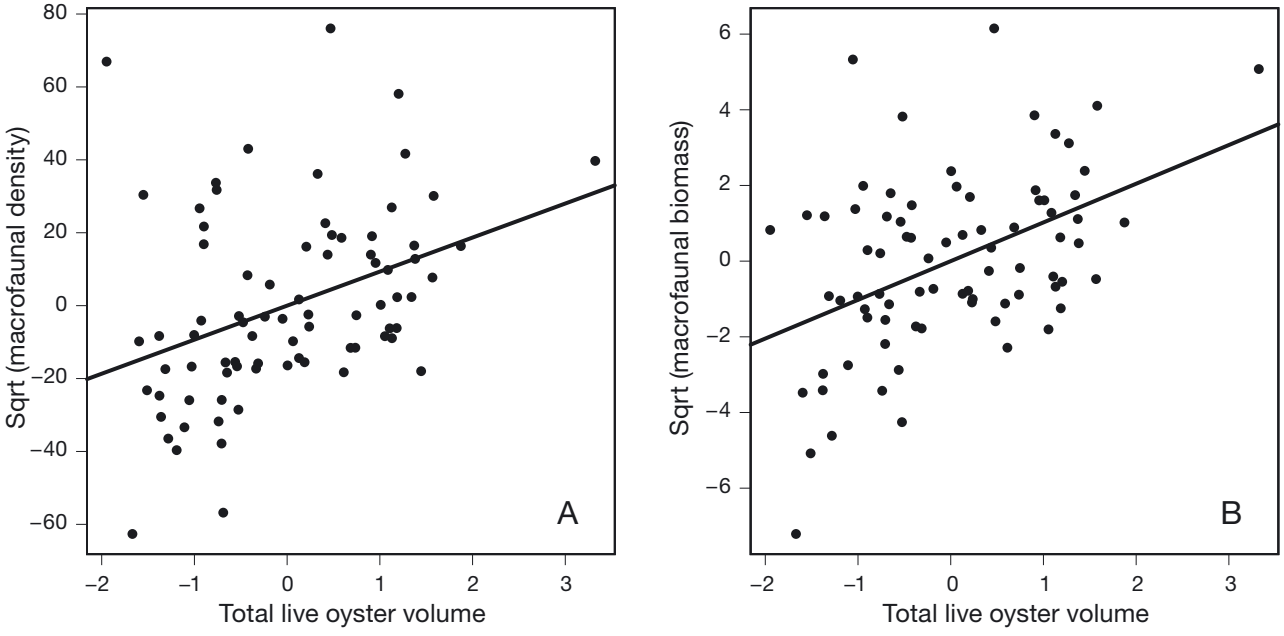

Fig. 7. Partial regression plots showing the relationship between total oyster volume, a significant predictor in the models of square-root transformed macrofaunal (A) density and (B) biomass. The partial regression plot shows the true relationship between a predictor in the model and the response variable, by holding all other predictors constant

consistent with the range in number of species (33 to 63) and macrofaunal densities (300 to 6000 ind. m^{-2}) compiled by Rodney & Paynter (2006) in a review of natural and restored reefs in the Gulf of Mexico and Atlantic coasts of the United States. Therefore, our study provides further evidence that some consistency exists in the species richness and density of organisms supported by oyster reefs across geographic regions. Furthermore, the macrofaunal assemblages described in this study were similar to those previously described for smaller Maryland reefs in Chesapeake Bay and elsewhere along the US Atlantic and Gulf of Mexico coasts. Two of the top 3 dominant taxa in our study, polychaetes and amphipods, were also among the top 3 dominant taxa in a similar study in the Maryland portion of Chesapeake Bay (Rodney & Paynter 2006). Consistent with our study, *Alitta succinea* was found in every sample at every site in Maryland (Rodney & Paynter 2006).

