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Informing Olympia Oyster Restoration: Evaluation of Factors That Limit Populations in a California Estuary

Kerstin Wasson

Abstract The goal of this investigation was to inform restoration strategies by determining which factors are most important in limiting Olympia oyster (*Ostrea lurida*) distribution and abundance at a Pacific coast estuary, Elkhorn Slough in central California, where Olympia oysters are currently extremely rare but were formerly abundant. An array of mensurative experiments and correlative analyses were used to examine the role of potential limiting factors. Absence of oysters was associated with symptoms of eutrophication, including elevated nutrient concentrations and turbidity. Oysters were also absent from all sites where water control structures resulted in minimal tidal exchange. Predation and competition did not appear to play a major role in surveyed oyster populations above Mean Lower Low Water but at lower elevations oysters were heavily fouled by non-native species. In most sites oysters were found only on large artificial substrates; survival on small natural hard substrates was apparently precluded by burial by fine sediments. Restoring more natural ecosystem processes by reducing nutrient and sediment inputs, increasing tidal exchange to areas behind water control structures, and preventing establishment of new non-native species would benefit Olympia oysters as well as support broader ecosystem-based management goals.

Keywords Ecosystem-based management · Elkhorn Slough · *Ostrea lurida* · Water quality

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Introduction

Bivalve shellfish restoration initiatives have become increasingly common in coastal habitats in recent decades because of increasing community awareness of declines in shellfish and their importance for ecosystem integrity, and as a result of increased funding (Brumbaugh et al. 2006). In estuarine ecosystems, oysters in particular have been the focus of conservation and restoration efforts. Oyster reefs have declined worldwide as a result of human exploitation and habitat alteration (Kirby 2004), and so have the ecosystem services they provide, ranging from commercial and recreational shellfish harvest by humans, provision of feeding habitat and refuge for fish and other invertebrates, and improvement of water quality through suspension-feeding activities (Brumbaugh et al. 2006; Coen et al. 2007).

Successful conservation and restoration depend on sound ecological frameworks, and an understanding of the mechanisms limiting distribution and abundance is necessary in order to protect and enhance a species that has declined (Salafsky et al. 2002). Many mechanisms have contributed to oyster declines globally, including overharvest, water quality degradation, habitat loss, and disease (Kirby 2004; Brumbaugh et al. 2006). Some oyster species, such as the Eastern oyster (*Crassostrea virginica*), have been intensively studied for decades, and ecological knowledge is supporting restoration efforts (Luckenbach et al. 1999). Even so, better links could be forged between ecological monitoring and restoration planning (Breitburg et al. 2000; Mann and Powell 2007).

The native oyster of the Pacific coast of the United States, the Olympia oyster (*Ostrea lurida*), has been the subject of relatively few ecological investigations (Baker 1995; Cook et al. 2000; Kimbro and Grosholz 2006; NOAA Restoration Center 2007; Trimble et al. 2009). A

literature search (Aquatic Sciences and Fisheries Abstracts) found 63 papers concerning Olympia oysters, vs. 2848 regarding Eastern oysters, highlighting the dramatic difference in scientific attention received by these oyster species (Trimble et al. 2009). The Olympia oyster has declined precipitously on the Pacific coast and community-based oyster restoration efforts are underway in many Pacific estuaries, focusing mainly on addition of hard substrates for settlement (NOAA Restoration Center 2007). Conservation and restoration planning for Olympia oysters could be enhanced by examination of the mechanisms that have contributed to their past decline and continued low abundance. The goal of this study was to identify the factors limiting oyster abundance at one Pacific coast estuary, Elkhorn Slough, in order to inform restoration strategies there and at other regional estuaries.

The Elkhorn Slough estuary (Fig. 1), located on the central California coast about midway between the coastal towns of Santa Cruz and Monterey, consists of a network of interconnected estuarine channels, the largest of which is

