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Title: **Restoration of native oysters in a highly invaded estuary**

Running head: Oyster restoration in an invaded estuary

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Abstract

Restoration of native species may be hampered by competition with non-native species. The outcomes of competition are often context-dependent, with one species dominating under some conditions but not others. Where non-natives differ from natives in their ability to tolerate stressful environmental conditions, restoration practitioners may be able to manipulate conditions or strategically locate restoration projects along naturally occurring stress gradients to favor native species. We tested the responses of native oysters and a suite of non-native sessile invertebrate species (mostly soft-bodied organisms) to varying tidal elevations, shoreline types, and distances from source populations. Cover of non-natives was lower at higher tidal elevation and far from adult populations. Native oyster recruitment was also reduced at the high tidal elevation. At this elevation oyster *dominance* was increased, but *abundance* was reduced. To test an adaptive management approach, we moved substrates from the low to high tidal elevations. Cover of non-natives had decreased dramatically one year later, while oyster metrics were unaffected or improved compared to those on substrates remaining at the low elevation. Our study indicates that reduction of non-native species abundance ,often an explicit goal of restoration, may be achieved by strategic location of restoration units, although abundance of target species may also be reduced, at least over the short term. However, restoration practitioners may be able to increase abundance of target species and reduce non-natives by applying stress differentially over time, with benign conditions during sensitive early life stages, and increasing stress after target organisms become more tolerant.

Key words: invasive species, *Ostrea lurida,* restoration design, stress gradient, tidal elevation

1. Introduction

Restoration frequently occurs in habitats that have been dramatically changed by human activities, which may result in conditions that no longer favor native species (Hobbs and Huenneke 1992, Miller and Hobbs 2007). One such change is the introduction of non-native species. Non-native species can pose direct threats to native species as competitors or predators, or by acting as ecosystem engineers, altering their surroundings in ways that negatively impact natives (Carlton 1999, Crooks 2002, Mack et al. 2000,Vitousek et al. 1996). The removal of non-native species is often not tractable at the landscape level, but eradication or control can sometimes be successful at smaller scales, allowing restoration of natives to proceed. Another potential option for restoration practitioners is to strategically select environmental conditions that reduce the impacts of non-native species on species targeted for restoration (Daehler 2003).

The importance of ecological interactions such as competition to species abundance and distribution is often context-dependent, such that some species or communities dominate in a certain set of conditions, but not in others (e.g., Bertness and Callaway 1994, He et al. 2013, Hutchinson 1961, Menge and Sutherland 1987). Restoration practitioners can take advantage of this by identifying and fostering conditions that shift dynamics to favor natives over non-natives (Daehler 2003). Sometimes this consists of restoring historic conditions under which native species thrive, such as through nitrogen reduction for native grasses and other plants (Blumenthal et al. 2003, Dalrymple et al. 2003, Holzel and Otte 2003, Perry et al. 2004, Prober et al. 2005), changing topography to increase flooding for meadow and riparian vegetation (Dalrymple et al. 2003, Holzel and Otte 2003, Nagler et al. 2005), or restoring more natural hydrology regimes for amphibians and a suite of marsh plants (Fuller et al. 2011, Rochlin et al. 2012).

The outcome of biotic interactions can also shift along an environmental stress gradient when native and non-native species differ in their tolerance to stress (Alpert et al. 2000, Daehler 2003, MacDougall et al. 2006). For example, some native plants outcompete non-natives under grazing or burning regimes or in shady understories; thus the creation of these stressful conditions can be a successful restoration approach for invaded grasslands (Buisson et al. 2006, Prober et al. 2005) and mangrove habitats (Chen et al. 2013). When large-scale manipulation of conditions is not an option, restoration practitioners might still be able take advantage of differences in stress tolerances, working within naturally occurring stress gradients and selectively restoring at sites where conditions are more stressful to non-native species than to target native species.

Restoration projects that use the methods described above frequently couple environmental manipulations with seeding or planting in cases where target species are also propagule-limited relative to non-natives (Frances et al. 2010, Holzel and Otte 2003). The seed bank or propagule pressure of non-native species at any given site also may need to be taken into account to avoid swamping effects, even when environmental conditions favor natives (Daehler 2003, Morghan and Seastedt 1999, Wilson and Gerry 1995).

To date, much of the restoration work examining the effects of environmental conditions and propagule limitation as they impact native species dominance has occurred in terrestrial plant systems. Here we apply some of these ideas in a marine system, testing several hypotheses about sites and conditions that would favor native oysters over a suite of non-native sessile invertebrates as part of a small-scale oyster restoration project in a Central California estuary.

The Olympia oyster (*Ostrea lurida),* native to the west coast of North America, is in decline from historic levels throughout its range from British Columbia to Baja California (zu Ermgassen et al. 2012). It is now the focus of restoration efforts in bays and estuaries along the West Coast (Dinnel et al. 2009, Pritchard et al. 2015). Olympia oyster restoration projects typically involve the provision of hard substrate in low intertidal and shallow subtidal zones, which is necessary for oyster settlement, but limited in the soft-sediment estuaries typical of the West Coast. However, many non-native species now found in these estuaries also require hard substrate and may compete with native oysters for settlement space and/or overgrow oysters after settlement (Deck 2011, Trimble et al. 2009). The issue of competition aside, concerns about the unintentional spread of non-native species through the additions of hard substrate have been raised during the permitting process for native-oyster restoration projects in some locations (Cohen and Zabin 2009, C.J.Z. pers. obs.). Thus the dual challenge for restoration in these invaded systems is to enhance native species while preventing increased abundance or distribution of non-natives.

