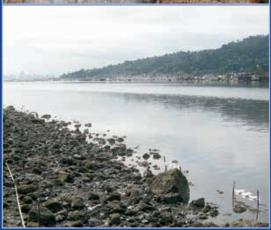


A Guide to Olympia Oyster Restoration and Conservation



















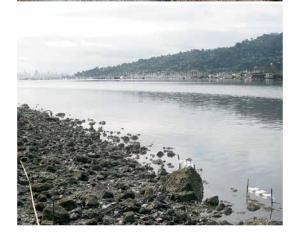


A Guide to Olympia Oyster Restoration and Conservation

ENVIRONMENTAL CONDITIONS
AND SITES THAT SUPPORT
SUSTAINABLE POPULATIONS
IN CENTRAL CALIFORNIA

Kerstin Wasson, Chela Zabin, Jillian Bible, Elena Ceballos, Andrew Chang, Brian Cheng, Anna Deck, Ted Grosholz, Marilyn Latta, Matt Ferner

September 2014















A Guide to Olympia Oyster Restoration and Conservation

Environmental conditions and sites that support sustainable populations in central California

This project was led by an interdisciplinary team from the San Francisco Bay and Elkhorn Slough National Estuarine Research Reserves, and has been developed in partnership with the University of California, Davis and the State Coastal Conservancy. The Smithsonian Environmental Research Center and the California Department of Fish and Wildlife are also partners in this effort. The management questions that we address have arisen directly from prior needs assessments of local and regional end-users: oyster restoration practitioners and the coastal decision-makers who set regional restoration policy and provide funding. The core project staff have worked for over ten years at the interface between science and estuarine management end-users, and have a successful track record of producing restoration planning tools which directly shape implementation of and policy for restoration projects. We are working in partnership with a range of local, state, and national partners.

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Synopsis

This guide identifies key environmental conditions that affect Olympia oysters in central California. Availability of hard substrate, abundance of phytoplankton, and relatively warm water temperatures are identified as important factors for supporting sustainable oyster populations. Low salinity, low dissolved oxygen, warm air temperatures and abundant predatory oyster drills are found to be the most important stressors negatively affecting oysters. In general, stressors already facing oysters today appear likely to exert more influence over Olympia oysters in coming decades than emerging climate-related stressors. Using data on oyster attributes and environmental conditions, the authors evaluated 21 sites in San Francisco Bay and Elkhorn Slough for their restoration and conservation potential.

Executive Summary

The Olympia oyster (*Ostrea lurida*) has declined at many estuaries in its native range along the Pacific coast from Baja California to British Columbia. In the past decade, efforts have begun to conserve, enhance or restore Olympia oyster populations in California, Oregon and Washington. The purpose of this guide is to inform these new initiatives, with emphasis on environmental conditions, including both supportive and stressful factors.

Recommendations in this guide are based on new field monitoring and laboratory experiments conducted in central California, as well as on an extensive review of the published literature for Olympia oysters across their range. The authors comprise an interdisciplinary team with expertise in estuarine ecology and oyster restoration science, practice and policy, working closely with oyster restoration and conservation stakeholders, with major funding from NOAA's National Estuarine Research Reserve System Science Collaborative. Our two study locations are only 100 kilometers apart, yet they encompass a broad range of conditions. San Francisco Bay is urban, much larger than Elkhorn Slough, and receives significant amounts of freshwater in rainy seasons. Elkhorn Slough is surrounded by agricultural fields and experiences high nutrient inputs but relatively low amounts of fresh water. In addition, within each estuary, we selected sites along the estuarine gradient from high to low salinity.

Sustainable oyster populations exhibit a suite of attributes. We evaluated nine of these attributes for sites in San Francisco Bay (SF Bay) (Figure 1) and Elkhorn Slough (ES) (Figure 2), and specified desirable thresholds for each attribute. These attributes could be examined by other investigators at additional sites.



High densities of Olympia oysters at China Camp State Park.

OYSTER POPULATION ATTRIBUTES

- · Adult oyster density
- Population estimate
- · Adult oyster size
- · Diversity of size classes
- Recruit density
- Reliable recruitment
- Larvae exported
- Survival rate
- · Growth rate

SUPPORTIVE ENVIRONMENTAL FACTORS

- Water Temperature
- · Chlorophyll a

ENVIRONMENTAL STRESSORS

- Salinity range
- Oyster drill predation
- Risk of high air temperatures
- · Low dissolved oxygen
- Risk of low salinity events



Olympia oysters and acorn barnacles.

We selected the following as important indicators of sustainable oyster populations: large adult population size, high density on hard substrates, high rate of juvenile recruitment, diversity of size classes, and high survival rate.

Numerous environmental factors affect the distribution and abundance of Olympia oysters. Based on results from field monitoring and laboratory experiments, combined with a thorough literature review and our own expert opinions, we have identified the factors that exert the strongest influence on Olympia oysters in our region. Some of these influences are positive.

- Availability of hard substrate in the low intertidal and shallow subtidal zone is a requirement for Olympia oysters, and in areas with deep mud, oysters only survive if large hard substrates are available.
- Phytoplankton is necessary to support suspension feeding; higher levels of chlorophyll *a* correlated with oyster attributes in our analysis.
- Warmer water temperatures also support growth and reproduction of Olympia oysters in this region.

Numerous environmental factors threaten oysters and serve as stressors. Some of these exert strong negative influences on oysters but only occur at certain sites. The expression of stressors is thus site-specific.

- Low salinity can very negatively affect oysters at sites with at least occasional high freshwater inflow.
- Predatory non-native Atlantic oyster drills (*Urosalpinx cinerea*) can have devastating consequences to oysters but are absent at many sites.
- Low oxygen (hypoxia) has negative effects but is only a problem at the most eutrophic sites in these estuaries.
- Warm air temperature during low tide exposure poses a potential threat at any site, but this threat is reduced at sites with more summer fog.

In contrast with our demonstration of strong negative effects by the above stressors, our work and that of others shows that other stressors are less important, at least during this study period and in this region. These include competition from non-native fouling species, sedimentation, contaminants, pathogens and disease, sea level rise and acidification of estuarine waters.

Olympia oysters face multiple environmental stressors due both to the natural dynamics of estuarine ecosystems and to anthropogenic modifications. We examined interactions between different stressors under laboratory conditions and found that the types of responses observed depended on the stressor and the timing of application. We documented some linear, additive relationships between stressors, and some that were non-linear and synergistic. It is clear that decreasing stressor levels through ecosystem management (such as reducing hypoxia resulting from nutrient loading) will support oysters, but it is hard to predict whether such stressor reduction will increase resilience to other stressors, such as those related to climate change.





Olympia oysters on hard substrate in SF Bay (top) and Elkhorn Slough (bottom).

Into the cold bay Place oysters where they can best Survive stressful times We evaluated twenty-one sites according to the oyster attributes, supportive environmental factors and stressors described above and have summarized these results in a Site Evaluation Table. Of the sites we evaluated, the top-scoring sites for restoration in San Francisco Bay were Berkeley Marina (Shorebird Park area), Strawberry (Brickyard Cove), San Rafael Shoreline and Point Pinole Regional Shoreline; however, in Elkhorn Slough, only Kirby Park and South Marsh received a high restoration score and more sites received low scores at this estuary than in San Francisco Bay. All of the high-ranked restoration sites also ranked high as conservation sites, but several additional sites ranked high for conservation: Richmond (Point Orient), Loch Lomond Marina, and Sausalito (Dunphy Park) in SF Bay and Whistlestop in Elkhorn Slough. The Site Evaluation Table can be used as a framework to assess other sites with new data. Because the overall score is an average of all parameters, it is possible to score new sites even if data are not collected for as many parameters as were used here.

This approach to quantifying the relative conservation value and restoration potential of 21 sites in central California estuaries can be used to inform future management actions. Agencies, non-governmental organizations, citizen science groups or others considering the launch of a new restoration project can determine whether a particular site is likely to yield success. Funding agencies can use scores to help evaluate multiple restoration proposals and regulatory agencies can use the scores to direct policy protecting valuable existing populations.

Our identification of the stressors that exert the strongest influences on oysters in these estuaries also can help inform ecosystem management efforts. For instance, reduction of hypoxia and prevention of the spread of oyster drills to new regions are both clear management recommendations. In general, these current threats to oysters should be of more concern to managers than those posed by climate change; our investigation suggests warming water temperatures over coming decades may benefit oysters, and threats posed by acidification of surface waters and sea level rise are likely to be lower than those posed by existing stressors. However, our analysis also suggests that projected increases in air temperature and increased variation in precipitation may threaten oyster populations, through overheating during low tide exposure and through low salinity during extended rains.

In summary, this guide supports Olympia oyster conservation and restoration and by enhancing understanding of the attributes of sustainable oyster populations, the environmental conditions that fosters them, and the sites that best support them.

Background

Purpose and development of this guide

The purpose of this guide is to inform restoration and conservation of Olympia oysters (*Ostrea lurida*). It was prepared by an interdisciplinary team from the California State Coastal Conservancy, University of California at Davis and the San Francisco Bay and Elkhorn Slough National Estuarine Research Reserves (SF Bay NERR and ES NERR) funded by the National Estuarine Research Reserve System Science Collaborative from 2011–2014 (Appendix 1). The intended audience includes oyster restoration practitioners, restoration scientists, and organizations involved in planning, funding, conservation, or permitting restoration. New field monitoring data were collected from Elkhorn Slough and SF Bay and form the basis for many of the recommendations presented here. However, many of the recommendations are likely to be applicable across a larger area, and many of the criteria for successful conservation and restoration sites probably apply across the entire range of the species.

