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RESEARCH ARTICLE

Successful initial restoration of oyster habitat in the lower Hudson River Estuary, United States

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The eastern oyster (*Crassostrea virginica*), has experienced dramatic declines throughout its range, and most U.S. states along the Atlantic and Gulf of Mexico coasts have restoration programs. Oyster restoration in the Hudson River Estuary has been a focus of management agencies for over two decades. The present project was initiated in 2013 after sampling for replacement of the Tappan Zee bridge determined live oysters would be lost during bridge construction, thus requiring mitigation measures. Preliminary studies identified three areas for pilot studies to inform the design of full-scale efforts. A pilot study involving deployment of oyster shell-filled gabions and two styles of Reef Balls, found all substrates supported oyster recruitment and growth but there were higher oyster densities on gabions. Some of the gabions, however, failed structurally necessitating a need for new design. For full-scale restoration, a total of 422 modified gabions and 881 Mini-Bay style Reef Balls were deployed across three sites which totaled approximately 2.4 ha (6 ac) in seafloor area. Both substrate types were heavily colonized by oysters and several other species at all three sites, essentially duplicating the findings of the pilot study. The final monitoring event in 2020 indicated a total of approximately 5.8 million live oysters were on the substrates deployed in 2018. This mitigation effort was the largest oyster habitat restoration project in, or north of, the New York Harbor region in recent decades based on restoration area and several oyster metrics of early success.

Key words: ecosystem services, gabions, mitigation, reef balls, shell

Implications for Practice

- This project demonstrates the value of empirical pilot studies for designing full-scale oyster restoration activities.
- This project also documents the impact that a broad coalition of partners knowledgeable in various components of the overall project can play in achieving success.
- The initial success of the full-scale restoration effort indicates excellent potential for additional oyster restoration in the lower Hudson River as well as additional topics for future research.
- The finding of wide variability of restoration success metrics among the study sites underscores the importance of site selection and suggests more needs to be learned about the distribution of live natural reefs and recruitment patterns in the study area.

Introduction

The eastern oyster (*Crassostrea virginica*) has experienced dramatic declines in many areas (Beck et al. 2011; zu Ermgassen et al. 2012), and most U.S. coastal states along the Atlantic and Gulf of Mexico have restoration programs (Bersoza et al. 2018). Some programs focus on restoration for human harvest, others are aimed at restoring the ecosystem services oysters provide, which include water filtration, habitat provision, benthic–pelagic coupling, and refugia from predation (Coen et al. 2007; Coen & Humphries 2017). In the Hudson River Estuary (HRE), the emphasis over the past two decades has been on these services, and restoration efforts have been highly collaborative involving a wide variety of partners (Levinton & Doall 2011; Lodge et al. 2015).

The eastern oyster has existed in the HRE for at least six millennia, their reefs at times covering hundreds of hectares of seafloor area in the Tappan Zee area (Snow 1972; Bell et al. 2006). The oyster's long-term history in the area includes at least two major declines, both associated with extreme warm–cool cycles (Carbotte et al. 2004). Declines since the 1700s, however, largely have been attributed to human overharvesting, pollution, and in recent decades, oyster diseases (Franz 1982; Kirby 2004; Beck et al. 2011). By the mid-1900s, only small, isolated populations of living oysters were known to occur in the New York Harbor region (Franz 1982; MacKenzie 1984). Recent studies, however, found live oyster

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populations in the HRE though their spatial extent and condition were not well-characterized.

Surveys from 1998 to 2004 mapped extensive dead reefs, some buried under 10 m of soft sediments, in the Tappan Zee area, and collected a few live oysters (Bell et al. 2006). More recent research demonstrated the viability of juvenile and adult oysters in several areas of the New York Harbor region, including the lower HRE (Medley 2010; Levinton & Doall 2011; Levinton et al. 2013). And a field experiment assessing the success of small, constructed reefs at five sites in the region found the highest natural recruitment at the Tappan Zee site, suggesting the presence of live reefs in the general area (Grizzle et al. 2013). Most recently, seafloor surveys conducted as part of the Tappan Zee bridge replacement planning and environmental review process found live oysters in several areas and determined that bridge construction would result in either temporary or permanent loss of oyster habitat. As a result, the New York Department of Environmental Conservation required the New York Thruway Authority to provide compensatory mitigation of the loss by construction (restoration) of new oyster habitat.

Oysters are sedentary, broadcast spawners that release their sperm and eggs into the water column where fertilization occurs. The resulting larvae develop in the water column for two or more weeks, then settle onto a hard substrate and metamorphose into juvenile oysters called "spat." Spat that survive and develop for a few months are considered recruits to the existing population. Restoration of oyster habitat typically at a minimum involves deploying hard substrate suitable for settlement of wild oyster larvae, particularly in areas thought to be substrate-limited, followed by laboratory-reared juvenile oysters if natural recruitment is also considered limited (see review by Coen & Humphries 2017). Previous studies in the Tappan Zee area had indicated some level of natural recruitment to experimental substrates (Carthan & Levinton 2013; Grizzle et al. 2013), but more extensive studies were needed. Thus, the mitigation process requiring construction (restoration) of new oyster habitat included formation of an Oyster Work Group (OWG) in 2013 consisting of researchers, regulators, consultants, and other stakeholders, to guide the overall effort (Gann et al. 2019). The OWG recommended a tiered approach overall where the results at each level informed the design of the next—an adaptive approach. The major findings of the Tiers 1 and 2 studies (2014–2015) were: (1) live oysters were collected at seven of nine study sites and (2) very low salinities were recorded at times at all sites. Densities of live oysters ranged from 0 to $30/m^2$ at the nine study sites, and live oysters ranged from spat (<25 mm) to large adults (115 mm). Although the water quality data indicated surprisingly low salinity (<1 psu) and dissolved oxygen (<1 mg/L) levels at times, the oyster data indicated that at least three sites should be considered for further studies because of high recruitment.