The goal of our study at Elkhorn Slough (Central California, USA, Fig. 1) to was examine whether under certain environmental conditions, native oysters could be enhanced relative to a suite of non-native species that are potential space competitors. In particular, we were interested in examining whether oysters were better at facing challenging environmental conditions than the sessile non-native invertebrates with which they co-occur, and if so, whether this could be used in the design of oyster restoration projects. Oysters are shelled bivalves that are adapted to the stressful conditions that are typical of the intertidal zone, such as periods of exposure to air and rapid temperature changes, and of estuarine systems, such as periodic fluctuations in salinity and sedimentation, because of their ability to close their shells (Berger and Kharazova 1997). In contrast, most of the non-native species on hard substrates at Elkhorn Slough are soft-bodied organisms such as sponges, tunicates and hydroids (Wasson et al. 2001, 2005), which are more vulnerable to desiccation, sedimentation and salinity stress. Non-native oysters are not currently present at Elkhorn Slough (Wasson et al. 2001).

Based on intertidal surveys, we hypothesized that while native oysters and a suite of non-native species broadly overlap in their distribution, there are some conditions under which oysters do better than the non-natives. These conditions, while perhaps not optimal, may be better tolerated by oysters than by the mostly soft-bodied non-natives, and thus could be incorporated into restoration design to promote dominance by oysters on our deployed substrates. For example at Elkhorn Slough, oysters extend higher into the intertidal zone than the non-native tunicate and sponge species (Fig. 2), which in this system are the taxa most likely to overgrow or prevent the settlement of native oysters. Research on eastern oysters *(Crassostrea virginica)* and Suminoe oysters *(Crassostrea ariakensis)* on the East Coast of the US found that those oyster species were more tolerant to aerial exposure than many of the other sessile invertebrates with which they co-occur such that that cover of potential competitors was reduced at higher tidal elevations (e.g., Bahr and Lanier 1981, Bishop and Peterson 2006, Fodrie et al. 2014). Indeed, it is common practice among commercial oyster growers to periodically expose oyster racks to air to remove soft-bodied fouling species. However, Olympia oyster settlement, growth and/or survival may be compromised at higher tidal elevations (Deck 2011, Kimbro et al. 2009, Parker et al. 2015, Trimble et al. 2009), possibly as a result of increased heat or desiccation stress and decreased feeding time.

At Elkhorn Slough, most non-natives also appear to do poorly compared to oysters in muddy locations, where hard surfaces are at least periodically buried in unconsolidated fine sediments (Fig. 2). But oysters certainly can also be challenged by muddy conditions, requiring increasingly larger substrates for attachment to prevent burial in locations with deeper mud (Wasson 2010) and may settle preferentially in shell (vs. mud) habitats (Trimble et al. 2009). Finally, some of the slough's non-native species, and particularly most of the non-native tunicate species, have relatively short larval durations (e.g. 1-10 hrs for *Molgula manhattensis,* Berrill 1931; typically within 2 hrs, max <1 d for *Botrylloides violaceus,* Berrill 1937, Epelbaum et al. 2009; <12 hrs for *Styela clava*, Davis and Davis 2007) and thus limited dispersal, so that natural recruitment to new substrates is limited by distance from established populations. In contrast, *O. lurida* has a longer larval duration of up to four weeks and can potentially disperse more broadly (Breese 1953). Larvae have been shown to disperse distances up to 75 km (Carson 2010). Still, oyster recruitment limitation might be a risk if oysters settle preferentially on conspecifics, as has been suggested by some (White et al. 2009), which would make restoration sites without adult oysters less favorable.

As part of a two-year restoration project, we tested the effects of tidal elevation, shoreline type (cobble vs. mud), and distance from established populations of oysters and other sessile species, evaluating various metrics of restoration success. Specifically, we first tested the hypotheses that oysters would not be affected but non-natives would be less abundant on substrates 1) higher in the intertidal zone, 2) in muddier locations, and 3) farther from adult populations of oysters and non-native species, which co-occur at sites with hard substrates in our study area. Next, based on our findings in the first year, we tested an adaptive management approach, moving restoration substrates to determine whether we could decrease non-native species without harming native oysters.

2. Materials and Methods

2.1 Restoration context and goals

Elkhorn Slough is a 1200-ha estuary, extending about 10 km inland from the town of Moss Landing in the Monterey Bay region (Fig. 1). The estuary receives only limited freshwater inputs, and water salinity in undiked regions is usually close to marine levels. Tides are semi-diurnal, with a maximum tidal range of ~2.5 m. The region has a Mediterranean climate, with all significant rainfall occurring between October and May. More background on the estuary can be found in Caffrey et al. (2002).

Olympia oysters have declined at Elkhorn Slough over the past century; for instance in the 1920s oystermen from San Francisco Bay collected 200 bushels (~80,000 individuals) in the lower estuary in a few days (Barrett 1963), while today an order of magnitude fewer individuals are present in the entire estuary (Wasson 2010). In many years, recruitment in the estuary is zero or negligible (Wasson et al. 2015), so this small population seems in danger of local extinction, as occurred at the nearest estuary to the south, Morro Bay (Polson and Zacherl 2009). The Elkhorn Slough National Estuarine Research Reserve thus embarked on a native oyster restoration project with the goal of doubling the oyster population on the Reserve over the next decade. Most of the Reserve is dominated by soft sediment, and oysters are limited in abundance by availability of substrates with sufficient vertical relief to avoid burial (Wasson 2010). The restoration approach taken was thus to supply hard substrate at appropriate elevations for oyster recruitment.

While native oysters have declined, non-native species have increased in both richness and abundance. Some 58 species are present at Elkhorn Slough and many are highly abundant (Wasson et al. 2001, 2005). Most of these organisms are sessile invertebrate animals, including sponges, tunicates, hydroids and bryozoans, which like native oysters, have free-swimming larval stages but need hard substrates on which to permanently attach and undergo metamorphosis to their adult forms.