Aside from providing habitat for an abundance and diversity of organisms, an additional ecosystem service provided by restored oyster reefs is the provision of food resources for upper trophic levels. Biomass is a common estimate of this service, serving as a proxy for secondary production, but comparison to other biomass estimates is made difficult by the paucity of previous studies that quantified biomass of the macrofaunal assemblage on oyster reefs. Nonethe-

less, the range of average macrofaunal biomass (42.87 to 113.8 g AFDW m^{-2}) reported in our study (not including oyster biomass) is consistent with the average biomass of resident fish and invertebrates supported by restored oyster reefs in Louisiana (50 g AFDW m^{-2}) (Humphries & La Peyre 2015). However, Humphries & La Peyre (2015) estimated macrofaunal biomass on intertidal oyster reefs, which may explain why their estimate is on the lower end of the range estimated in our study. Additionally, restored oyster reefs may potentially support greater macrofaunal biomass and therefore greater foraging opportunities for upper trophic levels compared with other structured habitats in the same system. In Chesapeake Bay, for example, macrofaunal biomass previously reported for seagrass habitats (11.7 to 47.2 g AFDW m^{-2}; Edgar 1990) or unstructured soft sediments (7 to 25 g AFDW m^{-2}; Lawless & Seitz 2014, Lovall et al. 2017), are lower than biomass estimates from restored reefs in our study. Future studies explicitly designed to compare biomass across these habitats are warranted.

Many of the organisms found in high abundance and biomass in this, and previous, studies are prey organisms often found in the diets of commercially and recreationally important fishes, such as striped bass *Morone saxatilis*, weakfish *Cynoscion regalis*, and white perch *Morone americana* (Harding & Mann 2001). For example, the mud crab *Eurypanopeus depressus* and fish *Gobiosoma bosc*, which were dominant species found on reefs in this study and in North Carolina (Meyer 1994), Maryland (Rodney & Paynter 2006), and Florida (Glancy et al. 2003, Tolley et al. 2005), are often found in the diets of transient fish predators (Pfirrmann 2017). This work further highlights the role of restored oyster reef habitats as foraging grounds for estuarine and coastal fishes.

Habitat complexity

The positive relationship we observed between habitat complexity and total macrofaunal biomass, density, and diversity is consistent with previous findings (Luckenbach et al. 2005, Tolley et al. 2005, Bergquist et al. 2006, Colden 2015, Margiotta et al. 2016, Hanke et al. 2017b) but expands our knowledge to large, restored, subtidal reefs in Chesapeake Bay. Macrofaunal density was greater in the interior of intertidal oyster reefs in North Carolina and was related to the increased oyster density in the interior compared with the edges of reefs (Hanke et al. 2017a,b). In our study, macrofaunal density increased with increasing live oyster volume, which was significantly and positively correlated with oyster density. The positive effect of live oyster volume and rugosity on mean mud crab density is not surprising given that mud crabs, such as *Panopeus herbstii* and *E. depressus* (Day & Lawton 1988), increase in density with increasing rugosity and live oyster density on intertidal oyster reefs (Margiotta et al. 2016) and prefer structurally complex habitats (Day & Lawton 1988). The positive association could be attributed to provision of refuges by live oysters resulting in decreased predation risk for mud crabs (Crowder & Cooper 1982, Warfe & Barmuta 2004, Humphries et al. 2011a). The positive relationship between oysters and mussel *Ischadium recurvum* density has been documented previously (Hadley et al. 2010, Colden 2015), however, to our knowledge, never before for large, subtidal restored oyster reefs. This relationship could be a result of reduced water flow over oyster reefs with high densities and volumes of live oysters, which is conducive to settlement of larval mussels (Soniat et al. 2004), combined with increased refuge from predation for newly settled mussels.

