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EXPLORING RESTORATION METHODS FOR THE OLYMPIA OYSTER *OSTREA LURIDA* CARPENTER, 1864: EFFECTS OF SHELL BED THICKNESS AND SHELL DEPLOYMENT METHODS ON SHELL COVER, OYSTER RECRUITMENT, AND OYSTER DENSITY

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ABSTRACT Oysters provide habitat, sediment stabilization, and improved water quality, and are important foundation species in many estuarine ecosystems. Worldwide oyster population declines have been dramatic and efforts to restore declining populations and the services they provide are ongoing. Several commonly used oyster restoration techniques were examined to determine which would be the most successful for restoring the Olympia oyster *Ostrea lurida* in Newport Bay, CA. Replicate ($n = 5$) 2×2 m shell beds were constructed of two initial shell planting thicknesses (bed thicknesses of 4 versus 12 cm) and two methods of deployment (bagged versus loose shell). Shell cover, oyster spatfall (settlement), oyster recruitment, and adult oyster densities were analyzed over 2 y; 12-cm-thick oyster beds maintained higher shell cover, experienced less sedimentation, and received greater numbers of oyster recruits than 4-cm-thick beds. There was no significant effect of shell deployment method on shell cover, recruitment, or adult density; however, spatfall was greater on loose shell beds compared with bagged shell beds in the final year of the study. Overall, augmenting mudflat habitat with oyster shell significantly increased adult *O. lurida* oyster density compared with unmanipulated plots and increased oyster density relative to the average density of oysters measured elsewhere in Newport Bay. Collectively, the data suggest that building thicker shell beds might increase the longevity of a constructed shell bed, and therefore, this approach is recommended for future restoration activities in southern California. This study highlights the advantages of augmenting habitat in a manner that provides vertical relief from sedimentation.

KEY WORDS: Olympia oyster, *Ostrea lurida*, oyster restoration, oyster reef, recruitment, shell bag

INTRODUCTION

Oyster reefs are among the most heavily affected habitats worldwide, with recent dramatic declines that have reduced once important habitat in estuaries to less than 15% of their historic occurrence (Beck et al. 2011, Zu Ermgassen et al. 2012). Recent interest in restoring oyster reefs can be attributed to this substantial loss of oyster reef habitat and the myriad ecosystem benefits that they provide (Brumbaugh & Coen 2009). Oyster reefs grow vertically, forming heterogeneous structured habitat that stabilizes sediments and shorelines (Meyer et al. 1997, Piazza et al. 2005, Grabowski et al. 2012). This habitat also provides refuge and foraging habitat for whole communities of invertebrates and fishes (Grabowski et al. 2005). In addition, oyster filter feeding activity can improve water clarity by capturing and depositing suspended particles, which may be beneficial to aquatic vegetation (Grizzle et al. 2008, but see Zu Ermgassen et al. 2012), and also contributes to denitrification of estuarine systems (Piehler & Smyth 2011, Kellogg et al. 2013). These ecosystem benefits, coupled with the economic value of oyster fisheries (MacKenzie 1996), have made restoration of oysters a key conservation priority worldwide.

The Olympia oyster *Ostrea lurida* Carpenter, 1864 is the only native oyster species on the U.S. and Canadian west coasts (Carpenter 1864, Polson et al. 2009). In California, it was once widely distributed in bays and estuaries (Bonnot 1935, and see Baker 1995 for review) and was a harvested food resource for Native Americans (Elsasser & Heizer 1966). Populations across the geographic range of the species declined dramatically in the early 1900s due to a combination of over-harvesting (Kirby 2004 and references therein), pollution (Hopkins 1935), and habitat loss/degradation (Dahl & Johnson 1991, Lotze et al. 2006). Restoration of the Olympia oyster is ongoing in Washington, Oregon, and California (Dinnel et al. 2009, McGraw 2009, White et al. 2009a and references therein).

A group of Olympia oyster restoration practitioners, convened at the 2006 West Coast Native Oyster Restoration Workshop, recommended using the term oyster "bed" as opposed to oyster "reef" when describing aggregates of Olympia oysters. There is a notable lack of quantitative data on the extent and dimensions of historical Olympia oyster aggregates, especially pre-exploitation (but see Blake & zu Ermgassen 2015); however, examination of photographs, fossil deposits, and qualitative descriptions of historical and extant oyster populations indicates that Olympia oysters may not form structures with as much relief as has been documented for other oysters [e.g., *Crassostrea virginica* (Gmelin, 1791) "reefs"]. Aggregates of Olympia oysters are thought to result in low-relief "beds" (NOAA 2007, Jacobsen 2009, B. Allen, Puget Sound Restoration Fund, personal communication, March 2015) that exist now as scatterings and occasional clumps of oysters on remaining hard substrata, but historically, consisted of several inches of dead shell covered with a thin veneer of living oysters (Steele 1957).

As is largely the case across the range of this species, no pre-exploitation quantitative data exist on *Ostrea lurida* density in southern California; however, historic documents indicate the presence of oyster beds in several southern California estuaries, including Newport Bay in Orange County (Gilbert 1889, Bonnot 1935). As well, evidence from fossil deposits indicates this species' presence in multiple locations in southern California extending back to the late Pleistocene (Howard 1935, Kern 1971). Oyster beds are now absent in California estuaries,

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although remnant low-density populations exist (Polson & Zacherl 2009), and, importantly, *O. lurida* larvae settle regularly throughout each reproductive season from May to September in Newport Bay (Seale & Zacherl 2009) and elsewhere in southern California, including Alamitos Bay and San Diego Bay (D. Zacherl, CSU Fullerton, personal communication, July 2015). Thus, *O. lurida* recovery in southern California may not be constrained due to insufficient larval availability, but instead, may be limited by lack of available suitable habitat (Wasson 2010).

In cases where oyster habitat is limited but larval supply is plentiful, restoration practitioners will first augment mudflat with oyster shell, cement "reef balls," or other hard substrata before considering the implementation of more aggressive restoration techniques like stock enhancement or oyster gardening (Brumbaugh & Coen 2009). Hard substrata provide habitat upon which larval oysters settle and recruit. Many (Mann & Powell 2007) consider oyster shell the preferred choice for habitat augmentation, and limited field evidence suggests that *Ostrea lurida* oyster spat may prefer to settle upon oyster shell versus gravel or bare mudflat (White et al. 2009b). This observation is supported with evidence from other species of oysters; *Crassostrea virginica* larvae are attracted to live oysters and oyster shell and will settle on or among them (Crisp 1967, Tamburri et al. 1992). This "gregarious" behavior produces a positive feedback cycle that can lead to the production of oyster beds/reefs.

When augmenting a habitat with oyster shell, the shell can be added using a variety of methods including applying it in varying initial shell planting thicknesses and in an unconsolidated (loose) or consolidated manner (e.g., bagging shell or embedding shell in cement, Brumbaugh & Coen 2009). Bagging shell into mesh bags may improve bed construction logistics because the bags are easy to deploy and provide a venue to engage volunteer participation (Hadley & Coen 2002). This technique may also decrease bed erosion and shell loss over time by increasing stability of out-planted oyster habitat. Despite the potential benefits of using bagged shell, the costs of the bagging material and labor as well as the introduction of plastic in the environment (many have used plastic mesh bagging materials) may outweigh the benefits of bagging. Minimizing shell loss is particularly important because oyster restoration projects are successful in the long-term only if the rate of shell accretion is greater than the rate of shell loss (Mann & Powell 2007). For this reason, Mann and Powell (2007) and others (Coen & Luckenbach 2000, Powell et al. 2006) have emphasized the importance of maintaining shell accretion and avoiding shell loss in any oyster restoration project design.