Fig. 1 Oyster survey sites. Numbered sites represent water monitoring sites, with hard substrate present, that were surveyed for oysters. Empty circles=sites without oysters, gray shaded circles=sites with low abundance of oysters, darkly shaded circles=sites with high abundance. Sites 4, 7, 8, 9, 10, and 11 were the locations of transects and recruitment studies. The unnumbered sites in Elkhorn Slough are sites dominated by soft sediments, none of which had oysters present
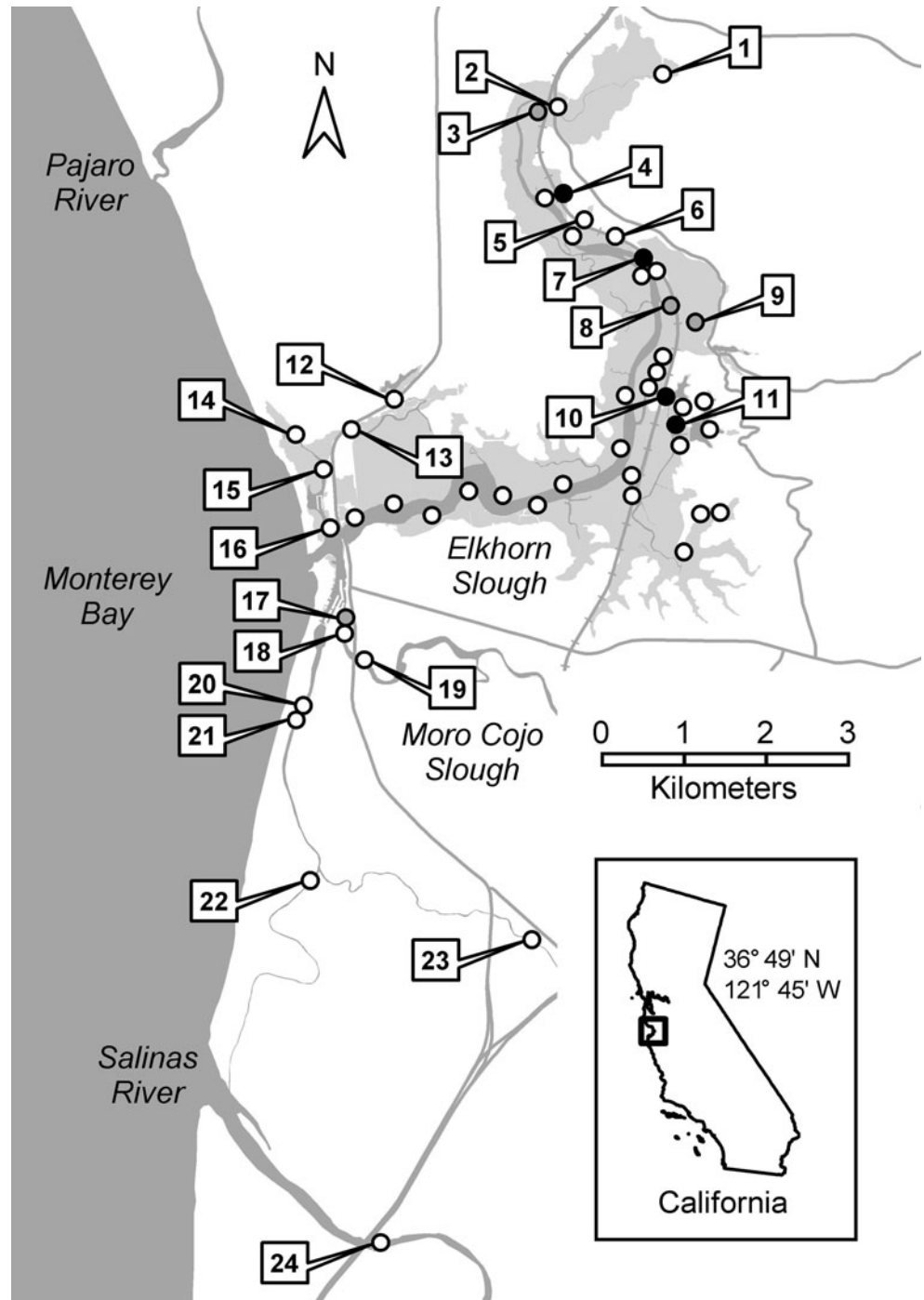
Elkhorn Slough. Other channels include Bennett Slough, Moro Cojo Slough, Tembladero Slough, and the old Salinas River channel. The Elkhorn Slough watershed has undergone significant land use changes over the past 150 years, and many parts are now intensively farmed (Caffrey et al. 2002). Estuarine habitats have also changed dramatically in this period, largely as a result of hydrological alterations (Van Dyke and Wasson 2005).

Olympia oysters have occurred at the Elkhorn Slough estuary from 10,000 years ago to the present, but little is known about their distribution and abundance in past periods. Paleoecological data indicate that oysters dominated benthic communities in the lower estuary from 10,000–4,000 years ago, in Bennett Slough, lower Elkhorn Slough, and lower Moro Cojo Slough (Hornberger 1991). Oysters are present at low abundance in all Native American middens from five sites distributed around different portions of the estuarine system, in all periods represented, from 8,000–300 years before present (Jones 2002). In the late 1920s, MacGinitie (1935) conducted extensive surveys of mudflat communities in the estuary, and reported that the Olympia oyster was "very plentiful in all parts of the slough where there are rocks or pilings to which it can attach", and mentioned various sites in the estuarine mouth area as well as a railroad bridge closer to the head of Elkhorn Slough having especially abundant populations. In 1926, oystermen from San Francisco Bay heavily harvested Elkhorn Slough oyster populations (Barrett 1963), which implies that abundance was sufficient to make harvest worthwhile. Today, Olympia oysters are very rare in the Elkhorn Slough estuary, mostly limited to larger artificial hard substrates in the intertidal zone of the mid-upper channel of Elkhorn Slough. Even sites with the most abundant oyster populations are very limited in extent and have relatively low densities. Extensive surveys suggest that perhaps 5000 live oysters remain in the entire estuary (Wasson, unpublished data). Thus Olympia oysters have undergone a significant decline in the past century.

To evaluate the role of water quality, tidal restriction, and substrate limitation on oyster distribution, I conducted surveys of adult oysters and hard substrates at sites throughout the whole estuarine network. To more closely examine the role of water quality, sediment depth, tidal restriction, competition and predation I assessed adult and juvenile oyster populations and environmental parameters at six sites in Elkhorn Slough where adult oysters were present.

