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Assessment of recent eastern oyster (Crassostrea virginica) reef restoration projects in the Great Bay Estuary, New Hampshire: Planning for the future

Raymond E. Grizzle
University of New Hampshire, ray.grizzle@unh.edu

Krystin M. Ward
University of New Hampshire - Main Campus, Krystin.Ward@unh.edu

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Raymond Grizzle and Krystin Ward
Jackson Estuarine Laboratory,
University of New Hampshire,
Durham, NH 03824

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Assessment of recent eastern oyster (*Crassostrea virginica*) reef restoration projects in the Great Bay Estuary, New Hampshire: Planning for the future

Raymond Grizzle and Krystin Ward
Jackson Estuarine Laboratory, University of New Hampshire, Durham, NH 03824

April 26, 2016

EXECUTIVE SUMMARY

Current oyster populations in New Hampshire total less than 10% of what they were in the 1980s, and the causal factors for the declines include disease, sedimentation, and human harvest. The two major results from a population ecology perspective have been dramatic losses of oyster shell (the major substrate on which oyster larvae typically settle) as well as juvenile annual recruitment to the remaining reefs. Experimental scale oyster restoration projects addressing these two limitations (substrate and natural recruitment) were initiated in the state in the early 2000s by scientists at the University of New Hampshire (UNH). Since the mid-2000s, the focus has been on full restoration-scale projects, and beginning in 2009 most projects have been collaborative efforts by UNH and The Nature Conservancy (TNC). The present study assessed nine recent collaborative efforts, and provided a comprehensive assessment of restoration success with the goal of determining how the restoration process might be improved.

Methods included measurement of the five "universal metrics" recommended for assessing oyster restoration projects: reef shape, reef size, reef height, oyster density, and oyster size-frequency distribution. Towed underwater video was used to determine the areal extent and shape of the constructed/restored reef areas focusing on the relative amounts of exposed surf clam shell originally used to construct the reef bases. Polygons delimiting the location and size of each "shelled" bottom area were manually constructed using ArcGIS software, and % coverage of the total restoration area was determined. Oyster density and size distribution were determined by taking replicate quantitative bottom samples on each reef using custom-made patent tongs with a sampling area of 0.16 m^2. All live oysters were counted and measured, and size-frequency plots were constructed to allow estimation of age/size relationships.

Initial areal coverage by seasoned surf clam shell originally used to construct the shell bases ranged from 20% to 60%. Video mapping in 2015 indicated that most reefs had experienced substantial losses of shell cover since initial construction, probably in most cases due to sedimentation. Initial oyster density also varied widely from no live oysters present to total oyster densities $>100/m^2$ at two sites. The 2015 data indicated substantial losses of live oysters on all reefs except one in the Piscataqua River. This site and one at the mouth of the Lamprey River also had natural recruitment densities $>50/m^2$ in 2015, indicating good potential for longer-term development. Additionally, size-frequency data indicated that these two sites and one at the mouth of the Squamscott River had multiple year classes present in 2015. In sum, these data strongly suggested that all three sites have good potential for longer-term development.

The two factors most strongly affecting restoration success appeared to be shell burial by fine sediments (sedimentation) and site location relative to proximity to a natural reef. *Three recommended changes in the current methods used in New Hampshire for oyster restoration projects include:* construct the reef base with enough shell to achieve vertical height of at least 0.3 m over as much of the restoration site as practical; arrange the reef base material (mollusk shell in most cases) in a pattern consisting of many small piles of shell so that the amount of reef "edge" is maximized; focus the site selection process on areas that are in close proximity (<0.5 km) to a healthy natural reef. *Three recommended changes in the current reef monitoring protocol include:* develop better methods for measuring reef height and overall reef rugosity; develop methods for assigning uncertainty levels to reef shape based on video mapping; and implement a comprehensive and adaptive long-term monitoring plan for all oyster restoration projects. *Suggested topics for future research include:* refine our understanding of the relationship between constructed reefs and natural reefs that act as potential larval sources; identify variables other than site location that potentially affect restoration success; assess the efficacy of spat seeding compared to shell base construction only; determine the potential effects of the rapidly expanding oyster farming industry on natural oyster reefs; and characterize the major ecosystem services oyster reefs (restored and natural) as well as oyster farms provide in the context of broader environmental management.

INTRODUCTION AND BACKGROUND

New Hampshire's native eastern oyster, *Crassostrea virginica*, has experienced dramatic declines throughout its range along the western Atlantic and Gulf of Mexico coasts (Beck et al. 2011; zu Ermgassen et al. 2012). The state's current oyster populations total less than 10% of what they were even in the 1980s (NH Fish and Game Department unpublished data), reflecting overall trends for the species. Although declines in the state's oyster populations had been documented well before 1980 (Jackson 1944; Ayer et al. 1970; Bolster 2002), oysters were abundant in many areas at that time and before the two major oyster diseases, MSX (*Haplosporidium nelsoni*) and Dermo (*Perkinsus marinus*), began to have noticeable impacts. The first documented major epizootic in New Hampshire was caused by MSX and occurred in 1996 (Barber et al. 1997). Since then, densities of adult (>60 mm shell height) oysters on the major reefs in the state declined through the 1990s and early 2000s from a high of ~250/m^2 to well below 50/m^2 (NHF&G unpublished data). As expected, these declines in adult oysters resulted in decreases in recruitment, with early recruit ("spat") densities typically <20 individuals/m^2 most years from 1995 through the mid-2000s. Some rebound in oyster densities and recruitment occurred in the mid-2000s, but have declined to near historical lows the past several years. Thus, since the 1980s there have been dramatic losses of oyster shell (the major substrate on which oyster larvae typically settle) as well as annual recruitment to the remaining reefs in New Hampshire.

The causes for oyster declines in New Hampshire also reflect trends in other areas and include disease, sedimentation, and human harvest (Langan 1997; Odell et al. 2006; Grizzle et al. 2006; Konisky et al. 2014). Management agencies in the state initiated oyster restoration programs in the early 2000s, and substantial progress has been made. However, much remains to be learned, particularly with respect to long-term success and the factors affecting success. The bulk of the research on eastern oyster reef restoration has occurred in the mid-Atlantic and southeastern US. In general, the amount of hard substrate suitable for oyster reef development in these areas has declined but natural oyster populations are still sufficient in many areas to consistently produce a substantial annual recruitment of young oysters (spat set). Thus, the major focus in many areas has been on determining the types and spatial arrangements of substrate material suitable for natural recruitment and subsequent reef development (Soniat et al. 1991; Luckenbach et al. 1999; Coen and Luckenbach 2000; O'Beirn et al. 2000; Luckenbach and Ross 2003; Piazza et al. 2005; Nestlerode et al. 2007; Powers et al. 2009; Brown et al. 2013; La Peyre et al. 2014). However, oyster populations in the northeastern US, including New Hampshire, are typically substrate *and* recruitment limited so more complex restoration methods must be developed (Grizzle et al. 2013; Lodge et al. 2015).

More than 20 oyster restoration projects involving a diversity of objectives, sizes, and methods have been completed in the state since 2000. Most of the early projects were experimental in nature and conducted by scientists at the University of New Hampshire (UNH). Total bottom area involved in each of the early projects was typically <1 acre and each was focused on particular research topics. Since the mid-2000s, the emphasis has been on full restoration-scale projects, most of which have been collaborative efforts between UNH and The Nature Conservancy (TNC), and building on what was learned from earlier work in the state and elsewhere. The present study assessed nine different projects representing the major collaborative efforts between UNH and TNC since 2009 (Fig. 1). The initial results of each project were described in previous final reports to the funding agencies (Konisky et al. 2011, 2012, 2014), but no longer-term assessments had been conducted. The goal of the present study was a comprehensive assessment of longer-term restoration success with the overall goal of determining how the restoration process might be improved.