The present paper describes the subsequent 5-year (2015–2020) collaborative restoration effort consisting of: (1) a 3-year pilot study to assess three sites and three substrates suitable for oyster recruitment; (2) a full-scale construction (restoration) of oyster habitat at three sites; and (3) assessment of full-scale restoration success for 2 years post-construction. We conclude with a discussion focusing on gaps in our knowledge for design of future oyster habitat restoration in the HRE.

Methods

Study Area

All studies were conducted in subtidal waters of the Tappan Zee portion of the HRE (Fig. 1), which has a combination of characteristics suitable for oyster reef development: oligohaline salinity regime, circulation patterns that potentially result in favorable larval transport, and widespread firm substrates (mainly sand and gravel) suitable for oyster recruitment (Starke et al. 2011). Maximum water depths in the study area are approximately 11 m below mean low water and there are extensive shoal areas (Starke et al. 2011). Bottom types include a mix of mud, sand, and cobble size sediments (Princeton Hydro 2015). Although oysters have been observed in the intertidal zone in the New York Harbor region (Medley 2010), they mainly occur in subtidal waters in the study area. Molluscan shellfish harvest is prohibited in the lower HRE due to water quality conditions. Thus, the present project was aimed at oyster habitat restoration for ecosystem services.

Pilot Study

The pilot study consisted of deployment of test substrates, assessment of oyster reef development, and monitoring of water quality. The experimental design was a 3 (sites) × 3 (substrate types) factorial. Three replicates of three test substrates: metal gabion cages containing oyster shells, small "Lo-Pro" Reef Balls, and larger "Mini-Bay" Reef Balls were deployed at Sites 1, 5, and 8 (Fig. 1) on 22 June, 2015. Both substrate types provided opportunities for students to participate in their construction and sampling (Fig. 2). Datasondes with sensors for salinity, temperature, and dissolved oxygen were also deployed in 2015 and 2016 at the three sites. Recruitment was determined by deploying spat collectors at Sites 1, 5, 8, and 0, in June 2015 and July 2016, and monitored monthly until October each year.

Somewhat different sampling methods were used to quantify oyster metrics during the 3 years of the pilot study (see Lodge et al. 2017 for details), but all were extractive methods (Baggett et al. 2014). Gabions were sampled by removing a consistent volume of shell "cultch" material and counting and measuring shell height on a subset of the live oysters on the shell. Reef Balls were sampled by counting and measuring all live oysters in replicate quadrats ($0.025\ m^2$ or $0.01\ m^2$), or all live oysters on the outside of each Reef Ball when density was low. Analysis of variance (ANOVA) was used to assess the effects of site, substrate type, and interactions on oyster metrics (mainly size and density). Size–frequency plots of shell height distributions were also constructed.

Full-Scale Restoration

Problems during the pilot study led to a new design for the gabions that included an internal cavity that made them more