Methods

Water Quality and Oyster Abundance

To test for a correlation between water quality and oyster distribution and abundance, I analyzed data collected as a part of a 20-year volunteer water monitoring program conducted at sites around Elkhorn Slough. Data were collected approximately monthly by a volunteer who measured salinity, temperature, turbidity, dissolved oxygen, and fluorescence with a Yellow Springs Instruments 6600 sonde in the field. The volunteer also collected water samples that were analyzed for nitrate, ammonium, and phosphate by the Monterey County Water Resources Agency at the Consolidated Chemistry laboratory. Nitrate and dissolved inorganic phosphate were analyzed using standard wet chemistry techniques and a spectrophotometer; ammonium was detected using an ion selective electrode. Water quality data were collected for this program at 23 sites: all the numbered sites shown in Fig. 1, except site 8. Since site 8 was an oyster site of interest, I averaged data from the two closest adjacent sites (7 and 9) to obtain an estimate of water quality. Of these sites (described in Table 1), seven had full tidal exchange (no water control structures; maximum tidal range about 250 cm, as on the adjacent open coast), four had muted tidal exchange (moderate daily exchange through water control structures, with maximum tidal range from 15–100 cm), and 13 had minimal tidal exchange (very little, often irregular tidal exchange through water control structures, with maximum tidal range from 1–15 cm). For all 24 of the sites, I calculated the average of each water quality parameter for five recent years (2002–2006). Although not all of these parameters are likely to be directly relevant to oysters, the goal was to use the suite of standard variables monitored in coastal water quality programs to detect signatures of water quality correlated with oyster presence.

At all 24 sites, I conducted field surveys during 2005–2007 to determine whether oysters were either absent, present at low abundance (<200 individuals within 100 m radius of water sampling site, or <5/m^2 of hard substrate), or high abundance (>200 individuals, or >5/m^2 of hard substrate). No sites differed among years of assessment. All sites had hard substrates, since these sites were chosen as regular water monitoring sites due to easy access along roads and bridges, which are typically reinforced in wetlands by rip rap or gravel berms. The area of hard substrate was estimated at all water quality sites with oysters present.

I conducted several related multivariate analyses (Clarke and Warwick 2001) of water quality vs. oyster abundance using the program Primer v. 6 (Clarke and Gorley 2006). I used draftsman plots to detect skew and log-transformed those parameters that were visibly skewed: the three nutrients, turbidity, and chlorophyll. I normalized all data and used Euclidean distance to create a resemblance matrix, which I used to conduct Analysis of Similarities (ANOSIM) to test for differences among oyster abundance categories. I used a non-metric multidimensional scaling (nMDS) to

Table 1 Description of sites. Numbers in the first column correspond to those in Fig. 1. Site names are given, as well as tidal exchange category (full, muted, minimal), as described in the Methods. Oyster relative abundance in the final column

Number	Site name	Tidal exchange	Oysters
1	Porter Marsh: Carneros Creek	minimal	absent
2	Porter Marsh: Hudson Landing East	minimal	absent
3	Hudson Landing West	full	low abundance
4	North Azevedo Pond	muted	high abundance
5	Central Azevedo Pond	minimal	absent
6	South Azevedo Pond	minimal	absent
7	Kirby Park	full	high abundance
8	North Marsh Exit	full	low abundance
9	North Marsh	muted	low abundance
10	Whistlestop Lagoon	muted	high abundance
11	South Marsh	full	high abundance
12	Struve Pond	minimal	absent
13	Bennett Slough East	minimal	absent
14	Bennett Slough West	minimal	absent
15	Bennett Slough: Jetty Road	muted	absent
16	Moss Landing North Harbor: Skippers-Sea Harvest	full	absent
17	Moss Landing South Harbor: Moss Landing Road North	full	low abundance
18	Moro Cojo: Moss Landing Road South	minimal	absent
19	Moro Cojo: Highway One	minimal	absent
20	Moss Landing South Harbor: Potrero Road North	full	absent
21	Old Salinas River Channel: Potrero Road South	minimal	absent
22	Old Salinas River Channel: Monterey Dunes Way	minimal	absent
23	Tembladero Slough	minimal	absent
24	Salinas River Bridge	minimal	absent

visualize clustering of sites according to these categories. I calculated Similarity Percentages (SIMPER) to determine which parameters contributed the most to observed dissimilarities between categories.

To summarize the water quality conditions associated with different levels of oyster abundance, I calculated the average value and range for each parameter for the 16 sites without oysters, the four sites with low abundance, and the four with high abundance. (Range in this case refers to the lowest and highest value observed among the sites falling into each of the three oyster abundance categories, but since the site data represent an average of 5 years of data, the true extremes detected at individual sites are greater.)

Substrate Amount and Size

To examine the role of substrate limitation, I conducted surveys at 25 haphazardly selected intertidal mudflat sites (shown as unnumbered circles in Fig. 1) in Elkhorn Slough in July 2007. Each survey began with rapid 10 min searches for oysters, followed by an estimate of the size of the search area (intended to range from 50–100 m²) and the percentage of this area that had hard substrate. Proportion of these sites with oysters present was compared to proportion of fully tidal water quality sampling sites with

oysters present using a Chi-Square test, to examine differences between sites with very little vs. abundant hard substrates, respectively.