We focus on environmental conditions that support Olympia oysters: which beneficial conditions to seek and which stressors to avoid when selecting a restoration or conservation site, or when directing ecosystem management efforts. This is not a "how to" manual for field restoration methods, nor does it address the human processes that are essential for restoration and conservation (permitting, community support, public outreach, etc.). Guides that address these issues are sorely needed and would complement the current effort.

End-users engaged in oyster restoration, planning, conservation, permitting or policy have been involved heavily during the development of this guide and in the scientific research behind it. Collaborators from Richardson Bay Audubon,



Dense oyster recruitment on the SF Bay Living Shorelines Project.

Below: lab studies at Bodega Marine Lab. Below right: field work at Hudson Landing in Elkhorn Slough.





The Watershed Project, and the state Coastal Conservancy assisted in collection of data from field sites. In January 2012, 48 end-users provided feedback through an electronic survey about priority questions, sites and stressors. The responses shaped the design of field monitoring and laboratory experiments (Wasson 2012). In January and February, 2013, more in-depth interviews were conducted with 15 end-users to characterize their decision-making regarding Olympia oysters. In April 2013, a workshop was held with 27 end-users to obtain formative feedback on key management applications of the new data from this project. That April workshop shaped the content and format of this guide (Wasson 2013). In September 2014, a final workshop facilitated dissemination of the guide to these end-users.



Large adult oysters sharing space with bay mussels at the Berkeley Marina.

Olympia oysters: challenges and opportunities

LIFE-CYCLE AND ECOLOGY

Olympia oysters are primarily estuarine and generally not found on the open coast (Baker 1995). In Central California, they are most abundant around the 0-meter tide mark, Mean Lower Low Water (MLLW) (authors' unpublished data), but have been reported from as high as 1 m above MLLW to depths of 10 m (Baker 1995). They require hard substrate on which to settle. They are sequential hermaphrodites—typically, but not always, starting out as males—and switch sexes several times within the course of a year. Females brood larvae in their mantles for 7–12 days (Coe 1931, Hopkins 1936, Strathmann 1987), after which they are released to swim in the plankton for 5 days (authors' personal observations) to 4 weeks (Breese 1953).

TRENDS IN DISTRIBUTION AND ABUNDANCE

Olympia oysters range from Central Baja California, Mexico, to British Columbia, Canada (Polson 2009). Abundance varies enormously from scant, but persistent, populations consisting of a handful of individuals, to locations with nearly 100 percent cover of oysters on hard substrates at MLLW (authors' personal observations). In most locations, the size of the pre-European-contact population is unknown. However, there were sufficient populations in SF Bay



Rocky substrate with oysters.



Intertidal community with oysters.

prior to the Gold Rush to support a commercial fishery (Conte and Dupuy 1982). Based on a review of the former extent of commercial oyster grounds from the earliest available records (mid-1800s to early 1900s), Zu Ermgassen et al. (2012) estimated oyster grounds in Puget Sound, Humboldt Bay, SF Bay, Elkhorn Slough and Mission Bay to be at 1% of historic levels.

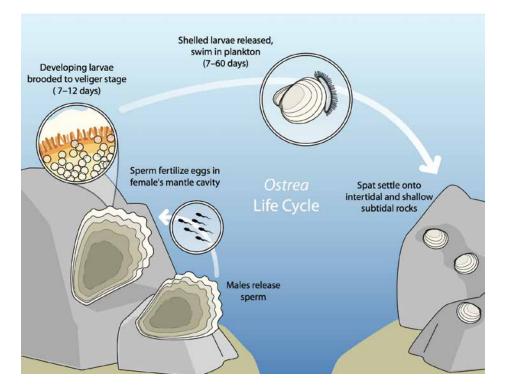
CONSERVATION AND RESTORATION

The earliest efforts to restore Olympia oysters began in Puget Sound in 1999 (Peter-Contesse and Peabody 2005) and included seeding oyster shell and large-scale deployment of Pacific oyster shell for natural set. Current smaller-scale projects in Oregon and in Central and Southern California range from deploying small structures to assess recruitment patterns and best methods, to larger-scale mixed species restoration projects with both physical and biological objectives in a "living shorelines" model.

Climate change is a challenge that must be understood and addressed as a part of restoration. Current model projections suggest rising temperatures, acidification of surface waters in some locations such as Tomales Bay and Puget Sound, and more frequent and severe flood events. These are likely to affect both existing oyster populations and restoration efforts. Climate change stressors may interact with and perhaps act synergistically with o ther anthropogenic stressors such as invasive species (for example, predatory oyster drills, the Pacific oyster *Crassostrea gigas*, and other potential space competitors), high nutrient levels, and pathogens and disease. Climate change effects are not likely to be the same in all locations, nor are other anthropogenic stressors equally important everywhere. Conservation and restoration efforts require a better understanding of the local importance of environmental factors, both now and in the future.

FIGURE 1

Schematic of Olympia oyster life cycle. Adult males release sperm that is taken up by nearby females. Eggs are fertilized within the mantle cavity and developing larvae are brooded to the veliger stage, released into the plankton, and transported with tides and currents. Larvae settle irreversibly onto hard substrate as juvenile oysters and grow to sexual maturity within months to a year. Each life stage is susceptible to a variety of environmental stressors, with younger stages being somewhat more susceptible than older stages.





Deploying monitoring tiles at Azevedo Pond in Elkhorn Slough.

LAB EXPERIMENTS

FIRST

- High water temperature
- · Low dissolved oxygen
- Low Salinity

SECOND

- Low salinity
- · High air temperature

THIRD

Salinity levels varying over different time frames

Information sources for this guide

NEW DATA

Field monitoring of oysters and environmental conditions

Field monitoring occurred from Spring 2012 through Fall 2013 at nine sites in Elkhorn Slough and twelve sites in SF Bay (Figures 2 and 3, pages 11 and 12), and included a range of oyster attributes and environmental parameters. Oyster attributes included density and size distribution of existing populations, growth rate, survival rate, and recruitment rate. These parameters were measured quarterly, with additional biweekly measurements of recruitment and fecundity at some sites in the summer. Scientists from the project team monitored most sites, but a subset of sites was monitored at a reduced level by collaborators from partner organizations (Appendix 1, 2). A suite of environmental parameters was measured at the same sites and additional continuous environmental data were made available from other sources (ES and SF Bay NERRs, USGS, www.mbari.org/lobo). We used statistical analyses to determine the importance of various environmental conditions to oyster performance.

Laboratory experiments examining stressors

We carried out three laboratory experiments testing the effects of single and multiple stressors on several life stages. The first lab experiment tested the potential interaction of multiple environmental stressors—including high water temperature, low dissolved oxygen, and low salinity—on juvenile oysters (Appendix 3). Hypoxia clearly resulted in sublethal impacts by reducing growth, and low salinity resulted in high oyster mortality, but only under extreme conditions. To our surprise, warming of water temperature enhanced growth and feeding, even under hypoxia. We found no synergistic interactions between stressors.

Our second lab experiment investigated the responses of juvenile Olympia oysters to the combination of low salinity (mimicking wet winter seasons) and

high air temperature (mimicking low tides and high air temperature in spring seasons), with different amounts of time between exposures to these stressors (Appendix 3). Both low salinity and high air temperature resulted in oyster mortality. When low salinity and high air temperature treatments were sequential, the combined impact was worse than the sum of the two stressors alone, thus a synergistic response. When stressor exposures lagged by two weeks, responses were additive, not synergistic.



Stressor experiments on oysters at Bodega Marine Lab.

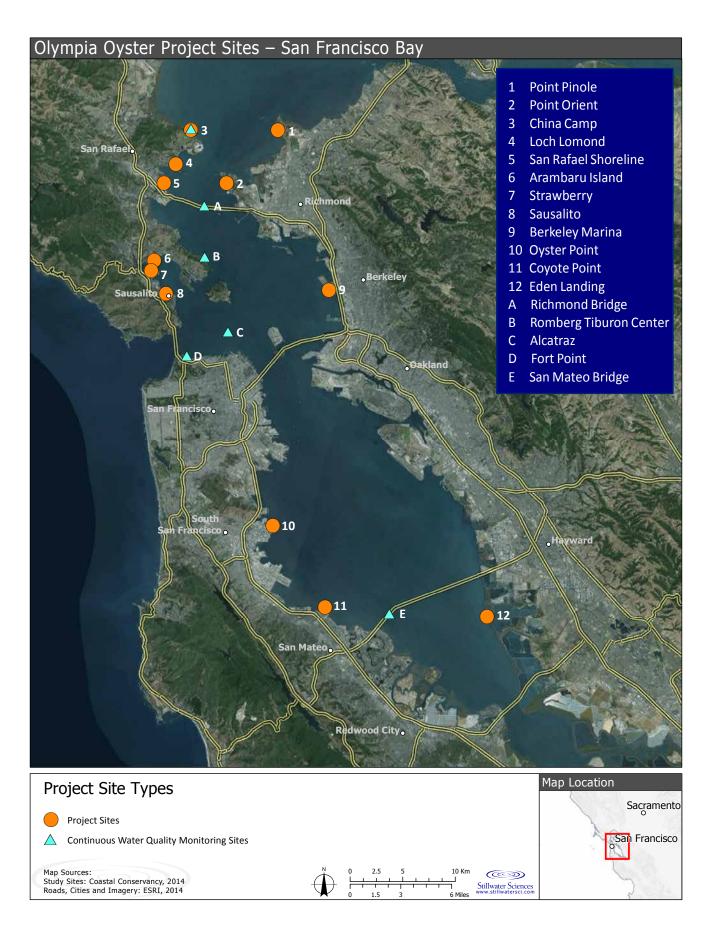
Winter storm, downpour Bay oysters shut their valves tight Long wait to exhale A third laboratory experiment (Appendix 3) investigated the response of adult oysters to different salinity levels, for different durations of exposure. We found that oysters survived short duration low salinity exposure by closing their shells, which resulted in cessation of feeding. However, longer duration events resulted in significant mortality. Oddly, the lowest salinities did not have the highest mortality rates, perhaps because exposure to very fresh water leads to immediate shell closure, offering greater protection.