The current oyster restoration process in New Hampshire includes the methods used in many areas where the oyster populations are substrate and recruitment limited (Brumbaugh and Coen 2009): construction of a hard substrate reef base followed by deposition of remotely set oyster spat-on-shell onto the reef base (Figs. 2 and 3). All nine of the study reefs for the current project included both components, with reef bases constructed of seasoned mollusk (mostly surf clams) shell. However, each project differed in total amount of shell deposited and how the shell was distributed (Table 1). For most projects, the shell was deliberately distributed unevenly to result in several heavily "shelled" areas within the overall restoration area footprint. The goal typically was 25% of the restoration area covered with shell.

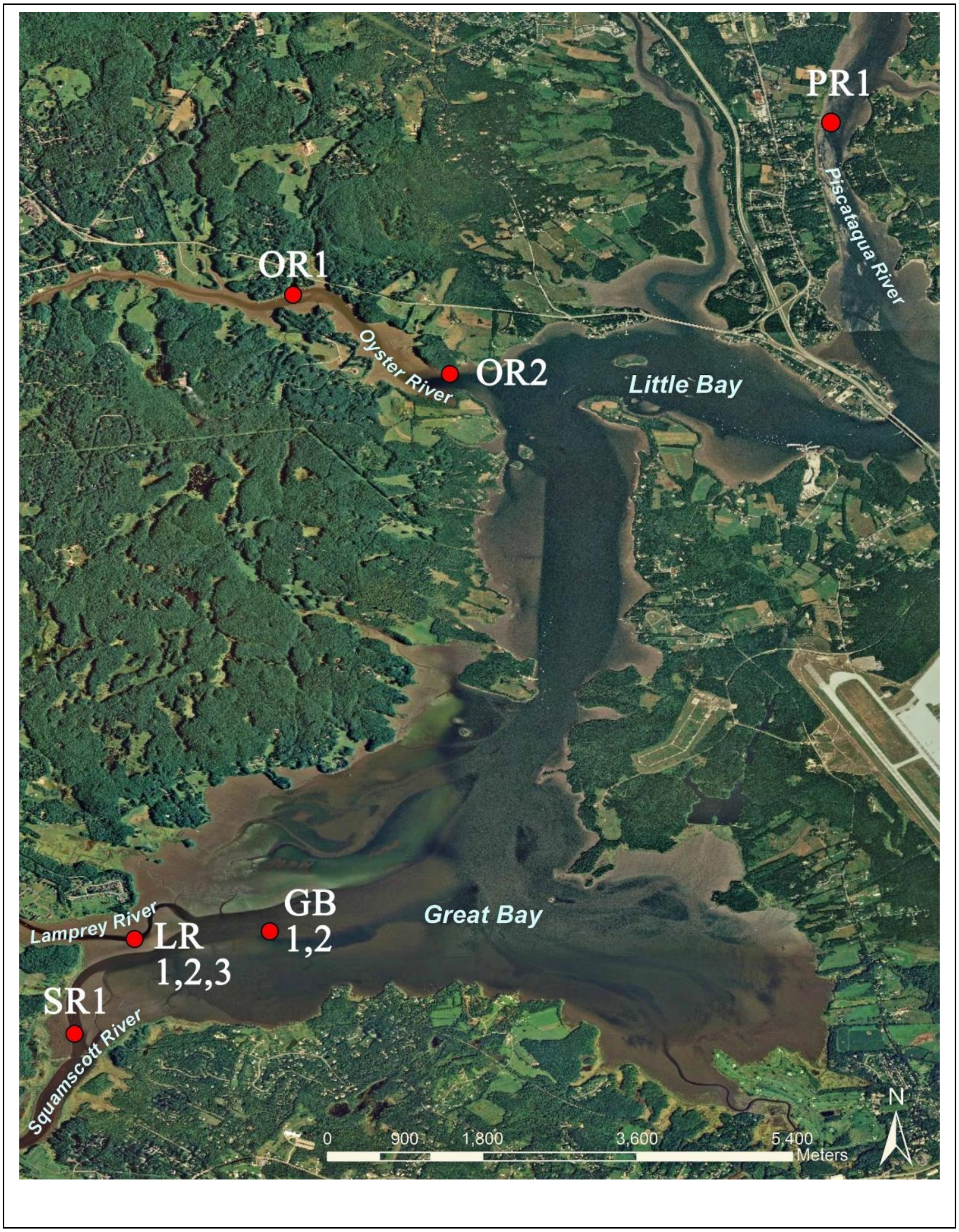

Fig. 1. Location of the nine oyster restoration sites assessed in the present study. Note three restoration projects occurred in close proximity at the Lamprey River and two in southwest Great Bay locations shown by red dots.

Fig. 2. Two methods used to construct reef bases. Left: mollusk shell deployed from bags. Right: shell pushed off barge at restoration site with firehose.

The remote setting process for production of spat-on-shell occurred at UNH's Jackson Estuarine Laboratory following the general methods in Castagna et al. (1996) and Supan et al. (1999)(Fig. 3). Seasoned recycled oyster shell obtained from citizens and local restaurants (via the NH Coastal Conservation Association and UNH's oyster shell recycling programs) was used as cultch, and oyster larvae were supplied by Muscongus Bay Aquaculture, Bremen, Maine. After setting, the spat-on-shell were moved to a nursery raft where they were held for ~2 months, then transferred to the restoration site and manually spread onto the shell base (Fig. 3). Spat-on-shell were also provided by volunteers participating in the New Hampshire Oyster Conservationist program which typically has been funded as part of the overall restoration project each year (Konisky et al. 2011, 2012).

Fig. 3. Remote setting process for producing oyster spat-on-shell at Jackson Estuarine Laboratory. Upper row: setting tanks and wire baskets filled with recycled oyster shell in setting tank. Lower left: nursery rafts with spat-on-shell in baskets suspended above the bottom. Lower right: towing 2-month old spat-on-shell to oyster restoration site.

The site selection process that has been followed in New Hampshire mainly consists of choosing sites based on where oysters occurred historically, and existing conditions that might affect success and be permitted by the regulatory agencies. Protected habitats such as eelgrass beds are avoided, and human uses such as navigation are not interfered with. However, there has been no rigorous consideration of environmental characteristics such as bottom type or water currents in the site selection process because oysters can be found throughout the Great Bay/Piscataqua River estuarine system and in a wide range of habitats.

METHODS

The present project consisted of the following three major tasks using the methods described for each. All five "universal metrics" recommended by Baggett et al. (2014, 2015) for assessing oyster restoration projects were measured at each of the nine restoration sites: reef shape, reef size, reef height, oyster density, and oyster size-frequency distribution.

Task 1: Video survey and mapping

The objectives of this task were to determine reef size, shape, and height, as well as to characterize any bottom conditions that might be relevant to restoration success. Towed underwater video was used to determine the areal extent of major bottom features, focusing on the relative amounts of exposed, un-silted surf clam shell (viable for setting) originally used to construct the reef bases, and live oysters (Fig. 4). Video imagery was classified in the laboratory at 2-second intervals (each a "sampling point") along each shiptrack into areas of high-density exposed clam shell (>20% cover), low-density exposed clam shell (<20%), and no clam shell; at each sampling point it also was noted whether live oysters were present. Polygons delimiting the location and size of each class of shell density were manually constructed using ArcGIS software, and % coverage (of the total restoration area) by each of the three classes was determined based on the percentage of the total sampling points assigned to each class.

Fig. 4. Towed underwater video system (SeaViewer Model 650) used to determine reef shape, size and height. Left: camera mounted on sled. Right: imagery recorder and GPS unit.

Reef height could only be accurately determined by direct visual inspection and measurement for that portion of each site in the low intertidal or shallow subtidal zones. Only three of the nine sites, OR1, OR2, and LR1, occurred in such shallow waters. Reef height at the remaining six sites that occurred in deeper waters could only be estimated from the video imagery.

