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OYSTER AND ASSOCIATED BENTHIC MACROFAUNAL DEVELOPMENT ON A CREATED INTERTIDAL OYSTER (*CRASSOSTREA ARIAKENSIS*) REEF IN THE YANGTZE RIVER ESTUARY, CHINA

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ABSTRACT Oysters and the reefs they build are being recognized and restored increasingly for the broad suite of ecosystem services they can provide. However, surprisingly little effort has been devoted to documenting the outcomes of such restoration or creation projects through time, or to comparing projects from different regions. In this study, we examined the oyster (*Crassostrea ariakensis*) and benthic macrofaunal development on a created intertidal oyster (*Crassostrea ariakensis*) reef along a salinity and exposure (vertical position on reef) gradient 5 y after creation in the Yangtze River estuary, China. Three years after reef creation, sustainable oyster populations were established successfully and market-size oysters accounted for more than 24% of the total reef cover, with mean abundances ranging from 95–225 adult oysters/m^2. Associated community metrics (species richness, abundance, and biomass) of benthic macrofauna showed generally increasing trends with reef development during the 5-y period; however, crustaceans and polychaetes were correlated most strongly with oyster development. Barnacle (*Balanus albicostatus*) abundance and biomass were correlated negatively with oyster and reef development. Salinity and exposure frequently interacted, suggesting that development at different places along the reef or salinity gradient was dependent on the vertical position along the reef or the degree of exposure at low tide. Oyster development on this created reef appears to be at a self-sustaining level and provides habitat for associated benthic macrofauna comparable with other regions globally.

KEY WORDS: restoration, oyster, reef, *Crassostrea ariakensis*, habitat, estuary, Yangtze, China

INTRODUCTION

Oyster reefs are being restored increasingly for the broad suite of ecosystem services they provide the surrounding environment (Coen et al. 2007a). Traditionally, many programs have been driven by managers with the specific goal of developing enhanced oyster fisheries or establishing oyster populations at self-sustaining levels (Breitburg et al. 2000, Coen & Luckenbach 2000, Coen et al. 2007b, Brumbaugh & Coen 2009). However, recent emphasis has shifted from focusing primarily on oysters, and the reefs they create, to the full array of ecosystem services and functions that oyster reefs provide (i.e., ecosystem engineering) (Jones et al. 1994, Coen et al. 2007b, Grabowski & Peterson 2007, Gregalis et al. 2009, Hadley et al. 2010, Beck et al. 2011). These services include water filtration (Newell 2004, Grizzle et al. 2006, Grizzle et al. 2008), erosion control (Meyer et al. 1997, Piazza et al. 2005), and the rebuilding of habitat that provide foraging, refuge, and nursery habitats for resident and transient macrofauna (Coen et al. 1999, Harding & Mann 1999, Peterson et al. 2003, Plunket & La Peyre 2005, Quan et al. 2009, Stunz et al. 2010). Because of spatial, temporal, or methodological differences among studies, consistent correlations between oyster reef development and the associated community have been somewhat equivocal and inconsistent (Luckenbach et al. 1999, Coen et al. 2007b).

Habitat restoration success should not be dependent solely on the growth and/or survival of the targeted species (Craft et al. 1999). Some studies judge the success of oyster reef restoration based solely on the abundance of market-size oysters or on total oyster counts (Tolley & Volety 2005, Powers et al. 2009). However, this ignores the other ecosystem services that nonmarket-size oysters or other sessile invertebrates (i.e., barnacles) may provide (Luckenbach et al. 2005, Coen et al. 2007b). In fact, a few recent studies have indicated that oyster reef ecological function does not necessarily require the presence of large oysters (Luckenbach et al. 2005, Hadley et al. 2010). For example, Hadley et al. (2010) showed that the habitat value of oyster reef for mussels and crabs was independent of large, dense oyster assemblages. More studies that determine oyster development and faunal utilization are needed because exclusive assessments of oyster population alone may not reflect the reef's full ecological function (Brumbaugh et al. 2006, Oyster Restoration Evaluation Team 2009, Powers et al. 2009).

The Yangtze River estuary is the largest estuary in China and has been recognized as one of the most important ecotones in the world (Chen et al. 1988, Quan et al. 2009). Since the early 1980s, the estuary has been going through profound physical and chemical changes as a result of extensive anthropogenic disturbances such as overfishing, environmental pollution, bioinvasion, wetland reclamation, and large-scale basin and estuarine projects (e.g., Chen et al. 2003, Quan et al. 2005, Chai et al. 2006). Some of these changes include increasing nutrient loads and frequency of red tides, loss or extinction of terrestrial and aquatic species, mass outbreaks of jellyfish (*Phylum Cnidaria*), decreased stock and biodiversity of benthos and fishes, as well as overall reclamation of wetlands (Chen et al. 2003, Quan et al. 2005, Chai et al. 2006). To mitigate some of these changes, there have been local efforts to cultivate and release native aquatic species for stock enhancement (Chen et al. 2003, Quan et al. 2006, Quan et al. 2009). In April 2004, creation of an intertidal oyster reef was initiated by transplanting hatchery-derived

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oyster (*Crassostrea ariakensis*; Fujita, 1913) seed to artificial concrete modular (dikes and groins) units as part of the Deepwater Navigation Channel Regulation Project (DNCRP). Before the DNCRP, few efforts had been made to restore or rebuild previous naturally occurring biogenic habitats (e.g., saltmarsh, oyster reef).

Previous studies have demonstrated that the created oyster reef is able to support sustainable oyster (*C. ariakensis*) populations (Quan et al. 2009), provide important ecosystem services (Quan et al. 2007), create significant habitat structure for resident and transient species (Quan et al. 2009), and maintain a higher average trophic level and more robust food web than adjacent saltmarsh (Quan et al. 2012). This study explored the development (from reef creation to year 5) of the oyster population and associated benthic macrofaunal communities using sites along an exposure and salinity gradient on the created intertidal reef in the Yangtze River estuary, China. Specifically, we ask the question: Can the created *C. ariakensis* reef be considered an "ecosystem engineer" in the Yangtze River estuary, China? We answer the question by examining oyster and associated benthic macrofaunal development on the created reef as well as the association between oysters and benthic macrofauna (e.g., species richness, abundance, biomass).