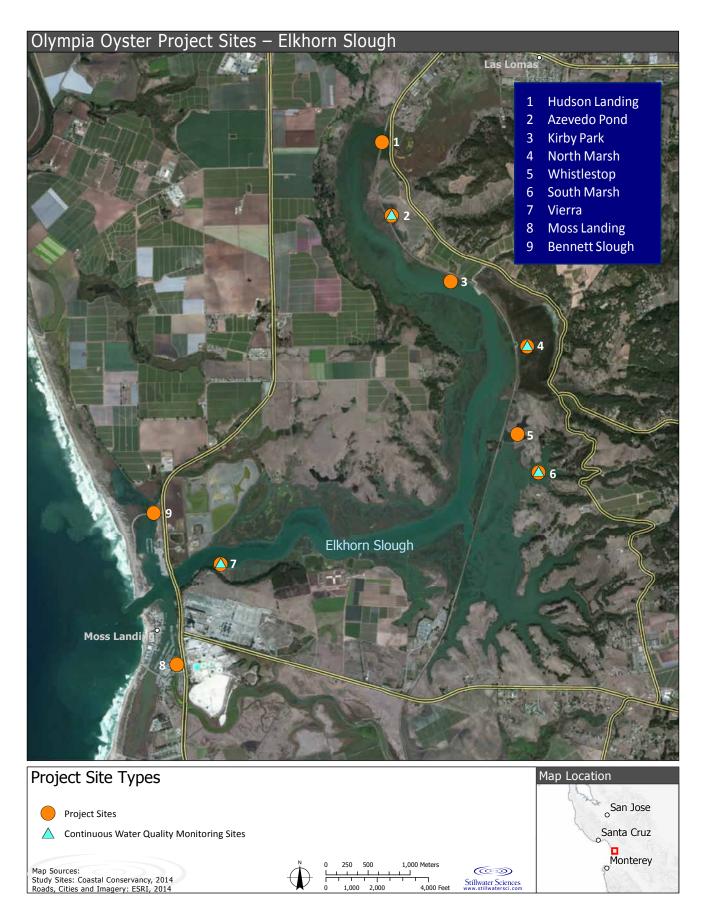
EXISTING DATA

In addition to the new data collected for this project, we also had access to several sources of data from our previous work, allowing us to expand our analyses and reach somewhat more general conclusions. One significant source of Olympia oyster demographic data and corresponding temperature and salinity data for SF Bay was a three-year project that one of us (A. Chang) led as a CALFED Bay-Delta Science Program Postdoctoral Fellow. From that project, we used bimonthly estimates of population density at 12 sites from December 2009 to December 2011, and estimates of growth and survival for the summer and fall in 2010 and 2011. Data on recruitment, growth and mortality, collected from field sites SF Bay from 2006–2008 as part of a California Sea Grant also helped guide the development of the Site Evaluation Table (Grosholz et al. 2008) (pages 32–38). We included data from the published literature in evaluating the relative importance of the selected oyster attributes and environmental conditions.

Azevedo Pond in Elkhorn Slough.







Attributes of Sustainable Oyster Populations

OVERVIEW

Successful oyster populations exhibit a suite of biological attributes that we characterized and describe below. Oyster populations along the entire coast likely show some amount of connectivity, due to dispersal of larvae among estuaries. However, most conservation planning occurs at smaller scales. Below, we focus on oyster populations at the scale of individual sites. We also consider the entire estuary-wide population of Olympia oysters when ranking the relative importance of different sites within the estuary. Site-specific estimates of oyster density, size distribution, and recruitment rates were chosen as indicators of healthy oyster populations. In particular, sites that experience regular and substantial recruitment often support a broad distribution of oyster sizes and high densities of adult oysters, but all of the factors listed are key attributes of sustainable oyster populations.





Top: new recruits. Middle: oysters in muddy conditions at Elkhorn Slough. Above: dense oysters in mixed mud/cobble in SF Bay.

Moderate-to-high adult densities (importance: very high)

The density of adult oysters at a site can serve as a cumulative indicator of its appropriateness for conservation or restoration; moderate to high adult densities result from one or more years of significant recruitment and survival. Current oyster density data are important for prioritizing conservation areas, yet some populations fluctuate from year to year and it is better to have multiple years of data for greater confidence. High oyster densities on existing substrate can be used to assess suitability for restoration at that site, provided there is existing hard substrate to begin with. At each site, we estimated oyster density on appropriate hard substrate along 30 m transects at the tidal elevation where oysters were most abundant. Across all sites adult oyster densities ranged from 0–961 individuals per m², with the lowest and highest densities in SF Bay being 3.5/m² and 961/m² at Eden Landing Ecological Reserve and Loch Lomond Marina, respectively, and the lowest and highest densities in Elkhorn Slough being 0/m² and 303/m² at Vierra and Kirby Park, respectively.

Total abundance at site (importance: very high)

An order-of-magnitude estimate of the total number of oysters living at a site is a good indicator of its relative conservation value. In some cases, adult density per square meter of hard substrate may not represent density at larger scales (e.g., hectares). For example, a site that has a million oysters within a hectare should have greater conservation value than a site that has a thousand oysters per hectare, and far greater than one that has ten oysters per hectare, even if all those sites have the same density per square meter. Therefore, it is important to establish where to draw the line around a site of interest and whether or not to include the full tidal range encompassing colonized hard substrate there. For







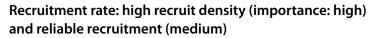
Top: field monitoring at the Berkeley Marina. Middle: juvenile oysters. Above: multiple age classes.

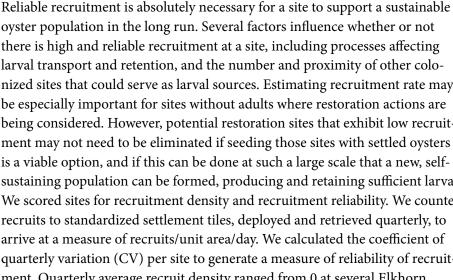
our assessment, we limited the total area for each site calculation to a 1-m wide band centered around our study transects at the tidal elevation of maximum oyster density and extending 300 m. We next estimated the percentage of cover of hard substrate to determine how much of the area was potential oyster habitat. We were then able to scale up from our density measurements (above) to generate order of magnitude estimates of total population. At our study sites, oyster populations ranged from 0 at several Elkhorn Slough sites to 100,000's of individuals at Loch Lomond Marina.

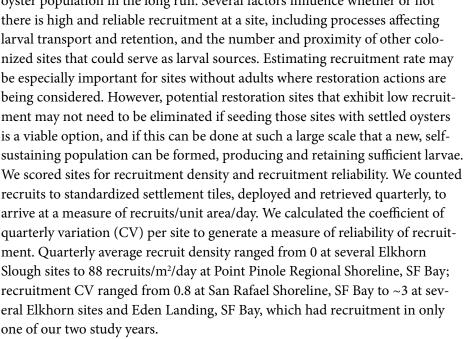
Oyster sizes: broad size distribution (importance: high) and large sizes (importance: medium)

The presence of oysters distributed among a broad range of size classes is a good indicator of a healthy population, indicating a combination of recent recruitment, growth, and long-term survival. Each is an important aspect of a sustainable population, but it is time-consuming and sometimes logistically challenging to measure each separately. Because recruitment can vary from year to year, the best estimates of size distribution will include several years of data. At the very least, estimates ought to be made after the recruitment season, to include newly settled juveniles. Absence of particular size classes does suggest potential limitations for populations. For example, absence of small sizes might suggest recruitment limitation or absence of large size classes might indicate a lack of long-term survival. However, although a broad range of sizes is regularly seen at high quality sites in central California, not all Olympia oyster populations show persistent evidence of previous recruitment, particularly if growth to adult size happens very quickly and subsequent growth of those same individuals is limited. We measured oysters in quadrats along our study transects, categorized these into 10 mm size classes, and generated a size-class diversity index using a formula typically used to compare species diversity, the Gini-Simpson index. This index ranges from 0 to 1, with 1 representing the greatest possible diversity. Our sites ranged from an index of 0.25 at a location where all oysters were from a single recruitment event (Hudson Landing, Elkhorn Slough), so that size diversity was very low, to an index of 0.876, at a site where there were many oysters in multiple size classes (Strawberry [Brickyard Cove], SF Bay).

In addition, when we included data on largest oysters, the table was more accurate in ranking sites that we know from previous research have had consistent recruitment and moderate to high densities of oysters over time frames longer than the current study. We used the mean of the upper quartile of oyster sizes measured in our quadrats. Including this measure slightly increased the scores of sites that had larger oysters, an indication of longer term survival and/or faster growth. At our sites, the average sizes of the largest oysters ranged from 12 mm (Eden Landing, SF Bay) to 66 mm (Moss Landing Harbor, Elkhorn Slough).







High juvenile survival rate (importance: high)

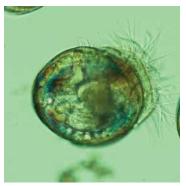
Juvenile stages are particularly susceptible to predation and other stressors that could lead to mortality. Survival to the adult stage is critical for reproduction and the overall sustainability of a population. In many cases, high rates of juvenile survival will be reflected in a broad range of oyster sizes present at a site (with the abovementioned exceptions). Thus, while survival rates are not critical to measure in situ, doing so allows for a more precise understanding of why certain size classes might be missing at a site. We allowed oysters to recruit to tiles in the field and then tracked the survival and growth of these oysters. For locations that did not have natural recruitment, we deployed tiles from nearby locations that had recruitment. Survival rates were calculated quarterly as the percentage of oysters surviving since the previous quarter, standardized by the number of days since last check. Survival ranged from a low of 99.45%/day at Loch Lomond Marina, SF Bay to a high of 99.90%/day at several tidally muted sites in Elkhorn Slough.