Mean fish density in our study was positively affected by live oyster volume, and negatively affected by increasing rugosity. The negative association between rugosity and mean fish density was somewhat unexpected, as rugosity has been previously reported to be positively associated with fish density and richness in other structured habitats, such as coral reefs (Gratwicke & Speight 2005). One explanation for this negative relationship in subtidal oyster reefs could be related to the larger body size and more mobile nature of fish compared with mud crabs, which were positively affected by increasing rugosity. For example, body size is an important factor influencing the response of gastropods to habitat complexity in coralline algal turf: as frond density increases, gastropod density, especially of the large bodied gastropods, decreases (Kelaher 2003). This suggests there is a threshold after which increasing habitat complexity no longer leads to increasing density of organisms, and may actually lead to a decline (Kelaher 2003). The threshold is proposed to depend on body size, with larger organisms reaching this threshold earlier than smaller organisms. As the complexity of the surface elements (rugosity) increases, the space between the structural elements (oysters) becomes smaller. This hinders the ability of larger-bodied organisms, such as fish, to enter and maneuver around within the reef matrix, and may thus decrease the number of larger organisms that can be supported, resulting in reduced densities.

The increase in macrofaunal diversity with increasing rugosity that we observed on restored subtidal oyster reefs in this study is also consistent with previous studies from other locations (Gratwicke & Speight 2005, Rodney & Paynter 2006), providing additional evidence to support the 'habitat heterogeneity hypothesis' (Tews et al. 2004). One explanation for this positive relationship is that habitat complexity increases niche diversification and amount of habitable area, which allows resource partitioning and coexistence of multiple species, leading to increased species diversity (Heck & Wetstone 1977, Tews et al. 2004).

Shorter-term studies utilizing small-scale experimental oyster reefs with dead shell failed to observe positive relationships between overall mean macrofaunal abundance and oyster metrics (Hadley et al. 2010, Humphries et al. 2011b) in contrast to what was observed in our study. Notably, small-scale experimental reefs with high oyster density and biomass did support high macrofaunal density and biomass (Colden 2015). This suggests that restoring for increases in live oyster volume and density, not just shell material, is necessary to increase macrofaunal density and biomass on restored reefs. One potential explanation for this is the structural refuge provided by aggregated live oysters, which is lacking when only dead shell material is present. In our study, dead shell volume was not a significant predictor of any community metric. However, another potential explanation is that live oysters also provide increased food resources on the reef both directly by being food themselves, and through converting suspended material in the water column into biodeposits which are rich in organic matter and provide food for deposit feeders such as snails and clams living on the reef. Additionally, oysters can improve water quality around the reefs by filtering large amounts of water and removing suspended particles (Grizzle et al. 2008). It is probable that both explanations are at work to increase macrofaunal density, however, separating the impact of structure from the other services provided by live oysters is an important area for future research that could result in better-informed restoration efforts. Regardless of the mechanism, it is clear that greater amounts of live oyster volume and higher densities are essential for development of productive macrofaunal communities.

Common measures of restoration success are the abundance of market-sized oysters (>76 mm SH) and oyster biomass; however, these measures may require time-consuming and destructive sampling techniques, which we suggest may be unnecessary to provide a measure of the habitat value of a restored reef. In this study, the total volume of live oysters, regardless of their size, was a significant predictor of mean macrofaunal density and biomass. In our study, many of the oysters collected in our samples were <76 mm SH (Fig. 8), and average oyster shell height in all but 2 of the rivers was less than market size. Of the 2 rivers that had average oyster shell height greater than market size, one had the highest average macrofaunal density (Piankatank in 2015), and the other had one of the lowest (Lynnhaven in 2014). This suggests that restored oyster reefs can provide valuable habitat and support productive macrofaunal communities with or without an abundance of market-sized oysters. This was particularly the case in the Great Wicomico and Piankatank Rivers, where restored reefs supported the greatest biomass and density of organisms. Similarly, an abundance of market-sized oysters was not necessary for supporting abundant and diverse macrofaunal communities on intertidal oyster reefs on the eastern shore of Virginia (Luckenbach et al. 2005, Hadley et al. 2010). Our results indicate that less destructive and less time-consuming measures, such as the volume of live oysters, and/or rugosity, could serve as indicators of restored reef habitat value. Estimating the volume of oysters and measuring rugosity can be accomplished relatively quickly in the field and oysters could be returned to the reef alive.