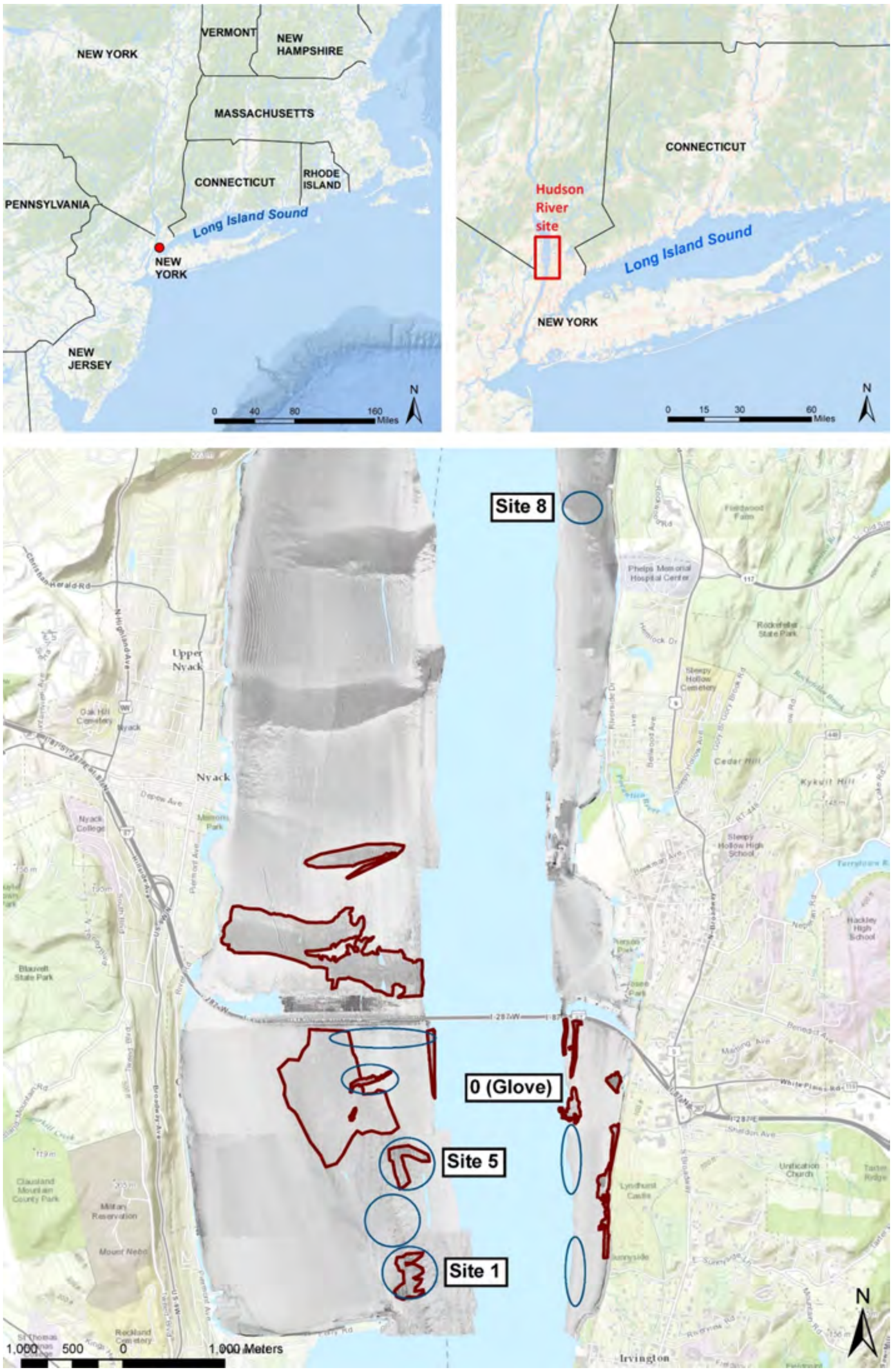

Figure 1. Sites for pilot study (1, 5, and 8), and for full-scale restoration (0 [Glove], 1, and 8). Red polygons indicate previously mapped historical oyster reefs. *Sources*: Esri, DeLorme, NAVTEQ, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, and the GIS User Community.

durable and potentially increased habitat provision (see below), and design of a "clustered" deployment for all substrates for the full-scale restoration effort. Mini-Bay Reef Balls and modified gabions were used for full-scale restoration which was initiated by deploying replicates of the two substrate types at three sites (Figs. 1 & 3). Based on the results of earlier surveys, and the pilot study, Sites 1 and 8 were judged to have the highest probability of successful restoration. A more limited effort was added at a third location (the glove [=Site 0]), as there was already a live oyster reef near that site.

The gabions were modified from the pilot study design by adding an internal cavity to provide space for fish and other