Until recently, restoration of *Ostrea lurida* mostly consisted of community-driven or nonprofit efforts that were not specifically designed with scientific monitoring in mind (Brumbaugh & Coen 2009, Trimble et al. 2009). One common practice has included substratum enhancement via spreading of shell on the mudflat haphazardly (Dinnel et al. 2009), resulting in a shell bed of uncontrolled thickness. No *O. lurida* restoration practitioners have yet published results from controlled experiments that monitored oysters' responses to bed thickness or the presence of unconsolidated (loose) versus consolidated (bagged) shell; however, several are actively investigating (or have recently investigated) aspects of these questions and other questions about restoration design in, for example, Washington (e.g., Brian Allen, Puget Sound Restoration Fund, personal communication, March 2015, Dinnel et al. 2009, White et al. 2009b) and central California (Latta & Boyer 2015).

Oyster bed thickness might be important for *Ostrea lurida* survival on beds because for other oyster species (e.g., *Crassostrea virginica*), their vertical location within a constructed oyster reef can significantly influence growth and mortality (Bartol et al. 1999, Lenihan 1999). In the case of *C. virginica*, an elevated vertical location on a subtidal oyster reef prevents exposure to deadly anoxic conditions; these findings may or may not be relevant to Olympia oysters in southern California, which are largely intertidal in their distribution. The lack of historical and published information on optimal and historical bed thickness for this species motivates a need to explore experimentally the effect of constructed bed thickness on *O. lurida* recovery. Together, consideration of both shell deployment method and initial shell planting thickness may be critically important to the success of future oyster restoration efforts (Brumbaugh & Coen 2009, Trimble et al. 2009, Hadley et al. 2010).

This study examines a 2-y experiment on an intertidal estuarine mudflat that assessed how oyster bed thickness and shell deployment method on constructed oyster beds affected larval oyster spatfall, recruitment, adult oyster density, and coverage of oyster bed material (shell cover) in Newport Bay, CA.

MATERIALS AND METHODS

Study Site

The study was conducted on a 100×2 m span of intertidal estuarine mudflat that was hard-substratum limited, with 97.8 ± 0.7% (1 SE) cover of mud prior to study initiation. The site was located in Upper Newport Bay, Newport Beach, CA, between N 33 ° 37′ 7.56″, W 117° 54′ 18.67″ and N 33° 37′ 17.04″, W 117° 54′ 8.86″ on land owned by the County of Orange (Fig. 1). The slope of the mudflat ranged between approximately 4–7 deg and was located in the back-bay region of the estuary adjacent to the Upper Newport Bay Nature Preserve along a no-wake boating channel. The mudflat substrate consisted of sediments composed of deep silty clay.

Bed Construction

In June 2010, a group of scientists and students from California State University Fullerton and community volunteers constructed oyster beds measuring 2×2 m each, using dead *Crassostrea gigas* (Thunberg, 1793) oyster shell purchased from Carlsbad Aquafarm (Carlsbad, CA). Prior to purchase, shell was stored in $20 \times 55 \times 55$ cm stackable plastic lattice trays that were air- and sun-exposed, located away from seawater for at least 6 mo, and inspected by California Department of Fish and Wildlife biologists to ensure that transport of invasive species into Newport Bay did not occur (Cohen & Zabin 2009).

Constructed bed treatments consisted of combinations of two initial shell planting thicknesses (resulting in bed thicknesses of 4 cm or 12 cm) and two deployment methods (loosely applied oyster shell, hereafter referred to as "loose," versus shells bagged into biodegradable jute bags with 1-cm mesh size, hereafter referred to as "bagged"). Bed treatments were deployed in a 2×2 factorial replicated design (Fig. 2). The jute bags were purchased from In2Bags, a Canadian jute bag

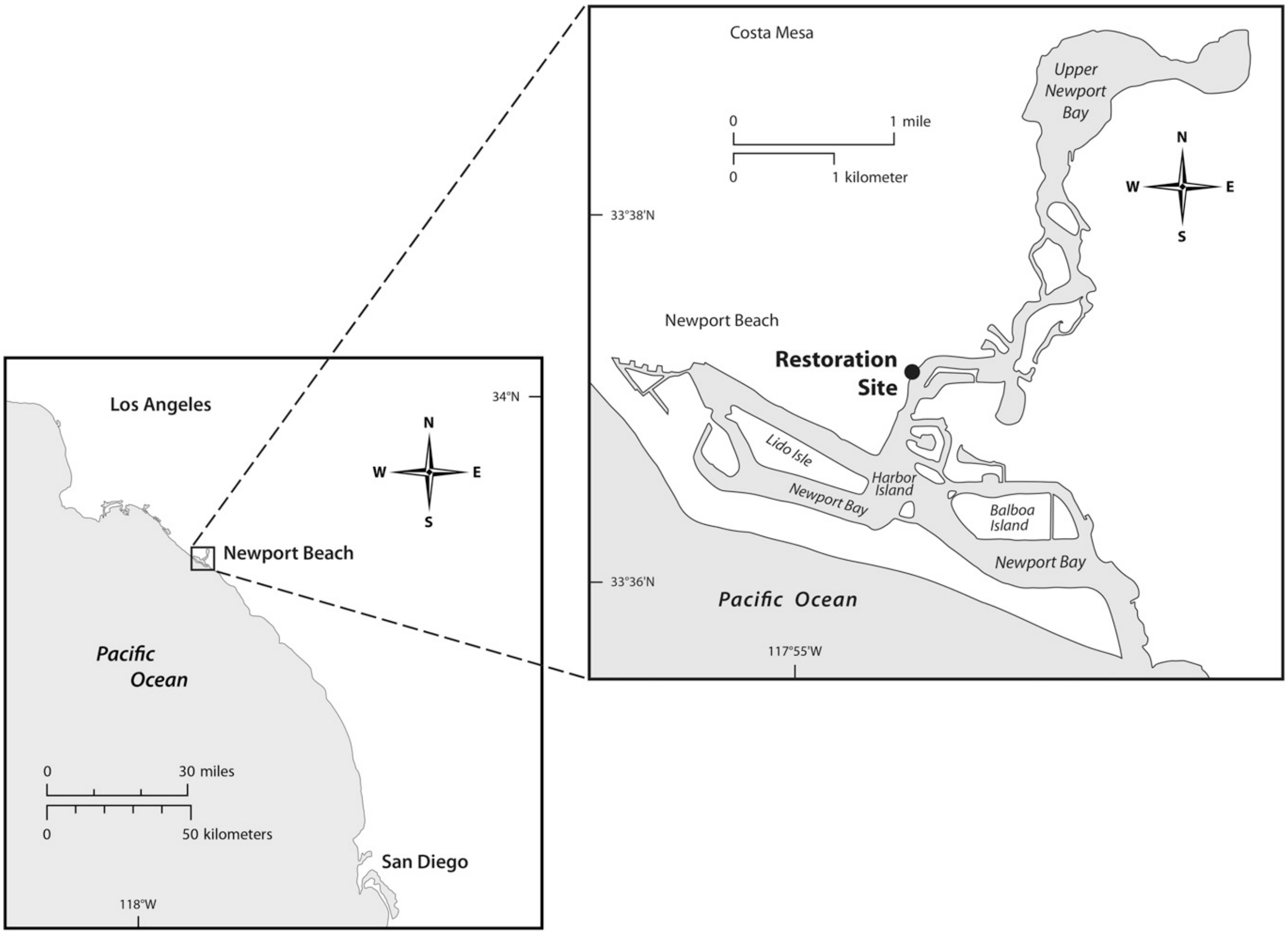

Figure 1. Study location in Newport Bay, CA.