2.2 Restoration methods

Restoration substrates were constructed from the shells of the gaper clam (*Tresus nuttallii*), which is an abundant, large native clam in the Slough. A resident population of sea otters (*Enhydra lutra*) near the estuary mouth preys on these clams, excavating them from the mud. These discarded shells are abundant along the shore at low tide, where teams of Reserve volunteers and staff collected shells ranging in size between 10 and 12 cm. Holes were drilled in the middle of each shell, and shells were strung onto “necklaces” of 15 shells along a 1-meter length of 0.5-cm diameter nylon line, again by volunteer teams (Fig. 3). The line was knotted between each shell to keep the shells separated, maximizing surface area for colonization by oysters. The necklaces were tied at each end to 1-cm diameter rebar poles, which were sunk into the mud such that about 100 cm remained above the sediment, suspending the necklace about 10 cm above the bottom at its lowest center point (Fig. 3). Previous work indicated that the shell necklaces were durable for at least five years and provided suitable oyster substrate (K.W., unpublished data). This method was developed because it primarily uses a substrate natural to the estuary (clam shells) and because the necklaces are mobile and modular, allowing their position to be adjusted adaptively if needed. While the necklaces are small, they are sufficient for achieving the restoration goal of doubling the size of the Reserve’s population, which involves providing substrate to support about 5000 oysters; this is a different scale of restoration than is conducted for other much more abundant oyster species elsewhere.

2.3 Experimental treatments

2.3.1 Overview

In July 2012, we deployed six necklaces at each of 10 sites (Table 1 and Fig. 1), for a total of 60 necklaces. Necklaces were first monitored in December 2012. Eight of the sites are fully tidal (maximum annual tidal range about 2.5 m) and two are located in a tidally muted lagoon (maximum tidal range about 0.5 m). The sites are all located within 1 km of each other in the Parsons wetland complex of the Elkhorn Slough National Estuarine Research Reserve. Eight of the sites experience strong tidal exchange and similar depths, are likely to have similar water quality conditions. We used these for experimental tests, and excluded the two tidally muted sites, as we anticipated conditions there would be quite different. Below and in Table 2 we detail the multiple comparisons made among different types of conditions represented by relevant sets of sites.

2.3.2 Tidal elevation

We determined tidal elevations at each site by placing flags on the mudflat at the waterline at the time the tide was predicted to be at MLLW, and did this repeatedly on multiple days. We also confirmed from a nearby (within 500 m of all stations) water level monitoring site that predicted and observed water levels were similar on these days. At each site, three necklaces were deployed so that the lowest shells on them hung at about 30 cm above Mean Lower Low Water (MLLW). Another set of three necklaces was deployed so that the lowest shells were at 30 cm below MLLW.

2.3.3 Shoreline type

Two of our fully tidal sites had artificial cobble and riprap deployed to protect berms (Sites 2, 7). We compared the necklaces at these cobble sites to those at two adjacent sites (within ~50 m) without cobble (Sites 1, 8; Tables 1, 2; Fig. 1). In December 2012, we also noted the depth of accumulated sediment on the shells of the necklaces, estimating in increments of 2 mm.

2.3.4 Proximity to established adult populations

To examine the effects of proximity to source populations, we compared sites immediately adjacent to established populations of oysters and non-native species (which co-occurred on all our cobble sites, but nowhere else) to sites far from these populations (~300 m). To remove the potentially confounding effect of shoreline type we only considered muddy sites in this comparison (near sites: 1, 8; far sites: 3, 5, 6; Tables 1, 2; Fig. 1).

2.3.5 Adaptive management: moving substrates to higher elevation

Based on the results of the above experiments, we also examined the effect of moving necklaces from lower to higher elevations after oysters had recruited. In early June 2013, at a subset of sites (Sites 1, 2, 7, 8), we moved a single necklace initially deployed in July 2012 from the lower elevation to the upper elevation. We began the experiment in summer, when the amount of cover of non-native species may be most critical, as it is just before the onset of the oyster recruitment season and the start of the season in which adult oysters are expected to undergo the greatest growth. At the start of this experiment and one year later (late May 2014), we assessed oysters and non-native species on the middle five shells of the experimentally moved necklaces and on control necklaces that were not moved from the low elevation. These middle shells were closest to the target tidal elevations, and limiting our measurements to these decreased monitoring time. Starting measurements were subtracted from ending measurements for each necklace to calculate change over the year. No oysters recruited in the estuary in 2013, so all oysters assessed were ones that had settled in 2012.

2.3.6 Monitoring of response variables

In December 2012, we assessed multiple indicators of restoration success as response variables for our experiments (Table 2). For most experimental factors, we estimated oyster recruitment and survival and percent cover of oysters and of non-native species. For our analysis of the effects of tidal elevation we assessed an additional parameter we thought likely to be affected, growth. We expected that distance from adult populations would affect recruitment and thus cover, but not survival, so we did not test the latter.

Recruitment and survival were estimated from counts of live and dead oysters on the necklaces. These counts are challenging due to the uneven surfaces of the clam shells and the sometimes heavy cover by other species, so should be considered estimates, not exact counts. We are able to detect oysters >5 mm in size with these quick counts. At our first assessment after 5 months, live oysters were generally 20-30 mm in maximum length; our anecdotal observations suggest they were all from a single recruitment pulse in late July. Recruitment tiles deployed at similar tidal elevations at Elkhorn Slough and checked quarterly confirmed no recruitment prior to July or after October (authors' unpublished data). To estimate recruitment (here defined as the number of oysters settling out from the plankton and growing to an observable size) we used the sum of live and dead oysters on the necklaces. We used the ratio of live to total oysters to estimate survival. (Dead oysters are recognized either by a top valve that is gaping rather than tightly sealed, or, if the top valve has fallen off, by the remaining bottom valve, which remains cemented to the substrate. Large dead oysters are easy to count and recognize; we probably missed dead shells <1 cm and thus could not quantify early mortality.)