To determine whether the size of substrates that can be used by oysters differs with sediment depth, I assessed depth of unconsolidated sediments and size of smallest substrates used by oysters at 10 locations. At each location, I spent 10 min searching for the 10 smallest substrates with live oysters attached, within a search area of about 100 m². I measured the longest axis of each of these 10 substrates to the nearest 0.5 cm. Within this search area, I obtained three haphazardly located estimates of sediment depth by dropping a metal rod (rebar 153 cm long, 1 cm in diameter) from a height of 50 cm and measuring to the nearest 1 cm the length of the rod that sunk into the mud. For each location, I calculated the mean of the 10 substrate sizes and three depth readings. I conducted a simple regression between the mean size of the smallest substrates used by live oysters and sediment depth.

Adult Density, Survival, and Size

Adult oyster populations were characterized in Fall 2007 at the three full exchange sites with the greatest oyster numbers (sites 7, 8, 11 in Fig. 1) and at three adjacent sites

with muted tidal exchange (4, 9, 10), which were the only sites in the estuary with oysters present in restricted tidal exchange (Table 1). These sites have a mean tidal range of about 100, 15, and 35 cm, respectively. At each site, permanent 10 m transects marked with metal rods (rebar) were established parallel to the shoreline to form the basis of a long-term oyster monitoring program. At full tidal exchange sites, transects were established in both the low intertidal (approximately at 10 cm above Mean Lower Low Water (MLLW)) and the mid intertidal zone (approximately at 50 cm above MLLW). These paired transects were located parallel to each other on the shoreline. At the muted exchange sites, which are lagoonal at all tides, with only a very narrow intertidal zone, transects were established in the shallow subtidal zone, in about 10–20 cm of water at low tide. At each site, either two or three transects (or transect-pairs, at full exchange sites) were established, depending on the horizontal extent of hard substrate available along the shoreline (three at sites 7, 10, 11, two at sites 4, 8, 9). My previous qualitative observations had suggested that greatest oyster densities occur at Elkhorn Slough in approximately the zone where low intertidal transects were located at fully tidal sites, and in the shallow subtidal zone where transects were located at muted tidal sites.

In each transect, a 50×50 cm quadrat was placed on the shoreward side of the transect tape at one meter intervals starting at zero, for a total of 10 quadrats per transect. In each quadrat, live and dead oysters were counted and live oysters were measured with calipers (maximum shell dimension measured to the nearest mm). Densities (m^{-2}) and percentage of oysters that were alive in each quadrat were calculated.

To assess the effect of tidal elevation on the various parameters measured in the transects, I averaged all the quadrats per transect for all the full tidal sites (the only ones where I had paired high and low transects). I then conducted a paired T-test using each transect-pair as the replicate ($n=8$). To examine the effect of tidal restriction, I averaged all transects per muted site, and all low transects per full site (because the low transects were most similar to the muted ones, in being submerged most of the time). I conducted a T-test using tidal exchange (full vs. muted) as the factor, using sites as replicates ($n=3$).

Recruitment and Juvenile Growth and Survival

Recruitment rates and juvenile growth and survival were assessed at the same six sites and transects surveyed for adults (see above). I deployed eight bricks haphazardly along the transects at each site in June 2007. At fully tidal sites, the bricks were placed along the low intertidal transect. Bricks were placed on the available substrates at each site, which varied from gravel bars to large rocks interspersed in mud. The bricks were retrieved in March 2008. Recruitment occurs from about May–November in this region (Wasson, unpublished). All eight bricks were retrieved at four of the sites; at site 4 I found seven and at site 7 I found six bricks. Each brick was scored qualitatively as having been subject to high sedimentation (mud adhering to brick or brick faces black with anoxic mud) or low sedimentation (no conspicuous signs of mud). I then cleaned off the mud to conduct further assessments.

On the sides and bottom of each brick, all live and dead juvenile oysters >3 mm were counted and measured. This allowed me to calculate density of live and dead juveniles (a proxy for recruitment rate), percentage of juveniles that were alive (a proxy for survival rate), and size (a proxy for growth rate). The smallest recruits (<3 mm) were not counted because they were difficult to detect, so mortality occurring in the earliest period following recruitment was not assessed. I estimated the percent cover of bare space (as a proxy for the strength of competition for space on the brick). I conducted a T-test to examine the effect of tidal exchange (full vs. muted) on the above parameters, using sites as replicates ($n=3$). I also conducted a T-test to examine the effect of sedimentation (low vs. high) on these parameters (comparing 19 bricks that were scored as having been subject to "low" sedimentation vs. 17 scored "high").

For all juveniles that were dead but still had the top valve attached, I noted whether there was evidence of predation (broken upper valve or small drill hole). Potential predators in Elkhorn Slough include sea otters, various sharks and rays, crabs, and native snails (small whelks and moon snails); non-native oyster drills do not occur in the estuary. Overgrowth (sessile organism growing over upper valve) was also assessed, because the estuary harbors extensive populations of non-native sessile species on hard substrates. I also noted if there was no obvious cause of death (upper valve intact, gaping). I then tallied these scores to determine frequency of evidence for predation, overgrowth, or other cause of death among recently dead juveniles.