We note that we did not measure all aspects of habitat complexity or heterogeneity in our study. For example, the size and spatial context of the reefs were not considered in this study. Reef size and location within the reef (edge vs. interior) impact reef complexity (e.g. oyster density) and macrofaunal community structure on intertidal reefs (Hanke et al. 2017a,b). We intentionally selected reefs of similar and large size and placed the settlement trays away from the edges of reefs to reduce the potential impacts that size and location on the reef may have had on our measurements of habitat complexity and community metrics. How these elements of complexity impact macrofaunal communities on subtidal oyster reefs has not received much attention and could be a fruitful area for future research.

Location (salinity) effects

In our study, oyster reef community structure was strongly related to salinity, a result that provides support for the conclusion drawn by Wells (1961) that salinity limits the upstream progression of some oyster reef associates in North Carolina. Eleven species

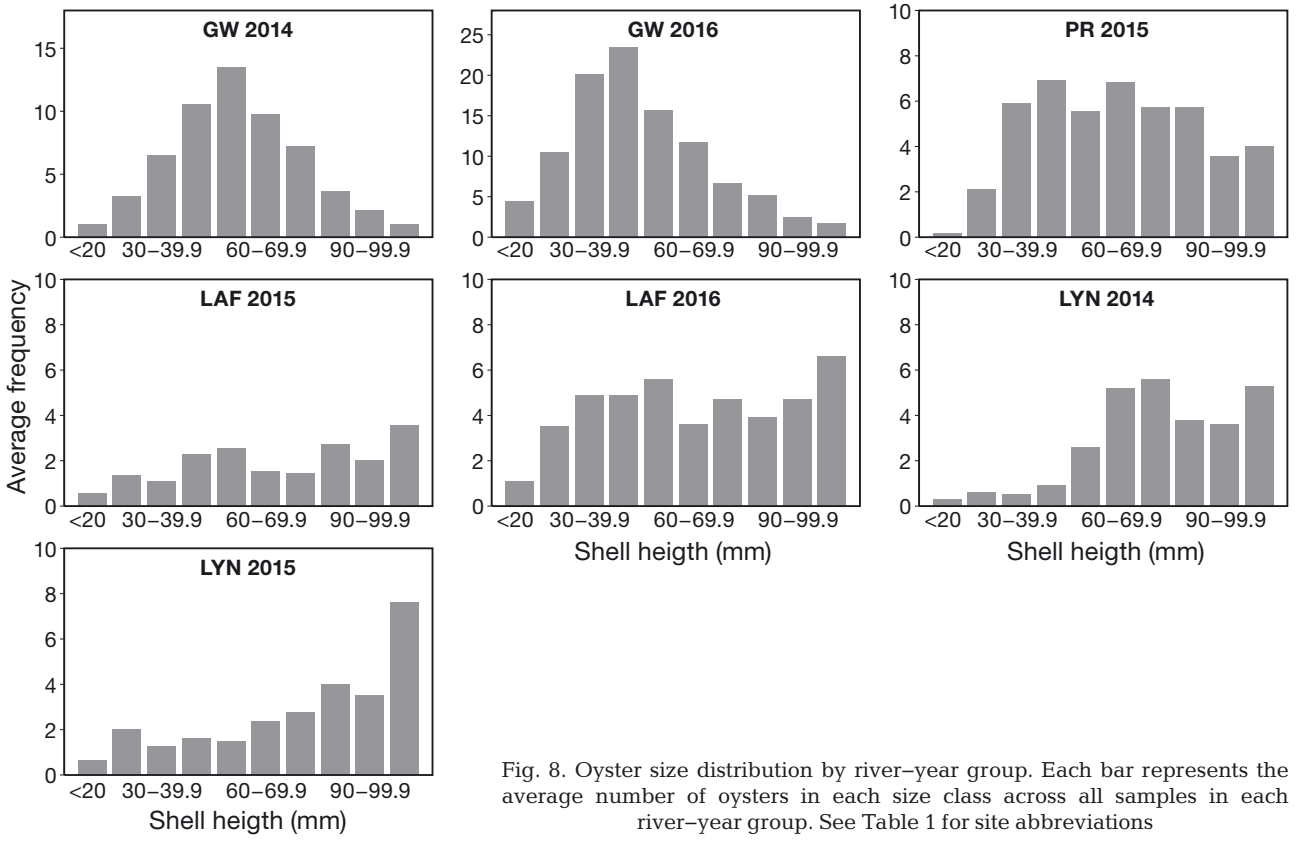

Fig. 8. Oyster size distribution by river–year group. Each bar represents the average number of oysters in each size class across all samples in each river–year group. See Table 1 for site abbreviations

were observed almost exclusively in the higher-salinity Lafayette or Lynnhaven Rivers, where significantly greater diversity and evenness occurred compared with reefs in lower-salinity rivers. Many of those species, such as *Alpheus heterochaelis*, *Crepidula plana*, and *Marphysa sanguinea*, prefer higher salinities, with the Lafayette River being at the lower range of their salinity tolerances. In addition to higher-salinity conditions, the southernmost rivers are closer to the mouth of the estuary and therefore have a greater connection to the coastal ocean, which may serve as a source of larvae of those species. Thus, proximity to the coastal ocean may be a factor contributing to the increased diversity observed in the Lafayette and Lynnhaven Rivers.