Growth rate is challenging and time-consuming to measure in the field, particularly on uneven substrates, and is often confounded with settlement density. Favorable sites may have such high oyster densities that size is constrained (many small oysters fill all available space). To try to avoid confounding effects of density, we examined maximum sizes rather than averages (maximum provides better estimate of growth potential, and these tended to be oysters that were not crowded). In May 2014, we measured the five largest oysters to the nearest 1 mm on each of two necklaces at the lower elevation and two necklaces at the higher elevation at five sites (N=27 oysters at high elevation, 36 oysters at low elevation; not all of the 10 necklaces had 5 oysters). As these measurements were made on animals ~2 years old, they represent the size of fully mature oysters.

In December 2012, we also made visual estimates in the field of percent cover of oysters and all sessile organisms occupying primary space (attached directly to the clam shells), identifying these to genus or species if possible. Nearly all sessile species other than oysters are non-native (Wasson et al. 2001, 2005); other native or cryptogenic (biogeographic status undetermined, sensu Carlton 1996) species typically made up <1% of total cover. For this study, we estimated percent cover of these non-natives as a group. We used percent cover estimates to examine abundance of oysters and total cover of non-native species under the different conditions. Percent cover of oysters was highly correlated with number of individuals (Pearson correlation 0.84, $p<0.0005$, df =49); we used cover as our main measure of abundance for ease of comparison to cover of non-native species, most of which were colonial organisms (sponges, tunicates, bryozoans and hydroids).

2.3. 7 Statistical analyses

To test for effects of tidal elevation, we used Analysis of Variance (ANOVA) with the factors of elevation, site, and the interaction between them to look for differences in recruitment and survival of oysters and cover of oysters and non-native species on high and low necklaces (each response variable assessed separately). We were unable to assess oysters on lower necklaces at one fully tidal site with very soft, deep mud; so only seven sites were used in these analyses (N=42 necklaces). We used nested ANOVAs to test for the effects of shoreline type and distance from adult populations, with site nested in each of these factors. In all cases, site was considered a fixed factor, as we were interested in determining the best restoration approach for our study sites. Necklaces were used as replicates (N=24 for shoreline type; N=30 for distance from adults).

We used paired t-tests to compare survival of oysters and differences in cover of oysters and non-native species on the four experimentally moved vs. four control necklaces. We used two-tailed tests for oyster measurements, with a null hypothesis of no difference between high and low necklaces, and one-tailed tests with a null hypothesis of lower cover of non-native species on the necklaces at higher tidal elevation.

We used R statistical software (version 3.1.2) for statistical analyses. We examined raw data to determine suitability for parametric tests, using graphical methods to determine normal distribution and Bartlett's test for homoscedasticity among treatment groups. We used various monotonic transformations of the response variables, in each case selecting the least drastic transformation that also allowed the data to meet test assumptions. For tests of shoreline type, we used a log transformation for non-native species cover, a cube-root transformation for oyster recruitment, and a logit transformation for oyster survival. For distance from adult populations, we used an arcsine transformation of non-native species cover.

3. Results

3.1 Overview

We counted 3584 oysters across all shell necklaces and sites in summer 2012. No oysters settled in 2013. Recruitment of non-native species occurred in both 2012 and 2013, and was comparable to that observed on other hard substrate at Elkhorn Slough in terms of percent cover and species composition. Our comparisons of treatments yielded variable results, with some environmental conditions apparently having strong effects on indicators of restoration success and others having weak or no effects.

3.2 Effect of tidal elevation

On average, more than twice as many oysters recruited to necklaces at the lower elevation, and cover of live oysters at the low elevation was more than double that on the high necklaces (Table 3; Fig. 4a, d; online Appendix A). Oyster survival post-recruitment did not differ between elevations (Table 3; online Appendix A). Mean size of the largest oysters was nearly identical (low: 59.9 mm, +/-1.1 SE; high: 59.0 mm, +/-1.1 SE). The factor "site" was also statistically significant in all oyster measures (online Appendix A); and the interaction between tidal elevation and site was significant for oyster recruitment, due to slightly higher recruitment on necklaces at the higher elevation at one site (Site 7). Cover of non-native species was greater at the lower tidal elevation (Table 3; Figs. 4d, 5; online Appendix A). The factor "site" and the interaction of site and tidal elevation were also statistically significant, with more non-native species at the higher elevation at one site (Site 3).

3.3 Effect of shoreline type

More oysters recruited to the cobble sites, but there was no difference in live oyster abundance, due to significantly lower survival at cobble sites (Table 3; Figs. 3b, e; online Appendix A). We observed numerous oysters with jagged, broken top shells consistent with crab predation at the cobble sites but not at the muddy sites. There was a trend toward higher cover of non-native species at mud sites, but this was not significant at alpha = 0.05 (Table 3; Fig 3e; online Appendix A). The muddy sites did not actually result in muddier conditions on the necklaces than the cobble sites; very little sediment had collected on the shell necklaces by December 2012. Most shells had no sediment, and in no case did we see sediment accumulation greater than 2 mm. The nested factor "site" was significant only for oyster cover (online Appendix A).

3.4 Effect of distance from established adult populations

Both oysters and non-native species settled on necklaces at sites near and far from cobble that contained adult populations of oysters and non-natives. On average, recruitment and cover of live oysters were similar between near and far sites, but the nested factor "site" was significant for these measures (Table 3; Fig. 4c, f; online Appendix A). Cover of non-native species at sites near adult populations was more than double sites far from adults, and differences by the nested factor "site" were also statistically significant (Table 3; Fig. 4f; online Appendix A).

3.5 Adaptive management: moving substrates to higher elevation

Over the course of the experiment, mean cover of non-native species and oysters changed on both the experimentally moved and control necklaces. Changes in oyster cover were highly variable, but on average increased to the same extent on both moved and control necklaces, resulting in similar cover at the experiment's end (Fig. 6; Table 3; online Appendix A). Oyster survival was 17% higher on the experimentally moved necklaces (Table 3; online Appendix A). Non-native species cover decreased on both treatments and controls, but to a greater extent on the necklaces that had been moved, resulting in much lower cover on the necklaces at higher elevation (Fig. 6; Table 3; online Appendix A).