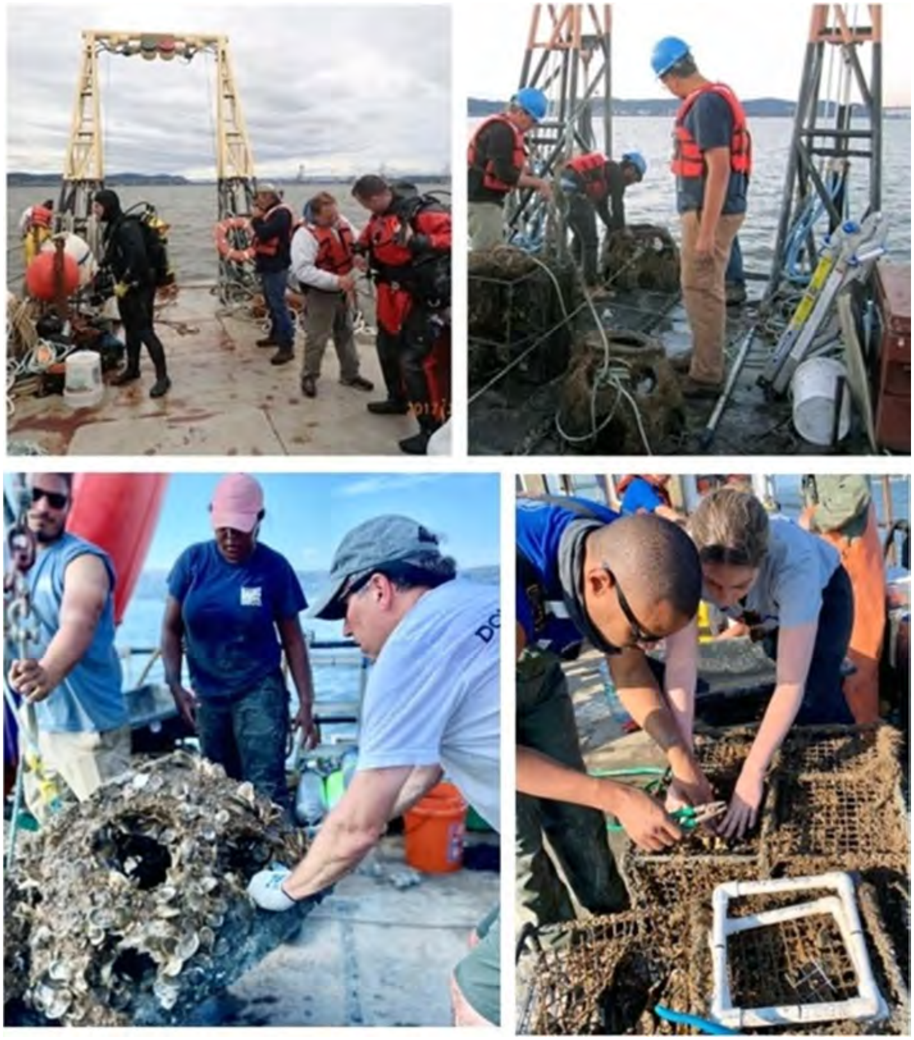

Figure 2. Retrieval of substrates involved divers attaching lines, then winching onboard for processing (photos by Katie Mosher).

organisms, and to increase their structural integrity. This design also increased the space available for larvae to penetrate and reduced the amount of recycled shell required for the project. Gabions were constructed of 12.5 mm rolled round bar frames with the resulting cube lined internally with 12.5-gauge, 24.5 mm mesh wire, and were filled with seasoned (dried onshore for a minimum of 12 months) oyster and clam shell collected from local restaurants (see Fig. 3 for dimensions of substrates). Site 0 encompassed an area of 0.03 ha (0.07 ac) and consisted of one cluster of 54 Reef Balls and one cluster of 36 gabions. Site 1 encompassed an area of 1.35 ha (3.35 ac) and consisted of 414 Reef Balls in 15 clusters and 193 gabions in 11 clusters. Site 8 encompassed an area of 1.04 ha (2.57 ac) and consisted of 413 Reef Balls in 15 clusters and 193 gabions in 11 clusters. All substrates were deployed in water depths greater than 3 m at mean lower low water during 10–31 July, 2018.

Oyster size and density were characterized by annual sampling in fall 2019 and 2020, thus providing three summer recruitment periods (2018, 2019, and 2020). After the substrates were removed from the water, the number and size (shell height measured with calipers or ruler to nearest 1 mm) of individual, live oysters were determined. For the Reef Balls, in 2019, if the number of oysters and oyster spat for the entire Reef Ball was less than 50, all oysters on the exterior and interior surfaces were counted and measured. If the number of oysters for the entire reef ball was greater than 50, individual live oysters in four replicate 0.04 m^2 (20 cm × 20 cm) quadrats placed randomly at multiple locations on the exterior of the reef ball were measured. In 2020, all counts and measurements were made using duplicate 0.04 m^2 quadrats placed at random locations on opposite sides of each Reef Ball. For gabions in both years, a section of the wire mesh from the tops of the gabion cages in two areas was opened using wire cutters and two 0.04 m^2 (20 cm × 20 cm) quadrats were placed haphazardly. All shells were excavated from the upper 2 cm, all live oysters were counted, and shell height (to nearest 1 mm) was measured.

Oyster metrics from both years were compared graphically but only the data from the final dataset (2020) were assessed statistically. The effects of site and substrate type on oyster size and density were compared among sites as well as the interaction of

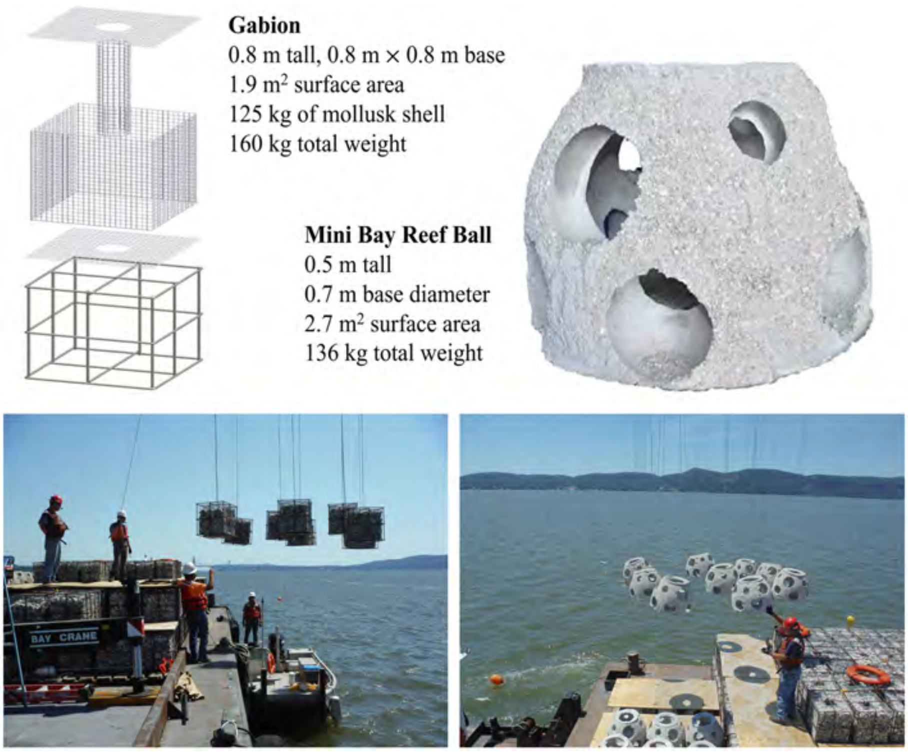

Figure 3. Top: shell-filled gabions and Mini-Bay Reef Balls used in full-scale construction. Bottom: deployment of the two substrate types, gabions and Mini-Bay style Reef Balls in July 2018 (photos by Brian DeGasperis/NYSDEC).

substrate and site in separate ANOVAs with post hoc Tukey's tests. The normality and homogeneity of oyster density and shell height datasets were visually confirmed. Two outliers were removed (Gabion treatment in Site 8) to improve normality of the oyster density dataset. Data analysis and visualization was conducted in R 2022.07.2 with *dplyr*, *stats*, *ggplot*, and *patchwork* packages (Wickham 2016; R Core Team 2013; Pedersen 2023; Wickham et al. 2023).