Conversely, mean total macrofaunal density was greater in the northern rivers (Great Wicomico and Piankatank) compared with the southern rivers (Lynnhaven and Lafayette), and salinity was a significant negative predictor of macrofaunal density. This pattern is consistent with several studies that reported an inverse relationship between salinity and macrofaunal abundances (Wells 1961, Bergquist et al. 2006). This also follows what might be expected based on the Menge & Sutherland (1987) model, in which the importance of predation and competition increases with decreasing environmental stress. In the estuarine environment, environmental stress decreases towards the mouth of the estuary, where daily or seasonal salinity fluctuations are generally not as great as those in brackish environment of the middle and upper estuary. This increased stability allows for increased diversity of organisms, thus more competition between those organisms and increased importance of predation. The increased role of predation and competition works to keep the abundance of dominant organisms low. In our study, *A. succinea* was a dominant oyster reef organism, but was more abundant in the 2 lower-salinity rivers compared with reefs in higher-salinity areas. *A. succinea* is a cosmopolitan species with a wide salinity tolerance, but in high salinity, *A. succinea* abundance may be suppressed due to increased competition with other polychaetes, particularly *M. sanguinea*, which was not present at lower salinities.

Mean oyster density, similar to mean macrofaunal density, was also greater in lower-salinity habitats, consistent with several other studies (e.g. Tolley et al. 2005, Bergquist et al. 2006). Increased predation pressure could also be contributing to the lower oyster densities in the higher-salinity waters. In addition to increased predation, prevalence of diseases such

as MSX and DERMO is often greater in higher-salinity waters (Haven et al. 1978, Tolley et al. 2005, Bergquist et al. 2006). Studies conducted on oyster reefs in estuaries in Florida, North Carolina, and China showed similar changes in both oyster and macrofaunal density and community structure along a salinity gradient (Wells 1961, Tolley et al. 2005, Bergquist et al. 2006, Shervette & Gelwick 2008, Quan et al. 2012), highlighting the importance of considering salinity during site selection for oyster restoration efforts.