To examine the potential effect of the invasive tubeworm *Ficopomatus enigmaticus* on juvenile oyster survival and growth, I conducted paired comparisons. On each brick face, I searched for any juvenile oysters surrounded by *Ficopomatus* (defined as having >50% of the shell perimeter surrounded). If I found such an individual, I searched for a second juvenile on the same brick face that was not surrounded (defined as having <20% of the perimeter surrounded by *Ficopomatus*); when there were multiple such individuals I chose the one closest to the surrounded individual. I then measured the size of these paired surrounded and non-surrounded juveniles and noted whether they were dead or alive. I conducted a paired T-test
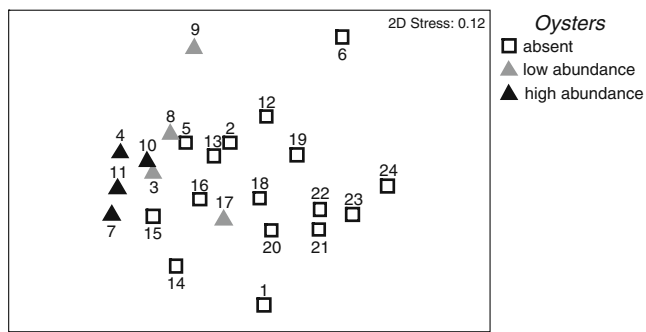
Fig. 2 Non-metric multidimensional scaling plot of 24 sites at Elkhorn Slough. Water quality differs significantly between sites without vs. with oysters

to determine whether size of surrounded vs. non-surrounded juveniles differed, and a Chi-Square test to determine whether mortality differed.

Results

Water Quality, Tidal Restriction, and Oyster Distribution

The multivariate analyses revealed that water quality differed for sites with different levels of oyster abundance. Using ANOSIM, I determined that sites with and without oysters were significantly different ($R=0.242$, $P=0.013$). For a finer scale comparison, I compared sites with oysters absent, present at low abundance, and present at high abundance. The overall ANOSIM was marginally significant ($R=0.147$, $P=0.098$); sites with oysters absent vs. at high abundance were significantly different ($R=0.294$, $P=0.025$); sites with oysters at high vs. low abundance were

marginally different ($R=0.25$, $P=0.057$); sites with oysters absent vs. at low abundance did not differ significantly ($R=0.078$, $P=0.29$). These patterns are visually apparent in a nMDS plot (Fig. 2), where sites with highly abundant oysters show no overlap with those without oysters and little overlap with those with oysters at low abundance, but sites with oysters absent and at low abundance show considerable overlap.

The nMDS plot also reveals that sites with high abundance of oysters are clustered most closely together, while those with low abundance of oysters show somewhat more spread, and those with oysters absent are most dissimilar from each other. This pattern is also apparent from average squared distances (as a measure of dissimilarity) among sites within the high, low, and absent categories (2.23, 6.41, and 8.58, respectively). Likewise, the ranges for most parameters (Table 2) are greatest for the absent and lowest for the high abundance categories.

The SIMPER analysis revealed five parameters each contribute more than 10% to the dissimilarity between the sites where oysters were absent vs. highly abundant. Turbidity, nutrients (phosphate, nitrate, ammonia), and dissolved oxygen were all higher at sites where oysters were absent than where they were highly abundant (Table 2). Four parameters contributed more than 10% to the dissimilarity between sites where oysters were at high vs. low abundance. Turbidity, dissolved oxygen, and chlorophyll were lower in sites with highly abundant oysters (Table 2). Temperature on average was similar between the two categories but was less variable at sites with highly abundant oysters (Table 2).

Tidal restriction was correlated with oyster distribution (Table 1). Oysters were absent from all 13 sites with

Table 2 Summary of water quality parameters related to oyster abundance. For each category, the average and range are calculated from the five-year-averages for all stations in each category. Parameters that contributed more than 10% to dissimilarity between

categories in a SIMPER analysis are marked with * if they distinguished oysters absent vs. present at high abundance, ** if they distinguished oysters present at low vs. high abundance, and *** if they contributed to distinguishing both of these

Parameter	Sites where oysters are…					
	Absent		Present at low abundance		Present at high abundance	
	Average	Range	Average	Range	Average	Range
Salinity (ppt)	19	(3.7–28)	25	(20–34)	27	(25–29)
Temperature (°C)**	17	(16–20)	18	(16–20)	18	(17–19)
pH	8.3	(7.8–8.6)	8.2	(8.1–8.4)	8.1	(8.0–8.2)
Dissolved oxygen (mg/L)***	9.4	(8.1–11)	9.2	(9.0–9.7)	8.5	(7.4–9.5)
Turbidity (NTU)***	59	(15–163)	45	(13–62)	13	(9.8–17)
Fluorescence (μg/L)**	38	(3.5–96)	28	(11–67)	15	(9.7–18)
Nitrate (mg/L)*	5.6	(0.21–22)	1.6	(0.65–3.0)	0.34	(0.25–0.44)
Phosphate (mg/L)*	0.36	(0.14–0.63)	0.22	(0.090–0.38)	0.11	(0.09–0.13)
Ammonia (mg/L)*	0.22	(0.09–0.37)	0.18	(0.14–0.23)	0.11	(0.10–0.12)

minimal tidal exchange. Of the four sites assessed with muted tidal exchange, oysters were absent from one, present at low abundance at one, and present at high abundance at two. Of seven sites with full tidal exchange, oysters were absent from two, present at low abundance at three, and present at high abundance at two.