High juvenile growth rate (importance: low to high)

As noted above, juvenile oysters are generally more susceptible to predators and environmental stressors than are adult oysters, suggesting the clear benefits of growing quickly after settlement. High juvenile growth rates indicate favorable conditions (such as available food and sufficiently high salinity and dissolved oxygen) and should lead to healthy adult populations. However, sites









From top to bottom: life stages of the oyster: gonads, brooded larvae, freeswimming veligers, "spat"—settled young oysters.





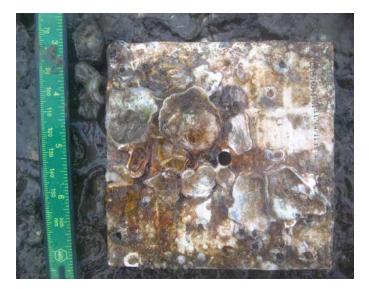
Tracking survival and growth of oysters on monitoring tiles.

with high food resources and warm water, which can promote growth, may also suffer from low dissolved oxygen. Additionally, low juvenile growth rate does not necessarily indicate poor field conditions. Growth may be limited by high recruitment densities rather than by a lack of food or by other unfavorable conditions. Marking and remeasuring oysters is time-consuming. Size-class distribution calculations, as mentioned above, provide indirect measurements of growth and survival. Such calculations could be substituted for direct measurement in sites with existing oyster populations. For sites without oysters or with few oysters, deploying settled oysters on tiles, as we did, to observe growth and mortality, can indicate whether conditions at a site are appropriate for restoration with seeded oysters. For such sites, we suggest weighting juvenile growth as high. We measured oysters settled on tiles once a quarter during our study, calculating average growth rates for each site in mm/day. Growth at our sites ranged from 0.037 mm/day at Coyote Point, SF Bay to 0.11 mm/day at four Elkhorn Slough sites and Berkeley Marina, SF Bay.

High larval contribution to region (importance: medium to high)

Sites that support significant adult populations also might export larvae and be of particular conservation value to the regional population. Measurements of fecundity and larval connectivity can help to identify what sites might most contribute to regional larval supply, but a thorough understanding of larval sources and sinks also requires an understanding of tidal currents and other transport processes around and between sites.

Using shell chemistry analysis, we were able to evaluate the relative contributions of larvae produced in regions within SF Bay to other regions in the Bay. Due to low adult densities and/or low fecundity at some sites, only six sites were evaluated in this portion of our research. For the locations we evaluated, our estimates ranged from 3 million larvae exported from Oyster Point to more than 26 million exported larvae from Loch Lomond Marina. Source and sink dynamics likely vary between years, so these results should not be considered definitive.



Shell scars from dead oysters.

ENVIRONMENTAL CONDITIONS AND OLYMPIA OYSTERS

OYSTER POPULATION ATTRIBUTES

- Adult oyster density
- Population estimate
- Adult oyster size
- Diversity of size classes
- Recruit density
- Reliable recruitment
- · Larvae exported
- Survival rate
- Growth rate

SUPPORTIVE ENVIRONMENTAL FACTORS

- Water Temperature
- Chlorophyll a

ENVIRONMENTAL STRESSORS

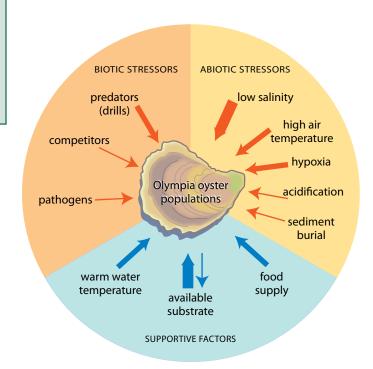
- Salinity range
- Oyster drill predation
- Risk of high air temperatures
- Low dissolved oxygen
- Risk of low salinity events

FIGURE 4

Conceptual diagram of main supportive factors and stressors affecting Olympia oyster populations in central California. Arrow thickness represents relative importance of factors (low, medium or high) based on our synthesis of regional data and literature.

OVERVIEW

The distribution and abundance of Olympia oysters is affected by numerous environmental factors. Through our newly collected data from field monitoring and laboratory experiments combined with a thorough review of the literature and our team's own expert opinion, we have identified the factors that appear to exert the strongest influence on Olympia oysters in our region (Figure 4). These include environmental factors that are beneficial or supportive to oysters, as well as environmental factors that pose threats or serve as stressors. Below, we describe the key factors, and explain the basis for our determination that they are of high, medium, or low importance to sustainable oyster populations. We have attempted to justify these classifications both transparently and robustly, pointing to the evidence on which they were based (Appendix 4). However, the identification of critical factors and classification of their importance should not be considered final and comprehensive; as new studies are conducted and new models created, our understanding is likely to evolve. It is also important to recognize that the general model of factors affecting oysters may not apply to every site. For instance, low salinity, oyster drills or hypoxia can exert strong negative effects on Olympia oysters at sites where they occur, but only were manifested at a subset of the sites we examined.





Large cobble provides hard substrate in Elkhorn Slough.

In stormy winters Many oysters do perish Empty shells linger

ENVIRONMENTAL FACTORS THAT SUPPORT OYSTERS

Hard substrate in low intertidal zone (importance: high)

Availability of hard substrate at the appropriate tidal elevation (e.g., from the mid-intertidal to the shallow subtidal) is a critical requirement for Olympia oysters. The size of hard substrates required to sustain oysters is a function of the depth of unconsolidated sediments at a site. At sites with deep mud, large hard substrates are required to prevent oyster burial, but at sites with little mud, oysters will survive on tiny hard substrates such as gravel or snail shells (Wasson 2010). Sites with otherwise appropriate environmental conditions for oysters will have none if substrate is lacking (Wasson 2010). For instance, at Elkhorn Slough there is a single site (Kirby Park) that has an order of magnitude more adult oysters than any other in the estuary; this site has an order of magnitude more hard substrate in the low intertidal zone than any other in the estuary, with the exception of the estuary mouth. Sites without hard substrate, but with appropriate environmental conditions, may be good candidates for restoration through substrate addition. Most restoration efforts provide hard substrate for oysters through addition of bare Pacific oyster half shell, reef balls, and other techniques. One example is the Coastal Conservancy's San Francisco Bay Living Shorelines Project, which constructed reefs in 2012 with mounds of clean Pacific half shell, and with artificial reef methods such as making reef balls using cement mixed with mined oyster shell and sand from SF bay. Up to 300 native oysters per square meter have settled onto the structures. The amount of hard substrate at each of our sites was an integral part of our population estimate, so we did not include this as a separate row in the Site Evaluation Tables.



Constructed reefs with Pacific shell bags provide hard substrate in SF Bay.

Chlorophyll *a* (importance: medium)

Phytoplankton (single celled planktonic algae) serves as food for filter-feeding oysters. Both food concentration and feeding time can be limiting, for example in intertidal areas with periods of aerial exposure compared with constantly submerged subtidal areas (Kimbro et al. 2009, Deck 2011). Limited food supply can result in reduced growth, shifts in size frequency, and reduced or delayed reproductive ability in other oyster species (e.g. Hofmann et al. 1994, Powell et al 1995). Food limitation also may lead to reduced growth and weight, and delayed time to settlement in Olympia oyster larvae (Hettinger et al. 2013). To estimate phytoplankton abundance at our sites, we measured the abundance of chlorophyll a, a plant pigment that is commonly used as a proxy for phytoplankton biomass. Our field data indicate that levels of chlorophyll a are positively correlated with oyster performance (Appendix 4). Measurements from our study sites ranged from an average for spring-fall of 3.1 μ g/L at Vierra, to 20.8 at Hudson Landing.

Warm water temperature (importance: medium)

Temperature is a major driver of virtually all oyster physiological processes, such as respiration, metabolism, filtration, and excretion (Hochachka and Somero 2002). Historical data and near-term models suggest that increased sea surface temperatures have occurred and will continue to occur in estuaries worldwide (Cloern et al. 2011). Our lab experiments indicate that near-term warming of estuarine waters is beneficial for oyster growth, as warming by 4°C increased oyster growth by 61% under unlimited food concentrations. Our field data showed a strong correlation between warm water measured at a site and several oyster attributes, including growth rate, average size, recruitment rates, and adult density (Appendix 4). Increasing water temperature can also ameliorate the effects of other environmental stressors (such as hypoxia), due to positive changes in metabolic rate, feeding, and so on. However, past a threshold (currently unknown for Olympia oysters), increasing water temperature likely has a negative effect and may also intensify the effects of other environmental stressors. Water temperatures were above 12°C 68% of the time at Point Pinole (SF Bay) and 95% of the time at Moss Landing Harbor (Elkhorn Slough).

ENVIRONMENTAL FACTORS THAT THREATEN OYSTERS (STRESSORS)

Low salinity (importance: high)

Salinity places basic physiological constraints on all marine and estuarine organisms (Hochachka and Somero 2002), and is a fundamental determinant of where species can live in an estuary (Remane and Schlieper 1971). Although Olympia oysters tolerate a range of salinity levels, low salinity exposure is stressful and can cause death in severe cases (Gibson 1974). Our field data showed a strong correlation between exposure to lower salinity levels and several oyster attributes, including average size, recruitment rate, and growth. In SF Bay, high freshwater flow following precipitation events and snowmelt can lead to low salinity conditions and subsequent massive die-offs in oyster

Blazing heat and air Meet a patch of oysters bare How will they now fare?