supplier based in British Columbia. There were a total of 20 constructed beds ($n = 5$ beds/treatment). Five unmanipulated areas of mudflat were also established as references, each also measuring 2×2 m. All oyster beds and reference plot locations were randomly designated along the mudflat at a standardized tidal elevation [centered at –0.15 m mean lower low water (MLLW)] and were spaced 2 m apart, except beds 20–21 (12 m apart), and 24–25 (8 m apart), due to discontinuities on the mudflat.

Shell Cover

Prior to oyster bed construction surveyors recorded percent shell cover (e.g., dead shell, *Mytilus* spp., *Ostrea lurida*, etc.)

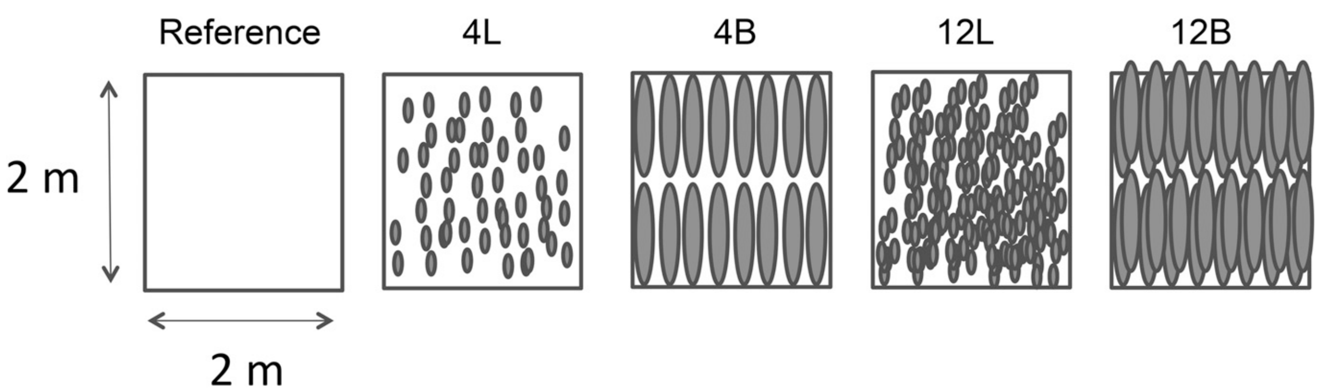

Figure 2. Experimental design including constructed oyster beds of two consolidation types (L = loose shell, B = bagged shell) and two thicknesses (12 = 12 cm thick, 4 = 4 cm thick), plus unmanipulated ("reference") plots. Beds and reference plots were ordered randomly along the mudflat at a tidal elevation centered at –0.15 m MLLW.

using 50 × 50 cm gridded point-contact quadrats. Immediately after oyster bed construction, shell cover was 100% for all treatment beds. Surveys were again conducted at 2, 7, 12, 19, and 24 mo after bed construction. All beds and reference plots were divided into four quadrants prior to the first sampling of percent shell cover. The first sampling period sampled the northeast quadrant and all subsequent samples were taken from quadrants in a clockwise direction. Within a quadrant, the exact location of the 50 × 50 cm quadrat was determined haphazardly for each period, but that haphazardly selected location was then standardized across all beds and reference plots within that period.

The purpose of the percent cover surveys was to assay the change in clean shell (free of sedimentation) available on the surface for spat to attach, because when the shells are fouled with sediments, they can no longer serve as adequate ''cultch'' for Olympia oysters (Fasten 1931 and references therein). Percent cover of shells could decline due to sedimentation (as our percent cover assay measured), but also could decline due to sinking, spreading, or being carried away by tidal currents and boat wakes. Therefore, to gain more insight into the cause of percent cover declines observed over the entire study period, surveyors augmented the percent cover surveys at 24-mo post-construction by estimating the depth of mud deposition upon shells and also by measuring the volume of shells excavated from 25 × 25 cm quadrats (see Spat Recruitment and Adult Density). In these additional surveys, surveyors recorded the percentage of point-contact locations where they encountered mud/sediment and then used a probe to estimate, to the nearest millimeter, the depth of sediment on top of shells when sediment was encountered at any point-contact location. To measure shell loss due to spreading or being carried away from the beds, surveyors measured the volume of shell excavated from the quadrats and calculated percent loss of shell volume per replicate. Starting volumes were calculated from initial bed thicknesses as 25 × 25 × 4 cm for the 4-cm-thick beds and 25 × 25 × 12 cm for the 12-cm-thick beds.

Spatfall

To monitor oyster settlement (spatfall), 15 × 15 cm ceramic tiles were deployed face down due to *Ostrea lurida*'s preference for settling on the undersides of substrata (Hopkins 1935), at a distance of 10–15 cm above the substratum of each constructed bed and unmanipulated plot, using polyvinyl chloride tees as in Seale and Zacherl (2009). Tiles were changed out every 2 wk from May to September, and once monthly from October to April. Laboratory technicians determined the number of oysters attached onto each tile using dissecting microscopes and converted the measure to per square meter. This method provided a standardized and relative measure of *potential* spatfall onto each constructed oyster bed and reference plot, but note that because reference plots generally had extremely low percent cover of hard substratum, especially relative to the constructed shell beds, these measures should not be construed as actual spatfall measures onto the shells/plots. Spatfall/m^2 was summed across all sampling periods within each year from early April to August, resulting in one cumulative spatfall data point per year per bed for ease of statistical analysis (n = 5 replicate beds per treatment). Note that the cumulative spatfall measure does not elucidate within-year seasonal patterns of settlement, but these are tangential to the central study questions focused on differences in spatfall as a function of initial shell planting thickness and shell deployment method; however, within-year seasonal patterns are briefly discussed in the Results. Seasonal patterns of settlement in southern California estuaries are also documented elsewhere (Coe 1931, Seale & Zacherl 2009).

Spat Recruitment and Adult Density

Prior to oyster bed construction, surveyors conducted adult oyster density surveys by searching for adult oysters on rocks and shells from within one 50 × 50 cm quadrat on each of the 20 bed plots and the reference plots. After bed construction, at 7, 12, 19, and 24 mo, the methods were modified by excavating quadrats of a smaller total area (25 × 25 cm) on each of the 20 beds and the reference plots. During each survey period, a new quadrant of each bed was sampled as described above in the methods for percent shell cover; the 25 × 25 cm quadrats were located within the 50 × 50 cm percent shell cover quadrats and excavations occurred at least 0.3 m away from the bed edge to avoid edge effects. No quadrant was surveyed more than once during the entire study period except that the same quadrant was sampled prior to construction and again at 24 mo. During excavation, we removed shells and rocks down to the mudflat base and rinsed them of sediments. We retained sediments for further studies on infaunal community diversity (beyond the scope of this article). On the rinsed shells and rocks, attached adult *Ostrea lurida* were identified and enumerated visually, and then all shells were stored at 0°C until they could be searched for microscopic recruit oysters. Adult and recruit data were sampled from an area measuring 0.0625 m^2 (25 × 25 cm excavation), but were converted to per square meter for ease of comparison across the literature.