Substrate Amount and Size

The searches of 25 intertidal mudflat sites in Elkhorn Slough yielded no oysters at any site. The search area averaged 83 m^2 per site, of which an average of 1.4% consisted of hard substrate; thus about 1.1 m^2 of hard substrate were available per search area at each site for oysters, but none of these hosted oysters. However, 17 of these sites were located within 1 km of a site where oysters were detected in the water quality surveys, and eight of them were located within 500 m. In comparison, five of seven of the fully tidal water quality sites (comparable water quality to the 25 mudflat sites) had oysters present, and this difference in proportion of sites with oysters present (0/25 vs. 5/7) was highly significant ($P<0.0001$) in a Chi-Square test. All sites in the estuary with oysters present had extensive hard substrate of anthropogenic origin (rip rap added to protect bridges, roads, etc.), with a range of 34–288 m^2 and an average of 121 m^2 per site.

The survey of the smallest substrates hosting live oysters yielded a significant relationship between depth of unconsolidated sediment and substrate size (Fig. 3, simple regression, $R^2=0.64$, $P=0.006$). At sites with deep mud, live oysters were found only on large rocks added to protect human infrastructure, while at sites with shallow mud, live oysters occurred on small natural substrates (Fig. 4),
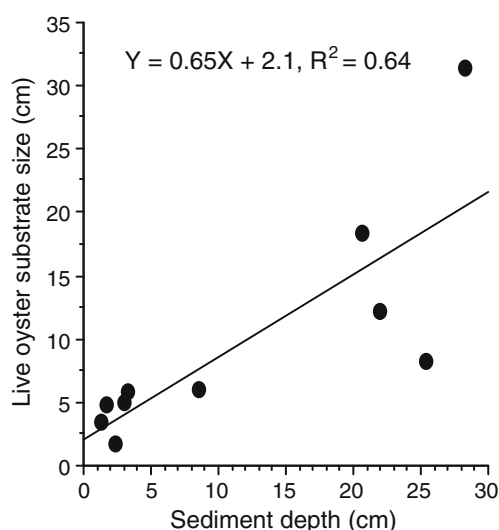

Fig. 4 Substrate size differences: **a** in areas with deep mud, live oysters are only found on large, artificial substrates such as rocks placed to protect bridges; and **b** in areas with shallow mud, live oysters are found on small natural substrates, such as shells of oysters and other molluscs

including dead and live oyster shells, clam shells, gravel, and live invasive mud snails (*Batillaria attramentaria*).

Adult Density, Survival, and Size

Tidal elevation affected some oyster parameters. A paired T-test revealed that density was marginally significantly higher in the low vs. mid intertidal (26 vs. 6 per m^2, $P=0.05$). The percent of oysters that were alive was marginally significantly higher in the low vs. mid intertidal (47% vs. 24%, $P=0.07$), while average size did not differ significantly with tidal elevation (43 mm for both, $P=0.87$). Tidal

Fig. 3 Relationship between size of substrates that host live oysters vs. depth of unconsolidated sediments at 10 sites

exchange did not have any significant effects on oyster density, percent alive, or size in the comparison of three full exchange vs. three muted exchange sites.

Recruitment and Juvenile Growth and Survival

Juvenile oysters colonized bricks at all sites assessed. Tidal exchange affected only a few of the parameters assessed on the recruitment bricks. Combined density of live and dead juveniles (a proxy for recruitment rate) did not differ significantly in full exchange (average 334 juvenile oysters/m^2) vs. muted exchange (average 236 juvenile oysters/m^2). The percentage of these juveniles that were alive (a proxy for survival rate) was significantly ($P=0.002$) lower in full tidal exchange (average 65%) than in muted tidal exchange (average 90%). Average size of live juveniles (a proxy for growth rate) did not differ significantly in full tidal exchange (average 16 mm) vs. muted tidal exchange (average 17 mm).

Sedimentation (1=low, 2=high) differed significantly ($P=0.006$) in full tidal exchange (average 1.8) vs. muted tidal exchange (average 1.1). Percent cover by bare space did not differ significantly, although it was higher in full (86%) than muted (56%) tidal exchange, but the difference was not significant ($P=0.26$). A T-test using sedimentation (high vs. low levels scored for the bricks) as the factor revealed no significant differences in juvenile size or density, but showed that survival rates were significantly ($P=0.03$) higher with low vs. high sedimentation (85% vs. 66%, respectively).

For all sites combined, there were 38 recently dead recruits with the upper valve still attached. Of these, 35 had no obvious cause of death, three appeared to have been overgrown by bryozoans, and none showed signs of predation. On 13 brick faces, there were co-occurring juveniles that were surrounded vs. were not surrounded by *Ficopomatus enigmaticus* to use for a paired analysis. A paired T-test revealed that the average size of surrounded juveniles (17.4 mm) was not significantly different from that of juveniles that were not surrounded (19.0 mm). Mortality was also not significantly different in a Chi Square test; 3/13 of surrounded juveniles were dead vs. 1/13 of the non-surrounded ones.