Results

Pilot Study

Details on the results of the pilot study are in Lodge et al. (2017). Here, we provide a summary of only the major findings relevant for design of full-scale restoration. Live oysters were found on all three deployed substrate types in all 3 years, with total mean densities by site ranging from 7 to 405/m^2. On the final sampling in 2017, live oyster density on the gabions (all three sites combined) was greater than 10-fold greater than either Reef Ball type. Both Reef Ball types had similar densities. The combined oyster size dataset (all substrates and sites) clearly showed 1 year class in 2015, 2 in 2016, and 3 in 2017. Overall, these data indicated successful recruitment for all 3 years.

Full-Scale Restoration

When considering datasets from the full-scale restoration (2019–2020), the 3-year pilot study (2015–2017; Lodge et al. 2017), and a preliminary recruitment study in the same area (2015–2016; AKRF 2016*a*, 2016*b*)—substantial annual spat sets were recorded throughout the study area for 6 consecutive years. And monthly monitoring of spat collectors during the pilot study indicated larval setting usually occurred between mid-August and mid-September. These are important findings for future restoration activities because they suggest that only addition of appropriate substrates during late spring/early summer will likely be necessary for restoration success.

A total of 37 Reef Balls and 20 gabions were monitored from the three sites in 2019, and sampling occurred on 6 days over two periods (30 September–2 October, and 29–30 October; approximately 14 months after deployment). In 2020, a total of 36 Reef Balls and 20 gabions were monitored from the three sites, and sampling occurred on 5 and 6 October, approximately 26 months after deployment. Sampling occurred in the fall so newly recruited oysters (spat from the typical summer spawn) would be detected. Both substrate types were heavily colonized by oysters and several other taxa at all three sites, essentially duplicating the general findings of the 3-year pilot study (Lodge et al. 2017; Fig. 4). At Site 0, oysters had achieved approximately 100% areal coverage of both substrates in some areas, and some oyster clusters projected greater than 10 cm above the substrate surface. Less oyster areal coverage and vertical height occurred at Sites 1 and 8, but development at both sites was substantial.

Site Differences in Oyster Metrics. There were marked differences in oyster density among the sites in both years, and both

Figure 4. Typical substrates retrieved from the three full-scale restoration sites in 2019 (left) and 2020 (right). Note greater oyster habitat development on both substrate types at Site 0 compared to other sites.

annual datasets (2019 and 2020) showed the same by-site trends for live oyster density: Site 0 greater than Sites 1 and 8 (Figs. 4 & 5). In 2020, mean oyster densities across both substrates were greatest at Site 0 and similar between the other two sites ($F_{[2,102]} = 17.30$, $p < 0.001$; Table S1), resulting in approximately 40% greater densities at Site 0. Mean shell height was approximately 25% greater at Site 0 than between the other two sites with similar oyster sizes ($F_{[2,104]} = 34.05$, $p < 0.001$).

Substrate Differences in Oyster Metrics. The effect of substrate type on oyster density also indicated similar relative trends in 2019 and 2020 (Fig. 5). There was no difference in oyster density between the Reef Balls and gabion treatments across sites ($t_{1,103} = 3.85$, $p = 0.053$), however oyster shell heights were greater on Reef Balls ($t_{1,105} = 3.97$, $p = 0.049$). It should be noted that the greater densities on the gabions compared to the Reef Balls during the pilot study (see above) may indicate that the magnitude of the differences between the two substrates decreases as populations develop.

Oyster Metrics by Site and Substrate. There were no significant interaction effects in 2020 between site and substrate types on both mean oyster density ($F_{[2,99]} = 1.43$, $p = 0.245$) and shell height ($F_{[2,101]} = 0.66$, $p = 0.52$), suggesting that the overall trends for the main effects of site and substrate type did not vary across the three sites.

Oyster Size Distributions by Site and Substrate. As already noted, three size/year classes of oysters were expected on the substrates sampled in October 2020 because their deployment in July 2018 allowed for three summer reproduction and recruitment periods. Size–frequency plots of the 2019 data indicated two size/year classes and the 2020 data indicated three classes, but perhaps only at Site 0 where the largest oysters in 2020 exceeded 120 mm shell height (Fig. 6). Data from the other sites and substrates were more variable, which may indicate variations in growth and/or survival. One major difference in patterns between the 2 years was strong small size classes (10–15 mm) at Sites 1 and 8 in 2019 but not 2020 (Fig. 6).