Upon examination, oysters of two distinct size classes (recruits versus adults) were found on the shell. ''Recruits'' were oysters smaller than 30 mm, whereas oysters that were larger than 30 mm were classified as adults. The classification of adults as those greater than 30 mm is consistent with the finding that *Ostrea lurida* is known to grow rapidly after settlement in southern California by as much as 30–37 mm in 16 wk, at which point all individuals have oogonia and spermatogonia present (Coe 1931). We use the term ''recruit'' operationally (*sensu* Hunt & Scheibling 1997) as spat that settled onto our oyster shell and likely experienced some postsettlement mortality. Because of their size, they likely lacked reproductive tissue (Coe 1931) and so were not classified as adults. Because they could have experienced significant postsettlement mortality and actually ''recruited'' to the shell, it is important to distinguish them from spatfall/settlers (i.e., individuals that attached to our tiles, described above, which were collected every 2 wk). The spatfall/settlers would not have experienced as much postsettlement mortality at the time of census and were not settling directly upon the shell. Spatfall could only have been at most 2 wk old and were less than 1 mm in size, whereas recruits ranged in size from ~1 mm to about 30 mm and could have been up to ~6 mo old. Spatfall could only have experienced postsettlement mortality across a 2-wk period, and thus are a better approximation of ''propagule pressure'' to the site, whereas recruits may have experienced significant mortality, and are much more likely to enter into the future reproductive pool.

TABLE 1.

Two-way repeated measures ANOVA statistics testing effects of shell bed thickness (bed thick), deployment method (deploy meth) and their interactions over time on mean shell cover, *Ostrea lurida* cumulative spatfall on ceramic tiles, recruits, and adults per meter square onto oyster beds constructed in Newport Bay, CA.

Response variable	Source	Test	Value	F	NumDF	DenDF	Prob > F
Shell cover	Bed thick	F test	1.9449	31.1192	1	16	**<0.0001**
	Deploy meth	F test	0.0989	1.5826	1	16	0.2264
	Bed thick × deploy meth	F test	0.0376	0.6008	1	16	0.4496
	Time	G-G	0.6981	37.4806	3.5	55.8	**<0.0001**
	Time × bed thick	G-G	0.6981	3.6808	3.5	55.8	**0.0131**
	Time × deploy method	G-G	0.6981	0.4461	3.5	55.8	0.7496
	Time × bed thick × deploy meth	G-G	0.6981	0.6560	3.5	55.8	0.6050
Ostrea lurida spatfall	Bed thick	F test	0.0002	0.0029	1	16	0.9578
	Deploy meth	F test	0.1639	2.6217	1	16	0.1250
	Bed thick × deploy meth	F test	1.4956e-6	0.0000	1	16	0.9962
	Time	G-G	0.6502	68.6401	1.3	20.8	**<0.0001**
	Time × bed thick	G-G	0.6502	1.3667	1.3	20.8	0.2659
	Time × deploy method	G-G	0.6502	5.9771	1.3	20.8	**0.0171**
	Time × Bed thick × deploy meth	G-G	0.6502	0.4179	1.3	20.8	0.5777
Recruit *O. lurida*	Bed thick	F test	2.1664	34.6620	1	16	**<0.0001**
	Deploy meth	F test	0.3631	5.8095	1	16	**0.0283**
	Bed thick × deploy meth	F test	0.43804	7.0086	1	16	**0.0176**
	Time	G-G	0.3615	38.2311	1.1	17.4	**<0.0001**
	Time × bed thick	G-G	0.3615	19.2796	1.1	17.4	**0.0003**
	Time × deploy method	G-G	0.3615	2.3195	1.1	17.4	0.1447
	Time × bed thick × deploy meth	G-G	0.3615	3.6273	1.1	17.4	0.0709
Adult *O. lurida*	Bed thick	F test	0.1755	2.8076	1	16	0.1132
	Deploy meth	F test	0.1817	2.9073	1	16	0.1075
	Bed thick × deploy meth	F Test	0.06219	0.9950	1	16	0.3334
	Time	G-G	0.5477	6.9403	2.2	35.1	**0.0023**
	Time × bed thick	G-G	0.5477	0.9708	2.2	35.1	0.3955
	Time × deploy method	G-G	0.5477	0.5554	2.2	35.1	0.5944
	Time × bed thick × deploy meth	G-G	0.5477	0.4411	2.2	35.1	0.6646

G-G, Greenhouse-Geisser correction was applied when the assumption of sphericity was violated. Between-subject factors are bed thick, deploy meth and bed thick × deploy meth, whereas within-subject factors are time and all interactions of between-subject factors with Time. Significant effects in bold.

Statistical Analyses

The effects of method of deployment and shell bed thickness and their interaction across time on shell cover, spatfall, recruit oyster density, and adult oyster density were tested with two-way repeated measures analysis of variance (ANOVA) using JMP 12.0 software. Data were evaluated to ensure that they met the assumptions of normality and multivariate homoscedasticity (sphericity). If Mauchly's test indicated that the assumption of sphericity had been violated, the critical P value was modified using a Greenhouse-Geisser correction. When interactions were found among effects, *post hoc* Tukey's comparisons were completed where appropriate. For percent shell cover and recruit oyster density, the data violated the assumption of normality and could not be transformed in a way that corrected the problem because of their significant right-skewed nature. Because ANOVA are robust to deviations from normality (Boneau 1960, Norman 2010), the decision was made to proceed with two-way repeated measures ANOVA with JMP 12.0 software.

Surveyors sampled percent volume shell loss on each bed and millimeters mud deposited onto shell only at the 24-mo sampling period, and tested the effects of method of deployment and shell bed thickness and their interaction on these response factors using two-way ANOVA with JMP 12.0 software. Data were first evaluated to ensure that they met the assumptions of normality and homoscedasticity. Millimeters of mud deposited onto shell were homoscedastic, but slightly deviated from a normal distribution. Multiple attempts at transformation were unsuccessful at correcting the departure from normality but because the deviation was extremely slight and ANOVA are robust to deviations from normality (Boneau 1960, Norman 2010), a parametric two-way ANOVA with JMP 12.0 software was the statistical approach used.