Die-off of oysters at China Camp after prolonged heavy winter rains in 2006.

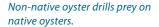


Monitoring at Elkhorn Slough.

populations (Appendix 4). Multiple lab experiments support these field observations, with juvenile Olympia oysters suffering significant mortality when exposed to salinity levels below 10 practical salinity units (psu) for five or more days. Our field data indicated that many oyster performance measures were negatively correlated with the average percentage of days when salinity at a site was below 25 psu; these data are captured in the Site Evaluation Tables in the "Salinity Range" row. Our field monitoring was conducted during a drought. Salinity was below 25 psu 36% of the time at Loch Lomond Marina (SF Bay) but never dropped below 25 at several sites in both estuaries. In addition, using longer term datasets (see Appendix 4), we indicated the percentage of years in which salinity at our sites had dropped below 5 psu for 4 days or more; these data are captured in the "Risk of Low Salinity" row. Most sites in the northern part of SF Bay had experienced such events in 25% of the years in the longterm data sets; while most mid-estuary sites at Elkhorn Slough and centralto-South Bay sites in SF Bay had no years with these low salinity events. More severe flood years are predicted for the region under climate change scenarios.

Predation by oyster drills (importance: medium)

Studies from other West Coast estuaries have shown that Atlantic oyster drills (*Urosalpinx cinerea*) can have substantial local impacts on oyster populations (Buhle and Ruesink 2009, Kimbro et al. 2009). *Urosalpinx cinerea* is well established in some parts of SF Bay, but recent work indicates that sites in the northern and central parts of the bay are unlikely to suffer oyster drill mortality due to absence of significant drill populations, with the exception of an oyster drill population within Richardson Bay (Zabin et al. 2010). However, oysters

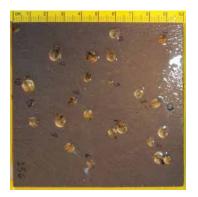




may be subject to significant predation south of the Bay Bridge, where drills are more abundant. These impacts have not been quantified. Oyster drills are not currently found in Elkhorn Slough but have been reported in Humboldt, Tomales, and Newport Bays (Carlton 1992). Most of our SF Bay sites had no drills, but drills were found at Aramburu Island, Oyster Point, Coyote Point, and Eden Landing. Highest drill counts were at Eden Landing where there was an average of 10 drills/m².

High air temperature (importance: medium)

Previous experiments have shown that Olympia oysters can tolerate high water temperatures, with an LT50 (50% mortality) between 38 and 39°C (Brown 2004, Cheng, unpublished data). How Olympia oysters respond to air temperature stress was previously unstudied, but may be important; air temperatures can reach and exceed oysters' thermal maximum, while water temperatures are unlikely to ever reach these high levels. Our lab experiments show that Olympia oysters can withstand high air temperatures during low tide exposure, even up to 40°C, but more frequent exposure and higher temperatures result in mortality (Appendix 3). Air temperatures high enough to cause mortality during low tide exposure currently occur rarely in central California (Appendix 4), but may occur more frequently in the future based on climate change projections. When paired with another stressor, such as low salinity, high air temperature can have more pronounced lethal effects (Appendix 3). We scored our study sites as potentially at risk for high air temperatures under future climate change in the "Risk of High Air Temperatures" row, using the number of days during our study period that sites experienced air temperatures above 30°C at MLLW. Coyote Point and Oyster Point in SF Bay both had 4 days above 30°C, while most of our sites had 0.



Oysters raised in the lab, subjected to low dissolved oxygen (top) and normal levels (above).

Low oxygen (importance: medium)

Hypoxia is the depletion of oxygen from water, typically defined as a dissolved oxygen threshold below 2-5 mg/L (by different standards). Estuaries and near-shore systems often exhibit hypoxia as a result of eutrophication. Eutrophication stimulates the primary production of plants, which then die and are decomposed via microbial consumption, which depletes the water column of oxygen. Overproduction of plants (e.g., algae) can also reduce dissolved oxygen at night when plants respire. Worldwide, hypoxia appears to be expanding in frequency and areal extent (Diaz and Rosenberg 2008). Locally, hypoxia is pervasive within Elkhorn Slough (Hughes et al. 2011) and has historically been an issue in south SF Bay. Our lab results suggest that diel-cycling hypoxia modeled after the conditions at Elkhorn Slough is not lethal, but has substantial sublethal effects on growth (Appendix 3). To score our sites by risk of hypoxia, we examined oxygen concentrations measured by day. We used the variance from typical fully-saturated oxygen conditions as the indicator, because we have found that it correlates with the duration of nighttime hypoxia (Appendix 4). Of our study sites, Azevedo Pond had the worst score, while most SF Bay sites did not appear to have a problem with very low dissolved oxygen.



Tube worms compete with oysters in Elkhorn Slough.

Acidification: low pH/alkalinity (importance: low)

One of the better-studied consequences of global change is the increasing acidity of ocean water due to the greater concentration of carbon dioxide (CO₂) in the atmosphere. However, the likely impacts of acidification for Olympia oysters are currently thought to be fairly low in central California. Estuaries such as SF Bay and Tomales Bay have relatively large seasonal and diurnal fluctuations in pH and carbonate saturation as the result of inputs from both watershed (river inflow) and nearshore oceans (via upwelling), and the influence of plant metabolism (daily cycles of photosynthesis and respiration) (Smith and Hollibaugh 1997). Consequently, organisms in these locations, including oysters, often already experience a very wide range of pH and carbonate saturation conditions. Potentially, these baseline conditions could worsen as increasing atmospheric CO₂ results in increasing water-column pCO₂, along with future changes in river inflows and upwelling inputs (Cayan et al. 2008, Checkley and Barth 2009). Such changes could produce an increasing frequency of low saturation conditions, with negative impacts on larval and juvenile oysters (Hettinger et al. 2012, 2013).

Competition from fouling species on hard substrates (importance: low)

Our field data showed no negative correlation between space covered by other sessile species and oyster density, recruitment, or growth at/near MLLW. The main groups of species present at MLLW were the green algae *Ulva* spp., red filamentous algae, and barnacles. Many sites were high in bare hard substrate availability. Previous work indicates that the effects of competition are variable, and more likely to have an impact on early life stages of Olympia oysters. The presence of competitors reduced total recruitment in SF Bay and reduced recruit size in nearby Tomales Bay, though effects varied by site (Deck 2011). Competitive effects increased at some sites at lower tidal heights, but this was not consistent across sites or bays. Only minimal effects were observed on other aspects of oyster life stages. Wasson (2010) found no correlation between recruit size or survival and distance to the nearest competitor near MLLW in Elkhorn Slough. However, greater low intertidal and subtidal coverage by



fouling species was observed, which could indicate potential effects at lower height. On the Pacific Northwest coast, Trimble et al. (2009) found that the presence of sessile invertebrate species reduced juvenile survival and growth, and tidal height did not affect this.

Olympia oysters growing on fence post in Elkhorn Slough. Extensive algal mats and low night-time oxygen result from inputs of agricultural nutrients.

FIGURE 18Other species on monitoring tiles at Vierra in Elkhorn Slough.



Sedimentation (importance: low)

Our field data show no negative correlation between oyster response variables and local sediment grain size, potential accumulation rate, or net change in sediment elevation, despite variation between sites in these factors. Other oyster species have been shown to be able to survive short term burial (Hinchey et al. 2006), but longer-term burial can reduce recruitment and increase mortality (Lenihan 1999). Grain size is an important aspect of sedimentation (Thrush et al. 2004); while significant accumulation of fine-grained sediment could limit water circulation and challenge feeding and respiration, even complete sediment burial in coarser-grained sands may not be detrimental. For example, some sandy sites monitored in this project have large oysters living on the undersides of rocks. It is important to note, however, that the impact of sedimentation is low only if sufficiently large hard substrates are available for oyster attachment. In the absence of attachment surfaces, oysters will be buried in deep mud. For instance, the majority of Elkhorn Slough consists of mudflats with deep fine sediments. Oysters are entirely absent from these areas, except where artificial hard substrates are available for attachment, allowing them to avoid burial (Wasson 2010). Sediment burial is thus an extremely important factor in explaining the distribution of oysters in this estuary. It is considered of low importance here because we have focused on sites with ample hard substrate and relatively low amounts of sediment accumulation; these are the typical conditions under which Olympia oysters currently occur in central California.



FIGURE 19Oysters in muddy conditions at Elkhorn Slough.

Contaminants (importance: low)

Despite the presence of contaminants at many central California sites, oysters do not appear to be very sensitive to them, generally. Current environmental laws have reduced the use and release of contaminants, such as organic biocides (Axiak et al. 1995), polycyclic aromatic hydrocarbons, and heavy metals (Connor 1972), which were previously found to affect oyster populations. Olympia oyster







Reef balls deployed in Elkhorn Slough (top) and SF Bay (middle). Above: SF Bay Living Shorelines Project constructed reefs at the San Rafael Shoreline.

populations exist in habitats formerly considered "polluted," such as near a wastewater treatment outfall in Humboldt Bay, CA, in marina basins in SF Bay, and in an area formerly contaminated with heavy metals and polychlorinated biphenyls near Stege Marsh, Richmond, CA (Hwang et al. 2013).