Assessment of Overall Mitigation Effort. Table 1 summarizes the results of the overall mitigation effort with respect to abundances of live oysters on the substrates. There were a total of approximately 5.8 million live oysters on the deployed substrates at the three mitigation sites in October 2020. Although most of the oysters were recent recruits (Fig. 6), substantial numbers of second and third year individuals (many >100 mm shell height) were present indicating good survival and growth for the 2.3-year development period.

Water Quality Trends. The present project also provided additional data on surprisingly robust oyster performance in waters of very low salinity (see AKRF 2021 for details). During the 5-year study period, spring, and early summer (April–July) salinity measurements were often less than 5 practical salinity unit (PSU) and sometimes less than 1. The observed strong oyster performance was surprising for such extreme conditions.

Discussion

The present mitigation effort was the largest oyster restoration project in, and north of, the New York Harbor region in recent decades. The final sampling in 2020 indicated a total of

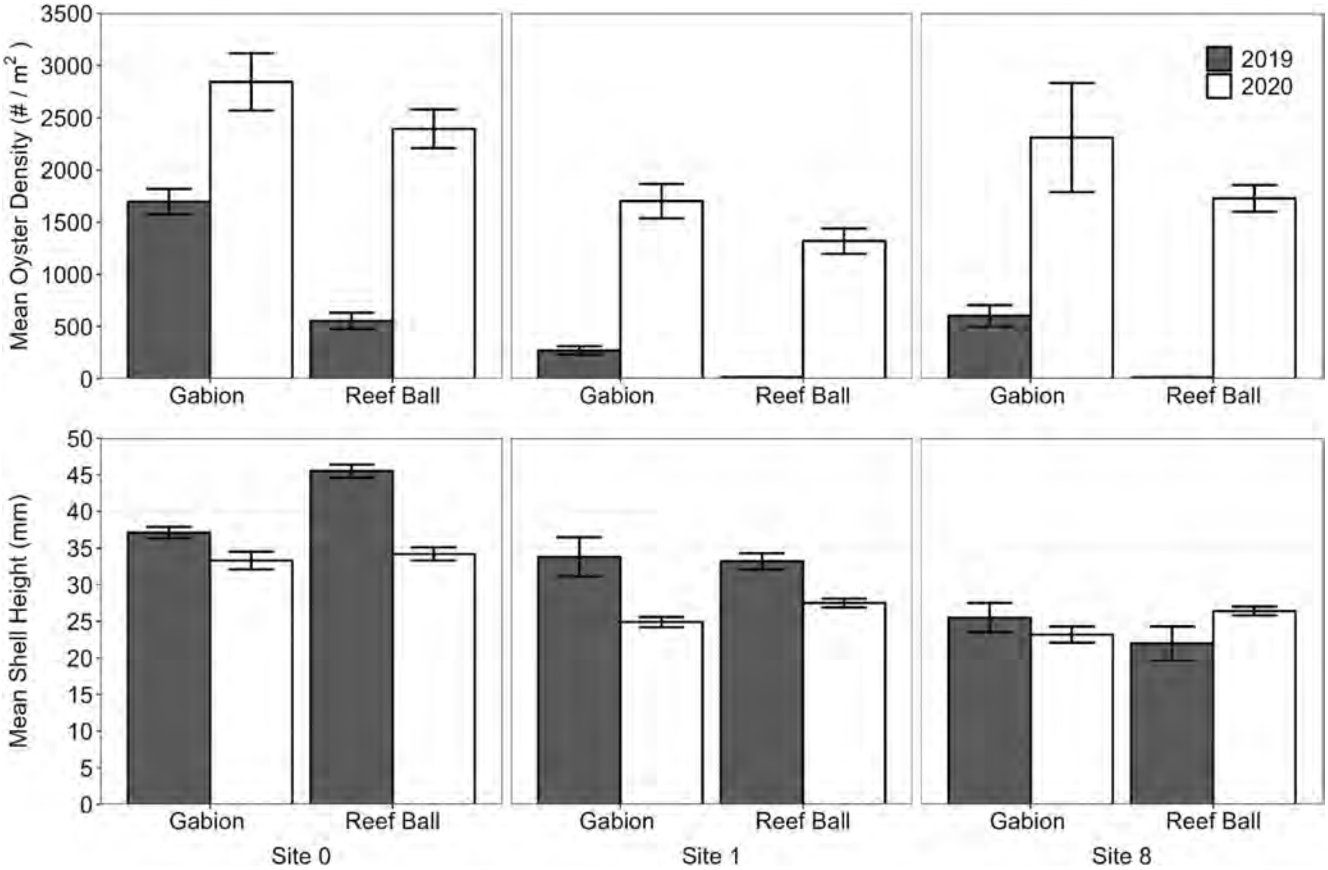

Figure 5. Mean (±1 SE) oyster densities (top) and oyster shell height (bottom) by site and substrate for 2019 and 2020.

approximately 5.8 million live oysters had recruited to the deployed substrates. The total permitted restoration area of the three sites was approximately 2.4 ha (6.0 ac) but the Reef Balls and gabions covered less than 5% of the total permitted area. Even so, they provided almost an acre (approximately 14% of the total area) of "hard substrate" potentially suitable for oyster colonization because of their structural complexity. Both substrates project about a meter above the seafloor and provide nearly 3 m^2 of surface area per unit. The gabions have much more small-scale surface area than the Reef Balls due to the rough surface provided by the oyster and clam shells, but this was not accounted for in any of the calculations. Reef Balls have been used extensively in many areas, and their effectiveness for habitat restoration in various respects is well-documented (http://www.reefball.org). In contrast, shell-filled gabions have only recently begun to be used for oyster restoration (e.g. Safak et al. 2020) and their initial effectiveness as well as durability and sustainability in the long term remain to be thoroughly tested. The similar short-term effectiveness of the two substrate types suggests that—as has been demonstrated in many studies (see Bersoza et al. 2018 for review)—larvae settle and oyster populations develop on many types of hard substrate. Nonetheless, we are aware of no long-term (>5 years) studies that compare different substrate types. Additional monitoring is needed to assess the long-term success of our project.