Task 2: Patent tong sampling

The objectives of this task were to provide data on oyster density and size distribution for live oysters. Replicate quantitative bottom samples were taken using custom-made patent tongs with a sampling area of 0.16 m^2 (Fig. 5). Five (5) to seven (7) replicate tong samples were taken at each site (Table 1). Each sample was processed by counting and measuring (shell height to nearest mm with calipers) all live oysters, and noting whether they occurred on clam shell (used in reef base construction) or oyster shell (used to produce spat-on-shell). This allowed us to differentiate between oysters (spat-on-shell) used in reef construction and natural recruitment which would at least initially have been only onto clam shell, and provided data on mortality and natural recruitment that had occurred since initial reef construction. Field observations (e.g., amount of shell burial or subsidence) relevant to assessing restoration success were also recorded.

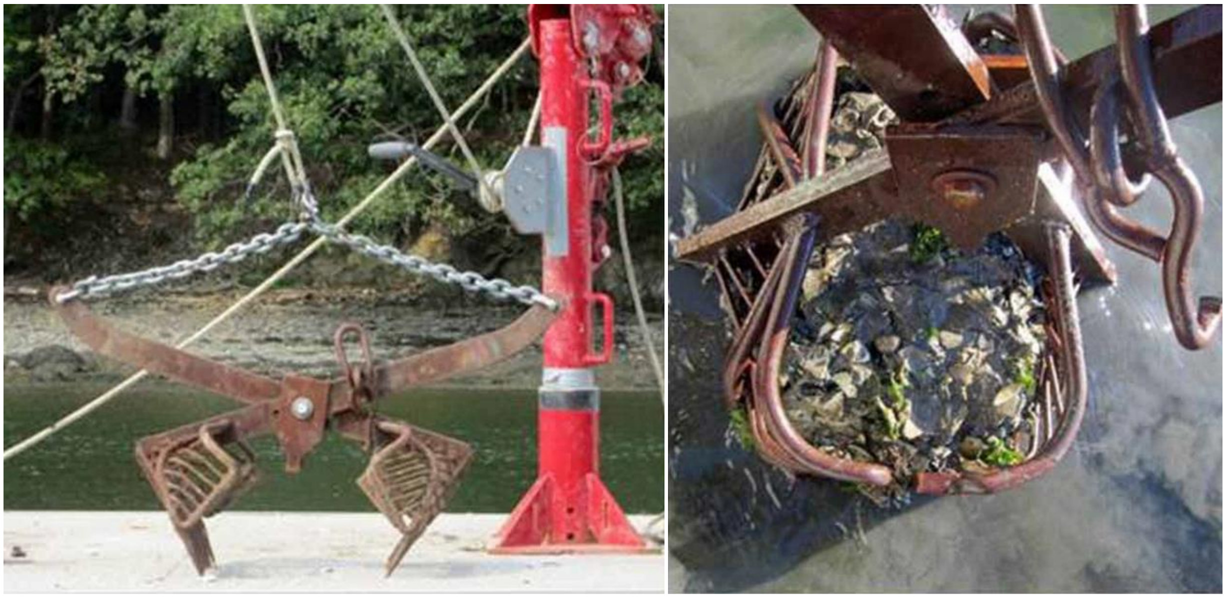

Fig. 5. Patent tongs used to take quantitative (0.16 m^2 surface area) samples to determine oyster density and size on restoration sites.

Task 3: Data analysis and assessment

The data from Tasks 1 and 2 were analyzed from the perspective of assessing the development and potential long-term sustainability of each restored reef, including the need for further reef enhancement actions. The overall approach was to compare the 2015 data with the data from initial reef construction/restoration, focusing on the four universal metrics. The 2015 data also were used to assess the notion that juvenile oyster recruitment is negatively correlated with distance from a healthy natural reef. These assessments were then synthesized to develop a set of recommended improvements in the existing reef restoration protocol, and to identify topic areas where more research is needed.

RESULTS

This section is arranged in four parts. The first two summarize the 2015 data for all nine restoration sites with respect to the universal metrics listed above and what they indicate with respect to restoration success. The third is an assessment of how location may have affected restoration success, focusing on distance from a natural reef. The final is a summary of the major factors that likely affected success of the nine projects and the implications for future projects.

Reef size, shape, and height

Physical characteristics of the shell base of each constructed reef varied by project (Table 1). In all cases, the result was a mosaic of surf clam shell piles of varying heights arranged haphazardly throughout the overall restoration area (Figs. 6 - 10).

Table 1. Summary data for reef shell base characteristics and spat-on-shell deployed to each site initially and in 2015. "(nd)" = no data.

Reef Name	Date constructed	Restoration area (ac)	Tong sample replicates	Number of spat-on-shell deployed	Volume of shell deployed (yd^3)	Initial shell cover (% of area)*	Maximum initial reef height (m)	2015 shell cover (% of area)	Maximum 2015 reef height (m)
Oyster River #1 (OR1)	2009	0.2	5	3000	30	20%	0.08	9%	0.01
Oyster River #2 (OR2)	2010	1.0	5	(nd)	100	(nd)	(nd)	7%	0.03
Lamprey River #1 (LR1)	2011	2.0	6	190000	200	60%	0.10	3%	0.10
Lamprey River #2 (LR2)	2011	1.0	5	145000	100	20%	(nd)	26%	0.20
Squamscott River (SR)	2012	2.0	7	85000	83	20%	(nd)	5%	(nd)
Lamprey River #3 (LR3)	2013	2.0	5	146000	200	38%	0.30	25%	0.20
Piscataqua River (PR)	2013	1.5	6	350000	150	54%	(nd)	23%	0.20
Great Bay #1 (GB1)	2014	2.5	5	226000	250	25%	(nd)	1%	0.02
Great Bay #2 (GB2)	2015	2.5	6	316000	250	21%	(nd)	4%	0.02

*Initial shell cover estimates from Konisky et al. (2011, 2012, 2014).

The major factors that affected physical characteristics of the reef shell base included how many positions ("spud-down points") were occupied by the barge during shell deployment, water depth, and water current flow speed. There also were two methods of shell deployment (Fig. 2): bagged shell spread by crane, and shell pushed from the barge deck with pumped water. Although there was no attempt to characterize the effects of the two methods on shell base features, deployment from bags seemed to provide more control by the operator on where the shell was dropped. Based only on observations of the two processes, there probably were differences related to the resulting distribution patterns of shell on the bottom.

The initial post-construction shell cover relative to the entire restoration area (i.e., reef size) ranged from 20% to 60% based mainly on shell cover data from annual reports (Table 1). Thus, most projects initially met or nearly met what has been considered in New Hampshire and elsewhere a minimum standard of 25% shell cover. Percent shell cover is largely controlled by the amount of shell used in base construction. For most of the nine projects, a design criterion of 100 yd^3 of shell per acre of restoration area was followed. The 2015 video mapping indicated similar shell coverage at some sites compared to initial shell cover (Sites LR2 and LR3), but greatly reduced at most. And there was no apparent correlation between reef age and changes in shell cover.

Changes in reef shape (comparing initial construction to 2015 data) also varied widely, ranging from minimal changes in overall pattern (Sites LR2 and LR3 [Fig. 8]) to substantial differences (Sites OR2 [Fig. 7] and GB1 [Fig. 11]). As might be expected, those reefs that showed the most change in size (% shell cover) also showed the most change in shape (Table 1).

Initial reef height among the nine sites ranged from 0.08 m to 0.3 m, but no data were available from most reefs (Table 1). It should be noted that the methods used for estimating reef height also varied widely and for most reefs should be considered a rough approximation because it was based mainly on video observations and not direct measurements. However, direct inspection of the condition of clam shell in the tong samples allowed confirmation of at least the relative amount of clam shell burial that had occurred because when buried in the soft mud found at most sites the shell became blackened in color.

Overall, and based on video observations and inspection of the tong samples, the changes in size, shape and height when comparing initial data with 2015 appeared to be mainly a result of loss of shell by burial (sedimentation) or subsidence, and possibly erosion and transport of shell out of the restoration area. These observations are discussed below in more detail.