Pathogens and diseases (importance: low)

Overall, oyster diseases and pathogens do not appear to be a major factor influencing native oyster populations in Central California. The most recent published surveys of disease in Olympia oysters in SF Bay (Friedman et al. 2005; Moore et al. 2011) reported that potentially pathogenic bacteria, viruses, and protists are present only in a minority of oysters, and typically at levels lower than those associated with disease. These studies showed little evidence for presence of disease except for disseminated neoplasia in Drakes Estero, and Candlestick Point, Oyster Point, and Coyote Point in SF Bay (Friedman et al. 2005, et al. 2008, Moore et al. 2011). The levels measured at these four sites are unlikely to seriously affect oyster populations or impact restoration efforts (Grosholz et al. 2008). However, disease may become more prevalent as a result of other stressors associated with climate change.

Sea level rise (importance: low)

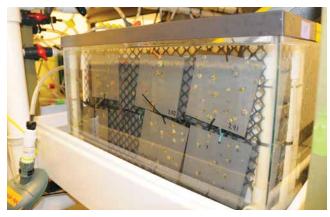
Sea level rise such as is projected to accompany global climate change should not inherently cause problems for oysters unless hard substrate is unavailable at new tidal elevations, or unless other stressors are exacerbated as the mean tidal elevation of existing hard substrate (and associated oyster populations) decreases. One potential impact of sea level rise could be increased local resuspension of sediment due to greater wave action and tidal currents associated with deeper waters. This could result in stressors associated with increased sediment burial in shallower areas. Shoreline hardening solutions to sea level rise could add significant hard substrate for oyster settlement and may support greater intertidal oyster populations in some areas. Despite the drawbacks of traditional shoreline hardening, such measures are increasingly being incorporated into thoughtfully planned nature-based solutions, such as living shorelines, that create habitat for multiple species.

Interactions between stressors

Environmental stressors often occur in combination. It is therefore important to understand not only the impacts of individual stressors but also the effects of combinations of multiple stressors on Olympia oysters. Multiple stressors can produce additive effects (i.e., equal to the sum of the stressor impacts alone), or interactive ones (i.e., either more detrimental or less detrimental than would be expected by simply adding the effects of the stressors alone).

We used field studies, combined with previous work to measure baseline patterns of potential environmental stressors in relation to oyster demographics. We used several multivariate analyses of a broad suite of environmental variables (including air and water temperature, salinity, and dissolved oxygen) and





Tank experiments at the Bodega Marine Lab.

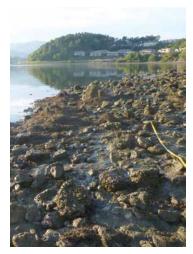
oyster demographic parameters (density, growth rate, size, recruitment rate) to identify which stressor or combinations of stressors explained the most variation in oyster demography. We identified no interactive effects.

We used laboratory experiments to more closely investigate causal relationships between multiple stressors and Olympia oyster survival and performance. In the first experiment, we examined interactions between warm water temperatures and low oxygen levels applied as simultaneous stressors, and then following a recovery period, applied low salinity stress, so interactions between all three stressors could be examined. Here, we found no evidence for interactive effects, but rather, these stressors were additive (Appendix 3). In the second experiment, we assessed the effects of low salinity and high air temperature simultaneously, and with different amounts of time between applying the two stressors. When applied simultaneously, we saw synergistic effects (detrimental effects beyond what would be predicted by simply adding the effects of low salinity and air temperature). When oysters were given recovery time between stressors, this synergistic response disappeared (Appendix 3). Previous studies have found interactive effects to be generally more common than additive effects (Crain et al. 2008, Darling and Cote 2008), but we found that results are dependent on the specific stressors and their timing. Although some stressors like low salinity and high air temperature may co-occur (for example, during springtime in some parts of SF Bay) and produce synergistic effects, realistic recovery time between stressors may lead to effects that are more additive in nature.

Site Evaluations

BACKGROUND AND GOALS

At our April 2013 project workshop, resource managers and restoration practitioners indicated that one of the most useful products that could come out of our current project was a report-card style table ranking our study sites in terms of their suitability for native oyster restoration and conservation. The Site Evaluation Tables evaluate our intertidal study sites using data collected in the field over the course of the project from April 2012 through November 2013, coupled with insights from our laboratory experiments, and, where possible,



Rocky intertidal habitat at Strawberry (Brickyard Cove).

long term data sets for key environmental and biological parameters. We have attempted to make the table easy to understand and use as well as transparent in terms of how scores were derived, so that users can adapt the table to their own purposes, including using it to score additional sites for which they have key data.

HOW THE TABLES WERE CREATED

The Site Evaluation Tables score sites based on oyster performance and on measurements of key environmental parameters. For each site, we included measurements of the oyster attributes described above, and factors that analysis of our field or laboratory data (or a literature search) indicated affected one or more of these attributes. We have created two versions of the Site Evaluation Table: an abbreviated summary version (see next page) and a longer version, with actual data values used for the scoring (pages 32–35). Both tables include three different overall scores at the bottom: 1) a score indicating suitability of the site for restoration through addition of hard substrates; 2) a score indicating suitability of the site for restoration through addition of hard substrates seeded with thousands of oysters, sufficient to establish a self-sustaining population supplying larvae to this area, and 3) a score indicating value of this area for conservation of existing oyster populations. Details on all the parameters included, their weighting, and calculation of the overall scores are included in the notes to the summary table. The longer table is also available online in a format that allows users to enter their own data to derive a site score.

Evaluation of 21 sites in San Francisco Bay and Elkhorn Slough

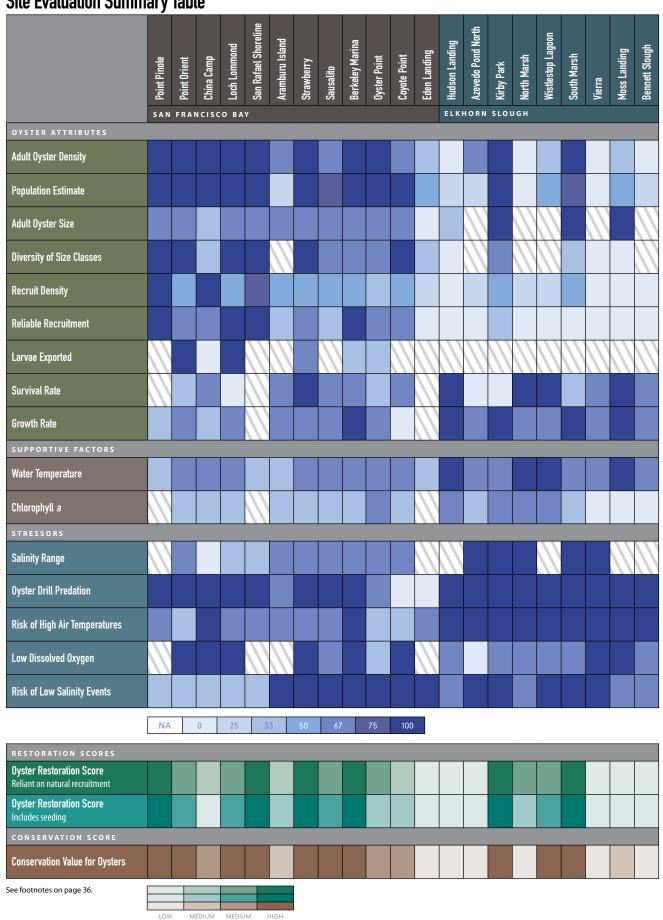
Twenty one sites were evaluated in the two estuaries (Figures 2 and 3). The Site Evaluation Tables show the overall restoration suitability scores for these sites. On the whole, sites in SF Bay scored higher than those at Elkhorn Slough. Top scoring sites were Berkeley Marina, Strawberry (Brickyard Cove), Point Pinole, San Rafael Shoreline in SF Bay; South Marsh and Kirby Park at Elkhorn Slough. At both estuaries, mid-estuary sites generally scored higher than other sites, which is consistent with our working knowledge of the sites. Although North Bay sites also were high-scoring in SF Bay during this relatively short study period, these sites are more vulnerable to low salinity events. Over the nearly 10 years we have been working in SF Bay, we have seen populations at these sites steeply decline during years of heavy rain. Sites in the South Bay, which have oyster drill

Urbanized conditions in SF Bay (near right) compared to rural conditions at Elkhorn Slough (far right).





Site Evaluation Summary Table









Top: monitoring tiles at Kirby Park in Elkhorn Slough. Middle: students with The Watershed Project. Above: sunset low tide monitoring at Point Orient.

populations and warmer air temperatures, such as Eden Landing and Coyote Point, scored lower. Aramburu Island in Richardson Bay, which lacks substrate at the appropriate tidal height and has a drill population, also received a low score. At Elkhorn Slough, several sites presumed to have favorable environmental conditions, but with little to no recruitment and/or adult oysters, such as Vierra and Moss Landing, also received low overall scores, as did some upper estuary and tidally muted sites with low recruitment and poor water quality.

DATA LIMITATIONS

It is important to keep in mind that the Site Evaluation Tables are based strictly on biological/ecological measurements and do not take into account other important considerations in site selection, such as community support, access, funding, and permit procedures.

Even from a strictly scientific perspective, there is still much to learn about native oyster population biology and ecology in our region, and of course there are many unknowns as we project into the future, given a changing climate. In many cases, data are available only for short time spans that likely do not represent the full range of conditions at a site over longer periods, or detailed data are only available at larger spatial scales, yet conditions may vary with microclimates at the site level. In the creation of this table, we relied on our expert opinion to weigh the relative importance of oyster performance data and the likelihood of extreme climate events at our study sites, particularly in converting raw data into weighted ranks. As such, the table represents a combination of empirically derived data and judgment calls.

Thus, site scores should be considered advisory only. For some sites, it is also possible that modifications to the restoration approach can help ameliorate stressors, such as deploying substrates in the shallow subtidal rather than intertidal zone to reduce heat stress at a site with frequent very-high air temperatures.

