Unprecedented Restoration of a Native Oyster Metapopulation

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Abstract

Native oyster species were once vital ecosystem engineers whose populations have collapsed worldwide due to overfishing and habitat destruction. In 2004 we initiated a vast (35 ha) field experiment with native oyster reefs in sanctuaries protected from exploitation in the Great Wicomico River, Chesapeake Bay using three reef types (high-relief, low-relief, unrestored) sampled in 2007 and 2009. We report an unparalleled restoration of this metapopulation, comprising 185 million oysters of four dominant year classes. A key mechanism underlying recovery was vertical relief—oyster density was fivefold greater on high-relief than low-relief reef—which explains the success of this restoration effort and the failures of past attempts. Juvenile recruitment and reef accretion correlated with oyster density, feedback processes that facilitate reef development and population persistence, suggesting the existence of alternative states. This re-established metapopulation is the largest of any native oyster worldwide, and validates ecological restoration of native oyster species.

Along North American, European and Australian coastlines, native oyster populations have been devastated to less than 10% of their historical abundance through overfishing and oyster reef destruction (*1-3*). Species such as *Crassostrea virginica* and *Ostrea conchaphila* in North America, *O. edulis* in Europe, and *O. anagasi* and *Saccostrea glomerata* in Australia were once vital ecosystem engineers influencing nutrient cycling, water filtration, habitat structure, biodiversity, and food web dynamics (*3, 4*). The widespread decline of these dominant suspension feeders was the predominant cause of eutrophication in estuarine ecosystems due to the shift from benthic to planktonic primary production and the accompanying hypoxia resulting from microbial decomposition (*3*). This phenomenon remains as a leading cause of ecosystem degradation in estuaries worldwide due to the largely failed efforts at oyster restoration (*5*). Consequently, non-native oyster species (e.g. Pacific oyster *Crassostrea gigas*) were introduced in many of these ecosystems to recover lost economic and ecological benefits (*6*), despite the unnatural alteration of the world's ecosystems (*3, 5*).

In Chesapeake Bay, oyster landings of the native *Crassostrea virginica* peaked in the 1880s at 20-25 million bushels per year, whereas recent landings are less than 200,000 bushels (*2*). Concurrently, the natural populations were reduced to approximately 1% of historical abundance (*2, 3, 5*), despite considerable expensive attempts to restore the populations. Introductions of *C. gigas* and other species were attempted through the 1900s, but failed due to biological and environmental impediments (*7*).

More recently it was concluded that revival of the native oyster is unlikely, and that introduction of non-native Asian oyster (*C. ariakensis*) merits consideration (*8*). This conclusion was based on the faulty premise that restoration failed largely due to the inability of *C. virginica* to resist the challenge of two diseases (MSX: *Haplosploridium nelsoni* and Dermo: *Perkinsus marinus*). However, various unfished populations have overcome disease pressure by being allowed to live in protected reefs conducive to growth, survival and disease resistance (*9-11*). Moreover, the currently accepted strategy of attempting to restore the wild fishery and native populations in tandem allows for destructive harvest practices that devastate the structural integrity of reefs (*12, 13*) and inhibit recovery. Recently, however, scattered small assemblages of *C. virginica* have been observed on natural and alternative oyster reefs protected from exploitation in Delaware Bay (*14*), North Carolina sounds (*12, 15*), and the Chesapeake (*16, 17*), suggesting that restoration of the native *C. virginica* is feasible using novel methods.

We report an unrivaled restoration of a native *C. virginica* metapopulation in the Great Wicomico River (GWR), a sub-estuary of lower Chesapeake Bay that was selected for restoration in 2004 by the US Army Corps of Engineers (USACE). Nine reef complexes covering 35.3 ha were declared permanent sanctuaries, free from oyster fishing (fig. S1). Pre-restoration surveys demonstrated that there was on average less than 2 oysters/m^2 throughout the nine reef complexes (see Materials and methods). The field experiment involved two restoration treatments [high-relief reef (HRR) and low-relief reef (LRR)] and a control treatment of unrestored bottom (UNB) spread over each of the reef complexes. In 2007 we sampled 85 one-square-meter plots, allocated randomly across the three treatments in the nine reef complexes, with patent tong and video surveys (fig. S1; see Materials and methods). We further sampled the reefs in March 2009 to verify long-term persistence of the reefs.

In 2007, the metapopulation on the nine reefs consists of an estimated 184.5 million oysters, comprising 119.2 million adults of two age classes (2005 and 2006) and 65.3 million juveniles of the 2007 year class (fig. S2), indicating protracted survival of settled individuals to adulthood and recruitment of larvae to the reefs. This represents a 57-fold augmentation of the resident GWR population (see Materials and methods), which greatly exceeds the previously unachieved restoration goal (10-fold increase of 1994 baseline by 2010) of the

Chesapeake Bay Program. Moreover, the reef complex continued to develop and persists to the present (March 2009), as evident in 2009 video and patent tong surveys (figs. S3-S5).

The 185-million-strong population dwarfs all individual populations throughout Maryland's 111,600 ha of public oyster grounds in upper Chesapeake Bay (*18*), and is nearly as large as the estimated 200 million oysters in all of Maryland waters. Comparisons to native oyster populations in other parts of the world similarly demonstrate the unrivaled magnitude of the restoration. The largest documented populations of native oyster species comprise 24 million flat oyster *Ostrea anagasi* in Tasmania (*19*) and 100 million European flat oyster *Ostrea edulis* in the Mediterranean (*20*). For all other native oyster species, there is little data but their populations are much smaller than the GWR population (*1, 3, 5, 6*).

The major influence upon oyster reef success was reef height, which drove abundance and density across the reef complexes (Figs. 1, S3-S5, M1-M6). Despite their much smaller area (12.1 ha), HRR segments harbored 67% or 123.8 million oysters (Figs. 1a, S5, M3-M6), whereas the 23.2 ha of LRR contained 32% or 58.1 million (Figs. 1a, S4, M2), and 43.5 ha of UNB held only 1% or 2.6 million (Figs. 1a, S3, M1). Irrespective of reef type, adults were twice as abundant as young juveniles (Fig. 1). Mean oyster density per m^2 was fourfold higher on HRR (1026.7 ± 51.5 SE) than on LRR (250.4 ± 32.3 SE); UNB only had 6.0 (± 1.5 SE) oysters/m^2 (Fig. 1b). The HRR density stands in sharp contrast to the typical average densities on Chesapeake Bay sanctuary reefs, which have 100-152 oysters/m^2. On harvested reefs in Chesapeake Bay, oysters exist at much lower densities (2-11 oysters/m^2); some harvested reefs harbor higher densities up to 350 oysters/m^2, but these are unusual.