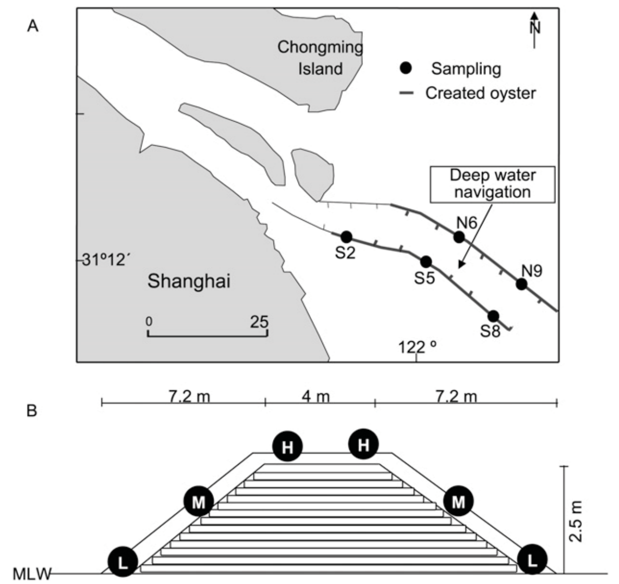

Figure 1. (A, B) Location of the created intertidal oyster reef in the Yangtze River estuary (A) and a schematic drawing of the sampling transect and cross-section of the artificial reef (B). High (H), middle (M), and low (L) intertidal zone, as well as mean low water (MLW) during spring tide are labeled.

MATERIALS AND METHODS

Study Site and Reef Construction

The Yangtze River estuary is well mixed, ranging from oligo- to polyhaline, with 4 major inlets to the East China Sea. Tides are semidiurnal, averaging 4.5 m and 2.6 m at spring and neap tides, respectively. The climate is characterized by an annual mean precipitation of 1,124 cm and a mean temperature of 15.7°C (Chen et al. 1988, Quan et al. 2009).

The Yangtze River originally carried 468 $\times$ 10^6 t/y of sediment into the East China Sea (Chen et al. 1988). More than half the sediment from the river was deposited in the estuarine area, which formed a large sand bar and decreased significantly the shipment capability of the Yangtze River (Chen et al. 1988). To deepen the navigation channel, the Chinese government authorized the DNCRP in 1997. The main structures of the DNCRP—including 2 dikes (south dike, 48 km; north dike, 49.2 km) and 19 groins (total length, 30 km)—were constructed in 1998 to 2003 in the north passage of the south channel (Fig. 1). One objective of the DNCRP was to increase water flow and decrease sediment deposition within the estuary (Quan et al. 2009). The dikes and groins of the DNCRP form an intertidal concrete modular structure, and provide hard substratum (~260 ha) for oyster settlement and growth, as well as associated benthic macrofauna. In April 2004, the East China Sea Fisheries Research Institute, working in cooperation with the Administration Bureau of Navigation in the Yangtze River Estuary, initiated a restoration project to establish a self-sustaining oyster population on the concrete modular structure. The restoration project aimed to mitigate the destruction and loss of suitable nekton habitats caused by DNCRP construction.

Low recruitment of larval oysters limited the success of the restored reef at the beginning of the DNCRP (Chen et al. 2003, Quan et al. 2009); therefore, broodstock enhancement was established in 2004 on the concrete modular structure (dikes and groins) (Chen et al. 2003). Seed oyster was obtained from the Xiangshan Bay (29°30′34.1″N, 121°28′39.2″E), approximately 160 km southwest of the DNCRP. In July 2002, the cultch were set for larval recruitment in the intertidal zone of the bay using recycled bicycle tires (external diameter, 58 cm; inner diameter, 50 cm). In April 2004, we seeded 786,000 (1,500 tires, 524 adult oysters per tire, and a total oyster fresh weight of 20 t) adult oysters (*C. ariakensis*; mean shell height (SH), 63 mm) to portions of the reef (Fig. 1A: N6, N8–N9, S5, S7–S8, S9), covering approximately 10 km of the reef at a mean density of 5.6 oysters/m^2. The oysters at the reef were identified initially as the jinjiang oyster (*Crassostrea rivularis*), but were later recognized as the Asian oyster (*C. ariakensis*) according to the recent classification based on shell morphology and flesh color (Wang et al. 2004, Quan et al. 2012). Furthermore, identification of oyster species at the DNCRP reef was completed using multiplex species-specific PCR genetic markers; more than 85% of oyster specimens were recognized as *C. ariakensis* (others were identified as *Crassostrea sikamea*) (Quan, unpubl. data). These 2 oyster species seem to have a zonal distribution—namely, *C. ariakensis* appears in the lower and middle zone, whereas *C. sikamea* can tolerate longer exposure durations and is distributed primarily in the high intertidal zone (Quan, unpubl. data).

The cross-section of the reef resembles an isosceles trapezoid, with a width of 4 m for the short parallel side and 18.4 m for the long parallel side, and it stands 2.5 m above mean low water (MLW) during spring tide (Fig. 1B). Dense oysters and typical 3-dimensional reef structure (dead and live oyster matrix) only appeared in the lower (MLW) and middle (1.2 m MLW) intertidal zone, whereas sporadic oysters are distributed in the high (2.5 m MLW) intertidal zone of the created reef (see Quan et al. 2009, Quan et al. 2012).

Sampling Regime

We sampled resident sessile (e.g., oysters, barnacles) and mobile benthic macrofauna (e.g., molluscs, crustaceans, polychaetes) at the reef 8 times since construction: September 2004, August 2005, August and November 2007, April and July 2008, and May and September 2009. All sampling took place when the reef was exposed during spring low tide, which allowed approximately 2 h to complete sampling on the reef. Each sampling period took 3–4 days to complete. We defined benthic macrofauna as those organisms exclusive of oysters and barnacles found within the shell matrix when exposed at low spring tide (Coen et al. 1999, Luckenbach et al. 2005), and we refer to these organisms as "benthic macrofauna" throughout this study. Species-specific data were not collected at the 2004 and 2005 sampling periods; therefore, only mean abundance and biomass of oyster and benthic macrofauna are reported.

The oyster *C. ariakensis* spawns primarily in June to July each year (Quan, unpubl. data); therefore, sampling in the mid spring (April to early June) and late summer (August to September) during 2007 to 2009 was carried out to describe the survivorship, growth, and mortality of the oyster population before and after spat recruitment. We set 5 sampling sites at the created reef along a salinity gradient to account for spatial variation within the estuary. Depending on the tide, runoff flow, and climate conditions, salinity ranged from 0.6–7.3‰ at site S2, from 2.5–16.8‰ at sites S5 and N6, and from 8.9–23.4‰ at sites S8 and N9 (Quan et al. 2009). Water temperature and dissolved oxygen at the reef were determined seasonally *in situ* during 2007 and 2008 (Hach Instruments, Sension5 model). Mean water temperature varies at the reef, from 4.2°C in winter to 30.8°C in summer, and dissolved oxygen ranges between 5.56 mg/L and 8.79 mg/L (Quan et al. 2010).