APPLYING SITE EVALUATION CRITERIA ELSEWHERE

The scoring system used in our table is based on the range of measurements from our study sites over a two-year period. Given the relatively broad distribution of our sites in the two estuaries, with reasonable confidence the table could be used to evaluate other sites in SF Bay and Elkhorn Slough, and, potentially, nearby sites that experience similar environmental conditions, such as Tomales Bay, Humboldt Bay and Morro Bay, if the user has site-specific data. The table structure could be used for other locations, but the ranges used to generate scores (such as water temperature, salinity, growth, size distribution) would need to be adjusted to accommodate local data.

The online version of the Site Evaluation Table in Excel allows users to populate the table with their own data. At an absolute minimum, we recommend collecting data on adult oyster densities and diversity of size classes for restoration sites being considered. As mentioned above, these surveys ought to be made shortly after recruitment season. These data, along with surveying the extent of shoreline



Installing monitoring tiles in SF Bay.

Elegant oysters, unique history and lore. Habitats prevail! with hard substrate at the appropriate tidal height, are the minimum that should be collected for sites under consideration. Data on recruitment rates, derived by deploying clean substrate at the start of recruitment season, should be collected if at all possible, and ideally these data should be collected over several years, as recruitment can be highly variable at some locations. Recruitment to deployed substrate and subsequent measurements of growth and survival should be evaluated for sites that do not have hard substrate but are being considered for restoration involving substrate addition. If possible, data on environmental variables should also be incorporated. Among these, the most important is an examination of longer-term salinity data from a nearby monitoring station to determine whether there is a risk of extended freshwater events during wet years. Assessing whether oyster drills are abundant at the site can also be done fairly easily.

Management Applications

OVERVIEW

The new science and tools presented in this guide have concrete applications to Olympia oyster restoration and management. The oyster restoration and conservation stakeholders involved in this collaborative project supplied the management questions they find of highest priority to address (Wasson 2013). For each question, we provide examples of management decisions and summarize the guidance this report provides for them.

Which sites currently support healthy and abundant existing oyster
populations that are most likely to be sustainable in the long-term? *Example of management decision:* strategic planners and resource agency
staff involved in permitting determine which sites/populations need special
protection from development or nearby disturbance; regulatory agency

considers oyster needs when designating a new marine protected area.

Guidance: site evaluation table above indicates which sites have the highest conservation score, and should thus receive priority: Point Pinole, Richmond (Point Orient), San Rafael Shoreline, Strawberry (Brickyard Cove), Loch Lomand Marina, Sausalito, and Berkeley Marina in SF Bay and Kirby Park, Whistlestop, and South Marsh in Elkhorn Slough. It is important to keep in mind that this prioritization is based on best current information; rankings may change as new data become available or as conditions change at these sites.

2. Which sites supply a disproportionate amount of larvae to other sites, thereby acting as a source of larvae rather than a sink?
Example of management decision: strategic planners and resource agency staff involved in permitting determine which sites/populations need special protection from development or nearby disturbance; regulatory agency considers oyster needs when designating a new marine protected area.

HIGHEST LIKELIHOOD OF RESTORATION SUCCESS

ELKHORN SLOUGH

- Kirby Park
- South Marsh

SF BAY

- Pt. Pinole
- Pt. Orient
- Strawberry
- · Berkeley Marina



Student volunteers with The Watershed Project monitor conditions at Point Pinole.

Guidance: the site evaluation table indicates the sites that contribute most to larval production for SF Bay. These were Richmond (Point Orient), Loch Lomond Marina and Strawberry (Brickyard Cove).

3. a) Which sites are best for success and long-term sustainability of oyster restoration projects?

Examples of management decisions: funder decides between competing projects in different locations; strategic planner for estuarine restoration picks target areas; restoration group decides where to propose next project.

Guidance: site evaluation table above indicates which sites have the highest restoration score, and should thus receive priority. The sites with the highest likelihood of restoration success are: Kirby Park, South Marsh, Point Pinole Regional Shoreline, Richmond (Point Orient), Strawberry (Brickyard Cove) and Berkeley Marina. Again, it is important to keep in mind that this prioritization is based on best current information; rankings may change as new data become available or as conditions change at these sites.

b) Is an oyster restoration project done at site X likely to be successful?

(This question is very similar to 3a, but in this case applied to a single site as a "yes/no" question about doing restoration, rather than involving prioritization between multiple sites.)

Example of management decision: restoration group decides whether to propose project at a particular site; funder decides whether to fund; conservation land trust or resource management organization decides whether to invest in oyster restoration at a particular property they own.

Guidance: the site evaluation tables provide evaluation of our study sites; the Excel version of this table (available online) can also be used as a tool for evaluating new sites.

4. How do effects of climate-related stressors compare to those of other stressors?

Example of management decision: estuarine ecosystem-based restoration initiative decides which stressors to focus on addressing in their strategic plan, and this decision is influenced by understanding the relative impacts of climate-related stressors compared with other stressors.

Guidance: synopsis of the environmental factors affecting Olympia oysters is provided in the text above: in a nutshell, current stressors such as episodic low salinity, hypoxia and oyster drills pose a greater threat than climate-related threats from increased water temperature, acidification, and sea level rise. However, projected increases in air temperature and storminess (leading to more extensive low salinity events in SF Bay) will pose threats.





Deploying monitoring equipment in Elkhorn Slough.

5. Can resilience of oysters to climate change be enhanced by decreasing other stressors?

Example of management decision: oyster restoration group decides to focus on stressor reduction (such as reducing nutrient run-off or removing a non-native species) at a site instead of (or in addition to) deployment of substrates if there is evidence for greater benefits from this approach; regulatory agencies decide to establish thresholds for stressors (for example, Total Maximum Daily Loads set by the State Water Resources Control Board) because of the demonstrated ecological benefits of enhanced climate change resilience as a function of stressor reduction.

Guidance: our field and laboratory experiments found strong negative effects of existing stressors, so there are definite benefits to addressing these factors (such as decreasing hypoxia or preventing oyster drills from colonizing new regions). In one of our experiments (Appendix 3), we found no synergistic effects between an existing stressor (hypoxia) and a climate-related stressor (warm water temperature). So in this case, decreasing the existing stressor does not enhance resilience to climate change. Indeed, in this experiment, this climate-related factor was revealed to be beneficial, not stressful. In another experiment we found negative effects of two climate-related factors (air temperature and low salinity), and interactions between them. In this case, resilience to one stressor could be enhanced by decreasing the other. However, the interactions between stressors disappeared if their timing was offset to allow for recovery. So we found that additive effects may be common under typical conditions faced by Olympia oysters.

Conclusion and Next Steps

This guide has synthesized data from recent laboratory experiments and field monitoring, and the published literature. We have used this information to identify the attributes of sustainable Olympia oyster populations, and to prioritize the supportive and stressful environmental factors that affect them most strongly in central California. Overall, we found that existing stressors such as eutrophication or invasive oyster drills exert more stress on Olympia oysters than stressors related to climate change, but eventually threats posed by factors such as warm air temperatures and increasingly variable salinity may become very important. We have developed a site evaluation tool and used it to assess restoration and conservation potential of Olympia oysters at 21 sites in SF Bay and nine sites in Elkhorn Slough. As more investigations are conducted and restoration projects are implemented, understanding of oyster sustainability will evolve, and these guidelines will need updating. We hope that in the coming years, the recommendations provided here support improved oyster conservation and restoration in California.

Site Evaluation Table: San Francisco Bay

		-			Point Pinole		Point Orien	nt	China Cam	р
PARAMETER	SCORING				DATA	SCORE	DATA	SCORE	DATA	SCORE
OYSTER ATTRIBUTES Adult Oyster Density		ard substrates at MLLW 33 10–100 = 67			177	100	737	100	250	100
Population Estimate		a covered by adults at N	MLLW 00 = 75 >10,000	= 100	10,000	100	10,000	100	10,000	100
Adult Oyster Size		tile on large hard subst $20-29 \mathrm{mm} = 33 \mid 3$	trates at MLLW 0—49 mm = 67 >	> 50 mm = 100	40	67	38	67	21	33
Diversity of Size Classes	· ·	, ,	rge hard substrates at l $-0.83 = 67 \mid > 0.83$		0.854	100	0.843	100	0.747	33
Recruit Density		•	on settlement plates a $0-40 = 75 \mid >40$		88	100	4	50	55	100
Reliable Recruitment		on of recruitment rate $2.6 = 33 \mid 1.3-1.9$	= 67 0-1.25 = 1 0	00	1.2	100	1.8	67	1.4	67
Larvae Exported	estimate of larvae estimate $0 = 0 \mid 1-10,000,0$	•	1–20,000,000 = 67	>20,000,000 = 100			22,000,000	100	0	0
Survival Rate		rly average, observed o 0.51–99.64 = 33 9	over time 9.65–99.80 = 67 >	-99.81 = 100			99.55	33	99.65	67
Growth Rate	mm/day, mean acro $< 0.05 = 0 \mid 0.0$		-0.099 = 67 >0.1	=100	0.05	33	0.08	67	0.06	33
SUPPORTIVE FACTORS Water Temperature		,	12° C, sampled at MLL'		68.8	33	85.9	67	86.3	67
Chlorophyll a	average μ g/L, sprin $<$ 5 = 0 5–10 =	g-fall = 33 10-25 = 67	7 >25 = 100				8.09	33	9.71	33
Salinity Range		year average salinity $<$ $-40\% = 33 \mid >0 \text{ to}$	25 ppt 0 25% = 67 0 = 1	00			13.4	67	42.2	0
Oyster Drill Predation	oyster drills/m ² $> 5 = 0 \mid 2-5 =$	= 33 < 2 = 67	0 = 100		0	100	0	100	0	100
Risk of High Air Temperatures	days with intertidal $5+=0 \mid 3-4=$	max temp $> 30^{\circ}$ C = 33 1-2 = 67	0 = 100		1	67	3	33	0	100
Low Dissolved Oxygen		ation from acceptable reconstruction $=$ 33 2–2.9 $=$ 67	_				1.70	100	1.90	100
Risk of Low Salinity Events	· ·	, , ,	pt) of ≥ 4 consecutive d 0-24.99% = 67 0	•	25	33	25	33	25	33
RESTORATION SCORES Oyster Restoration Score Reliant on natural recruitment	LOW < 75	MEDIUM LOW 76–84	MEDIUM HIGH 85-94	HIGH >94	HIGH	101	MEDIUM HIGH	93	MEDIUM LOW	80
Oyster Restoration Score Includes seeding	LOW <75	MEDIUM LOW 76–84	MEDIUM HIGH 85–89	HIGH >89	HIGH	92	MEDIUM HIGH	89	LOW	74
CONSERVATION SCORE Conservation Value for Oysters	LOW < 80	MEDIUM LOW 81–90	MEDIUM HIGH 91–100	HIGH >100	HIGH	122	HIGH	108	MEDIUM HIGH	92