The key feature mediating the abundant restored population was the vertical relief of the restored reefs, specifically the height above the river bottom (HRR: 25-45 cm and LRR: 8-12 cm, prior to subsidence of 2-6 cm due to settling) of the oyster shell used to build the reefs. As the proportion of HRR increased on any particular reef, oyster density rose sharply from 200 oysters/m^2 when a reef was 10% HRR to over 1000 oysters/m^2 when a reef was 90% HRR (Fig. 2, r^2 = 0.86). For every 10% increase in the proportion of HRR, oyster density rose by 100 oysters/m^2 (Fig. 2). Similarly, oyster size (shell height) on HRR (47.3 mm ± 1.2 SE; Fig. S2a) was 15% larger than that on LRR (41.0 mm ± 1.1 SE; Fig. S2b). The mechanism mediating the superiority of HRR over LRR was most likely due to the optimal flow rates and corresponding healthier physiological condition of oysters on HRR, which maximize growth and survival and minimize disease influence and sedimentation (*9, 12*).

The sharply magnified oyster densities on HRR had two profound benefits for the long-term sustainability of the restored population (Fig. 3a) and the persistence of the associated reef matrix (Fig. 3b). First, there was a positive feedback between adult density and subsequent juvenile recruitment such that spat density was a positive parabolic function of adult density, with a peak at an adult density of 850 oysters/m^2, after which juvenile recruitment declined (Fig. 3a). Variance in juvenile recruitment also differed by reef type (Fig. 3a), and was distinctly lower on HRR (CV = 43%) than on LRR (CV = 129%). Thus, recruitment was not only much greater on HRR, but it was also more consistent than the variable and lower recruitment on LRR (Fig. 3a).

Oyster reefs require an accumulation of accreting shell (i.e. the conglomeration of shell from living and dead oysters) that develops vertically with a complex architecture, and which serves as the base for the extant population, spat settlement and reef persistence. Accretion rate of shell material on restored reefs was a sigmoid function of total oyster density and differed substantially by reef type: 6-16 L/m^2 on HRR and $<$ 4 L/m^2 on LRR (Fig. 3b). Historically, accretion rates exceeding 5 L/m^2 characterized successful native oyster reefs (*21*). The vertical growth and cohesiveness of HRR indicate that they are coalescing into the historic, natural oyster reef architecture typical of pre-exploitation reefs (*21*), as evident in the photographs and video clips of 2007 and

2009 (Figs. 1, S5, M3-M6). These results suggest that oyster reefs exist in two alternative states, one a heavily-sedimented degrading state characterized by low oyster densities, recruitment and growth, and the other a vertically accreting, elevated reef configuration comprised of abundant oysters of various age classes, which provide a positive feedback to reef integrity. These alternative states have characteristics similar to those observed in marine and aquatic ecosystems (*22*).

It has been suggested recently that native oyster restoration cannot succeed because restored reefs do not accrete reef material at sufficient rates to compensate for losses due to shell degradation and sedimentation (*23, 24*). This conclusion is based on data from restored reefs characterized by poor habitat quality (e.g. low reef height), low recruitment, low standing stock, and ongoing exploitation, which destroys the reef architecture and removes large adults from the population (*13*). Such reefs are comparable to the poorly performing LRR in the GWR. In contrast, HRR are accreting shell at rates significantly faster than 5.0 L m^{-2} yr^{-1}, indicating that HRR has developed into a robust, permanent reef structure, whereas much of the LRR is not likely to persist more than a few years. The HRR exhibit both vertical and cohesive growth, in contrast to the pattern of reef degradation typically observed on previous native oyster restoration projects (*25*). Our recent patent tong samples and UW ROV observations in March 2009 indicate that recruitment of the 2008 year class was very successful and that the reefs are continuing to develop and grow, attesting to the expansion and persistence of the reef matrix. The HRR system has persisted and, more importantly, thrived for nearly five years, well past the typical longevity of failed oyster reefs (*25*). The HRR are gaining shell material and establishing oyster densities at rates previously unrecorded on native oyster restoration projects.

The native oyster metapopulation on the restored reef system in the GWR greatly exceeds recently proposed criteria for sustainability (*15*): (1) it is comprised of multiple year classes at high abundance, which buffers year-to-year variation in spat settlement; (2) it is composed of young and old adults that have survived disease challenge; (3) the reefs are accreting (i.e. growing) at a rate that will provide settlement habitat for future generations; and (4) it receives sufficient spat settlement and recruitment to sustain the population over the long term.

The recent recovery of a native *Crassostrea virginica* metapopulation in the Great Wicomico River of Chesapeake Bay, as well as limited successes in other North American estuaries (*14-17*), highlight the critical importance of two common features of successful reefs—protection from fishing and high vertical relief (*9, 10, 12, 13*). Past oyster restoration efforts operated under the mistaken premise that fishery and ecological restoration could be accomplished simultaneously (*7, 8*). This approach failed to stem the decline in oyster stocks, and led to the widespread use of more efficient fishery methods such as power dredging, the most destructive technique of harvesting oysters (*13, 25*). This strategy promoted partial fishery recovery via put-and-take fisheries at the expense of ecological restoration, and consequently perpetuated the precipitous decline of oyster populations in Chesapeake Bay as well as along the Atlantic and Gulf of Mexico coasts of North America (*1-3, 5*).

The GWR restoration project deviated significantly from prior restoration attempts in the Chesapeake Bay by building oyster reefs of high vertical relief at a broad spatial scale in large sanctuaries protected from fishery exploitation, and in locations characterized by high recruitment (*26*, also see Materials and methods). Typical restored sanctuaries prior to this project amounted to 1% or less of an estuary's original oyster reef extent. The GWR reef network encompasses approximately 40% of the original oyster reef extent (*27*) within a hydrodynamically restricted system (*26*). This metapopulation connectivity promotes persistence of individual populations in the network and larval subsidies from protected source reefs to fished reefs (*28*) with the attendant economic benefits (*4*). Designation of the reefs as sanctuaries protects the reefs both from exploitation of the spawning stock and physical destruction of the critically important vertical structure. Significant vertical relief and reef persistence were accomplished by building a substantial portion of the reef system as high as 45 cm (HRR) in contrast to the 8-12 cm LRR, which typically does not promote reef persistence more than 3-5 years (*25*). Low-relief reefs have been the construction method of choice by fishery management agencies in the Chesapeake and several other estuaries. The ephemeral nature of low-relief reefs has proven to be one of the main impediments to the recovery of native oyster habitat wherever they are used.