At each of the 5 sampling sites, the reef was subdivided further into 3 tidal strata: high (reef crest, 2.5 m above MLW), middle (reef flank, about 1.2 m above MLW), and low intertidal zones (reef base, at the MLW; Fig. 1B). At each tidal level, 3 0.3×0.3-m quadrats were collected from each side of the reef to avoid the bias of wave energy. All the material in each 0.09-m^2 quadrat was excavated down to the surface of the modular concrete reef, then sorted using a 1.0-mm mesh sieve. All live oysters (exclusive of recruits, SH $\geq$ 20 mm) were measured to the nearest millimeter and weighed to the nearest 0.1 g, and barnacles (*Balanus albicostatus* Pilsbry; hereafter, "barnacle") were enumerated and weighed. Remaining benthic macrofauna (e.g., molluscs, crustaceans, polychaetes) were preserved in 75% ethanol, then enumerated and identified to the lowest possible taxonomic level, and weighed to the nearest 0.01 g wet weight. Mollusc weights were converted to flesh biomass based on an established ratio of flesh to shell (Quan et al. 2009). The abundance and biomass of benthic macrofauna were expressed as the individuals per square meter and wet weight per square meter, respectively. Species richness was represented as the mean species number in each quadrat.

Statistical Analyses

Oysters were sorted for market size (SH, $\geq$70 mm), and total counts exclusive of recruits (SH, <20 mm). The market-size ratios of oysters were calculated based on the size–frequency distribution. Separate 2-factor analysis of variance (ANOVA; STATISTICA 6.0) were carried out to examine differences in the abundance and biomass of oyster, barnacles, and the benthic macrofaunal communities for each sampling event (Factors: sampling site and tidal level). Prior to all analyses, data were tested for normality (Kolmogorov–Smirnov test) and homogeneity of variances (Cochran's test). If necessary, the data were $\log(x + 1)$ transformed. Post hoc pairwise comparisons were made on least-squared means using Tukey's HSD ($P < 0.05$). Correlations between oyster metrics (abundance and biomass) and associated benthic macrofaunal descriptors (species richness, abundance, and biomass) of the total and major taxonomic groups (e.g., molluscs, crustaceans, polychaetes) were explored further using Pearson's product–moment correlation coefficients.

RESULTS

Oyster and Barnacle

Immediately after reef creation, mean oyster abundance (new recruitment) increased rapidly and peaked in summer 2005 at 3,410 oysters/m^2 (Fig. 2A). Abundance then decreased

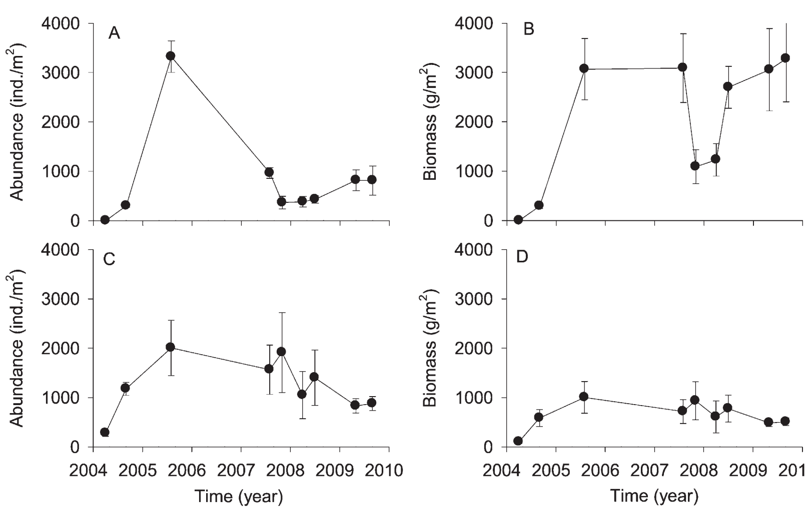

Figure 2. (A–D) Temporal variation of oyster abundance (A), oyster biomass (B; tissue fresh weight), barnacle abundance (C), and barnacle biomass (D; tissue fresh weight) on the created intertidal oyster reef in the Yangtze River estuary. Mean values ± 1 SE (*n* = 5).

until fall 2007, when the reef reached 366 oysters/m^2, then increased slightly until fall 2009 with 810 oysters/m^2. Mean oyster biomass followed similar trends as abundance; however, a greater increase was observed in biomass from 2008 to 2009 (Fig. 2B). Barnacles displayed similar temporal patterns as oysters in mean abundance and biomass during 2004 to 2007 (Fig. 2B). Thereafter, mean abundance and biomass decreased gradually from 2007 to 2009.

Oyster size–frequency distributions varied with reef age, and mean oyster size generally increased throughout the study period (Fig. 3). Maximum SH was no more than 40 mm, and no market-size individuals (SH, ≥70 mm) appeared at the reef 1 y after construction (Fig. 3A). By the third year, mean SH had increased to more than 50 mm, and market-size oysters represented more than 20% of the total population (Fig. 3B). Through time, interannual differences in oyster size–frequency distributions were less distinct, and there were similar ratios of market-size oysters (>20%) from 2007 to 2009 (Fig. 3B–D).

Mean biomass (tissue wet weight) of oysters and barnacles varied significantly ($P < 0.05$) among sampling sites and among intertidal levels (Table 1). A strong interaction was present in 2007 and 2009 ($P < 0.05$, Table 1). Abundance followed similar trends as biomass. There was significantly ($P < 0.05$) greater oyster biomass in the low intertidal zones than in the high

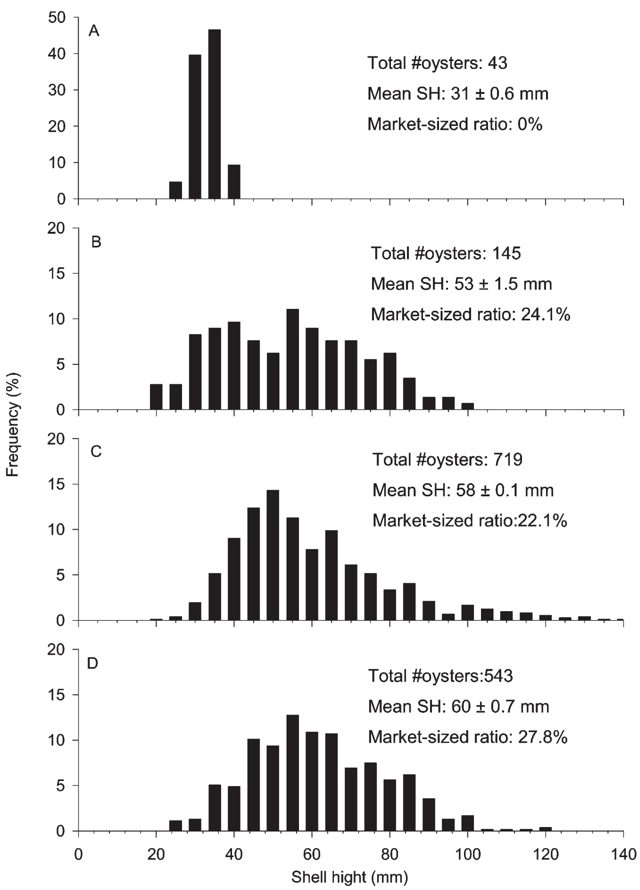

Figure 3. (A–D) Frequency distribution of shell height (SH), as well as mean SH and percentage of market-size (SH, ≥70 mm) oysters (*Crassostrea ariakensis*) in June 2005 (A), August 2007 (B), July 2008 (C), and September 2009 (D) on the created intertidal oyster reef in the Yangtze River estuary. The reef was created in April 2004.