RESULTS

Shell Cover

Before construction of the beds, shell coverage across all plots ($n = 25$) averaged 1.4 ± 0.4% (1 SE). After shell additions, cover was 100% on all treatment beds and 1.2 ± 0.8% on references plots. Percent shell cover decreased significantly on 12-cm-thick beds from time of construction (June 2010) to 2 mo postconstruction (August 2010), and thereafter stabilized (Fig. 3). Percent shell cover also decreased significantly on 4-cm-thick beds, but in this case, decreased from time of construction (June 2010) to 7 mo postconstruction (January 2011), and thereafter

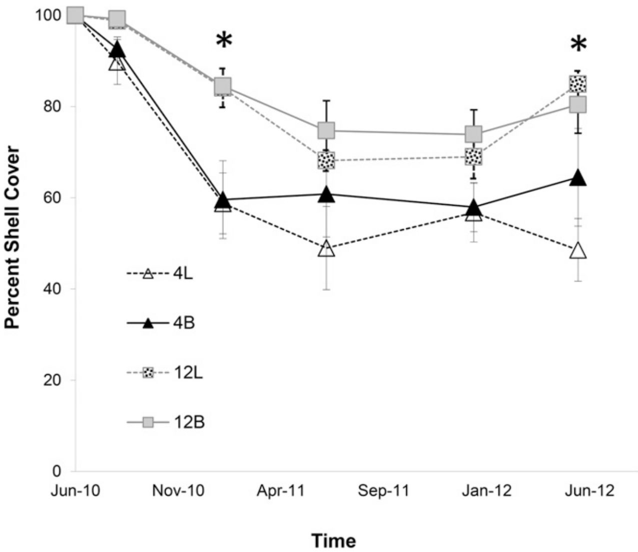

Figure 3. Mean percent shell cover (±1 SE) on experimental oyster beds (*n* = 5 per treatment) 0, 2, 7, 12, 19, and 24 mo after bed construction in Newport Bay, CA. Shell cover was 100% at time 0 for treatment beds. L = loose shell, B = bagged shell, 12 = 12 cm thick shell bed, 4 = 4 cm thick shell bed. Asterisks indicate significant differences between 12 cm thick beds and 4 cm thick beds, based on *post hoc* Tukey's comparisons.

stabilized (two-way repeated measures ANOVA, significant time × bed thickness interaction, Table 1, Fig. 3). The 12-cm-thick beds maintained significantly greater cover than the 4-cm-thick beds by the end of the study (82.7 ± 3.3% versus 56.5 ± 6.6% shell cover for 12- and 4-cm-thick beds respectively, *post hoc* Tukey's comparisons, Fig. 3). There was no effect of shell deployment method on shell cover (Table 1, Fig. 3). On reference plots, shell coverage increased over time from 1.2 ± 0.8% in June 2010 to 18.8 ± 10.2% in June 2012, and qualitative observations indicated that these increases in shell coverage were due to dead *Crassostrea gigas* shell drift from constructed oyster beds.

At the termination of the study in June 2012, 62% of shells on 12-cm-thick beds had some mud deposited upon them, at an average depth of 2.1 ± 0.2 mm, compared with 88% of shells on the 4-cm-thick beds, with significantly higher average mud depth measuring 3.7 ± 0.3 mm (two-way ANOVA, significant effect of shell bed thickness, Table 2).

After 24 mo, the oyster bed treatments all lost shell volume at the same rate. The percent of shell loss did not differ significantly across treatments (two-way ANOVA, Table 3), but ranged from averages of 35.47%–64.0% within treatments and with an average across-treatment shell volume loss of 52 ± 6.42%.

Spatfall

Generally, greatest spatfall occurred during 2012, ranging from 1,459.2 ± 238.8 to 2,259.2 ± 373.6 cumulative settlers/m^2, and the lowest amount of spatfall occurred in 2011, ranging from 451.2 ± 50.7 to 630.4 ± 121.9 cumulative settlers/m^2 (Fig. 4). Spatfall in 2010 was intermediate relative to 2011 and 2012, ranging from 918.4 ± 81.1 to 1,209.6 ± 105.5 cumulative settlers/m^2.

TABLE 2.

Two-way ANOVA test statistics for effects of shell bed thickness (bed thick), deployment method (deploy meth) and their interactions on millimeter of mud deposited onto shell 24 mo after oyster beds were constructed in Newport Bay, CA.

Source	*df*	Sum of squares	Mean square	*F* ratio	*P*
Bed thick	1	12.17	12.17	22.28	**0.0002**
Deploy meth	1	1.41	1.41	2.58	0.1279
Bed thick × deploy meth	1	0.18	0.18	0.33	0.5711
Error	16	8.75	0.55		
Total	19	22.52			

Significant effects in bold.

There was a significant interaction between time and deployment method on cumulative spatfall, with a significant effect of year that varied according to treatment (Table 1, Fig. 4). This interaction was evident in 2012, where *post hoc* Tukey's tests indicated that cumulative spatfall was greatest on the beds where shell was deployed loosely (Fig. 4), whereas in other years, there were no differences in cumulative spatfall across treatments.

The greatest pulse of spatfall occurred at a different time each year (Table 4). In 2010, it occurred in mid and late June, whereas in 2011 spatfall was consistently low from mid-April through August, with no significant pulse (Table 4). In 2012, there was a substantial pulse in late May and a smaller pulse in mid-August. Across the entire 2-y period, all beds and reference plots experienced pulses of spatfall in synchrony, such that the greatest pulse occurred during the same census period regardless of treatment.

Spat Recruitment

Across the study period, *Ostrea lurida* recruit densities onto excavated shell ranged from 0 to 348.8 ± 75.6 recruits/m^2. Greatest *O. lurida* recruit densities were recorded in June 2012 (ranging from 38.4/m^2 ± 13.0 to 348.8 recruits/m^2 ± 75.6) with the 12-cm-thick beds receiving significantly greater recruitment than 4-cm-thick beds. When comparing the 12-cm-thick shell beds in June 2012, the bagged shell beds experienced significantly greater recruitment than the loose shell beds (two-way repeated measures ANOVA, significant time × bed thickness and bed thickness × deployment method interactions, Table 1, Fig. 5). Reference beds experienced no detectable recruitment over the course of the study period.

Adult Oyster Density

The method of shell deployment and the shell bed thickness had no effect on adult density; however, adult density did change significantly over time (two-way repeated measures ANOVA, Table 1) on all oyster beds. *Post hoc* Tukey's tests indicated that adult *Ostrea lurida* density increased significantly on all oyster beds from June 2010 compared with all subsequent sampling events (Fig. 6). The density of oysters at the site prior to oyster bed construction averaged 2.2 ± 1.4 oysters/m^2 and thereafter ranged from 38.4 to 172.8 oysters/m^2 across the study period. At study termination, 24 mo after the oyster beds were constructed, the average oyster density was 26.4 times the

TABLE 3.

Two-way ANOVA test statistics for effects of shell bed thickness (bed thick), deployment method (deploy meth) and their interactions on percent volume shell loss 24 mo after oyster beds were constructed in Newport Bay, CA.