Aside from salinity, differences in overall water quality among the rivers could also affect community structure. In this study, only DO, salinity, temperature, and depth were considered, but other environmental factors that were not measured, such as total suspended sediments, chlorophyll *a*, or turbidity, and temporal fluctuations in those parameters that were not captured in the sampling could also affect biological communities. For example, 2 filter feeders, the hooked mussel *I. recurvum* and barnacles *Balanus* spp., had higher mean densities in the Great Wicomico and Piankatank Rivers than in the Lynnhaven and Lafayette Rivers. Mean water clarity in the Piankatank and Great Wicomico Rivers was greater throughout the sampling periods compared with the Lafayette and Lynnhaven Rivers (M. A. Karp pers. obs.). This may be because the Lynnhaven and Lafayette Rivers are surrounded by urban areas, whereas rural and forested lands surround the Piankatank and Great Wicomico Rivers. Barnacles and mussels may experience increased clogging of their gills in the siltier waters of the Lynnhaven and Lafayette Rivers compared with the less silty Great Wicomico and Piankatank Rivers, which may enable their populations to increase in the less-silty rivers. Conversely, the tunicate *Molgula manhattensis* had higher mean densities in the Lafayette and Lynnhaven Rrivers than the Great Wicomico and Piankatank Rivers. Tunicates are fouling organisms that can often tolerate poorer water quality (Lippson & Lippson 2006), and therefore may be able to thrive in the Lafayette and Lynnhaven Rivers.

CONCLUSIONS

An important ecological service of oyster reefs is the provision of habitat for a diversity of macrobenthic organisms that utilize the crevices within the shell matrix for habitat, refuge, and foraging. The 3-dimensional structure of oyster reefs that provides this habitat is largely created by the vertical orientation and aggregation of oysters. In the 4 rivers that we sampled, subtidal restored oyster reefs developed distinct communities, likely in response to salinity. Although community composition and diversity were related to salinity, our results suggest that the mean density and biomass of reef organisms were positively related to the volume of live oysters. Species diversity was also positively related to habitat complexity, as measured by rugosity. Based on our observations, the location and structural configuration of oysters on restored reefs could have a significant impact on oyster reef community development. In particular, our results suggest that restoration efforts with a goal of enhancing the utilization of oyster reef habitat by resident fish and invertebrates should take into account the salinity of the proposed location. Further, habitat complexity of restored reefs may be efficiently monitored by measuring the amount and configuration of live oyster material on the reef.

Acknowledgements. This research was funded through the National Oceanic and Atmospheric Administration Chesapeake Bay Office, Grant NA14NMF4570288, awarded to R.D.S. and R. Lipcius. Additional funding was provided through the Virginia Sea Grant Graduate Research Fellowship awarded to M.A.K. The authors thank the following staff and students of the Marine Community Ecology and Marine Conservation Biology (R. Lipcius) labs at VIMS for all their help with field sampling and species identification: Katie Knick, Mike Seebo, Alison Smith, Bruce Pfirrman, Mandy Bromilow, Cassie Glaspie, and Megan Wood. A special thanks goes to Katie Knick for creating the site map. Additionally, we thank 2 governor school interns, Willow AbshireSims and Jack Huguenin, and an REU intern, Julia Carrol, for their help in the lab and field. Special thank you to the 2 divers, Jim Goins and Dr. Solomon Chak, without whom we could not have carried out our field work. Lastly, the authors thank Mark Luckenbach and John Brubaker for their thoughtful comments and edits to earlier versions of this manuscript as members of M.A.K.'s thesis committee, as well as 3 anonymous reviewers for their comments. This paper is Contribution No. 3730 of the Virginia Institute of Marine Science, College of William & Mary.

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Editorial responsibility: Lisandro Benedetti-Cecchi, Pisa, Italy

Submitted: August 1, 2017; Accepted: December 23, 2017
Proofs received from author(s): February 24, 2018