Our study also provided strong evidence of the potential for additional restoration of oyster habitat in the general area of the Tappan Zee involving only the addition of appropriate hard substrates. Work on several topics, however, is needed to move the process forward. Foremost is the need for more information on the spatial extent of live oysters and bottom types potentially suitable for oyster restoration. As discussed in the Introduction section, bottom surveys in the early 2000s (Carbotte et al. 2004; Bell et al. 2006), and more recently as part of the preliminary studies for the present mitigation project (AKRF 2016*a*, 2016*b*), provided evidence that substantial live oyster populations existed in the lower HRE. None of these studies, however, provided information sufficient to characterize the spatial extent of live oysters. Thus, additional acoustic surveys coupled with extensive bottom sampling are needed to adequately characterize the spatial extent and condition of live oyster habitat in the lower HRE.

The Tappan Zee area was the location of a historical (1950s) major commercial oyster industry that involved transferring adult oysters from Long Island Sound onto approximately 5000 acres of leased bottom in the HRE with the aim of enhancing spawning and local recruitment, followed by removing "seed" (juvenile) oysters presumably produced by the transferred adults, for transplanting to growing areas in Long Island Sound (Bromley 1954). The overall process was perhaps patterned after the long-recognized notion that recruitment is

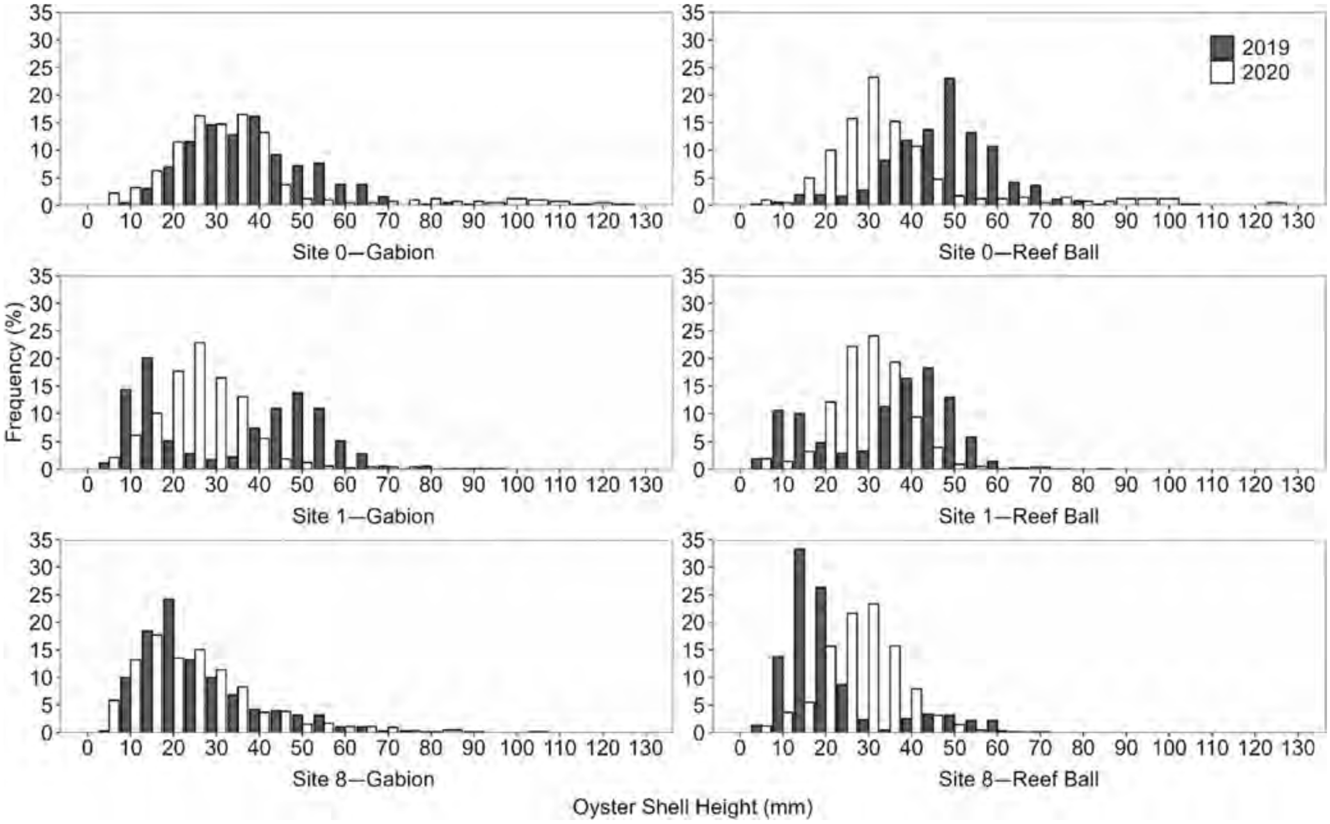

Figure 6. Size–frequency distributions by site and substrate type for fall 2019 and 2020 oyster data, representing three recruitment periods.