Final cover of non-natives (in 2014) was lower on the necklaces moved to high elevations than the cover of non-natives we had documented originally on high necklaces (in 2012) (Fig. 4d). We attribute this difference to seasonality; the original assessments shown in in Fig. 4d were conducted in December, when cover of non-natives was fairly high both in the low and high intertidal. By summer 2013, we noted that cover of non-natives was much lower on high necklaces in general compared to low necklaces, perhaps because desiccation stress is greater in the warm season.

4. Discussion

4.1 Context-dependence of competitive dynamics

One potential approach for restoration in invaded habitats is to shift competitive dynamics to favor the target species or community by strategically siting projects within naturally occurring stress gradients. We found that selective placement of restoration substrates resulted in reduced cover of a suite of potential non-native competitors at the physiologically more stressful higher tidal elevation.

Evidence from other locations has indicated that fouling species can strongly impact fitness of *O. lurida*, with effects on growth, survival, and recruitment. Deck (2011), studied the effects of a similar suite of non-native species on *O. lurida* in two California estuaries. She found reduced recruitment of oysters with increased cover of fouling species in San Francisco Bay and reduced recruit size (but not reduced recruitment) with greater cover of fouling species in Tomales Bay. In Willapa Bay, WA Trimble et al. (2009) reported strong impacts of sessile invertebrate cover (mostly barnacles and tunicates) on juvenile Olympia oyster survival and growth. Negative impacts of fouling species, particularly other filter feeders that may compete for food, have been documented in other oyster species in other locations (e.g., Bahr and Lanier 1981, Bishop and Peterson 2006, Fodrie et al. 2014). Competition with fouling species might also be expected to become more important on restoration substrates over time as these species accumulate, and these negative interactions may eventually outweigh the physiological benefits of lower tidal elevations (Bishop and Peterson 2006, Fodrie et al. 2014, Zabin et al. 2015). While we did not have evidence that competition with non-native fouling species was a limiting factor for oysters at Elkhorn Slough in Year 1 of our study, in Year 2, we found a suggestion of competitive effects on one metric, oyster survival, which was greater on necklaces moved to the higher tidal elevation relative to controls that remained at the lower elevation. Taken together, this body of research suggests that the placement of restoration structures at higher tidal elevations may be key to reducing oyster competitors and increasing restoration success, particularly over the longer term.

We were also interested in another type of stressor that might be important in soft-bottomed estuaries like Elkhorn Slough -- sediment burial, which shelled oysters should tolerate better than their soft-bodied competitors. While sedimentation can be detrimental to oysters when it results in total burial (Blake and Bradbury 2013, Trimble et al. 2009, Wasson 2010), we have observed good survival of oysters in locations where ~5 mm of fine sediment covers hard substrate, and we have observed long-term survival of oyster clusters partially buried at very muddy sites. We were not able to test our hypothesis properly; our substrates deployed over muddy shorelines were no muddier than the ones above cobble. Future experimental restoration studies could test whether oyster dominance over non-natives can be achieved in sites with moderate sediment burial (such as shown in the lower left of Fig. 2).

Another condition we tested was distance from adult source populations, as a proxy for propagule limitation. Non-native species cover was lower at sites farther from conspecific adults, while oyster abundance was unaffected by distance from adult oysters. Although we did not specifically test this, these differences are most likely the result of differences in larval duration and thus dispersal. However, not all of the non-native species have short larval periods, and some of these did settle on substrates at distant sites, which then became potential sources of non-native propagules in subsequent years. Thus, at least on the spatial scale we tested at Elkhorn Slough, restoration projects located a modest distance from source populations might not reduce non-native species abundance over the longer term.

Exploiting differences in tolerance to environmental stress to the benefit of target native species might be easier when native and non-native species are very different from one another, as they are at Elkhorn Slough. The strategies we employed to promote native dominance would not be effective, for example, in reducing abundance of the non-native Pacific oyster, *Crassostrea gigas,* a larger, faster-growing oyster present in many West Coast estuaries. Where it is abundant, *C. gigas* presents a challenge to native oyster restoration both in terms of potential negative impacts on the native *O. lurida* (Trimble et al. 2009) and for practitioners who do not wish to inadvertently promote the non-native. In three Southern California bays, where both oyster species co-occur, researchers have documented higher recruitment and survival of native oysters relative to *C. gigas* at lower tidal elevations (Parker et al. 2015). Restoration projects there have been able to exploit these differences, placing restoration substrates below the *C. gigas* zone but above the zone in which fouling species are most abundant (Parker et al. 2015).

4.2 Using environmental stress to meet restoration goals

An approach that makes use of the context-dependence of competition that has been used in terrestrial systems is enhancing stress-tolerant communities by locating restoration projects in more stressful places (such as in sites with alkaline soils) or by restoring stressful disturbances such as fire and grazing (Daehler 2003, Goergen and Daehler 2002, Mesleard et al. 1993). Such measures are appropriate when these conditions are less challenging for natives well-adapted to this stress than for non-natives that may be generalists with lower tolerance to a particular local stressor, as they help to shift competitive dynamics to favor native species. This approach has not been commonly used in marine or estuarine restoration (but see Chen et al. 2013, Rochlin et al. 2012).

However, we found trade-offs between maximizing oyster *abundance* and maximizing *dominance*: the former was maximized at low elevation and the latter at high elevation. This raises an important question about restoration goals. For oysters, restoration metrics are typically focused on attributes of the oyster populations, such as density and size distribution (Baggett et al. 2015). By such metrics, the less stressful conditions are better. However, broader goals are often a part of ecological restoration, such as having a characteristic assemblage of native species (Society for Ecological Restoration 2004). By these metrics, the more stressful conditions are better at accomplishing restoration goals. The decision whether to use stress as a tool may thus depend on restoration goal(s), i.e., not promoting non-natives might be an explicit goal or condition of restoration, as well as on the strength of competition between natives and non-natives. This highlights the need to clearly define restoration goals and definitions of success (Zedler 2007).