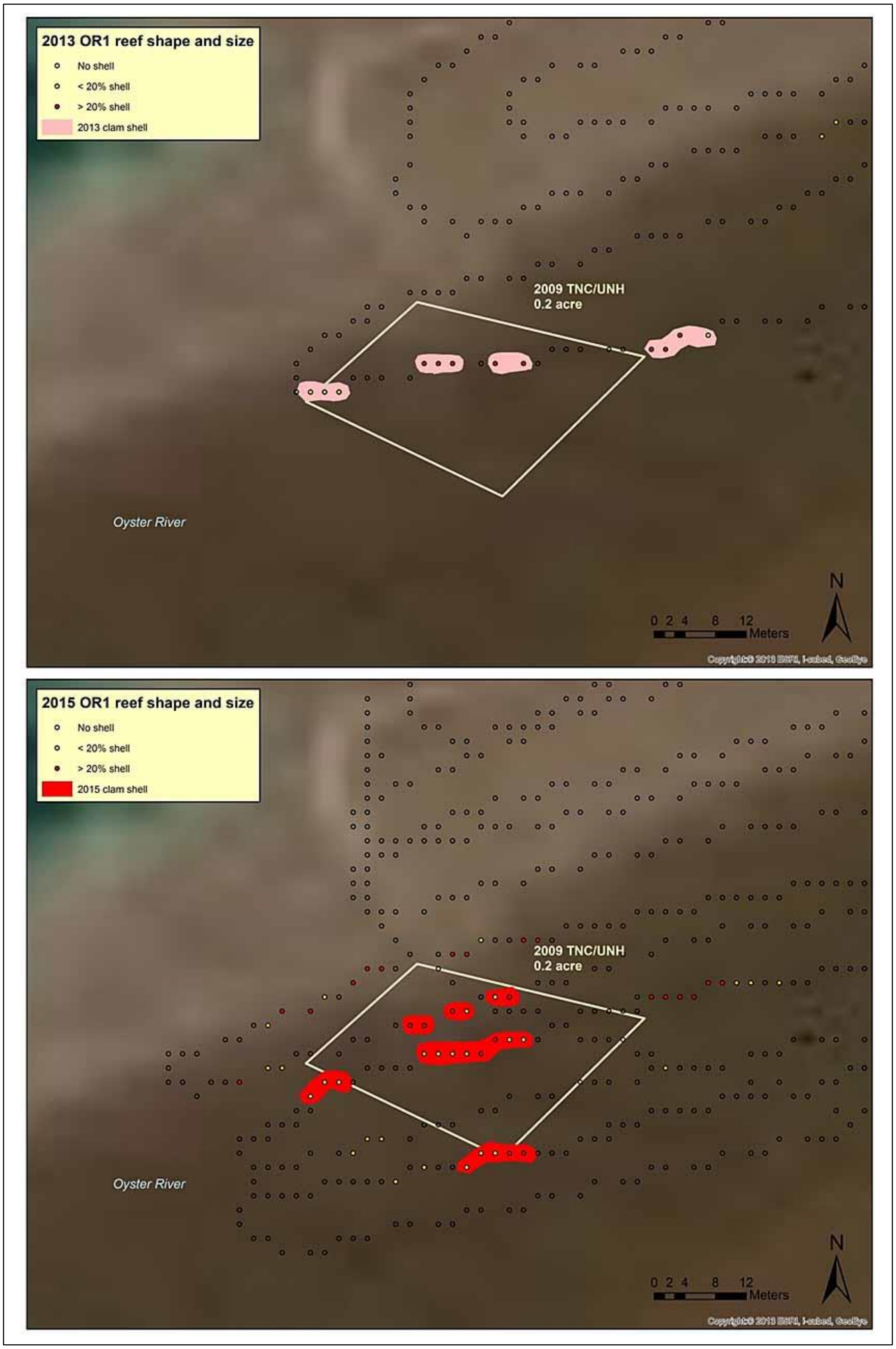

Fig. 6. Site OR1 towed underwater video based map of clam shell cover in 2013 (4 years post-construction; no earlier imagery was available) and 2015. Each small circle represents a video sampling point where position was recorded and imagery at that point was classified into the three categories shown in the inset.

Fig. 7. Site OR2 towed underwater video based map of clam shell cover in 2013 (3 years post-construction) and 2015.

Fig. 8. Sites LR1, LR2 and LR3 towed underwater video base map of clam shell cover in 2013 and 2015.

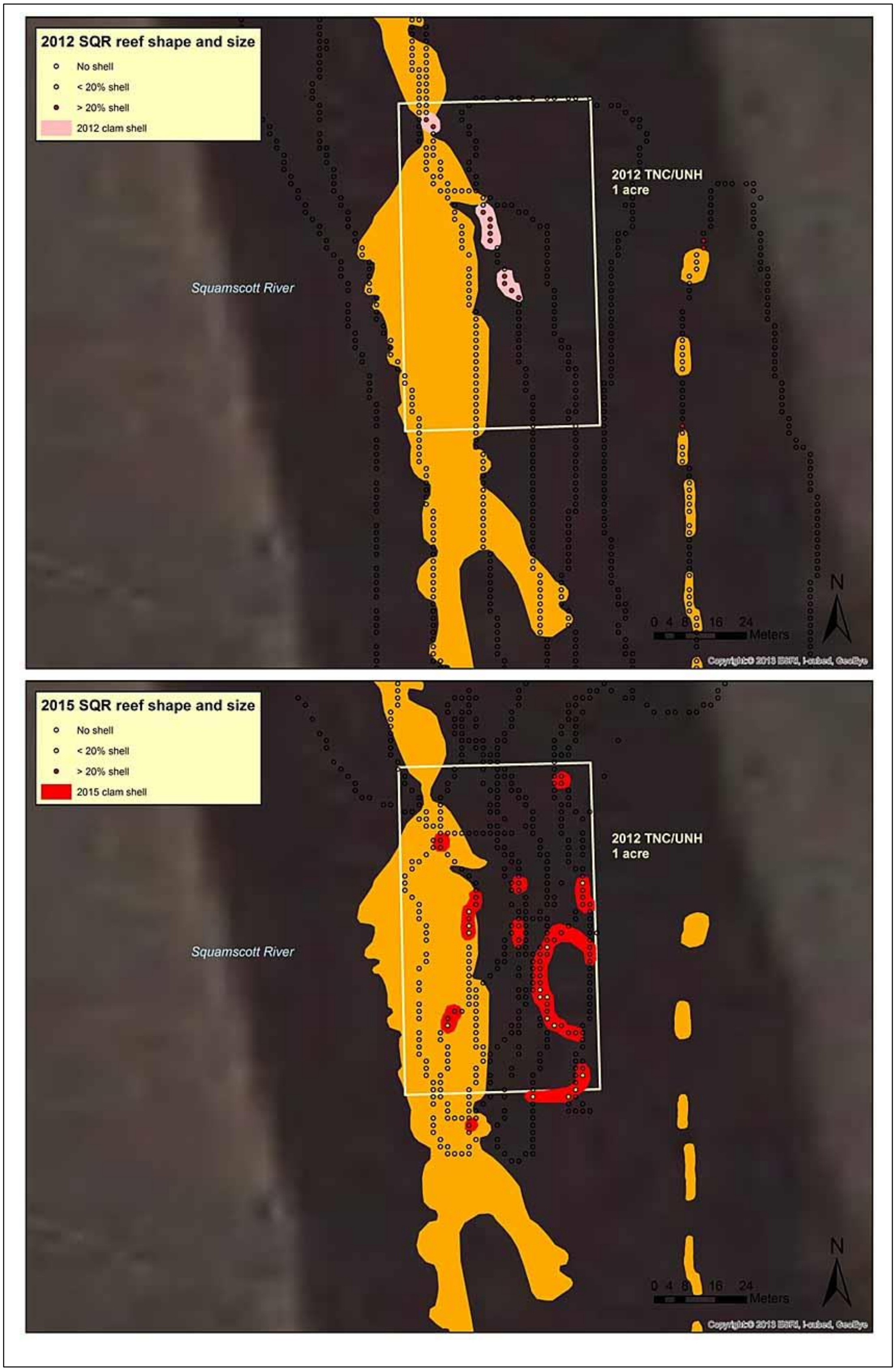

Fig. 9. Site SQ towed underwater video based map of clam shell cover in 2012 and 2015.