Source	*df*	Sum of squares	Mean square	*F* ratio	*P*
Bed thick	1	1,046.90	1046.90	1.24	0.2820
Deploy meth	1	989.82	989.82	1.17	0.2951
Bed thick × deploy meth	1	99.90	99.90	0.12	0.7354
Error	16	13,515.17	844.70		
Total	19	15,651.81			

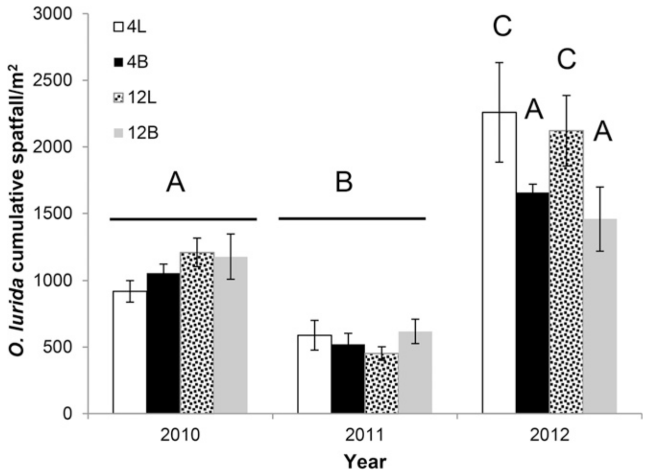

Figure 4. Mean *Ostrea lurida* cumulative spatfall onto deployed ceramic tiles per square meter across treatments per year. Error bars = ±1 SE. L = loose shell, B = bagged shell, 12 = 12 cm thick shell bed, 4 = 4 cm thick shell bed. Groups with different letters over bars (e.g., A, B, or C) are significantly different, based on *post hoc* Tukey's comparisons.

starting density, at 59.2 ± 3.2 oysters/m^2 across all oyster beds. In contrast, while oysters were also present on the reference plots in low densities prior to oyster bed construction (5.6 ± 3.2 oysters/m^2), they were not detected on the reference plots at the termination of the study (0.0/m^2 ± 0.0) nor throughout the study period. There was one notable exception, when a medium-sized rock was encountered in one reference plot quadrat during January 2012 that contained 13 (unlucky) oysters.

DISCUSSION

Despite significant loss of shell volume from constructed oyster beds, the combined settlement, recruitment, and adult density data gathered during our study provide evidence that oyster densities in Newport Bay, CA, can be increased significantly by augmenting habitat with oyster shell. Our constructed oyster beds, regardless of method of deployment or initial shell planting thickness, quickly and significantly increased adult *Ostrea lurida* density relative to unmanipulated mudflat. After only 2 y, average oyster density on the constructed beds was greater than 26 times the starting density at the site. In other locations, depletion of Olympia oyster populations has necessitated the introduction of seed stock to revive locally extinct oyster beds (Dinnel et al. 2009). When restoration can be accomplished via simple habitat augmentation, the risk is lowest for unintended genetic impacts (Camara & Vadopalas 2009). Addition of seed stock does not appear to be necessary to increase the local density of Olympia oysters in Newport Bay, CA. Others have similarly found that simply adding oyster shell to mudflat quickly augments eastern oyster (*Crassostrea virginica*) and Olympia oyster densities (O'Beirn et al. 2000, Piazza et al. 2005, Nestlerode et al. 2007, Dinnel et al. 2009).

After 2 y, the 12-cm-thick shell beds attracted greater recruit densities, maintained higher percent shell cover, and accrued less sedimentation than did 4-cm-thick beds. Over the course of the 2-y study, this did not yet result in significantly greater adult oyster densities on thick shell beds; however, given the exceptionally strong recruitment pulse associated with the last (June 2012) sampling period (Fig. 5), coupled with the much higher retention of shell (Fig. 3) and lower rate of mud deposition on thick beds, the long-term stability of thick shell beds may be greater than thin beds. Together, these findings argue for implementing thicker shell beds that provide higher relief and are more resistant to sedimentation.

Mann and Powell (2007) argued that maintaining structured shell cover is a critical element of any restoration effort because without a clear settlement destination for spat, oysters cannot self-perpetuate. Others (Bartol & Mann 1997, Lenihan & Peterson 1998, Lenihan 1999) found that subtidal oysters (e.g., *Crassostrea virginica*) experience increased survival when located higher on a reef (allowing them to escape hypoxic events near the bottom) or within the interstices of a reef (subsurface reef habitat provides refuge from environmental elements and predation). Collectively, these studies highlight the importance of reef height and the value of three dimensional habitat. Whereas in the case of the Olympia oyster (this study), thicker beds appeared to be favorable because of their ability to alleviate sedimentation and maintain shell cover, thus providing more potential spat habitat, they may also provide more refuge opportunities than thinner beds, as with other oyster species on subtidal reefs. This unexplored aspect of shell bed thickness provides an excellent venue for future research on Olympia oysters.

Shell deployment method was not a significant factor in determining adult oyster density, shell volume loss, or maintaining shell cover. Based on qualitative field observations, the jute began to degrade within 4 mo of bed construction. Subsequently, in samples excavated at 6–7 mo after construction, jute fragments were abundantly evident in the excavated material. The rapid degradation of the jute bags may have contributed to our inability to observe an effect on shell cover, shell volume loss, and other response factors. Reasonably strong recruitment of adult oysters was observed (and many other sessile marine invertebrates) during the first 6 mo of the study (see Fig. 6), which may have at least partly consolidated the loose shell beds and confounded the ability to measure an effect of deployment method. Regardless of the cause of the lack of effect, the use of biodegradable jute bagging appears unwarranted, and this will save time and money. For this study, the decision to use biodegradable jute was necessitated by permitting restrictions (although the authors agreed with permitting agency concerns about introducing plastic mesh into

TABLE 4.

Average *Ostrea lurida* spatfall/m^2/day (with SD) onto ceramic tiles deployed facedown 10–15 cm above the substratum on constructed oyster beds and unmanipulated reference plots as a function of treatment in Newport Beach, CA, from June 2010 to August 2012.