Adaptive management may be one solution for optimizing both abundance and dominance. For our small-scale project, moving the restoration units proved to be successful, allowing us to take advantage of higher recruitment at the low tidal elevation, and then reduce survival of non-natives at the high elevation without any obvious negative effects on the oysters. This could potentially be used as a future restoration approach at Elkhorn Slough and at other small estuaries with very small oyster populations: oyster substrates, if light enough, could be "seeded" via natural recruitment at lower tidal elevation, then moved higher to reduce cover of non-native species. This would not be feasible for larger projects, but the deployment of substrates seeded with hatchery-reared oyster spat might help overcome the expected lower recruitment at high tidal elevations.

A conceptually similar adaptive management approach that could be used more broadly by restoration practitioners might be to apply stress differentially over time at a stationary restoration site. For example, early spring mowing was found to shift a grassland from non-native to native-dominated; phenology differences between native and a dominant non-native grass species meant that more biomass was removed from the non-native, allowing greater growth and flowering of the native (Wilson and Clark 2001). In serpentine grasslands, enhancement of soils with nutrients initially leads to increased production by native species, but eventually leads to native forbs being outcompeted by non-native annual grasses (Huenneke et al. 1990). In such an example, restoration of a serpentine site might involve fertilization of newly planted natives followed by cessation of fertilization after their establishment.

4.3 Value of experimental restoration and monitoring

Despite calls for conducting large-scale experiments in wetland habitats in general (Wagner et al. 2008), and oyster restoration in particular (Walles et al. 2016), application of an experimental approach remains relatively rare. Resources for restoration are often so limited that practitioners often try what seems like the best possible approach and hope for the best. This greatly limits our ability to learn from failures or successes. Our study illustrates the value of conducting restoration experimentally: we detected strong differences among sites and conditions, which would have been impossible if we had conducted restoration only at one site. Taking an adaptive management approach allowed us to improve restoration design in the second year based on our findings in the first year. Scaling up at the best sites and tidal elevations would be an appropriate next step.

Monitoring also allowed us to learn from mistakes: we realized that we did not properly test sediment burial, and that seasonality was important in the assessment of non-native species and bare space. It also allowed us to better understand mechanisms behind observed effects. For example, the number of oyster recruits was higher on cobble shores than adjacent mud, but crab predation at those sites led to reduced survival, so that total number of live oysters was similar after six months.

Understanding the physiological tolerances of desired and undesired species to different environmental conditions can help inform the location, design and approach to monitoring of restoration efforts (Cooke and Suski 2008). Manipulating specific environmental conditions in the field rather than just comparing site differences is one approach to learning about the effect of individual parameters, which may be increasingly important when planning for restoration in ecosystems that have been highly altered by human activities.

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Tables

Table 1. Site characteristics for study locations.

Site Name	*Site*	*Tidal Regime*	*Shoreline Type*	*Distance from Adult Population*
South Marsh Footbridge West	1	full	mud	near
South Marsh Footbridge East	2	full	cobble	near
Cattail-Rookery	3	full	mud	far
Five Pannes South*	4	full	mud	far
Five Pannes Middle	5	full	mud	far
Five Pannes North	6	full	mud	far
Middle Culvert	7	full	cobble	near
Hummingbird	8	full	mud	near
Whistlestop East**	9	muted	N/A	N/A
Whistlestop West**	10	muted	N/A	N/A

*This site not used in analyses because lower necklaces inaccessible; **tidally muted sites also excluded from analyses

Table 2. Details of experimental set up and analysis.

Experiment	*Sites Used*	*Response Variables*		*Statistical Test*
Tidal Height	7 fully tidal sites: 1-3, 5-8	oysters: # of live, oysters, survival, recruitment, cover	non-native species: cover	2 way ANOVA
Shoreline Type	Sites near adult populations: 2 mud: 1,8; 2 cobble: 2,7	oysters: recruitment, cover, survival	non-native species: cover	Nested ANOVA
Distance from Adult Population	Muddy sites: 2 near: 1,8; 3 far: 3,5,6	oysters: recruitment, cover	non-native species: cover	Nested ANOVA
Adaptive Management	One control, one treatment necklace at 4 sites: 1,2,7,8	oysters: cover, survival	non-native species: cover	Paired T Test

Table 3. Experimental results; statistically significant differences are in bold. Means and standard errors shown are untransformed data.

Experiment	*Oyster Recruitment (Total Oysters)*	*Oyster Survival (%)*	*Oyster Cover (%)*	*Invasive Cover (%)*
Tidal Elevation				
Low (sites 1-3, 5-8)	122.4 (+/-10.9)	88.7 (+/-6.2)	19.52 (+/-2.0)	25.3 (+/-4.0)
High (sites 1-3, 5-8)	70.0 (+/-10.4)	85.7 (+/-8.2)	11.9 (+/-1.5)	19.9 (+/-3.4)
Significance	***p*<0.0005**	*p*=0.12	***p*<0.0005**	***p*=0.016**
Shoreline type				
Cobble (sites 2,7)	138 (+/-10.4)	60.9 (+/-4.5)	15 (+/-2.1)	26.3 (+/-2.3)
Mud (sites 1,8)	83 (+/-13.6)	98.8 (+/-0.5)	18 (+/-2.4)	31.4 (+/-4.4)
Significance	***p*<0.0005**	***p*<0.0005**	*p*=0.18	*p*=0.45
Distance from Adult Population				
Near (sites 1,8)	83.3 (+/-9.6)	Not Tested	14.2 (+/-2.2)	31.4 (+/-3.1)
Far (sites 3,5,6)	76.9 (+/-12.4)		15.3 (+/-3.5)	14.2 (+/-4.0)
Significance	*p*=0.712		*p*=0.71	***p*<0.0005**
Adaptive Management				
Sites (1,2,7,8)				
Necklaces Moved to + 30 cm	NA	94 (+/-0.04)	41.25 (+/-8.3)	3.75 (+/-2.4)
Controls at -30 cm	NA	77 (+/-0.05)	43.75 (+/-8.3)	42.5 (+/-8.6)
Significance		***p*=0.036**	*p*=0.653	***p*=0.031**

Figure legends:

Figure 1: Location of restoration project (inset); and sites within restoration project.