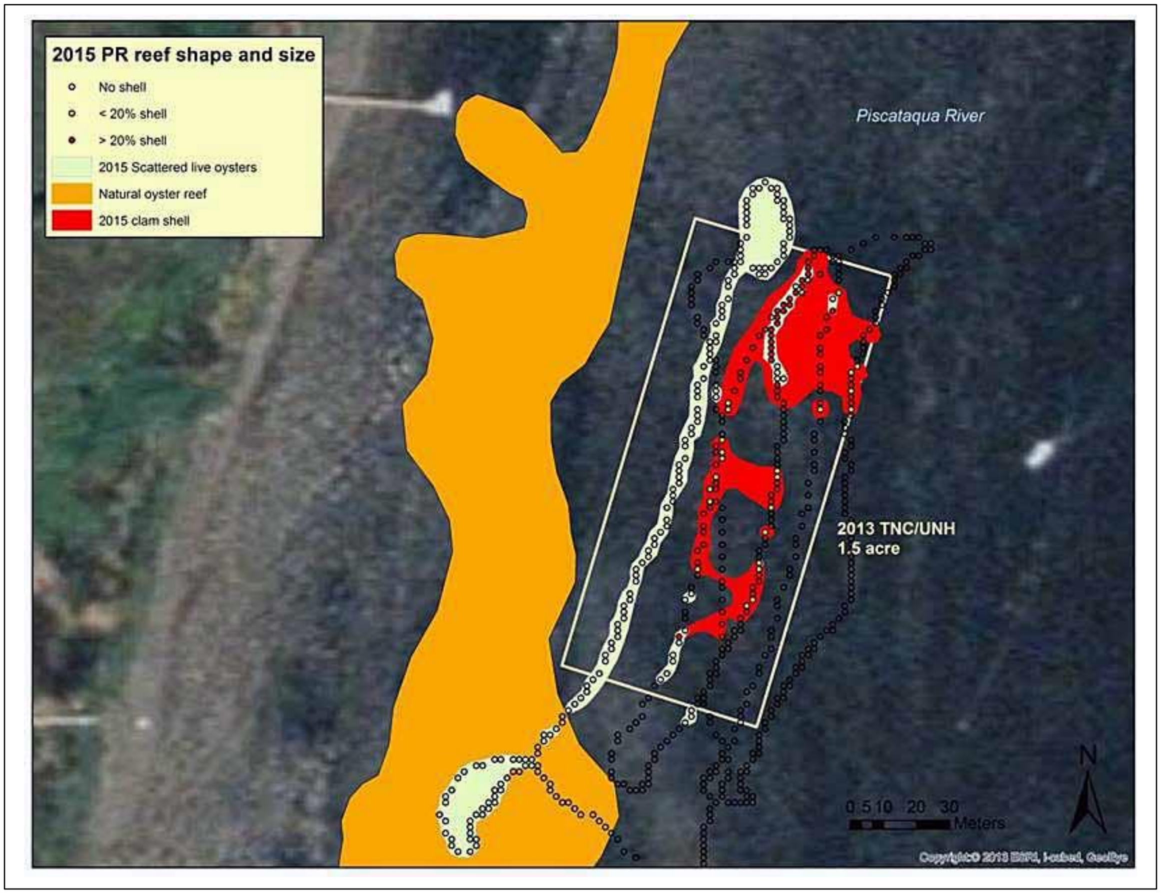

Fig. 10. Site PR towed underwater video based map of clam shell cover in 2015 (no earlier imagery available).

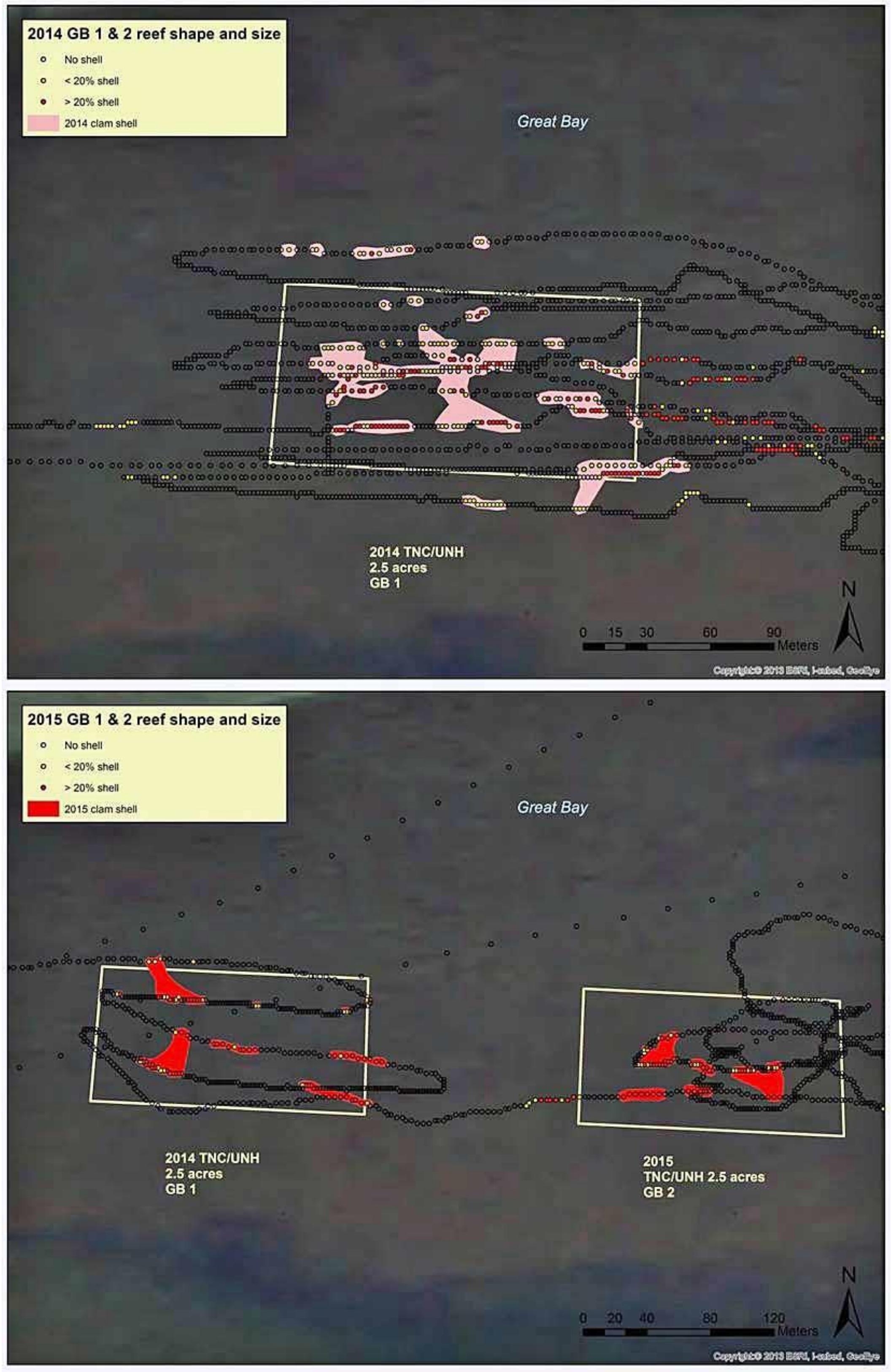

Fig. 11. Sites GB1 and GB2 towed underwater video based map of clam shell cover in 2014 and 2015 (note that GB2 was constructed in 2015).