The vertical growth and cohesiveness of HRR indicate that they are coalescing into the historic, natural architecture typical of pre-exploitation oyster reefs (*29*), as evident in the photographs and video clips (Figs. 1, S5, M3-M6). Winslow (*29*), during his historic survey of oyster reefs, documented perhaps the last unexploited reefs in Chesapeake Bay. These reefs consisted of "long, narrow oysters…no single oysters of any [age] class, but all grew in clusters of 3 to 15. The shells were clean and white, free from mud and sand. The mature oysters were covered and the interstices between them filled with younger oysters." Moreover, he noted that it was very difficult to sample these reefs due to their cohesive nature, which we also experienced when attempting to sample HRR during our 2009 survey.

Although disease will kill some oysters in the GWR, the recent development of disease tolerance in oysters on sanctuary reefs of lower Chesapeake Bay (*11*) bodes well for the long-term persistence of the GWR metapopulation and its attendant ecosystem benefits (*4*). Similar approaches with other natural (*14*) and artificial reefs (*30*) could lead to recovery of the native oyster throughout North America, as well as other ecosystems worldwide where native oysters have been functionally extirpated (*3, 5*).

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Figure legends

Figure 1. (a) Oyster abundance and (b) Density on each of the reef types across the nine-reef system. Values for UNB are magnified to demonstrate the similar pattern in adult and spat abundance as on the HRR and LRR patches. Abundance estimates for the system of nine reefs consisted of a total of 184.5 million oysters (95% CI: 165.0-204.0 million), 119.2 million adults (95% CI: 104.5-133.9 million) of the 2005 and 2006 year classes, and 65.3 million spat (95% CI: 59.7-77.2 million) of the newly recruited 2007 year class (Fig. S1).
Error bars represent 1 SE. n = 22 for HRR, 41 for LRR, and 22 for UNB. The underwater photograph below each of the reef types represents average conditions for each type of reef type.

Figure 2. Combined spat and adult oyster density as a function of the proportion of sampled HRR plots on each of the nine reefs [Least-squares regression; Spat and adult density = 165.5 + 992.8 x (Proportion HRR), $r^2 = 0.86$, $n = 9$].

Figure 3. (a) Spat density as a function of adult density and (b) Accretion rate as a function of adult and spat density on each of the 85 one-square-meter plots sampled across the nine reefs. [Non-linear least-squares regression; (a) Spat density = 4.672 + 0.818 x (Adult Density) - 0.001 x (Adult Density)^2, $r^2 = 0.54$, n = 85; (b) Accretion rate = -0.302 + 16.860 x (1 – $e^{-0.001 \times \text{Adult and Spat Density}}$), $r^2 = 0.86$, n = 85]. In (b) the squares and associated crosses represent the means and SEs for each of the three treatments.

Figure 1.