Figure 2. Top left and right photos: Non-native fouling species are abundant on hard substrates but do not extend as high in tidal elevation as do native oysters. Bottom left: in muddier locations, oysters are present, but non-native fouling species are rare or absent.

Figure 3. Top photo: shell necklaces, constructed by volunteers just prior to deployment. Bottom photo: Sets of necklaces placed at two tidal elevations; the tops of the lower necklaces are just barely visible above the water.

Figure 4. Left side of panel: comparisons of recruitment and number of live adult oysters per necklace, on necklaces placed a) at low vs. high elevation; b) at cobble vs. muddy shores; c) near and far from source populations. Right side of panel: percent cover of bare space, non-native sessile species and native oysters on necklaces placed d) at low vs. high elevation; e) at cobble vs. muddy shores; f) near and far from source populations. Bars are standard error; numbers indicate statistically significant differences in tested factors. Uppercase letters in d) are used to indicate that differences in cover of non-native species were statistically significant between treatment types; lower case letters indicate the same for oysters.

Figure 5. Top: a necklace at the higher tidal elevation; bottom, low elevation necklace. Photos taken in December 2012 following July 2012 deployment of necklaces.

Figure 6. Percent cover of bare space, non-native species and native oysters on necklaces at the start and end of the Adaptive Management Experiment. Treatment necklaces were moved from the low to high tidal elevation; control necklaces remained at the low elevation. Bars are standard error; lower case letters indicate statistically significant differences between groups.

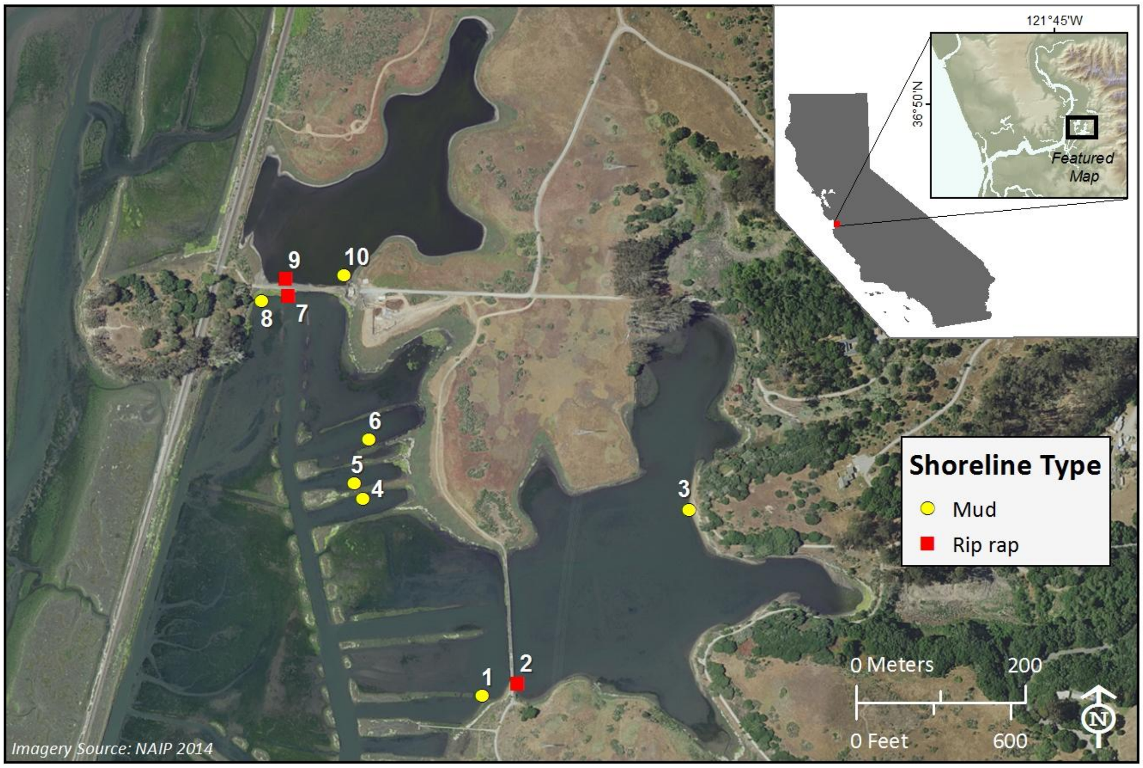
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Figure 1