intertidal zones (Table 1). Conversely, the greatest barnacle biomass (tissue wet weight) was found in the high intertidal zone (Table 1). There were significant negative correlations between oysters and barnacles (abundance and biomass) for all years ($P < 0.001$, Table 2).

Benthic Macrofauna

Thirty-six species (Table 3) of benthic macrofauna were collected within quadrats during the 5-y study period. Crustacea (14 species) represented the most abundant phylum, followed by Mollusca (12 species) and Polychaeta (5 species). Other phyla observed included Chordata (2 species), Echinodermata (1 species), Platyhelminthes (1 species) and Cnidaria (1 species).

From 2007 to 2009, abundant benthic macrofauna (taxa accounting for greater than 5% of total abundance combined) at the reef included the nerite *Nerita yoldi* Recluz, the Asian periwinkle *Littorina brevicula* (Philippi, 1844), the periwinkle *Littoraria intermedia* (Philippi, 1846), and the nereid worm *Perinereis aibuhitensis* Grube. The microcotylid monogeneans *Lutianicola* sp. increased in 2008 and accounted for 13% of the total abundance for that year. Overall, *N. yoldi* accounted for 39.6% of the total abundance and was the most abundant reef resident, followed by *L. brevicula* (19.4%), *P. aibuhitensis* (13.1%), and *L. intermedia* (12.1%). Mollusca dominated the samples in abundance regardless of sampling period (Table 3, Fig. 4). Relative abundance of molluscan species declined with reef development, whereas crustaceans and polychaetes increased (Fig. 4).

Species richness of benthic macrofauna increased throughout the course of the study (Fig. 5A, B). There was a general trend of increasing absolute abundance and biomass of all organisms and several taxonomic groups (crustaceans, molluscs, and polychaetes) with reef development (Fig. 5C–J). The total abundance and biomass of benthic macrofaunal communities differed significantly ($P < 0.05$, Table 1) among sampling sites (salinity) and among intertidal levels (exposure), with greater values found in the lower intertidal zone and at sites with higher mean salinity ($P < 0.05$, Table 1). There was a significant interaction ($P < 0.05$, Table 1) between site and intertidal level for the total biomass of benthic macrofauna in most years. The mean abundance and biomass of benthic macrofauna generally showed increasing trends along the salinity gradient.

Correlations Between Oyster and Benthic Macrofauna

Correlation coefficients between oyster biomass and the overall benthic macrofaunal community (species richness, abundance, and biomass) varied considerably. Generally, the oyster abundance showed similar correlations with benthic macrofaunal community descriptors as did oyster biomass. There were significantly ($P < 0.05$) positive correlations between oyster biomass and polychaetes (abundance and biomass), with one exception being biomass in July 2009 ($P > 0.1$, Table 2). There were consistent negative correlations between molluscs and oysters; however, only 4 of the 12 paired components across the study were statistically significant ($P < 0.05$) (see Table 2). In 6 of 12 observations, crustaceans were positively correlated with oyster biomass (Table 2).

TABLE 1.

Mean biomass by site (see text for abbreviations) and 2-way ANOVA results for the oyster *Crassostrea ariakensis*, barnacle *Balanus albicostatus*, and benthic macrofauna on the created reef.

	Mean biomass (g/m^2)						2-Way ANOVA		
	S2	S5	S8	H	M	L	Sites (*df* = 4)	Intertidal (*df* = 2)	Site × Intertidal (*df* = 8)
Oysters									
August 2007	986	1,897	5,096	391	3,008	4,309	**19.56 (<0.001)**	**31.88 (<0.001)**	**13.53 (<0.001)**
November 2007	769	1,561	409	101	531	2,632	**12.09 (<0.001)**	**16.97 (<0.001)**	**11.87 (<0.001)**
April 2008	812	2,192	703	183	1,376	2,122	**3.69 (0.023)**	**30.73 (<0.001)**	0.87 (0.531)
July 2008	2,308	3,414	3,363	601	3,013	4,481	**4.08 (0.009)**	**21.13 (<0.001)**	0.99 (0.462)
May 2009	919	4,153	4,590	440	2,737	5,988	**6.83 (<0.001)**	**18.69 (<0.001)**	**3.70 (0.003)**
September 2009	1,798	5,533	2,320	1,555	2,687	5,584	**40.84 (<0.001)**	**68.40 (<0.001)**	**16.86 (<0.001)**
Barnacles									
August 2007	275	1,041	1,429	1,343	699	110	**15.90 (<0.001)**	**260.60 (<0.001)**	**15.91 (<0.001)**
November 2007	512	486	1,703	1,139	1,091	569	**7.25 (0.003)**	**16.80 (<0.001)**	**7.79 (<0.001)**
April 2008	19	879	1,514	1,038	522	266	**11.40 (<0.001)**	**5.29 (0.011)**	1.12 (0.377)
July 2008	1,667	703	250	1,575	567	188	**2.83 (0.042)**	**11.39 (<0.001)**	1.09 (0.396)
May 2009	17	676	961	958	517	463	**26.64 (<0.001)**	2.85 (0.073)	**5.95 (0.007)**
September 2009	404	416	476	2,458	175	0	2.09 (0.111)	**16.74 (<0.001)**	**3.90 (0.002)**
Benthic macrofauna									
August 2007	14.75	21.22	51.82	51.28	38.47	33.48	**10.30 (<0.001)**	**12.46 (0.001)**	**3.06 (0.012)**
November 2007	10.03	30.07	36.96	28.46	23.76	25.06	**6.95 (<0.001)**	1.94 (0.158)	**4.05 (0.003)**
April 2008	13.47	31.57	83.23	51.51	36.05	32.55	**7.27 (<0.001)**	**1.24 (0.304)**	0.72 (0.640)
July 2008	21.20	51.32	70.98	29.84	55.04	54.60	**4.53 (0.006)**	**6.85 (0.004)**	**3.31 (0.008)**
May 2009	11.31	51.18	170.09	27.26	63.54	122.35	**18.55 (<0.001)**	**14.93 (<0.001)**	1.72 (0.141)
September 2009	18.41	28.78	96.69	47.12	19.38	69.644	**19.24 (<0.001)**	**14.70 (<0.001)**	**6.82 (<0.001)**

F values are shown with significance level (*P* value) in parenthesis. Bold type indicates statistical significance ($p < 0.05$).