Oyster density

Initial post-construction density of live oysters on the nine restoration sites varied widely, ranging from none present at Site GB2 (due to high mortality of "seeded" spat-on-shell and no initial natural recruitment) to relatively high densities at sites SR (115/m^2) and LR3 (301/m^2)(Fig. 12). Although there are no formal design criteria for initial density, restoration projects in New Hampshire typically attempt to initially achieve a total oyster density of 50/m^2; this was exceeded at three sites (LR1, SR, and LR3) and nearly met at another (LR2). The data are not presented herein, but it should be noted that initial total oyster density (Fig. 12) included the remotely set spat-on-shell deployed onto the site and natural recruitment that had occurred the first year.

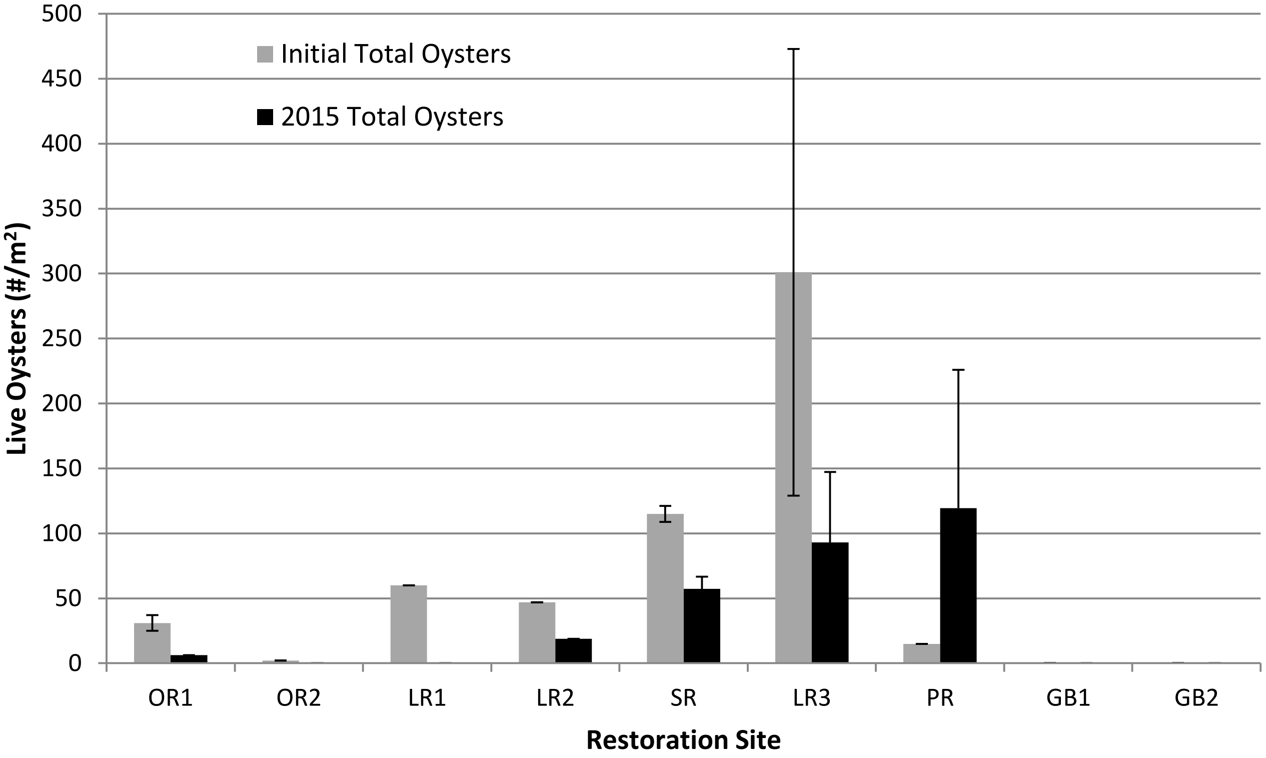

Fig. 12. Total live oyster density initially (see Table 1 for reef construction dates) and in 2015. Note: OR2 had an initial density of 2 oysters/m^2 and no data were available for GB1. Note that the sites are arranged chronologically from left (OR1 constructed in 2009) to right (GB2 constructed in 2015).

In addition to total live oyster density on each reef (Fig. 12), the 2015 sampling and analysis also provided data on the two major subpopulations potentially present: the originally deployed spat-on-shell (live oysters attached to oyster shell), and naturally recruited spat (live oysters on surf clam shell) for all years subsequent to reef construction (Fig. 13). These two subpopulations provide information on the overall suitability of the site for oyster growth and survival as well as long-term sustainability. Sites LR3 and PR had high natural recruitment in 2015, and Sites SR and PR showed good survival of older oysters. In sum, these data indicate that these three sites likely have good potential for longer-term sustainability (see more discussion below).

Oyster size-frequency

The distribution of size classes within the total live oyster population reflects the representation by different age classes, which provides additional information on potential sustainability of the reef. For the 2015 data, it was possible to separate total live oyster density at each site into different probable age classes represented in the overall population. Beginning with the 2015 annual recruitment (oysters <40 mm shell height and attached to surf clam shell), three sites showed successful recruitment (OR1, LR3, and PR; Fig. 13). However, only LR3 and PR had recruitment levels above the 50/m^2 typically considered to be "good" recruitment in New Hampshire. This suggests good potential for longer-term development of the constructed reefs at these two sites if natural recruitment regularly occurs.

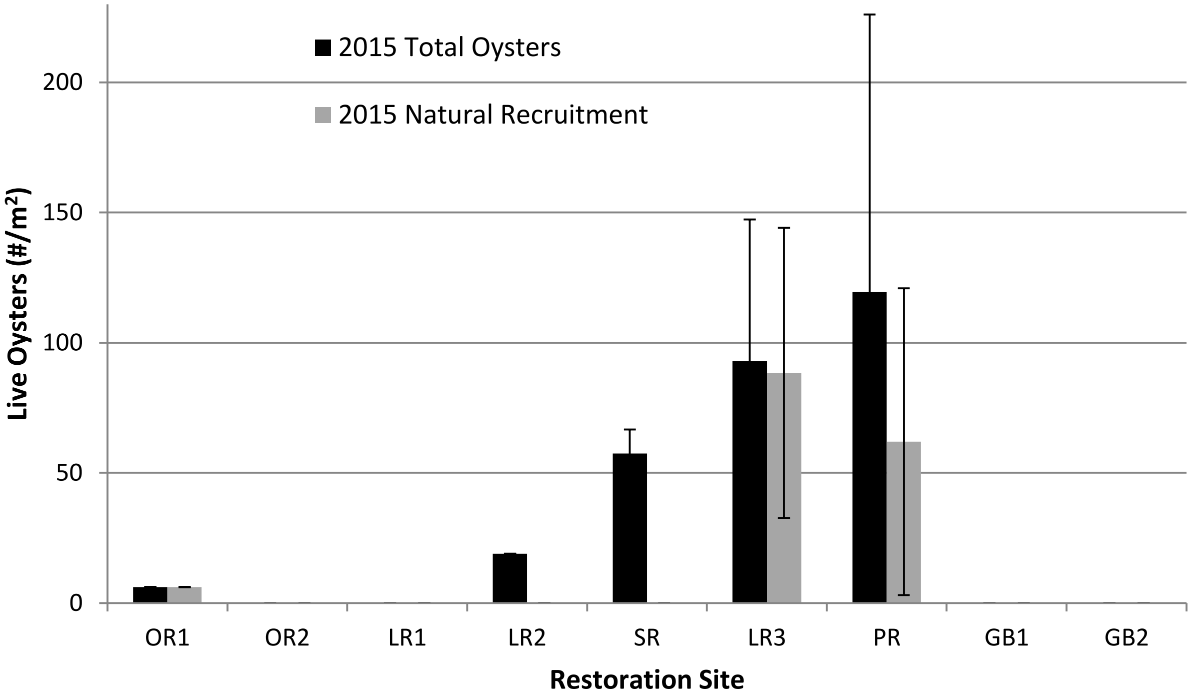

Fig. 13. Total live oyster density in 2015 on the nine restoration sites showing the component of the total oyster density (black bars) represented by 2015 natural recruitment (oysters <40 mm shell height; gray bars).