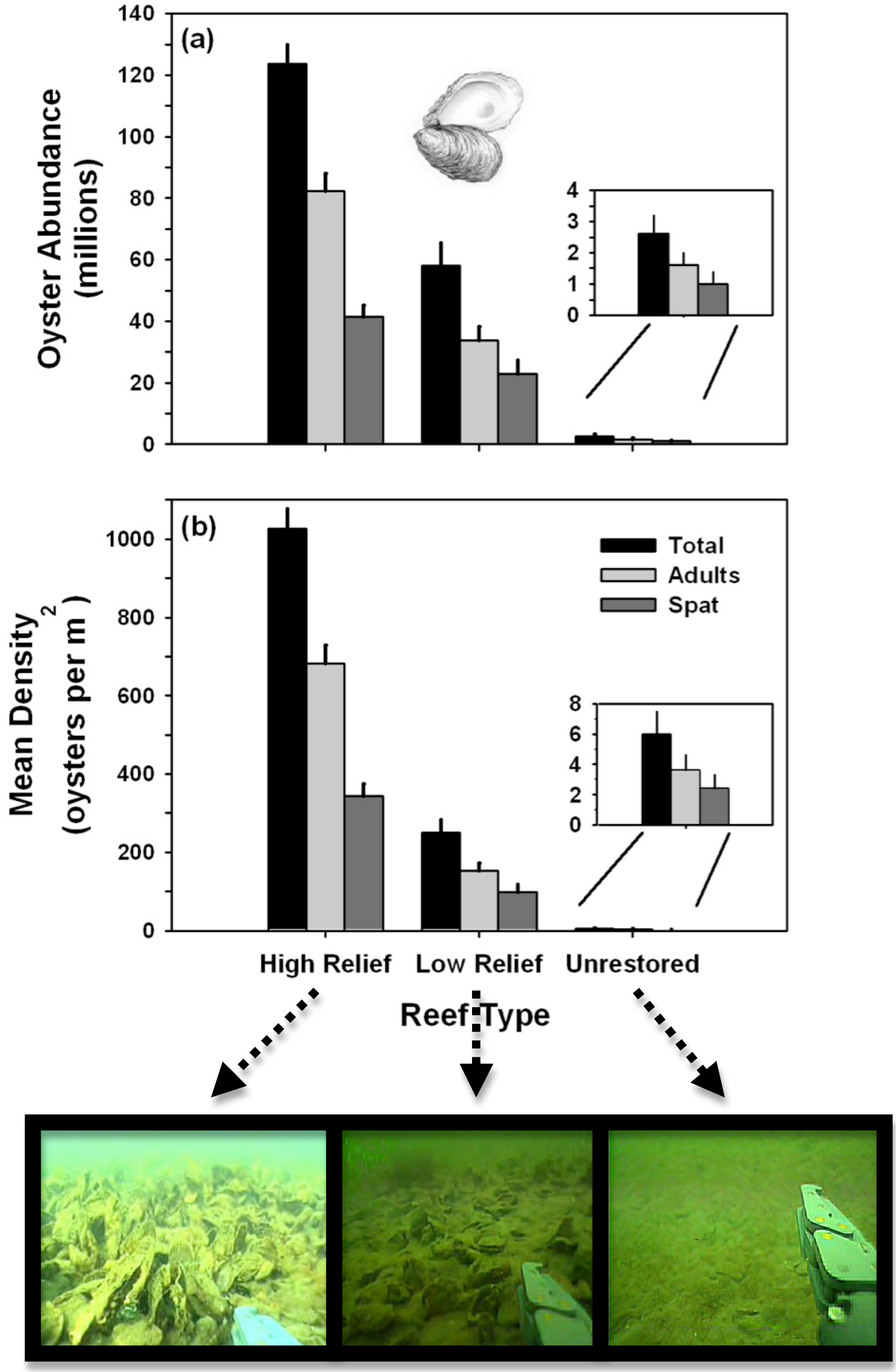
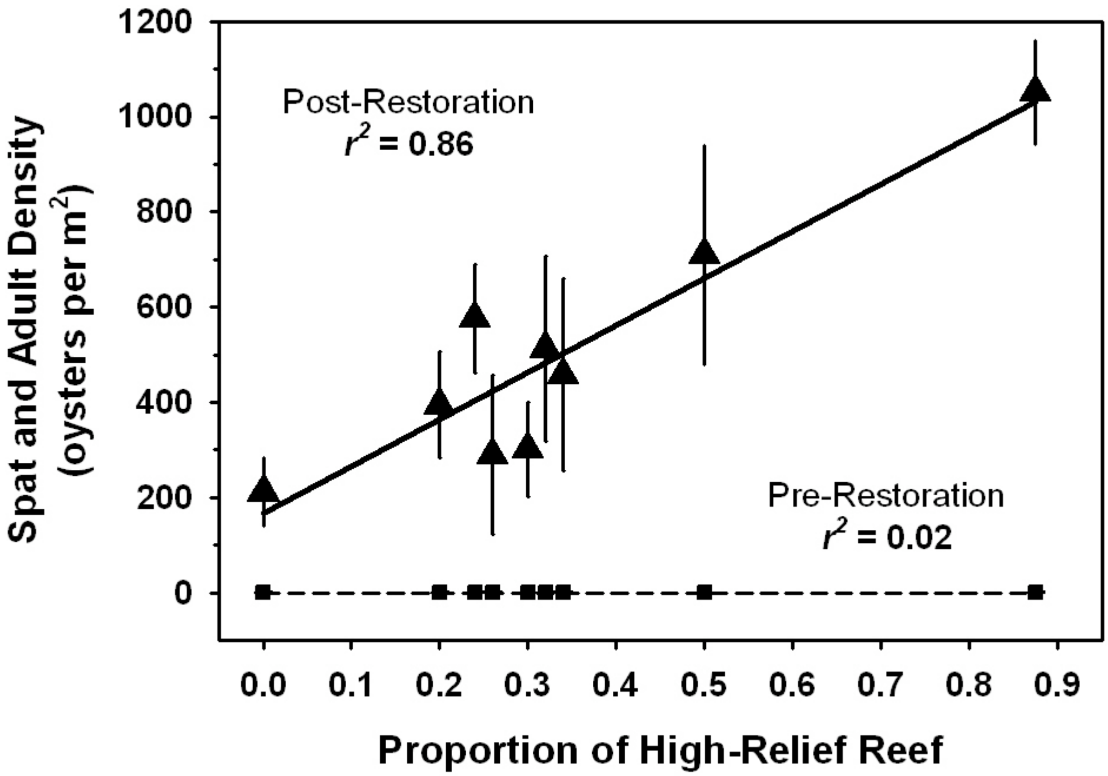
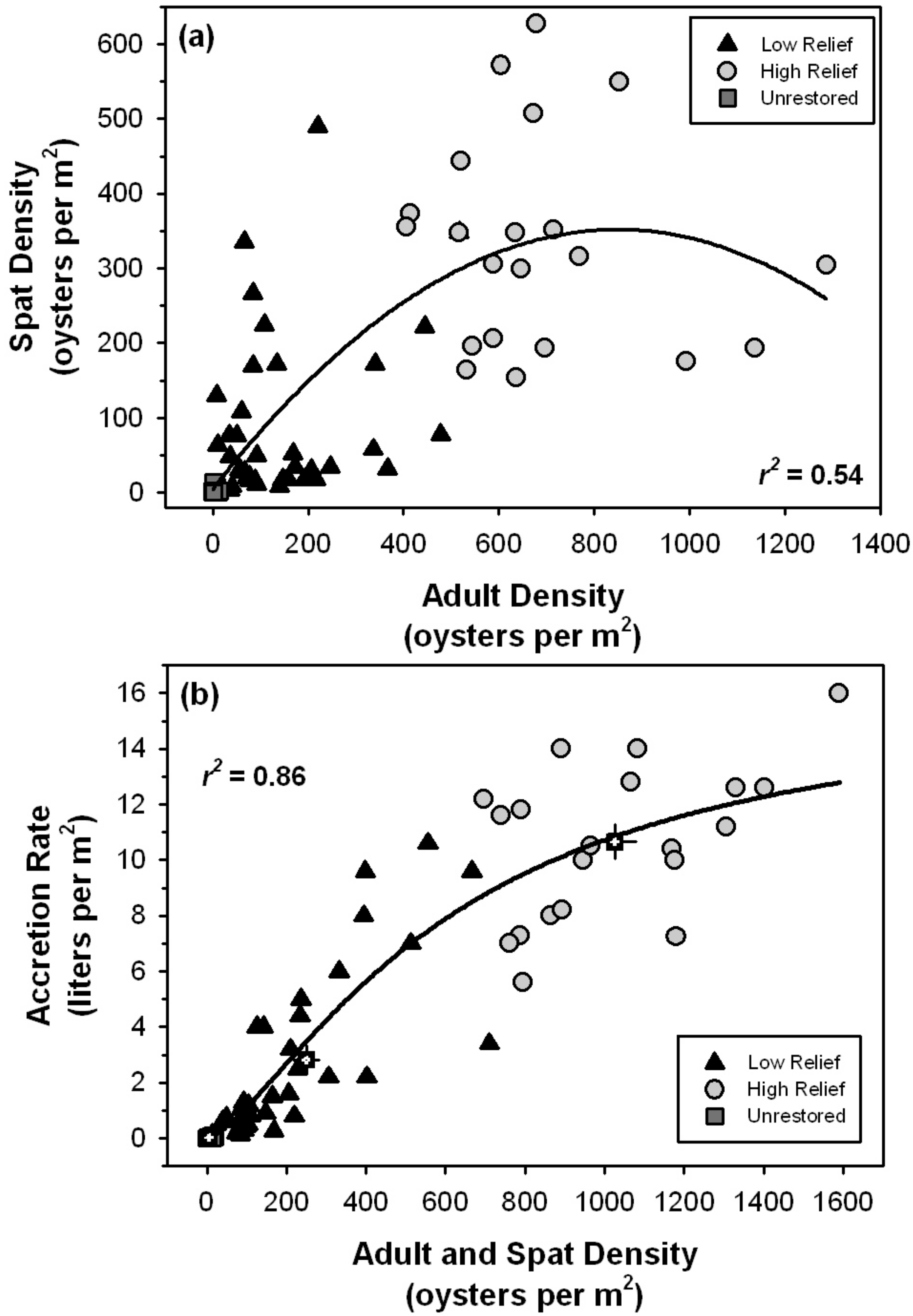

140
120
100
80
60
40
20
0
(a)
Oyster Abundance
(millions)
4
3
2
1
0
1000
800
600
400
200
0
(b)
Mean Density
(oysters per m 2)
Total
Adults
Spat
8
6
4
2
0
High Relief
Low Relief
Unrestored
Reef Type

Figure 2.