DISCUSSION

Crassostrea ariakensis: *An Ecosystem Engineer*

Through the recruitment, settlement, and growth of the larvae released by transplanted *C. ariakensis* seed, a complex 3-dimensional habitat was created for other benthic macrofaunal species. Our results using *C. ariakensis* provide results similar to studies that examined reefs created by the Eastern oyster *Crassostrea virginica* (Gmelin, 1791) (e.g., Rodney & Paynter 2006, Hadley et al. 2010), the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) (e.g., Lejart & Hily 2011), the Olympia oyster *Ostrea lurida* (Carpenter 1864) (e.g., Dinnel et al. 2009), and the European oyster *Ostrea edulis* (e.g., Smyth & Roberts 2010) in which structure facilitated habitat creation for reef-associated species. Harwell et al. (2010) concluded functional equivalency between *C. virginica* and *C. ariakensis* through comparisons of habitat complexity and associated benthic communities in the Chesapeake Bay. The oyster *C. ariakensis* can provide suitable habitat for benthic communities that is similar to that of other species and can therefore be considered an ecosystem engineer (Coen & Luckenbach 2000) in the Yangtze River estuary, China.

This study shows that *C. ariakensis* can establish self-sustaining oyster populations and create a complex 3-dimensional reef structure in the intertidal zone. We found that *C. ariakensis* had generally greater abundance in the low intertidal zone than the high intertidal zone, but that *C. ariakensis* could survive for relatively long emersion periods (approximately 3 h) in the middle and high intertidal zones. This contrasts with previous findings in the Chesapeake Bay, where no *C. ariakensis* survived in the high intertidal (3.5-h emersion) and middle intertidal (2-h emersion) zones (Kingsley-Smith & Luckenbach 2008). Kingsley-Smith and Luckenbach (2008) also reported that *C. ariakensis* suffered from higher mortality when exposed in the high intertidal zone, but that *C. ariakensis* grew faster than *C. virginica* in subtidal locations. One possible explanation for this is that local variations (native vs. nonnative) in emersion time resulting from the neap–spring cycle and meteorological conditions affected the tolerance of *C. ariakensis* to aerial exposure, desiccation, and thermal stress (Kingsley-Smith & Luckenbach 2008).

Oyster Development

Oyster spat began to settle on the artificial modular reef immediately after seed transplanting in 2004, and the highest abundances were present 1 y later. After this initial colonization, a rapid decrease was observed in mean oyster abundance, possibly because of a self-thinning process. As in plants, the explanations for self-thinning in marine organisms emphasize intraspecific competition (Woodin & Jackson 1979). The crowded conditions reduce the per-individual ration of food and space (Petraitis 1995, Fréchette et al. 1996).

The mean oyster abundance (exclusive of oyster spat < 20 mm in SH) on our created reef at the end of the 5 y of sampling (810 oysters/m^2; mean size, 60 mm; September 2009) was higher than those recorded from restored/created subtidal reefs (Table 4), such as the Great Bay estuary, NH (200–600 oysters/m^2) (Greene & Grizzle 2005); Chesapeake Bay, MD (173 oysters/m^2) (Rodney & Paynter 2006); Indian River Bay, DE (254 oysters/m^2) (Erbland & Ozbay 2008); Rappahannock River, VA (77–257 oysters/m^2) (Luckenbach et al. 2005); and Inlet Creek, SC (497 oysters/m^2) (Luckenbach et al. 2005). Our values were more similar to the restored subtidal reef (850 oysters/m^2) located in Mobile Bay,

TABLE 2.

Correlations between oyster biomass and reef community metrics (species richness, abundance, biomass) by sampling date for the created intertidal reef in the Yangtze River estuary.

		Barnacle		Total		Crustacean		Mollusca		Polychaetes	
Oyster	*S*	Abundance	Bio-mass	Abundance	Bio-mass	Abundance	Bio-mass	Abundance	Bio-mass	Abundance	Bio-mass
Oyster biomass in August 2007											
r	**0.464**	**–0.639**	**–0.712**	–0.130	–0.037	0.248	**0.362**	–0.188	–0.169	**0.522**	**0.429**
P	**0.001**	**<0.001**	**<0.001**	0.385	0.805	0.093	**0.013**	0.206	0.256	**<0.001**	**0.003**
Oyster biomass in November 2007											
r	0.041	**–0.539**	**–0.605**	–0.196	0.102	0.066	–0.002	–0.261	–0.240	**0.620**	**0.728**
P	0.780	**<0.001**	**<0.001**	0.181	0.492	0.657	0.988	0.073	0.100	**<0.001**	**<0.001**
Oyster biomass in April 2008											
r	0.030	**–0.715**	**–0.657**	–0.173	0.112	0.268	0.288	–0.262	–0.269	**0.560**	**0.630**
P	0.852	**<0.001**	**<0.001**	0.272	0.479	0.086	0.065	0.094	0.085	**<0.001**	**<0.001**
Oyster biomass in July 2008											
r	0.096	**–0.547**	**–0.550**	–0.259	**0.324**	**0.465**	**0.538**	–0.235	–0.167	**0.325**	0.234
P	0.531	**<0.001**	**<0.001**	0.085	**0.030**	**0.001**	**<0.001**	0.121	0.274	**0.029**	0.122
Oyster biomass in May 2009											
r	**0.488**	**–0.558**	**–0.549**	**0.409**	**0.584**	**0.453**	**0.476**	**–0.293**	**–0.463**	**0.683**	**0.630**
P	**<0.001**	**<0.001**	**<0.001**	**0.005**	**<0.001**	**0.003**	**0.001**	**0.050**	**0.001**	**<0.001**	**<0.001**
Oyster biomass in September 2009											
r	–0.158	**–0.426**	**–0.425**	**–0.440**	0.015	0.163	**0.312**	**–0.601**	**–0.439**	**0.397**	**0.410**
P	0.172	**<0.001**	**<0.001**	**<0.001**	0.894	0.159	**0.006**	**<0.001**	**<0.001**	**<0.001**	**<0.001**

Sample size, $n = 90$ for overall sample number (5 sites × 3 tidal levels × 6 quadrats).
P, probability of $r = 0$. *r*, Pearson product coefficients; *S*, species richness (species each 0.09/m^2). Bold type indicates statistical significance ($p < 0.05$).