Figure 2

Figure 3

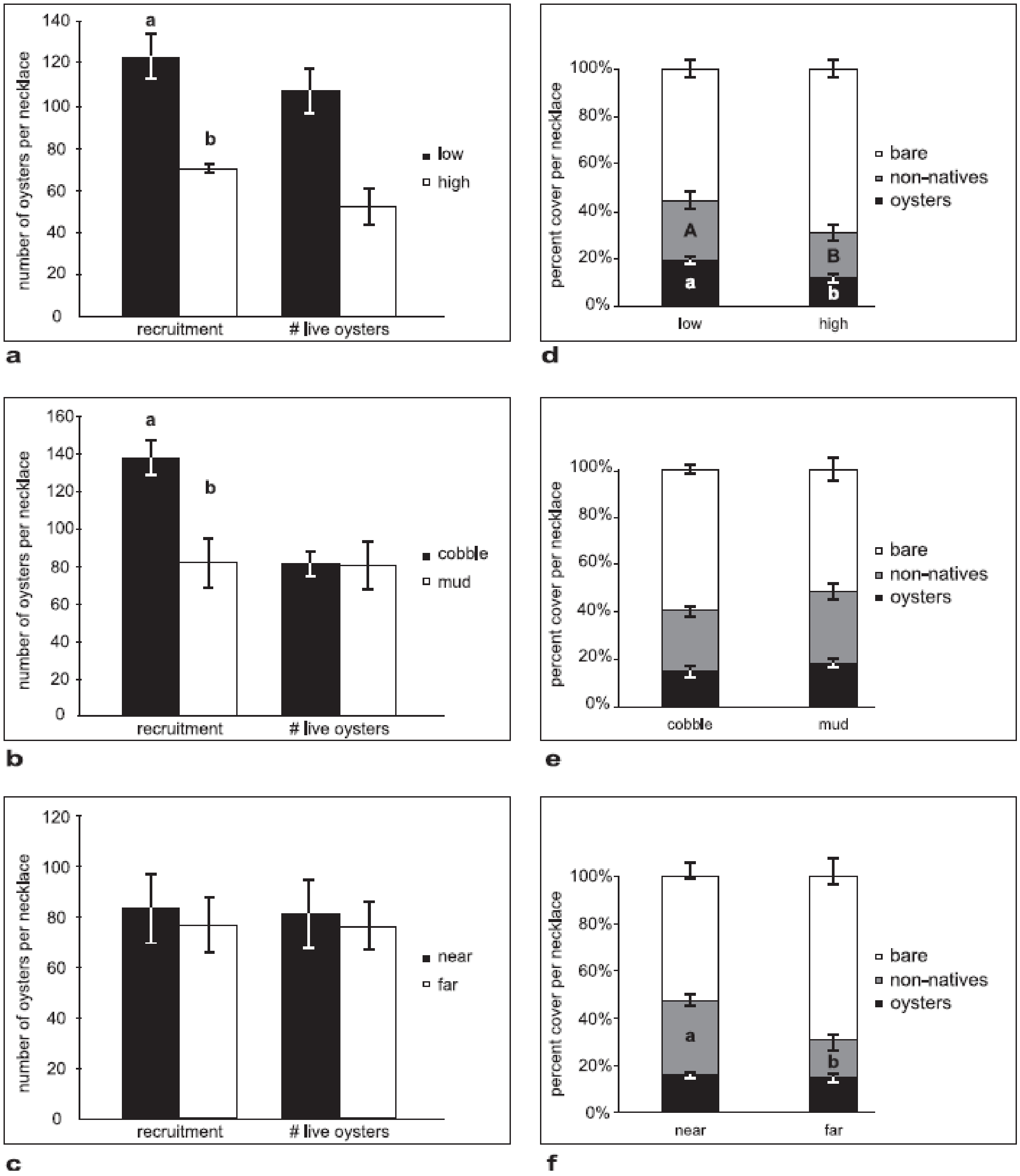
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Figure 4

Figure 5

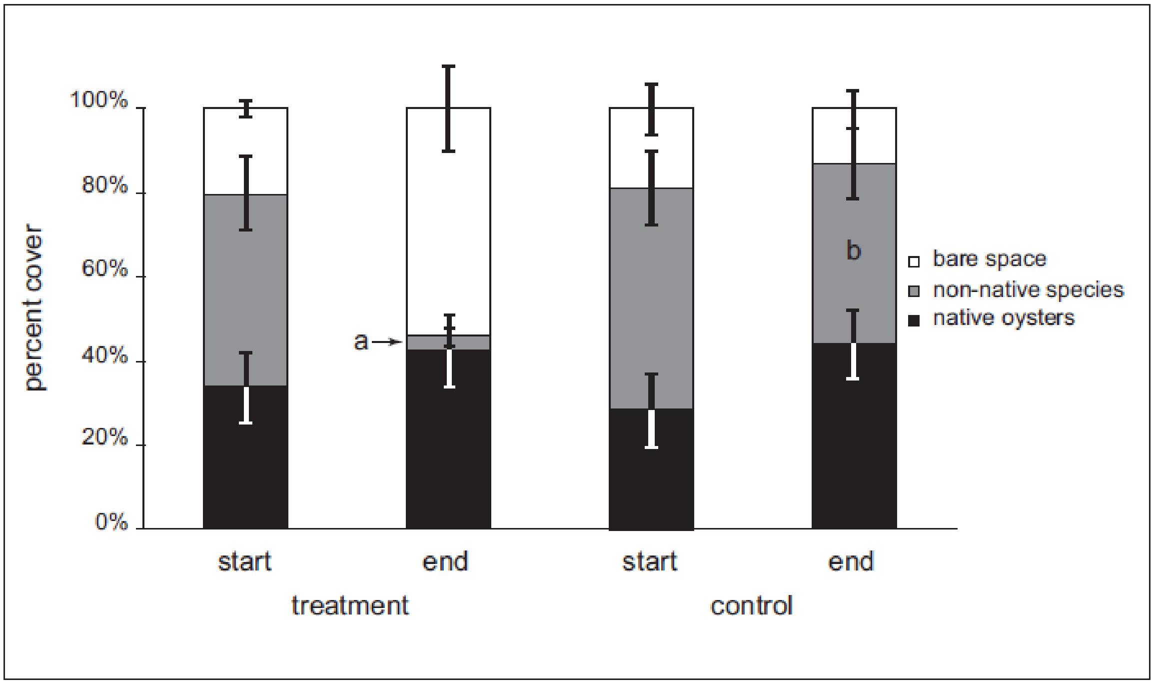
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Figure 6

Highlights

- Native oysters tolerate some stressful conditions better than non-native competitors
- Abundance of both oysters and non-natives increases at lower tidal elevations
- However, dominance by oysters increases at higher tidal elevations
- Mobile restoration units allow for adaptive management to optimize native cover
- Using environmental stress gradients may improve restoration outcomes