1200
1000
800
600
400
200
0
Spat and Adult Density (oysters per m2)
Post-Restoration
r2 = 0.86
Pre-Restoration
r2 = 0.02
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Proportion of High-Relief Reef

Figure 3.



(a)
Low Relief
High Relief
Unrestored
Spat Density
(oysters per m2)
0
100
200
300
400
500
600
0
200
400
600
800
1000
1200
1400
r2 = 0.54
Adult Density
(oysters per m2)
(b)
r2 = 0.86
Accretion Rate
(liters per m2)
0
2
4
6
8
10
12
14
16
Low Relief
High Relief
Unrestored
0
200
400
600
800
1000
1200
1400
1600
Adult and Spat Density
(oysters per m2)

SUPPORTING ONLINE MATERIAL

Materials and methods

Pre-Restoration survey

A pre-restoration survey with patent tong samplers was conducted throughout the unrestored, potential oyster reef habitat in the Great Wicomico River (GWR), a small sub-estuary on the western shore of the Chesapeake Bay just South of the Potomac River (Fig. S1) in Northumberland County, Virginia at approximately N 37.8043 and W -76.268. The survey consisted of 63 samples across the nine reef complexes (*S1*), and none of the samples had more than 2 oysters per m^2 (Fig. 2). This pre-restoration survey served as the "Before-Control" element of a "Before-After Control-Impact" experimental design.

Construction

The U. S. Army Corps of Engineers (USACE) attempted to construct approximately 42.5 ha of oyster reef habitat in fall of 2004 by placing dredged and washed oyster shells removed from former productive reef footprints in the lower James River. These areas were not the most suitable habitat available in the river, but were areas classified as “shell-sand” and “shell-mud” rather than high-quality hard bottom known as “oyster rock” in a 1981 survey (*S2*). Areas of high-quality bottom were set aside for the public common-access oyster fishery by the Virginia Marine Resources Commission. This practice is common when combining fishery and ecological restoration, forcing sanctuaries for ecological restoration to be placed on marginal bottom (e.g. soft muds), which hinders reef performance and persistence, thereby fostering the belief held by some that native oyster restoration cannot succeed. The USACE responded to the problems of having to build reefs on sub-optimal bottom and the suspected ephemeral nature of low-relief reefs by constructing high-relief reefs over a large portion of the project area to increase the chances of project success. This proved to be a wise decision.

Post-Restoration survey

The patent tong survey was conducted throughout the restored oyster reef areas (Fig. S1). Underwater video was used to document the reef condition and appearance at various locations during the patent tong survey. The filming occurred immediately adjacent to the patent tong sample sites. The patent tong survey, along with associated underwater video, indicated that the USACE reefs encompassed 38.7 ha initially and as of fall 2007, 35.2 ha remained, an approximately 9% rate of loss over the four year period since the reefs were constructed. Due to the vagaries of the shell placement technique, which consisted of blowing the dredged shells, with a water cannon, over the area to be restored from a barge into the water, approximately 10% of the area the USACE had attempted to build reefs on never received any shells. Due to subsidence, a significant portion of the HRR strata had essentially degraded to LRR. This resulted in a 33.9% loss of HRR acreage to the LRR strata, which gained in size as a result. Much of this loss occurred toward the main channel of GWR on reefs in waters deeper than 6 m. The reef areas lost were typically on areas of softer sediments and had little shell; in some cases only approximately 2-4 cm of shells remained. The shells became completely covered with sediment and were no longer available as settlement substrate for oyster larvae. Any spat or adults observed on these shells had died due to anoxia. The restored reefs were all constructed above Sandy Point, in a stretch of river known to have a relatively small tidal exchange. All restored reefs were intended to be fully within various Baylor (public) oyster grounds, but a substantial percentage of most of the nine reefs extended outside of the Baylor grounds. Though bottom categorized as Baylor grounds did not necessarily include all natural oyster reefs, it is a reasonable guide for the location of subtidal oyster reefs in Virginia waters of the Chesapeake Bay. The Baylor grounds encompassing the project cover a total of 194.2 ha and contain many habitat types, including former reef footprints consisting of hard shell, sand-shell and mud-shell mix, sand, clay, and mud. Due to the inherent difficulties in deploying shells off a barge using a water cannon to create shell beds of uniform thickness, some areas intended to receive shells did not, and some areas near but outside the Baylor grounds did. This heterogeneous placement of shell is typical of such construction, and the area of bottom covered is not strongly correlated with the volume of shell used (*17*). The direct result was the deployment of reefs of various heights and configurations, as well as areas devoid of shell, within the Baylor areas targeted for restoration.

Estimate of 1994 oyster population in Great Wicomico River (GWR)

To generate the population increase due to the restoration effort in the GWR over a historical time frame, we used estimates of abundance derived from the 1994 dredge survey by the Virginia Institute of Marine Science and Virginia Marine Resources Commission (the status of Virginia's public oyster resource 2004 report). From the dredge survey, abundance of spat, small adults and large adults were combined into a total average of 110 per bushel (16 spat + 87 small adult + 7 large adult per bushel). Each dredge tow collected 1.5 bushels and sampled 55 m^2, with an average efficiency of 18% and range in efficiency from 2-26% (*S3*). The area of bottom inhabited by the oyster population was estimated as 19.425 ha, which represents areas of high-quality oyster habitat (= "oyster rock") as defined in previous surveys (*S4*). The resultant average estimate = 1.5 x 110 oysters/55 m^2 x 100/18 x 194250 m^2 = 3.244 million oysters. If the dredge efficiency was 2%, estimated abundance = 9.011 million, and if 26% it would be 0.693 million.

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Figure S1. Map of the reef sites in the Great Wicomico River, Chesapeake Bay. HRR is indicated in red, LRR by stippling, and UNB by the remaining area in each of the Baylor Ground polygons.