AL (Gregalis et al. 2009), but were lower than those in most of the restored intertidal reefs, such as Cape Shore of Delaware Bay (2,100 oysters/m^2) (Taylor & Bushek 2008), Fisherman's Island (~1,800 oysters/m^2) (Nestlerode et al. 2007), and the South Carolina coast (1,460–2,887 oysters/m^2) (Hadley et al. 2010). There was greater oyster abundance on our created reef than on natural reefs in James River, VA (300–500 oysters/m^2) (Mann et al. 2009); West Bay, TX (38 oysters/m^2) (Zimmerman et al. 1989); and Suwannee River estuary, FL (511 oysters/m^2) (Bergquist et al. 2006), but means remained well below abundance found on natural reefs in Charleston harbor, SC (861–1,646 oysters/m^2) (Luckenbach et al. 2005) and Crystal River, FL (3,800 oysters/m^2) (Lehman 1974). The potential underestimation at our reef as a result of the exclusion of oyster spat is a possible reason for the relative low abundance compared with other restored intertidal reefs.

The trends observed in overall size distribution and SH indicated that a sustainable oyster population had established on our created reef 5 y after creation. The abundance of market-size oysters (SH ≥ 70 mm, 95–225 oysters/m^2) in 2007 to 2009 was comparable with that reported on natural intertidal reefs along the South Carolina coast (25–472 large oysters/m^2, SH > 60 mm), and was consistently greater than those from 45 restored reefs (77 large oysters/m^2, SH > 60 mm) throughout South Carolina (Hadley et al. 2010) and natural intertidal reefs in the Suwannee River estuary, FL (37 3-in oysters/m^2) (Bergquist et al. 2006). Similar values were reported on the natural or constructed reef in South Carolina, with a maximum market-size percentage of 18% (Luckenbach et al. 2005).

Developing metrics to evaluate the success of restored or created oyster reefs is vital for managers and future projects (Coen & Luckenbach 2000, Powers et al. 2009, Harwell et al. 2010). A workshop sponsored by South Carolina Sea Grant in 2004 presented the most appropriate success metrics (e.g., oyster density, size frequency, associated reef fauna, reef size, reef architecture, landscape fragmentation, and water quality parameters) for oyster reef restoration based on identified project and site-specific characteristics (Coen et al. 2007b). Powers et al. (2009) evaluated the success of 94 oyster reefs (88 constructed, 6 natural) within 11 no-harvest sanctuaries located in North Carolina using the following success criteria: vertical relief more than 20 cm in height, living oyster more than 10 oysters/m^2, evidence of recent recruitment in 1 of 2 y of the survey. Harwell et al. (2010) set a target density of ~400 oysters/m^2 as success criteria for 4 restored oyster reefs in Chesapeake Bay. Our reefs (810 oysters/m^2, persistent recruitment, and complex 3-dimensional reef structure) satisfy all the aforementioned criteria and can therefore be considered a viable model to create and restore self-sustainable oyster reefs in the Yangtze River estuary, China.

Associated Assemblage Metrics

The structurally complex surface that oysters create can provide a unique habitat for reef-associated benthic organisms that serve as prey for economically and ecologically important nekton species (Harding & Mann 2001, Luckenbach et al. 2005, Quan et al. 2012). A number of studies have used quantitative or qualitative methods to investigate species demographics on natural or restored oyster reefs (e.g., Dame 1979, Larsen 1985, Zimmerman et al. 1989, Wenner et al. 1996, Luckenbach et al. 2005, Rodney & Paynter 2006, Walters & Coen 2006, Taylor & Bushek 2008, Lejart & Hily 2011). In these studies, community metrics varied substantially with site location, reef characteristics, sampling method, and physiochemical factors (Table 4). The total abundance of reef-associated benthic

TABLE 3.

Total number of benthic macrofauna (total area surveyed, 16.2 m^2) collected on the created intertidal oyster reef in the Yangtze River estuary, China.

Phylum	Species	2007	2008	2009	Total
Crustacea	*Alpheus japonicus* (snapping shrimp)	4	0	52	56
	Eriocheir leptognathus (grapsid crab)	18	13	17	48
	Gnorimosphaeroma rayi (isopod)	0	0	109	109
	Hemigrapsus penicillatus (grapsid crab)	1	0	6	7
	Hemigrapsus sanguineus (grapsid crab)	0	0	6	6
	Metopograpsus latifrons (grapsid crab)	15	30	2	47
	Metopograpsus frontalis (grapsid crab)	1	0	0	1
	Metopograpsus quadridentatus (grapsid crab)	1	0	6	7
	Orchestia platensis (amphipod)	0	0	44	44
	Pilumnus scabrisculus (xanthid crab)	19	36	50	105
	Sesarma dehaani (grapsid crab)	13	0	8	21
	Sesarma bidens (grapsid crab)	14	0	9	23
	Sesarma tripectinis (grapsid crab)	2	0	0	2
	Synidotea laevidorsalis (isopod)	12	0	23	35
Mollusca	*Barbatia bistrigata* (ark clam)	61	77	182	320
	Diodora mus (fissurellid snail)	0	1	0	1
	Littoraria intermedia (littorine snail)	963	192	237	1,392
	Littorina brevicula (littorine snail)	686	1,031	509	2,226
	Modiolus flavidus (mytilid mussel)	30	0	13	43
	Nerita yoldi (nerite snail)	1,887	1,079	1,579	45,45
	Purpura clavigera (muricid snail)	4	0	17	21
	Pyrene bella (pyramid snail)	1	0	46	47
	Rapana bezoar (muricid snail)	0	0	1	1
	Sinonovacula constricta (razor clam)	0	1	0	1
	Trapezium liratum (trapezid clam)	0	0	16	16
	Vignadula atrata (mytilid mussel)	48	72	51	171
Polychaeta	*Amaeana occidentalis* (terebellid worm)	1	0	5	6
	Neanthes japonica (nereid worm)	98	0	0	98
	Nephtys polybranchia (nephtyid worm)	0	0	7	7
	Perinereis aibuhitensis (nereid worm)	222	404	874	1,500
	Perinnereis nuntia (nereid worm)	0	0	110	110
Echinodermata	*Protankyra bidentata* (synaptid sea cucumber)	0	0	1	1
Platyhelminthes	*Lutianicola* sp. (microcotylid monogeneans)	8	440	0	448
Cnidaria	*Haliplanella* sp. (acontiate sea anemone)	0	6	4	10
Chordata	*Liciogobius guttatus* (goby)	1	2	11	14
	Omobranchus elegans (blenny)	1	0	0	1

organisms at our created intertidal reef was most similar to those found at restored and young subtidal reefs (1–2 y) in the Rappahannock River, VA (Luckenbach et al. 2005); Indian River Bay, DE (Erbland & Ozbay 2008); and Mobile Bay, AL (Gregalis et al. 2009); but was below the values observed at older restored (e.g., Luckenbach et al. 2005, Rodney & Paynter 2006) or natural reefs (e.g., Frey 1946, Bahr 1974, Lehman 1974, Dame 1979, Larsen 1985, Coen et al. 1999, Walters & Coen 2006). Reef age seems to be an important factor controlling oyster development and therefore associated species demographics (Burt et al. 2011); abundance of reef-associated benthic organisms gradually increases with reef development (e.g., the current study, Coen & Luckenbach 2000, Luckenbach et al. 2005, Hadley et al. 2010), which provides evidence for the positive effect reef age has on the community metrics of other species.