positively related to proximity to broodstock (Brooks 1891, pp 204–205). More recent research in Chesapeake Bay has also demonstrated the importance of proximity to broodstock oysters for restoration success (Schulte et al. 2009; Schulte & Burke 2014). Recent research in New Hampshire similarly found that most successful oyster reef restoration projects were less than 1 km from a healthy natural reef (Grizzle et al. 2021), and experiments involving three natural reefs found that most recruitment occurred less than 500 m from the reefs (Atwood & Grizzle 2020). Previous studies in the Tappan Zee area documented oyster recruitment but were not aimed at determining spatial gradients in lower reaches of the HRE (Carthan & Levinton 2013; Kulp & Peterson 2016; McFarland & Hare 2018). Future mapping work focused on live oyster habitat and natural recruitment patterns are clearly needed.

The oyster metrics from all study sites indicated surprisingly robust performance in waters of very low salinity during the warmer months. Previous field studies (Levinton et al. 2011; Grizzle et al. 2013; McFarland & Hare 2018) and multi-factor spatial modeling of restoration suitability for the eastern oyster (Starke et al. 2011) identified the Tappan Zee area as potentially providing a low-salinity refuge from disease and predators, but with a tradeoff of higher mortality due to sporadic storm events that could result in prolonged salinity below the oyster's

Table 1. Abundances of live oysters in 2020 (2 years post-deployment) by site and substrate type. Estimated no. of live oysters = total no. of substrates deployed × surface area of each substrate × mean live oyster density.

	Substrate type	*Total no. of substrates deployed*	*Surface area of each substrate (m^2)*	*Mean live oyster density (no./m^2)*	*1 SE*	*Estimated no. of live oysters*	*1 SE*
0	Reef Ball	54	2.74	2394	186	354,216	2,7521
0	Gabion	36	1.94	2844	275	198,625	1,9206
1	Reef Ball	414	2.74	1315	125	1,491,683	14,1795
1	Gabion	193	1.94	1702	165	637,263	6,1779
8	Reef Ball	413	2.74	1965	185	2,223,633	20,9350
8	Gabion	193	1.94	2311	522	865,285	19,5447
					Total	5,770,705	

tolerance. During the present 5-year study period (pilot and full-scale), spring, and early summer (April–July) salinity measurements were often less than 5 PSU and sometimes near zero (AKRF 2021), far below what is generally considered optimum (Shumway 1996; Starke et al. 2011). There is a growing literature that documents tolerance of some populations of the eastern oyster to low salinities and the genetic basis for such tolerance (e.g. McCarty et al. 2022; Swam et al. 2022). This is an important research topic relevant to the design of future restoration projects in the HRE and elsewhere.

Additionally, our data suggested individual growth rates comparable to other studies in the region. Individual oyster growth was not directly determined in our study, but it can be estimated based on size-frequency data. Growth rates for shell height of 25–40 mm/year for the first few years have been reported in earlier studies in the New York Harbor area (Cerrato 2006; Medley 2010; Levinton & Doall 2011; Levinton et al. 2013). Although rates can vary widely, using 35 mm/year as an approximate mean value, the size-frequency data from Site 0 for both years (for full-scale restoration) indicate 2-year classes in 2019 and 3 in 2020. Data from the other two sites, however, were more variable which may indicate variations in growth and/or survival rates among the sites and between the substrates.

Although the major focus of the monitoring effort was oysters, other species occurred in the "fouling" communities (i.e. all species that typically occur on hard substrates) that developed on the experimental substrates, and two taxa (barnacles and mussels) were at much higher densities than oysters (Lodge et al. 2020). The timing of larval settlement among the fouling community species could not be determined but based on the approximately 100% cover of barnacles (*Balanus improvisus*) and mussels (*Ischadium recurvum*) observed in some areas it is possible they could have inhibited oyster settlement. The relationships among species in fouling communities is complex and includes the obvious competition for space as well as predation on settling larvae (Kochman et al. 2008; Boudreaux et al. 2009; Barnes et al. 2010). Further studies might yield relevant information relevant to the timing of restoration activities such as substrate deployment. Although our study was not designed to unravel the effects of various species interactions, no potential causes (e.g. known predators) for their declines were evident and there were wide variations in seasonal and year-to-year abundances of both taxa. Thus, the developing oyster populations on the experimental substrates provided habitat for other sedentary species, and *presumably* other motile species typically associated with oyster reefs in the region (Peterson & Kulp 2013; Glenn et al. 2020). The new fouling communities on the deployed substrates also provided considerable, though unmeasured, water filtration due to the substantial abundances of at least three filter feeding groups (oysters, mussels, and barnacles). The provision of these and other ecosystem services by the new oyster habitat should be important topics for future research in the HRE.

Acknowledgments

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Compiled Student *t* tests and ANOVAs with post hoc Tukey's tests on the final (2020) dataset for oyster density and oyster shell height by site, substrate, and the interaction of site and substrate.

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