Discussion

Water Quality

Multivariate analysis revealed that sites with and without Olympia oysters at Elkhorn Slough differ significantly in water quality. Furthermore, sites with high oyster abundance had the least variation in water quality parameters, suggesting that oysters can only thrive in a relatively narrow range of the water quality conditions available in this estuary. Water quality is well known to affect benthic invertebrate populations, but few previous studies have linked Olympia oyster abundance to estuarine water quality. However, it is known that prolonged periods of low salinity can result in die-offs (Grosholz et al. 2008), and that temperature can play an important role in reproduction (Hopkins 1936; Baker 1995).

The particular parameters that contributed most to dissimilarity between sites with and without oysters at Elkhorn Slough are mostly ones associated with eutrophication: sites without oysters had higher nutrient concentrations, fluorescence (a proxy for water column productivity), daytime turbidity, and dissolved oxygen. Elevated daytime oxygen is correlated with night-time hypoxia at sites in this estuary because daytime oxygen production by phytoplankton is highest in the same shallow, nutrient-loaded wetlands where night-time consumption by benthic and planktonic communities is greatest. Studies elsewhere have shown that increased nutrient levels may increase oyster recruitment (Minchinton and McKenzie 2008) and moderate eutrophication may enhance oyster growth (Kirby and Miller 2005). The negative correlation of oyster abundance with indicators of eutrophication may be due to the more extreme nutrient loading of Elkhorn Slough (Caffrey et al. 2002).

Artificial Tidal Restriction

In the Elkhorn estuary, Olympia oysters were only present at three of 17 sites with artificially restricted tidal exchange. Oysters were not present at any sites with very limited tidal exchange. Minimal tidal exchange sites tend to have persistent low salinities in the rainy season and, resulting from lack of dilution by tidal currents, tend to have higher concentrations of agricultural pollutants and more hypoxia. Negative effects of artificial tidal restriction have been shown for various estuarine invertebrates and fish (Raposa and Roman 2003; Ritter et al. 2008), but effects on Olympia oysters had not been previously reported.

While oysters were entirely absent from sites with minimal tidal exchange, they were present at three of four sites with more moderate, muted tidal exchange. Indeed, comparison of adult and juvenile parameters revealed few significant differences between full and muted sites, although replication was low and variation was very high among the three muted sites. Juvenile survival was significantly greater in muted exchange, perhaps as a function of sedimentation, which was significantly lower at these sites. Therefore, artificially restricted tidal exchange may be suitable for Olympia oysters as long as tidal flushing is sufficient to allow passage of larvae and to prevent water quality problems. Indeed, Olympia oysters were once successfully cultivated in diked beds with artificially muted tidal exchange in Washington State (Baker 1995).

Tidal Elevation

At Elkhorn Slough, Olympia oyster density and proportion of individuals that were alive were marginally higher in the low vs. mid intertidal zone. Likewise, in Washington State, Olympia oysters have been shown to have better growth and survival at very low intertidal or shallow subtidal elevations than mid intertidal elevations (Trimble et al. 2009). For another oyster species (*Crassostrea ariakensis*), it has been shown that lower tidal elevations may pose less physiological stress and provide more time for suspension feeding, but competition from other fouling species may be less intense at higher tidal elevations (Bishop and Peterson 2006). Similar mechanisms may operate at Elkhorn Slough, where oysters are virtually absent from the subtidal zone apparently due to overgrowth by non-native fouling species (Wasson, unpublished). Determining the optimal elevational zone for oyster restoration via addition of hard substrates should balance these trade-offs between higher recruitment and growth of oysters at lower tidal elevations, but decreased competition with fouling species at higher tidal elevations.

Substrate Size and Sediment Depth

At Elkhorn Slough, the presence of hard substrates alone does not predict oyster distribution—many sites with no oysters had very extensive hard substrates. Similarly in San Francisco Bay, numerous sites with ample hard substrate yielded no oysters (Harris 2004). A major strategy for oyster restoration has been addition of hard substrates, on the assumption that the available area of substrate is limiting population sizes (Brumbaugh et al. 2006). Clearly this assumption does not hold for some estuarine sites at Elkhorn Slough or San Francisco Bay, where factors other than limited availability of hard substrates for attachment, perhaps poor water quality or insufficient larval supply, explain oyster absence.

While *presence* of hard substrates did not accurately predict presence of oysters at Elkhorn Slough, *absence* of hard substrates perfectly predicted absence of oysters. No oysters were found at any of 25 intertidal mudflat sites that lacked extensive hard substrates, even though the majority of these sites fell within the known distribution of oysters in the estuary, where water quality conditions should be appropriate. The only sites in the estuary where oysters were found were ones where there has been addition of hard substrates to armor banks to protect railroads, roads, water control structures and bridges. Estuarine sites at Elkhorn Slough thus appear to fall into two categories: either they are dominated by soft sediments and have no oysters, or they have substantial amounts of artificial hard substrate, on which oysters may or may not be present.