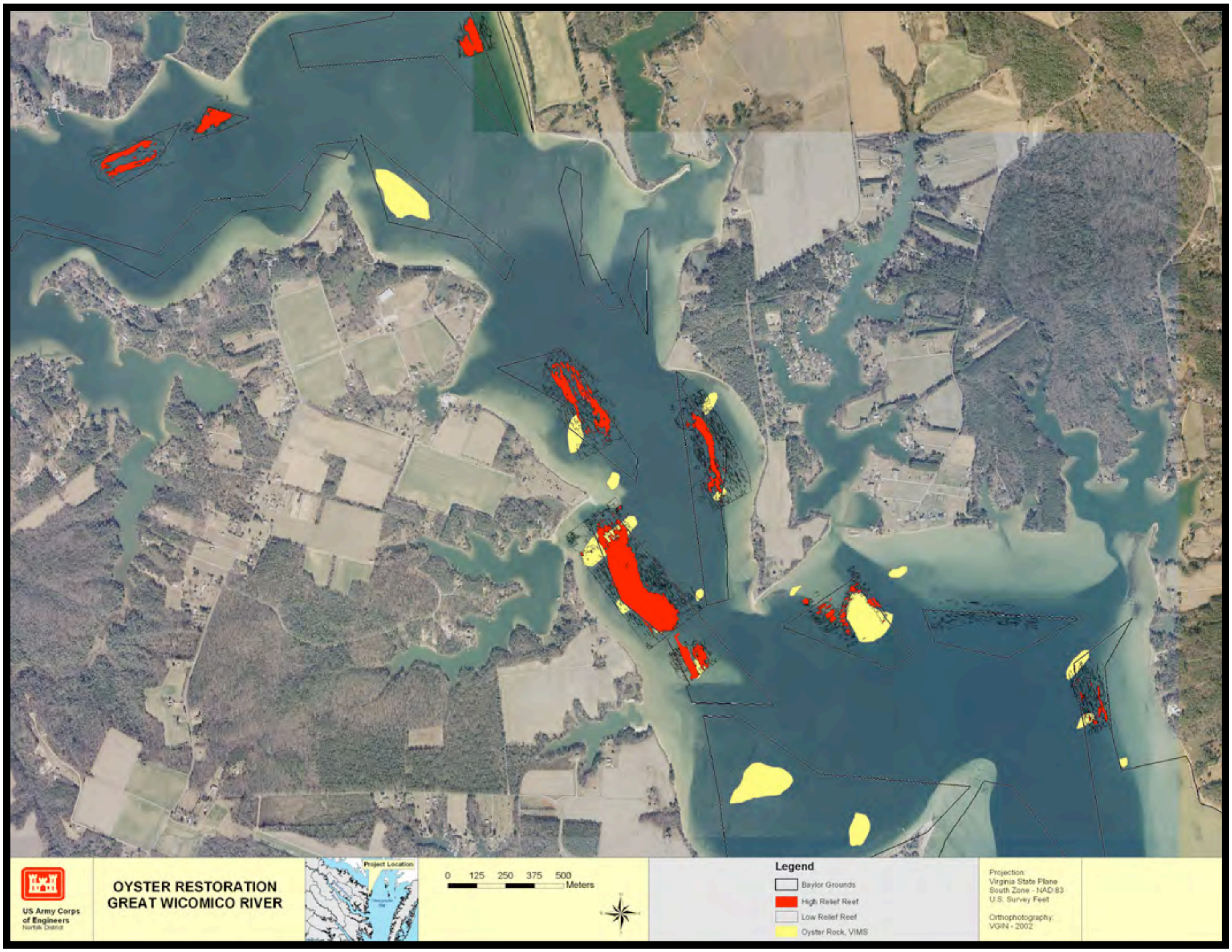


Figure S2. Size-frequency distributions of *Crassostrea virginica* on (a) HRR and (b) LRR treatments.

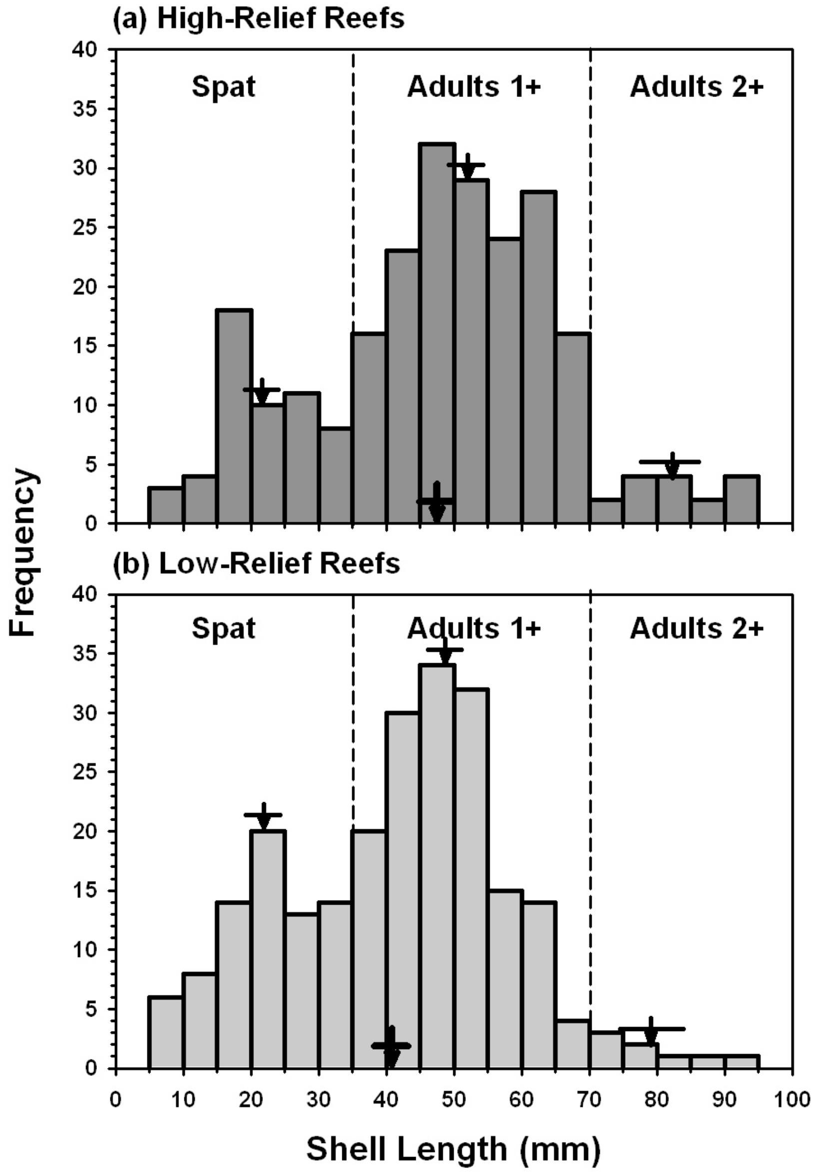


Figure S3. Representative photograph of unrestored bottom prior to the restoration and on unrestored-bottom control areas after the restoration.