Date deployed	12B spatfall/m^2/ day (SD)	12L spatfall/m^2/ day (SD)	4B spatfall/m^2/ day (SD)	4L spatfall/m^2/ day (SD)	Reference plots spatfall/m^2/day (SD)	Average across treatments spatfall/m^2/ day (SD)
June 15, 2010	39.31 (12.08)	39.09 (6.78)	41.37 (13.68)	35.43 (10.38)	38.40 (16.05)	38.72 (11.31)
June 29, 2010	36.57 (19.51)	41.37 (16.4)	29.94 (7.25)	26.06 (5.85)	30.17 (8.02)	32.82 (12.83)
July 13, 2010	6.40 (3.29)	3.89 (1.53)	2.97 (1.73)	2.74 (2.23)	3.89 (3.49)	3.98 (2.70)
July 27, 2010	1.37 (1.49)	1.6 (1.30)	1.14 (0.81)	0.91 (0.96)	1.83 (1.73)	1.37 (1.23)
August 10, 2010	0.27 (0.60)	0.27 (0.60)	0.00 (0.00)	0.27 (0.60)	0.27 (0.60)	0.21 (0.50)
August 22, 2010	0.23 (0.51)	0.23 (0.51)	0.00 (0.00)	0.23 (0.51)	0.23 (0.51)	0.18 (0.43)
September 5, 2010	0.68 (0.55)	1.07 (0.80)	0.68 (0.81)	3.49 (4.87)	1.07 (0.87)	1.40 (2.35)
October 8, 2010	0.43 (0.70)	0.11 (0.24)	0.32 (0.81)	0.21 (0.29)	0.64 (0.88)	0.34 (0.55)
November 7, 2010	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.23 (0.51)	0.05 (0.23)
December 5, 2010	0.00 (0.00)	0.00 (0.00)	0.11 (0.26)	0.00 (0.00)	0.00 (0.00)	0.02 (0.11)
January 2, 2011	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.11 (0.26)	0.11 (0.26)	0.05 (0.16)
January 30, 2011	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
February 27, 2011	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
March 20, 2011	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
April 17, 2011	5.24 (2.15)	3.10 (2.34)	3.30 (1.05)	3.10 (2.62)	3.39 (2.38)	3.63 (2.16)
May 20, 2011	0.46 (0.63)	0.00 (0.00)	0.69 (0.63)	1.14 (1.98)	0.46 (1.02)	0.55 (1.05)
June 3, 2011	1.14 (1.62)	1.60 (1.91)	1.14 (0.81)	1.60 (1.02)	2.06 (0.96)	1.51 (1.27)
June 17, 2011	7.77 (3.74)	3.20 (1.88)	8.23 (5.56)	8.23 (5.38)	9.60 (3.93)	7.41 (4.53)
July 1, 2011	4.57 (3.23)	4.11 (3.49)	3.89 (1.53)	3.66 (2.96)	5.26 (2.37)	4.30 (2.62)
July 15, 2011	8.91 (6.33)	8.23 (3.17)	8.46 (2.87)	12.57 (6.46)	11.89 (4.61)	10.01 (4.87)
July 29, 2011	3.20 (2.85)	3.89 (1.73)	3.20 (1.70)	2.51 (1.7)	3.43 (1.14)	3.25 (1.80)
August 12, 2011	4.57 (5.42)	2.74 (1.91)	2.97 (2.87)	2.97 (2.63)	2.29 (1.62)	3.11 (3.02)
August 26, 2011	1.14 (1.98)	1.14 (1.62)	0.91 (2.04)	2.06 (1.49)	2.06 (2.48)	1.46 (1.85)
September 9, 2011	0.64 (0.67)	0.48 (0.44)	0.32 (0.44)	0.96 (0.36)	1.92 (2.30)	0.86 (1.18)
September 29, 2011	0.11 (0.24)	0.32 (0.48)	0.43 (0.45)	0.43 (0.45)	0.75 (0.48)	0.41 (0.44)
October 28, 2011	0.00 (0.00)	0.00 (0.00)	0.11 (0.24)	0.00 (0.00)	0.21 (0.48)	0.06 (0.23)
November 27, 2011	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
December 26, 2011	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
January 19, 2012	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
February 19, 2012	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
March 18, 2012	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
April 8, 2012	2.17 (0.99)	2.06 (2.28)	1.96 (1.12)	1.65 (0.67)	2.99 (1.48)	2.17 (1.37)
May 9, 2012	12.8 (8.06)	17.16 (11.24)	16.00 (5.34)	14.55 (4.93)	19.2 (7.37)	15.94 (7.40)
May 20, 2012	48.23 (31.67)	57.60 (17.61)	60.80 (20.27)	70.86 (26.11)	59.66 (14.64)	59.43 (22.16)
June 3, 2012	7.68 (8.24)	50.77 (39.69)	20.91 (10.19)	51.2 (38.03)	23.04 (24.68)	30.72 (30.79)
June 18, 2012	2.29 (3.96)	3.66 (4.38)	2.74 (2.08)	3.66 (3.17)	0.46 (1.02)	2.56 (3.13)
July 2, 2012	0.56 (0.84)	1.69 (2.34)	1.13 (1.03)	1.32 (1.57)	1.32 (1.57)	1.20 (1.48)
July 19, 2012	0.23 (0.51)	0.00 (0.00)	0.23 (0.51)	0.23 (0.51)	0.69 (1.02)	0.27 (0.60)
August 2, 2012	2.97 (2.08)	4.34 (4.23)	1.83 (2.87)	1.83 (1.73)	2.51 (2.2)	2.70 (2.70)
August 16, 2012	26.74 (8.34)	11.43 (8.67)	12.11 (3.84)	13.26 (16.49)	19.20 (11.41)	16.55 (11.34)
August 30, 2012	2.06 (1.49)	0.91 (1.25)	0.23 (0.51)	1.83 (2.37)	3.20 (3.47)	1.65 (2.17)

Experimental design including treatment beds ($n = 5$ beds per treatment) of two consolidation types (L = loose shell, B = bagged shell), two thicknesses (12 = 12 cm thick, 4 = 4 cm thick), plus five unmanipulated plots (“reference plots”).

the environment, see Laist 1997, Katsanevakis 2008); however, the results of this study cannot be extended to consolidation of shell using plastic mesh bags, some of which may have maintained their integrity throughout the course of the study (Coen et al. 2013).

Other shell restoration practitioners point to the many benefits of shell bagging for smaller-scale restoration efforts including providing ease of logistics, providing the ability to engage and educate community volunteers while preparing and building reefs (Hadley & Coen 2002, Taylor & Bushek 2008, Brumbaugh & Coen 2009), and improving ability to control reef height during the deployment phase. To our knowledge, although both unconsolidated and consolidated shell deployments are widely used, no published studies until this one have directly compared the effectiveness of the methods in augmenting oyster density.

Curiously, method of deployment did affect spatfall onto our settlement tiles in the last year of our study, 2012, although the mechanism is unknown. These findings are incompatible with all of the other findings in this study, where method of

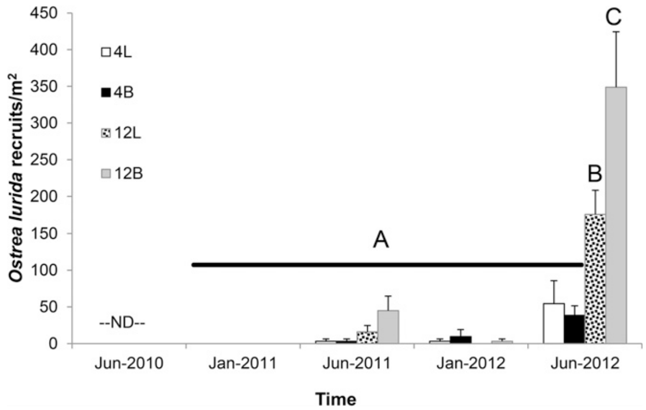

Figure 5. Mean *Ostrea lurida* recruits on excavated shells per square meter as a function of treatment per period. Error bars = ±1 SE. ND = no recruitment data were collected on any treatment for June 2010. L = loose shell, B = bagged shell, 12 = 12 cm thick shell bed, 4 = 4 cm thick shell bed. Groups with different letters over bars (e.g., A, B, or C) are significantly different, based on *post hoc* Tukey's comparisons.

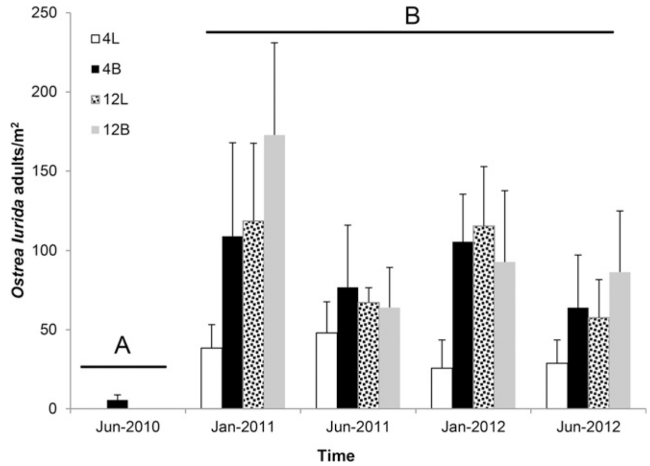

Figure 6. Mean *Ostrea lurida* adults on excavated shells per square meter as a function of treatment per period. Error bars = ±1 SE. L = loose shell, B = bagged shell, 12 = 12 cm thick shell bed, 4 = 4 cm thick shell bed. Groups with different letters over bars (e.g., A, B, or C) are significantly different, based on *post hoc* Tukey's comparisons.

deployment had the opposite effect on recruit density and no effect on adult density; however, spatfall monitoring extended through September 2012, with a significant pulse of settlement occurring in August 2012 (Table 4), whereas the census of recruits and adults occurred in June 2012. Because of the short time span of the study, it is difficult to assess whether this increase in spatfall would have been reflected in increased recruitment of oysters to the constructed beds in subsequent months.