The limitation of Olympia oysters to areas where artificial hard substrates have been added is puzzling given the historical record of Elkhorn Slough. Olympia oyster shells occur in all major Native American middens across the estuary, and were consistently present from 8,000–300 years before the present. Local geology—hills with sandy soils—would not have provided large rocks to the estuary, so these oysters must have been successfully growing on naturally occurring, small pieces of hard substrate, such as clam shells and on other oysters. However, today Olympia oysters only rarely occur on such small hard substrates in Elkhorn Slough. Harris (2004) found subtidal oysters to be absent from most parts of San Francisco Bay sampled, which are soft-sediment dominated, except for one site where fast currents allowed shells and rubble to persist unburied on the surface.

The correlation found between size of substrate used and sediment depth suggests that small natural substrates can only be used successfully in areas with shallow sediment depths. This is also supported by the lower survival of juvenile oysters on bricks with high sedimentation. Burial by sediments may lead to anoxic conditions or may interfere with feeding. So the absence of oysters from the majority of the estuary, which is dominated by soft sediments, can be considered an interaction between substrate limitation and burial by sediment. It has been suggested that Olympia oysters may be absent from estuaries with high sediment deposition rates, such as Bolinas Lagoon or Morro Bay (Barrett 1963), and that they may have declined in San Francisco Bay because of increased sedimentation resulting from hydraulic mining (Barrett 1963). Sedimentation rates at many estuaries have increased as a result of anthropogenic alterations, and may explain the current absence of Olympia oysters from soft sediment habitats where they formerly persisted on small bits of natural hard substrate.

Predation and Competition

Our study found no evidence for predation playing an important role in limiting oysters at our focal study sites in Elkhorn Slough. No recently dead juveniles showed signs of predation (such as shell breakage); 92% of recently dead juveniles had intact, gaping top valves suggesting that they may have died of anoxia resulting from burial in mud or from water column hypoxia.

Competition for space also did not appear to play a major role in this study. Only 8% of recently dead juveniles appeared to have died as a result of overgrowth. Juveniles surrounded by a common fouling species (the tubeworm *Ficopomatus*) did not have significantly lower growth or survival rates than nearby juveniles that were not surrounded. Bare space was abundant on the recruitment bricks, as well in the transects for adult oysters. However,

these results may be misleading. Non-native species account for 77% of the species richness and 84% of the cover of sessile species on hard substrates in Elkhorn Slough (Wasson et al. 2005). On clean surfaces such as the recruitment bricks, competition may take longer to manifest itself; bare space was still high on most bricks after nine months but may become limiting later. Moreover, data from more recent surveys (Wasson, unpublished) suggest that competition with non-native fouling species becomes very important for Olympia oysters at Elkhorn Slough at tidal elevations below those that were assessed in this study, i.e. at and below MLLW. In Willapa Bay, non-native fouling species have been shown to limit the growth and survival of Olympia oyster recruits in the low intertidal and shallow subtidal zone (Trimble et al. 2009).

Conclusions and Management Recommendations

At Elkhorn Slough, poor water quality associated with stagnant or eutrophic conditions, especially in wetlands with artificially restricted tidal exchange, is associated with the absence of oysters from much of the estuary. Burial by unconsolidated sediments that prevents oysters from surviving on small natural hard substrates (bits of shell or gravel) appears to be responsible for oyster absence in regions with appropriate water quality. In regions with appropriate water quality and sufficiently large hard substrate to prevent burial by sediments, non-native species may limit abundance at low tidal elevations. Water quality degradation, altered sedimentation rates, and introduction of non-native species have all resulted from anthropogenic activities at Elkhorn Slough (Caffrey et al. 2002) and may account for the decline of Olympia oysters since the 1930s, when they were reported to be highly abundant (MacGinitie 1935). Such anthropogenic alterations are widespread in estuarine systems (Emmett et al. 2000, Kennish 2002), and are likely to contribute to observed oyster declines in other Pacific coast estuaries as well.

Negative human-induced changes have been somewhat mitigated by the addition of hard substrate—without these additions there might be no oysters in the Elkhorn Slough estuary today. To enhance oyster populations in the estuary, additional hard substrates could be added. Addition of large hard substrates, however, in itself represents an anthropogenic alteration to Elkhorn Slough and to most Pacific coast estuaries, which are naturally dominated by soft sediments (Emmett et al. 2000). While it might prove beneficial from a single-species management perspective, it might not be appropriate from an ecosystem-based management perspective, taking into account multiple species and ecological processes (Christensen et al. 1996). One should consider oyster restoration as a part of a larger attempt to reverse human alterations to estuarine habitats. Oysters are only

substrate limited because deep unconsolidated sediments lead to burial on small, natural hard substrates. Instead of focusing only on substrates, restoration efforts should also attempt to decrease high sedimentation rates in areas where they are higher than natural baseline levels. Likewise, improving water quality by reducing nutrient loading and increasing tidal exchange to stagnant areas with artificially restricted tidal exchange, and trying to prevent or eradicate new invasions by non-native fouling species would benefit native oysters, and also restore more natural estuarine ecosystem processes.

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