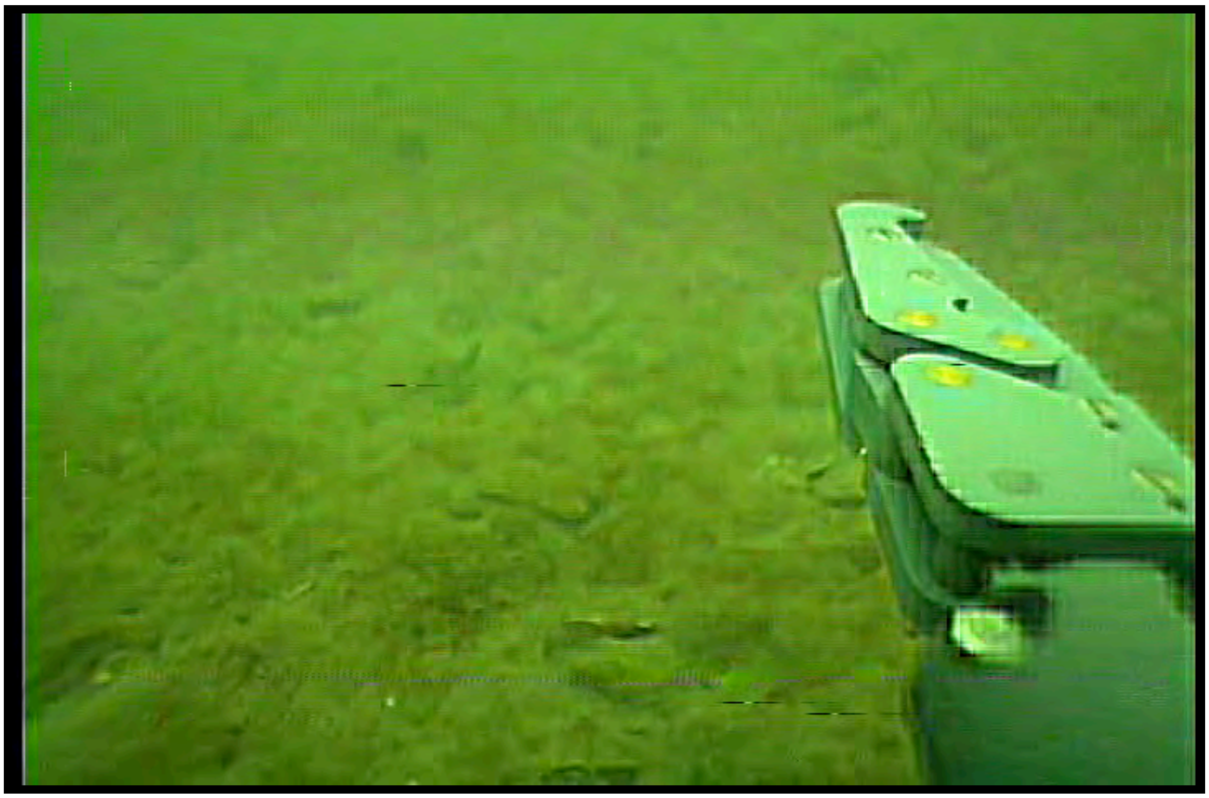
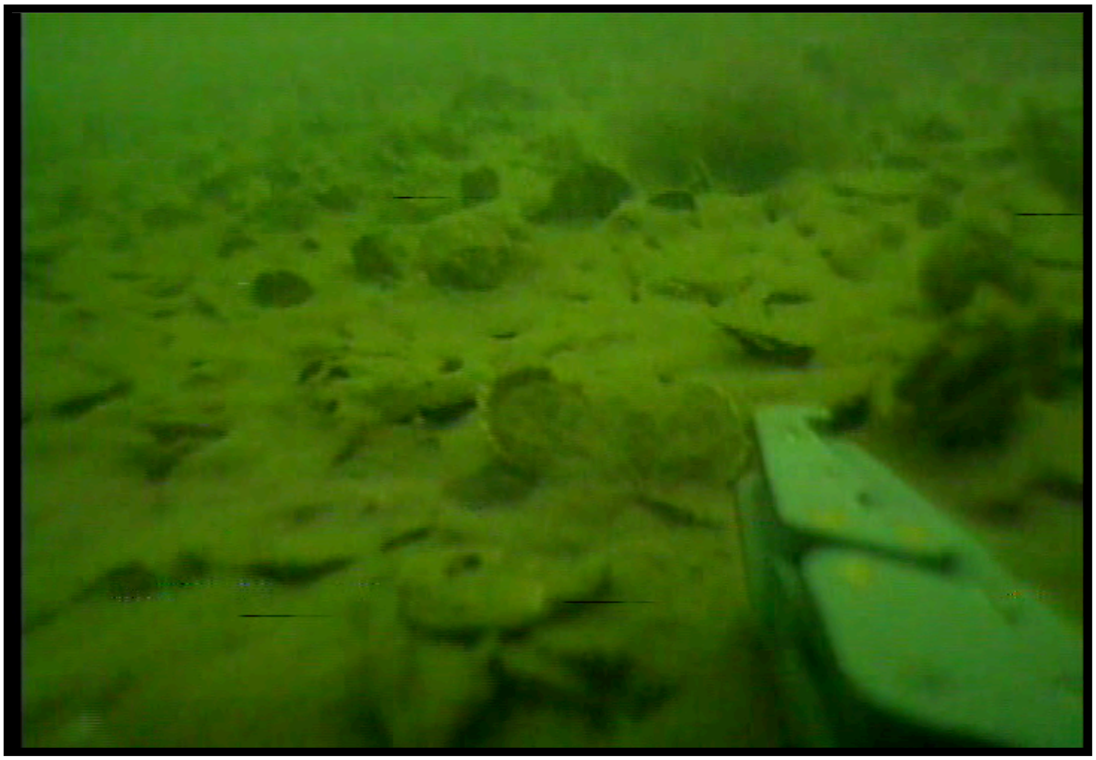


Figure S4. Representative photographs of low-relief reefs in 2007 (top) and 2009 (bottom). Note the heavy sedimentation and relatively low vertical relief.