Oyster densities were sufficient at three of the nine sites to assess the 2015 data in more detail with respect to age distribution by constructing size-frequency charts (Fig. 14). The size-frequency data from Sites SR and LR3 indicate that they probably only consisted of two age classes, oysters set in 2014 and 2015; SR was constructed in 2012 and LR3 in 2013 (Table 1). Field inspections of Site LR3 in fall 2013 confirmed a good natural spat set onto the clam shell reef base (Fig. 15), but subsequent high mortality in 2014. Although these data indicate poor survival of the originally deployed spat-on-shell and naturally recruited oysters at both sites, it does indicate good potential for natural recruitment. The data from Site PR (constructed in 2013) indicate the presence of three year classes, thus there was some level of survival of the originally seeded spat-on-shell as well as successful natural recruitment in 2014 and 2015 (Figs. 14 and 16).

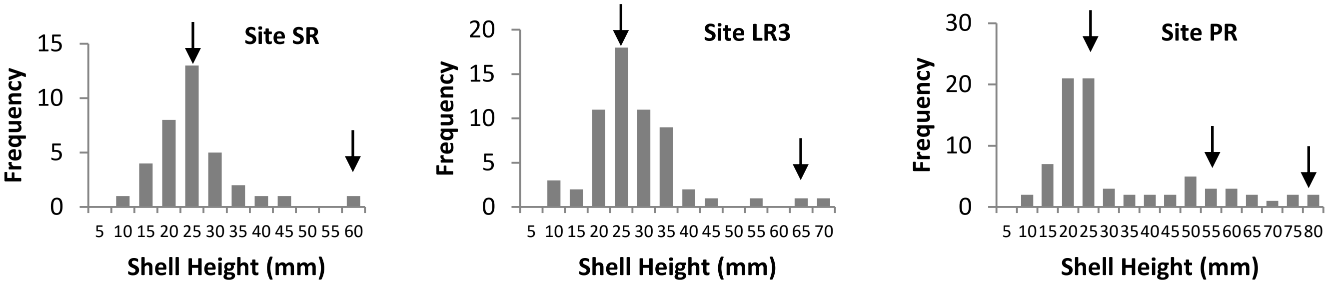

Fig. 14. Size-frequency distributions for 2015 data from three restoration sites. Arrows indicate mean size of probable age classes.

Fig. 15: Site LR3 in 2013. Left: portion of shell pile exposed on spring tide in late August showing initial natural recruitment (arrows indicate small spat). Right: underwater photo in September showing growth and vertical extension of spat set earlier in the summer (arrows).

Fig. 16: Surf clam shell from reef base at Site PR showing at least two year classes of oysters, October 2015.

Restoration success

As discussed above, the nine restoration sites varied widely in all four metrics used to assess restoration success. However, there were trends among the sites, particularly with respect to the underlying factors likely affecting success. Here we interpret the among-site metrics in the context of causal factors and the implications for design of future restoration projects.

All of the sites except PR were negatively affected by loss of clam shell used to construct the reef bases, probably as a result of burial (sedimentation) by silt and/or subsidence of shell into the soft sediments. This may be *the* major obstacle to oyster restoration in many areas of the Great Bay system. However, it does not preclude restoration projects in these areas because increasing height of the shell base during initial construction will result in clam shell remaining (for some period of time) elevated above the bottom and thus available for oyster larval settlement. In one case (Site LR2; Fig. 8) surf clam shell may have been eroded by tidal currents and transported off the site after initial construction, indicating that exposure to storm currents and waves should also be considered. The overall implication for future projects is that design features of the shell base should be determined on a site-by-site basis, and reef height should be at least 0.3 m across as much of the restoration area as practical.

A second factor that probably strongly affected restoration success among the study sites is location. A previous study in New Hampshire based on field sampling in 2013 of twelve restoration projects with initial construction as early as 2000 and eight natural reefs resulted in an important finding relevant to the present study: natural recruitment onto the constructed/restored reefs was strongly negatively correlated with distance from the nearest natural reef (Eckert 2016). Eckert's subsequent field studies over two years at three different natural reefs indicated that most annual recruitment to experimental shell bags occurred within 0.5 km of the reef. Data from the present study were not sufficient to provide a rigorous quantitative test of Eckert's findings due to the likely effects of burial of the shell base so that no suitable substrate was available for natural recruitment, but they nonetheless provide additional evidence supporting the notion that restoration success is affected by distance to a natural reef. The three restoration sites (SR, LR3, and PR) that had high levels of natural recruitment in 2015 and had multiple year classes of live oysters were <1 km from a natural reef. Three of the remaining six sites also were <1 km from a healthy natural reef, but all had substantial losses of clam shell base which may have affected natural recruitment potential. The remaining three sites did not have good natural recruitment and all were >1 km from a healthy natural reef. In sum, these data strongly indicate that future restoration projects should be located as close as practical to a healthy natural reef.

A final factor that may have affected success of some of the projects, but could not be adequately assessed in the present study, was the effect of addition of remotely set oyster spat-on-shell to the constructed shell base. The rationale for putting spat-on-shell onto the reef base is that it insures that live oysters are initially present on the site, as well as potentially enhancing natural recruitment. A short-term (a few years) positive effect seems quite likely, but the long-term (after the initially "seeded" oysters have died) has not been tested. All nine of the projects assessed in the present study involved this treatment, so no comparison sites were available. At least some level of testing of the overall efficacy of seeding with spat-on-shell should be considered in future projects.

DISCUSSION

Since initiation of oyster restoration projects in New Hampshire in 2000, the restoration protocol has been changing as we learned what worked and what did not on a short term site-by-site basis (Grizzle et al. 2003, 2006, 2009; Konisky et al. 2011, 2012, 2014). The present study and a similar one by Eckert (2016) discussed above are the only attempts at comprehensive multi-site and long term assessments of oyster restoration success in the state. These longer term studies have yielded important information relevant to moving forward. Here we discuss each of the three major factors affecting restoration success identified and briefly described above in the context of previous research in New Hampshire and elsewhere.

Sedimentation

Langan (1997, 2000) identified burial by fine sediments (sedimentation) as one of the major causes of recent dramatic declines in New Hampshire's oyster populations, and it has been a persistent problem at least since the early 1900s (Jackson 1944; Ayer et al. 1970). Great Bay is not unique in this respect. One focus of eastern oyster restoration research in general has been on determining how reef height is related to reef development and ecological functioning (Lenihan 1999; Lipcius and Burke 2006; Powers et al. 2009; Schulte et al. 2009; Scyphers et al. 2011; Harding et al. 2012; Breitburg et al. 2015). In general, this research has found that reef height is positively related to oyster health and condition, and the potential for restoration success. Thus, one way to at least potentially ameliorate the impacts of excessive sedimentation and increase the probability of restoration success is to construct reefs with sufficient height.

In New Hampshire we have constructed reef shell bases of heights ranging from a few centimeters to ~0.3 m (Grizzle et al. 2006, 2009, 2014; Konisky 2011, 2012, 2014). Although we have not assessed the long-term persistence of reefs of different heights in a rigorous comparative manner, the general trend has been that reefs in deeper mud-bottom areas are more prone to sedimentation than those in shallower waters with coarser sediments. For example, shell bases of only a few centimeters height have persisted at some sites for >5 years (e.g., recent personal observations of sites "Little Bay" at Fox Point and "Oyster River" described in Grizzle et al. 2014), compared to others that have shown substantial sedimentation within 2 years after construction (e.g., Sites LR1 and GB1 herein). Based on our current understanding (including reef height criteria used in other areas), we suggest that initial reef height should be determined on a site-by-site basis and based mainly on tidal flow conditions and bottom type, but should fall within the range of 0.1 to 0.5 m.