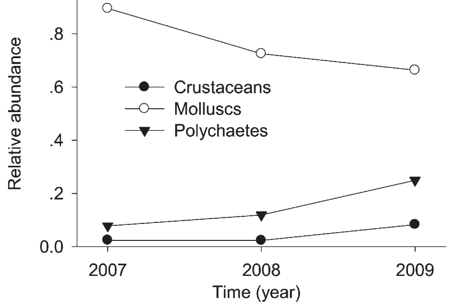

Figure 4. Change in relative abundance of resident benthic macrofauna on the created intertidal oyster reef in the Yangtze River estuary.

In the current study, we found that the abundance and biomass of the oysters and associated benthic macrofaunal communities generally increased from the upstream to downstream portions of the reef along the salinity gradient. The greatest abundances often appeared at sampling sites S5 or S8, where higher salinities facilitated greater larvae recruitment and growth (Quan et al. 2009). Similar patterns have been recorded at natural or restored reefs (e.g., Tolley et al. 2005, Rodney & Paynter 2006, Harwell et al. 2010); however, Bergquist et al.

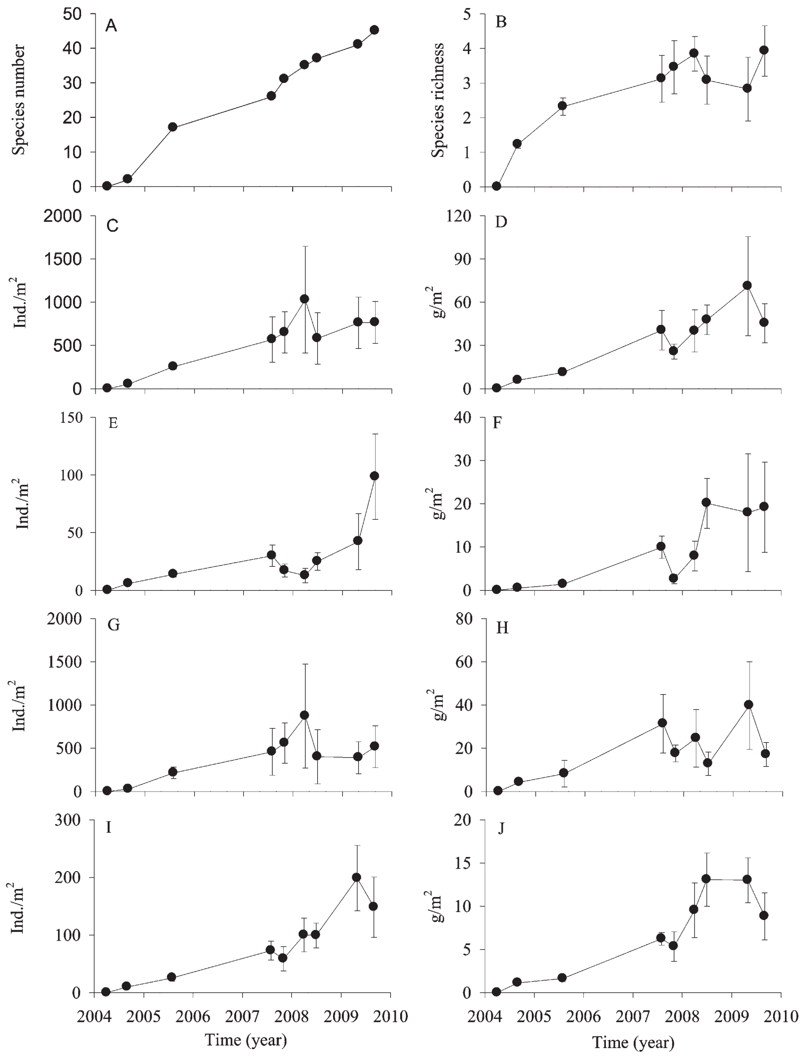

Figure 5. Temporal variation of resident benthic macrofauna. (A–J) Total species number (A), mean species number within each quadrat (B), total abundance (C), total biomass (D), crustacean abundance (E), crustacean biomass (F), molluscan abundance (G), molluscan biomass (H), polychaetes abundance (I), and polychaetes biomass (J) of resident benthic macrofauna on the created intertidal oyster reef in the Yangtze River estuary. Mean values ± 1 SE.

(2006) found that percentage cover and density of live oysters were correlated inversely with salinity (10–30) in the Suwannee River estuary, FL. This was likely a result of increased predation and parasitic Dermo infection under higher salinity conditions (Bergquist et al. 2006), and these factors do not seem to be significant in the Yangtze River estuary.

Molluscs, polychaetes, and crustaceans typically dominate the benthic macrofaunal communities at natural or restored oyster reefs (Zimmerman et al. 1989, O'Beirn et al. 2004, Rodney & Paynter 2006). For example, several studies (e.g., Wells 1961, Larsen 1985, O'Beirn et al. 2004, Rodney & Paynter 2006) demonstrated that these 3 taxonomic groups accounted for approximately 70% of the total species number of benthic organisms in natural and subtidal oyster reefs. However, polychaetes (5 species) recorded at our created reef were less abundant in the total species assemblage compared with other studies (Wells 1961, Larsen 1985). The main contributors (>75%) to species richness in our created reefs were crustaceans (14 species) and molluscs (12 species). Rank and composition within each taxonomic group was similar to results from previous oyster reef studies in the United States (e.g., Zimmerman et al. 1989, O'Beirn et al. 2004, Rodney & Paynter 2006); gastropods ranked first in abundance followed by crustaceans. Interestingly, the relative abundance of molluscs generally decreased with reef development, whereas an increasing trend was evident for crustaceans and polychaetes. In addition, crab densities (98 crab/m^2 in September 2009) at our intertidal reef were considerably lower than those reported on restored intertidal oyster reefs along the North Carolina coast (150 crab/m^2) (Meyer & Townsend 2000); the South Carolina coast (158–360 crab/m^2) (Hadley et al. 2010); Mobile Bay, AL (~170 crab/m^2) (Gregalis et al. 2009); and the Caloosahatchee estuary of Florida (640 crab/m^2) (Tolley & Volety 2005); but were similar to those on the restored subtidal reef at Inlet Creek, SC (100 crab/m^2) (Luckenbach et al. 2005) and the natural subtidal oyster beds in Barataria Bay, LA (111 crab/m^2) (Plunket & La Peyre 2005). Similarity, the mean abundance of polychaetes (<200 individuals/m^2) at our reef was lower than those observed from restored subtidal reefs in the Chesapeake Bay (approximately 1,300 polychaetes/m^2) (Rodney & Paynter 2006) and

TABLE 4.