This study was set up as a replicated design to explore techniques that may be valuable in restoration for this species and was not explicitly a restoration project. Rather, it aimed to determine which methods are most advantageous for achieving increased Olympia oyster density, and these data will be useful for future restoration projects. Restoration ecologists have underscored the importance of using reference sites in establishing target metrics for restoration goals (Brumbaugh et al. 2006, Baggett et al. 2014). For the Olympia oyster throughout its range, it remains difficult to establish these metrics due to the lack of suitable reference sites and quantitative data on historical species abundance and density. For example, elsewhere in Newport Bay, there are no existing Olympia oyster beds against which to compare our adult oyster density data. Although beds of oysters were observed and known to exist throughout southern California estuaries through the early 1900s (Ingersoll 1881, Gilbert 1889, Bonnot 1935), quantitative data on density of Olympia oysters in beds are nonexistent; however, the average density (59.2 oysters/m^2) and the maximum density (172.8 oysters m^2) recorded after 2 y on the constructed beds are much greater than the maximum density of Olympia oysters (19.2 oysters/m^2) on any other habitat (e.g., cobble, mud, riprap, seawall, pier piles) in Newport Bay recorded by Polson and Zacherl (2009) in their 2005 surveys. The recorded densities are also higher than the average densities of oysters surveyed elsewhere in Newport Bay more recently. For example, in 2012, at an adjacent site with 65% cover of hard substrata (mix of shell, cobble, and concrete) surveyors measured oyster density at 40.4 ± 6.7 oysters/m^2, and across multiple habitat types (e.g., seawall, dock piling, mudflats), surveyors measured average density at 30.7 ± 2.9 oysters/m^2 (D. Zacherl and N. Tronske, CSU Fullerton, personal communication, July 2015).

Elsewhere across the U.S. West Coast, sites in San Francisco, CA, which underwent recent restoration (e.g., Point San Quentin), achieved a maximum density as high as or higher than the maximum density in this study (compare 172.9 oysters/m^2 in this study to 146–961 oysters/m^2; Polson & Zacherl 2009, Wasson et al. 2015). In British Columbia, Olympia oyster density at multiple sites (at 240–360 oysters/m^2) exceeds that recorded in this study (Gillespie 2009, Jacobsen 2009).

Based on these results and other published studies, one might infer that the existing substrata in Newport Bay (e.g., pier piling, rip rap, mudflat, and seawalls) cannot support oyster densities as high as that on oyster shell beds or reefs. This is impossible to directly measure outside of this study because of the complete absence of natural Olympia oyster beds, as discussed above; however, there are multiple reasons to expect that this might be the case. First, an oyster shell bed or reef offers significantly higher rugosity per unit area compared with dock piling or seawalls. Also, the oyster beds in this study were purposefully sited at a low tidal elevation (–0.15 m MLLW, where oysters are known to reach their density maximum; D. Zacherl, personal observations) on a mudflat with a shallow slope, compared with dock piling and seawalls that provide vertical substrata with little surface area at the appropriate tidal elevation. Finally, other restoration studies provide evidence that oyster shell supports higher adult oyster density than alternate substrata. White et al. (2009b) found consistently higher oyster recruitment on beds built with oyster shell compared with beds made of gravel or bare substrata. Oyster shell is more stable than clam shell or coal ash (Coen & Luckenbach 2000), which can be broken into smaller fragments that fill in interstitial space and decrease oyster survival and density. Nestlerode et al. (2007) also observed higher oyster density and survival on oyster shell reefs versus clamshell reefs and O'Beirn et al. (2000) observed greater oyster survival on constructed oyster reefs versus clamshell and coal ash reefs. Collectively, these studies suggest that oyster shell beds may be a more suitable habitat for oysters than both artificial (e.g., sea walls, dock piling, but see Theuerkauf et al. 2015) and other natural substrata (e.g., gravel, clam shells).

Importantly, only one nonnative Pacific oyster *Crassostrea gigas* recruited into the constructed beds in this study, although adults of this species are present throughout the estuaries in southern California, including Newport Bay in Orange County, Alamitos Bay in Los Angeles County, and estuaries throughout San Diego County, especially San Diego Bay (Crooks et al. 2015). The Pacific oyster is now recruiting throughout southern California estuaries (H. Henderson, Merkel Consulting, personal communication, August 2014; D. Zacherl, CSU Fullerton, personal communication, July 2015). One plausible explanation for no observed recruitment of *C. gigas* in this study could be that *C. gigas* shows zonation patterns with other oyster species (Krassoi et al. 2008). This is the case in southern California, where *C. gigas* reaches its maximum density well above +0.5 m MLLW, whereas *Ostrea lurida* achieves highest densities at –0.1 m MLLW and lower (D. Zacherl and T. Parker, CSU Fullerton, personal communication, July 2015). The constructed beds in this study were located at a tidal elevation that, perhaps, did not favor the recruitment of *C. gigas*.

Significant loss of shell volume occurred on the constructed beds, although percent shell cover stabilized within 6 mo of bed construction regardless of bed thickness (Fig. 3). Because surveyors measured shell volume only at study termination, it is difficult to assay the trajectory of shell volume loss, although qualitative and quantitative observations of the reference plots suggest that shell migrated from constructed beds onto the reference plots in the first year after bed construction and thereafter stabilized at ~18% shell cover. Collectively, the percent shell cover data suggest that shell volume loss may have stabilized after the first year, but that does not ameliorate the finding that shell loss was significant. Clearly, shell loss should be a major consideration for future restoration projects (Coen & Luckenbach 2000, Powell et al. 2006, Mann & Powell 2007) and these study findings reinforce the need to monitor this important metric. This study was designed as a short-term research project, but if constructed beds are to be maintained in the long term (i.e., restoration), shell beds will likely require ongoing augmentation.

Because there is no information available on the effect of shell bed height or shell deployment method for *Ostrea lurida* restoration, this study begins to illuminate the relative importance of both factors. The results point toward the advantages of using oyster shell to augment habitat in a manner that provides vertical relief from sedimentation. Thicker oyster shell beds maintained higher shell cover, less sedimentation, and higher recruit densities than thin shell beds. With limited available scientific information on *O. lurida* restoration in many locations throughout its range, the integration of science-based planning and monitoring as part of any future restoration effort is crucial. Monitoring provides valuable data that can drive the direction of future restoration goals and efforts, inform adaptive management, reveal variation of method efficacy across regions, and bolster success in restoring this ecologically important and recovering species.

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