Reef shape should also be considered when designing reef height. We previously tested how reefs of different sizes and configurations compared with respect to short-term development and ecological functioning (Grizzle et al. 2006, 2009). In brief, these experiments indicated that there were no differences in oyster metrics (including natural recruitment) comparing "mini-reefs" varying from 3 m to 6 m in diameter (and 0.2 m height). However, the constructed mini-reefs overall had higher densities of oysters and associated resident fish and invertebrates than the adjacent natural reef. From the perspective of full-scale restoration projects, these findings suggest that a reef base consisting of many multiple mounds of shell might be more ecologically important that a more uniformly distributed shell base.

A final topic to consider here is how reef height changes with time. Post-construction and long-term development of reef height is strongly affected by growth of the spat-on-shell initially deployed to the reef and new oysters that recruit to the reef surface. Our recent studies of oyster growth rates in New Hampshire (Grizzle et al. 2016), and our general observations of growth and development of constructed oyster reefs, indicate that formation of significant vertical structure requires 5 or more years of reef development. Thus, studies of at least that duration are needed to adequately characterize development and sustainability of constructed reefs.

Site location

Site location has long been a major topic of research by oyster restoration practitioners because it determines the variety of uncontrollable environmental factors that strongly affect restoration success (Mann and Evans 2004). For example, reef base material, shape, size, and height can all be optimal, but if the constructed reef is located in an area where water quality conditions are outside the range of the oyster's tolerance, then the constructed reef will fail. Although long-term experiments have not been conducted in New Hampshire, data from the UNH/TNC Oyster Conservationist (OC) program have consistently demonstrated that oysters can do well in the short-term throughout the Great Bay/Piscataqua River estuarine system (Konisky et al. 2014; Grizzle et al. 2015). The OC program has also yielded data indicating that the highest growth rates usually occur at riverine sites generally coinciding with the historical locations of large natural oyster reefs (Odell et al. 2006). The implication for future oyster restoration projects in New Hampshire is that site selection and reef construction design criteria should focus on those factors such as sedimentation that have been identified as site-specific controls on oyster survival.

Recent research in New Hampshire has indicated that site selection criteria should include oyster recruitment potential because it can strongly vary on spatial scales of <1 km, as discussed above. Thus, natural recruitment potential should be considered in selecting restoration sites. This is not at all surprising as a general recommendation, but the spatial scales involved are. It has long been known that site selection is critical for collecting adequate natural spat (Brooks 1891, p. 104). However, the fact that oyster larvae can be dispersed widely during their ~2-week larval period has also been well demonstrated. Unfortunately, we are aware of very little research (other than Eckert 2016) that has attempted to characterize the spatial scales involved in oyster larval dispersal and settlement in the context of site selection for oyster restoration projects.

Mann and Evans (2004) discussed some of the unknowns with respect to site selection in the restoration process, and argued that improvements in our knowledge and modeling of larval dispersal and settlement are critical to long-term oyster restoration success. Several field studies have documented a positive relationship between adult oyster densities and recruitment to restoration sites (Southworth and Mann 1998; Schulte et al. 2009; Lipcius et al. 2015), but we are aware of only one study other than Eckert (2016) providing data on the spatial dimensions involved. Harding et al. (2012) reported high recruitment levels on constructed reefs within 1 to 2 km of productive natural reefs. In sum, available research confirms the notion that site location is important to good natural recruitment, but does not comprehensively quantify the relationships involved. We suggest that a reasonable conclusion with respect to selecting future oyster restoration sites in New Hampshire is that they should be as close as practical (<0.5 km where possible) to a healthy natural oyster reef consisting of multiple year classes.

Addition of spat-on-shell

Few studies have been published on how the common practice of "seeding" a constructed reef base with remotely set spat-on-shell affects long-term success. Geraldi et al. (2013) is the only explicit test we are aware of, and the title of their paper reflects their overall finding: "Addition of juvenile oysters fails to enhance oyster reef development in Pamlico Sound." Their study reefs, however, had substantial natural recruitment that apparently "…overwhelmed any benefit of seeding." Thus, direct applications of their findings to areas such as New Hampshire that are recruitment limited probably are not warranted. Nonetheless, any advantages of spat seeding, particularly for long-term restoration success, remain to be demonstrated. We suggest that for future restoration projects in New Hampshire, spat seeding should be conducted where possible. And such projects should be designed to provide tests of the efficacy of spat seeding compared to shell base construction only.

A final topic relevant to spat seeding is oyster disease. Probably the most damaging effect ecologically of disease has been a dramatic decrease in individual oyster longevity, in some areas from a maximum of perhaps >20 years to <5 years (Mann et al. 2009; Southworth et al. 2010). There have been no explicit recent studies in New Hampshire on oyster longevity, but unpublished NH Fish and Game Department data show a steady decrease over the past two decades in the maximum oyster size observed on the natural reefs from 200 mm in 1993 to <120 mm in 2013. Large, which equates in most cases to older, wild oysters are not known to occur in New Hampshire today.

Much of the early research in New Hampshire involved testing different strains of oyster broodstocks based on the notion that the major need was to introduce some level of disease-resistance into the wild stocks by constructing reefs using spat-on-shell produced from larvae from disease-resistant broodstocks. By the mid-2000s we had conducted five experiments involving larvae from four different broodstocks and three hatcheries: Cooperative Regional Oyster Selective Breeding (CROSBreed) broodstock from a mid-Atlantic consortium; native New York broodstock from Frank Flower & Sons Hatchery; native New England broodstock from Damaristcotta River, Maine, from Muscongus Bay Aquaculture; and native Great Bay, New Hampshire broodstock spawned at Muscongus Bay Aquaculture (Grizzle et al. 2006). Larvae and spat from most broodstock sources demonstrated characteristics showing potential for use in restoration in New Hampshire. However, the New England oysters (Maine and New Hampshire) performed best overall when considering remote setting success, spat survival, and early reef performance (up to 3 years post-construction). In particular, the most variable short-term outcome among the larval sources was in remote setting success, which varied from <10% to >50%. It cannot unequivocally be stated that larval source was the reason for variations in remote setting success because each year involved a different combination of salinity, temperature and other conditions that are known to affect setting success. In any case, it was decided in the mid-2000s to only use larvae from New England broodstock and provided by Muscongus Bay Aquaculture because of consistently high remote setting success as well as good growth and survival of the resulting juvenile oysters. All nine of the projects assessed in the present study used larvae from either Damariscotta River (Maine) or Rutgers NEH broodstock.

CONCLUSIONS

The overall aim of the present study was to assess restoration success at the nine study sites from the perspective of how the restoration protocol might be improved. Sufficient data were obtained to make several recommendations for the design and assessment of future oyster restoration projects as well as suggestions for where additional studies are needed. Thus, we offer the following three-tiered set of conclusions.

Recommended changes in the New Hampshire oyster restoration protocol

- Construct the reef base with enough shell to achieve vertical height of at least 0.3 m over as much of the restoration site as practical
- Arrange the reef base material (mollusk shell in most cases) in a pattern consisting of many small piles of shell so that the amount of reef “edge” is maximized
- Focus the site selection process on areas that are in close proximity (< or = 0.5 km) to a healthy natural reef (i.e., population of potentially reproducing adult oysters)

Recommended changes in reef monitoring protocol

- Develop better method for measuring reef height and overall reef rugosity
- Develop method for assigning uncertainty levels to reef shape based on video mapping
- Implement a comprehensive long-term monitoring plan for oyster restoration projects

Topics for future research

- Refine our understanding of the relationship between constructed reefs and natural reefs that acts as potential larval sources
- Identify other variables that potentially affect restoration success
- Assess the efficacy of spat seeding compared to shell base construction only
- Determine the potential effects of the rapidly expanding oyster farming industry on natural oyster reefs
- Characterize the major ecosystem services oyster reefs (restored and natural) provide in the context of broader environmental management

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