Comparisons of oyster and associated benthic macrofauna at various natural or restored oyster reefs worldwide.

Location	Reef Characteristics	Reef Age (y)	Oyster abundance (individuals/m^2)	Resident Epibenthic Macrofauna: Species no.	Resident Epibenthic Macrofauna: Abundance (individuals/m^2)	Source
Great Bay Estuary, NH	Restored, subtidal	1	200–600*			Greene and Grizzle (2005)
Potomac River, MD	Natural			41	~4,000	Frey (1946)
Chesapeake Bay, MD	Restored, subtidal	3–5	173 ± 25.5*	35	4,057	Rodney and Paynter (2006)
Cape Shore, DE	Restored, intertidal	1	2,100*			Taylor and Bushek (2008)
Indian River Bay, DE	Restored, subtidal	2	254.4 ± 73.6*		414	Erbland and Ozbay (2008)
Rappahannock River, VA	Restored, subtidal	2	77–257*		~900§	Luckenbach et al. (2005)
Fisherman's Island, VA	Restored, intertidal	3	~1,800*			Nestlerode et al. (2007)
James River, VA	Natural		300–500*			Mann et al. (2009)
James River Estuary, VA	Natural			142	5,757–57,857	Larsen (1985)
Great Wicomico River, VA	Restored, subtidal	3	1,026.7 ± 51.5 (HRR) 250.4 ± 32.3 (LRR)			Schulte et al. (2009)
North Inlet, SC	Natural, intertidal			37	2,476–4,077	Dame (1979)
Inlet Creek, SC	Restored, intertidal	6	497 ± 282*		~2,200	Luckenbach et al. (2005)
Charleston harbor, SC	Natural, intertidal		861–1,646[a]			Luckenbach et al. (2005)
South Carolina coast	Restored, intertidal	3	1,460–2,887*		418–3,989 mussel/m^2, 158–360 crab/m^2	Hadley et al. (2010)
Sapelo Island, GA	Natural, intertidal			42	3,800	Bahr (1974)
Mobile Bay, AL	Restored, subtidal	1	850*	21	900	Gregalis et al. (2009)
West Bay, TX	Natural, intertidal		38*	63 (winter), 59 (summer)	56,400 (winter), 34,200 (summer)	Zimmerman et al. (1989)
Suwannee River estuary, FL	Natural, intertidal		511*	31		Bergquist et al. (2006)
Crystal River, FL	Natural		3,800*	31	6,200	Lehman (1974)
Yangtze River estuary, China	Restored, intertidal	5	810 ± 295†	45	765 ± 241‡	Current study

* All live oysters.
† Oyster shell height ≥ 20 mm exclusive of recruits.
‡ Exclusive of barnacles, the barnacle *Balanus albicostatus* was the most abundant reef resident exception for the oyster *Crassostrea ariakensis*.
HRR, restored high-relief reef; LRR, restored low-relief reef.

natural intertidal reefs in West Bay, TX (about 3,000 individuals/m^2) (Zimmerman et al. 1989).

Relationship Between Oyster Population and Benthic Macrofaunal Community

The barnacle *B. albicostatus* was the most abundant sessile invertebrate other than *C. ariakensis* on the reef. The barnacles had greater settlement and recruitment than oysters during the early stages of reef deployment (April to September 2004); however, its mean abundance and biomass declined with reef development. Luckenbach et al. (2005) also observed a decline in barnacle densities on a restored subtidal oyster reef in the Rappahannock River, VA. In contrast to the spatial patterns of the oyster, the mean abundances and biomass of *B. albicostatus* gradually decreased from the high intertidal zone to the low intertidal zone throughout the current study. Other studies have recorded similar zonation patterns for oysters and barnacles as a result of competitive exclusion for space and food (Luckens 1975, Lohse 2002, Luckenbach et al. 2005).

Associations between overall benthic macrofauna descriptors and oyster population metrics (abundance and biomass) were not always consistent at our created reef (Table 2). However, when benthic macrofauna were examined by phylum or functional group, stronger correlations were present. Polychaetes and crustaceans were consistently correlated with oyster development in the current study. This result is consistent with other studies (e.g., Bergquist et al. 2006, Hadley et al. 2010) and may indicate that reef structural complexity and interstitial space provide refugia for crustaceans and polychaetes. Conversely, molluscs failed to be consistently correlated with oyster development and, therefore, may be less dependent on oysters for habitat. Similar patterns have been reported for the Chesapeake Bay in that there were no significant correlations between oyster metrics and overall assemblage parameters of resident benthic organisms (Luckenbach et al. 2005, Hadley et al. 2010). These results may demonstrate that other factors such as environmental (e.g., salinity) or spatial (e.g., setting, landscape fragmentation, connectivity) characteristics could mediate benthic macrofauna more so than oyster populations (Grabowski et al. 2005). For example, several studies indicated that salinity appeared to be a stronger predictor of community metrics of benthic organisms than oyster reef development (e.g., Tolley et al. 2005, Bergquist et al. 2006, Harwell et al. 2010). Future studies should aim to determine the relative contributions of these factors and the interplay between biotic and abiotic interactions.

Conclusions and Implications

This study showed that self-sustaining oyster populations have been established through transplanting seed oysters at a created reef in the Yangtze River estuary, China, and may be considered an ecosystem engineer in this system. Oysters colonized the reef quickly, grew to market size, and now represent a thriving population. Greater abundance of oysters was found in the lower intertidal zone and at higher salinities, whereas barnacles showed opposite trends. The species number, abundance, and biomass of associated benthic macrofauna generally showed increasing trends with reef development, or age. However, oyster abundance appeared to be a stronger predictor for barnacles, crustaceans, and polychaetes rather than total abundance and diversity of overall benthic macrofauna or molluscs. In the future, additional monitoring of reef development and function is needed to track ecological succession of restored and created oyster reefs to determine the relative contributions of oyster development and environmental forcing in mediating associated organisms.

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