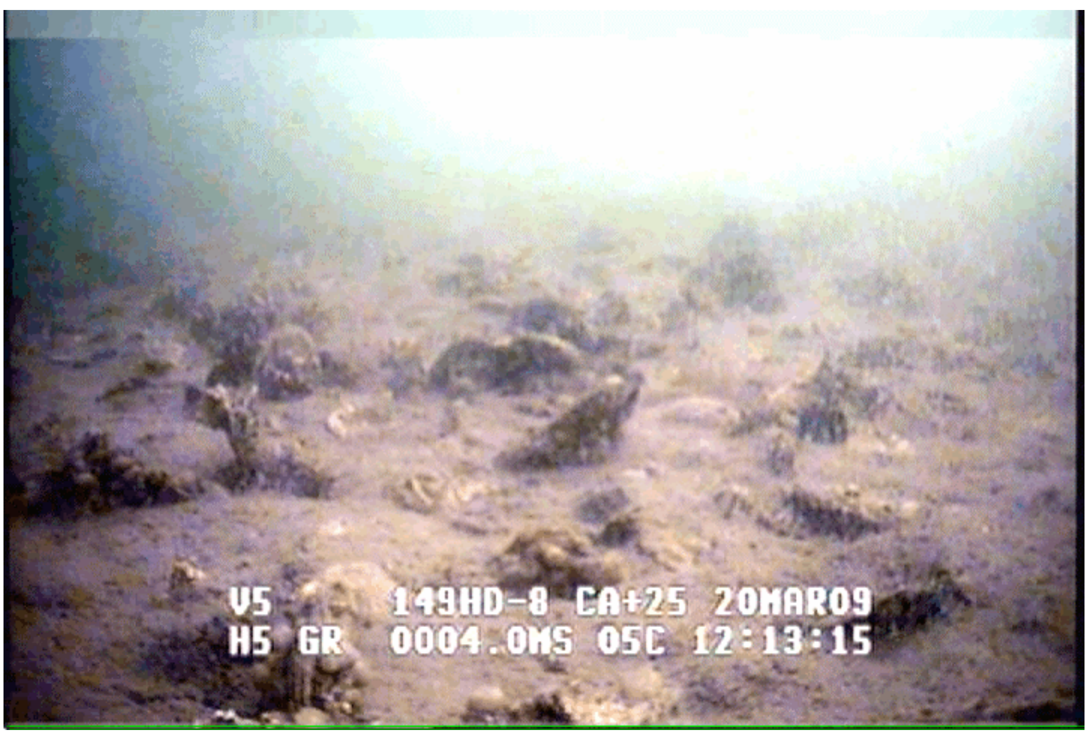


Figure S5. Representative photographs of high-relief reef in 2007 (top) and 2009 (bottom). Note the abundant large live oysters, high vertical relief, and broad reef extent. In 2009 the reef has a developed faunal and floral assemblage.

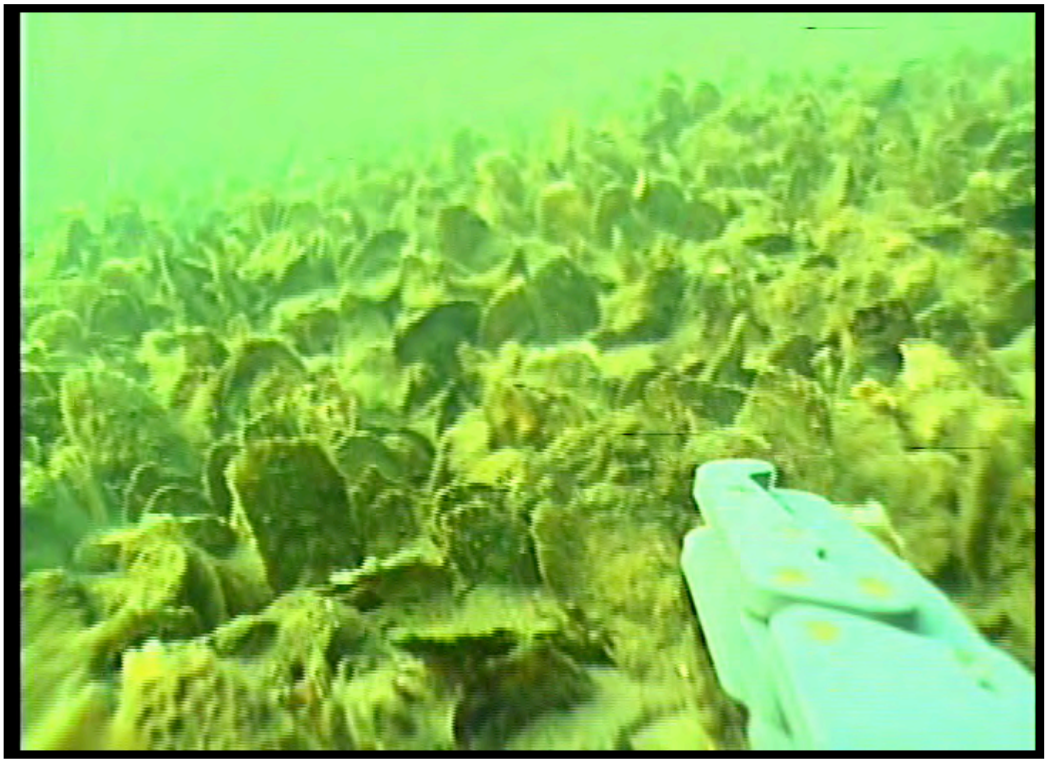


Figure M1. Video clip from one of the control treatment areas of unrestored bottom.

Figure M2. Video clip of one of the low-relief reef areas. Note the lack of vertical relief and heavy sedimentation across the reef.

Figure M3. Video clip of one of the more productive low-relief reef areas. Note the intermediate degree of vertical relief and moderate sedimentation across the reef.

Figure M4. Video clip of a typical high-relief reef. Note the high abundance of live adults, strong vertical relief, numerous cohesive clusters, and light sedimentation.

Figure M5. Video clip of another typical high-relief reef. Note the spatial extent of the thriving reef, irrespective of the specific location being filmed. All of the high-relief reefs were similar to this reef.

Figure M6. Video clip of goby, shrimp and live oysters on high-relief reef. Note the "smoke ring" (i.e. pseudofeces) blown by the "happy" oyster on the thriving high-relief reef.