Loch Lomo	ond	San <u>Rafae</u>	l Shoreline	Aramburu Island Strawber			vberry Sausalito		Berkeley Marina Oyster Poi		Oyster Poi	ster Point Coyote Po		e Point <u>E</u> o		Eden Landing	
DATA	SCORE	DATA	SCORE	DATA	SCORE	DATA	SCORE	DATA	SCORE	DATA	SCORE	DATA	SCORE	DATA	SCORE	DATA	SCORE
961	100	476	100	35	67	314	100	48	67	266	100	433	100	64	67	3.52	33
100,000	100	10,000	100	10	25	10,000	100	1,000	75	10,000	100	10,000	100	10,000	100	100	50
35	67	38	67	40	67	46	67	41	67	39	67	31	67	32	67	12.3	0
0.852	100	.849	100			0.876	100	0.821	67	0.824	67	0.818	67	0.749	100	0.397	33
2	50	10	75	3	50	2	50	1	50	4	50	2	25	3	50	0.089	25
1.2	100	0.82	100	2.4	33	1.3	67	2	33	1	100	1.5	67	1.6	67	3.18	0
26,000,000	100					12,000,000	67			8,000,000	33	4,000,000	33				
99.45	0			99.72	67	99.85	100	99.71	67	99.79	67	99.61	33	99.77	67		
0.09	67			0.08	67	.08	67	0.08	67	0.1	100	0.09	67	0.037	0		
86.6	67	81.7	33	73.6	33	87.6	67	84.7	67	87.3	67	86.3	67	86.8	67	83.3	33
8.29	33			5.66	33	5.49	33	6.87	33	6.29	33	20.46	67	9.47	33		
35.9	33	35.9	33	0.2	67	0.2	67	0.2	67	1.8	67	12.9	67	13.1	67		
0	100	0	100	1	67	0	100	0	100	0	100	0.1	67	8	0	10	0
1	67	1	67	1	67	1	67	1	67	0	100	4	33	4	33	2	67
1.98	100					1.70	100	2.20	67	1.81	100	2.11	33	1.72	100		
25	33	25	33	0	100	0	100	0	100	0	100	0	100	0	100	0	100
MEDIUM HIGH	90	HIGH	98	MEDIUM LOW	80	HIGH	103	MEDIUM HIGH	88	HIGH	102	MEDIUM HIGH	86	MEDIUM LOW	80	LOW	44
MEDIUM HIGH	86	HIGH	91	MEDIUM LOW	78	HIGH	97	MEDIUM HIGH	85	HIGH	98	MEDIUM LOW	82	MEDIUM LOW	76	LOW	42
HIGH	104	HIGH	118	MEDIUM LOW	82	HIGH	118	HIGH	101	HIGH	116	MEDIUM HIGH	98	MEDIUM HIGH	97	LOW	58
NA	0	25	33	50 67	75	100											

Site Evaluation Table: Elkhorn Slough

					Hudson Land	ing	Azevedo Pond North		
PARAMETER	SCORING				DATA	SCORE	DATA	SCORE	
OYSTER ATTRIBUTES Adult Oyster Density	•	nard substrates at MLLW 33 10–100 = 67		10	0	87.5	67		
Population Estimate		a covered by adults at <i>N</i>		10	25	100	50		
Adult Oyster Size		rtile on large hard subst 20—29 mm = 33 3		> 50 mm = 100	29	33			
Diversity of Size Classes		of size frequency on la 25–0.80 = 33 0.81-	•		0.25	0			
Recruit Density		eraged across quarters, 25 1–9 = 50 1	·		0	0	0.366	25	
Reliable Recruitment		ion of recruitment rate $-2.6 = 33 \mid 1.3-1.9$	= 67 0-1.25 = 1	00	4	0	2.89	0	
Larvae Exported	estimate of larvae e 0 = 0 1–10,000,	exported 000 = 33 10,000,00	1–20,000,000 = 67	>20,000,000 = 100					
Survival Rate	2.1	rly average, observed o		>99.81 = 100	99.9	100	99.48	0	
Growth Rate	mm/day, mean acro $< 0.05 = 0 \mid 0.0$	oss quarters 05–0.069 = 33 0.07	7-0.099 = 67 >0.	0.11	100	0.087	67		
SUPPORTIVE FACTORS Water Temperature		temperature average > 0-85% = 33 85-9	•	91.3	100	88.5	67		
Chlorophyll a	average μ g/L, sprir $<$ 5 = 0 5–10	ng–fall = 33 10–25 = 67	7 >25 = 100	20.8	67	7.27	33		
Salinity Range		/year average salinity $<$ $-40\% = 33 \mid > 0 \text{ t}$		100			0	100	
Oyster Drill Predation	oyster drills/m ² $> 5 = 0 \mid 2-5 =$	= 33 <2 = 67	0 = 100		0	100	0	100	
Risk of High Air Temperatures	days with intertidal $5+=0 \mid 3-4=$	max temp $> 30^{\circ}$ C = 33 1-2 = 67	0 = 100		0	100	0	100	
Low Dissolved Oxygen		ation from acceptable r $0 = 33 \mid 2-2.9 = 67$	-		2.27	67	4.5	0	
Risk of Low Salinity Events		low salinity event (\leq 5 p -49.99% = 33 >	•		67	0	100		
RESTORATION SCORES Oyster Restoration Score Reliant on natural recruitment	LOW < 75	MEDIUM LOW 76–84	MEDIUM HIGH 85-94	HIGH >94	LOW	0	LOW	73	
Oyster Restoration Score Includes seeding	LOW < 75	MEDIUM LOW 76–84	MEDIUM HIGH 85-89	HIGH >89	LOW	67	LOW	73	
CONSERVATION SCORE Conservation Value for Oysters	LOW < 80	MEDIUM LOW 81–90	MEDIUM HIGH 91–100	LOW	78	LOW	72		

Kirby Park		North Marsh		Whistlestop Lagoon		South Marsh		Vierra		Moss Landing		Bennett Slough	
DATA	SCORE	DATA	SCORE	DATA	SCORE	DATA	SCORE	DATA	SCORE	DATA	SCORE	DATA	SCORE
303	100		0	3.27	33	205	100	0	0	3	33		0
10,000	100	0	0	100	50	1,000	75	0	0	100	50	10	25
57	100					53	100			66	100		
0.817	67					0.789	33			0	0		
4	50	0.72	25	0.337	25	2	50	0	0	0	0	0	0
2.4	33	2.94	0	3.1	0	2.9	0		0		0		0
99.46	0	99.9	100	99.9	100	99.59	33	99.75	67	99.89	100	99.75	67
0.11	100	0.092	67	0.078	67	0.11	100	0.09	67	0.11	100	0.095	67
89.6	67	90.5	100	90.2	100	89.2	67	88.5	67	95.2	100	88.9	67
13.23	67	12.1	67	12.25	67	8.8	33	3.1	0	4.23	0	3.77	0
0	100	0	100			0	100	0	100				
0	100	0	100	0	100	0	100	0	100	0	100	0	100
0	100	0	100	0	100	0	100	0	100	0	100	0	100
2.47	67	2.95	67	2.6	67	2.83	67	1.33	100	1.3	100	2.49	67
0	100	7.14	67	0	100	0	100	0	100		67		67
HIGH	100	MEDIUM HIGH	85	MEDIUM HIGH	88	HIGH	94	LOW	0	LOW	0	LOW	0
HIGH	96	MEDIUM LOW	83	MEDIUM HIGH	87	HIGH	91	LOW	65	MEDIUM LOW	78	LOW	61
HIGH	115	LOW	0	HIGH	103	HIGH	102	LOW	0	MEDIUM LOW	89	LOW	71

Notes to the Site Evaluation and Summary Tables

The Site Evaluation Tables show the site data and scores for each parameter for sites in the Elkhorn Slough area and the San Francisco Bay. The Site Evaluation Summary Table shows only the assigned scores, represented as color-coded cells.

In the Site Evaluation Tables, there are two columns for each study site: the first shows the raw data for each parameter and the second indicates the score to which the raw data were converted. The lower the score, the poorer the site. For each site, the three lowest right-hand cells give the overall scores, which are the weighted average of all parameter scores, and the left-hand cells show color-coded qualitative scores. The three overall scores for each site are: 1) for restoration that is reliant on natural recruitment; 2) for restoration that includes seeding; 3) for site conservation value. These overall scores were translated into one of four qualitative rankings (low, medium low, medium high or high), based on the spread of scores across all sites.

We used three major categories of parameters used in the table:

- 1. Oyster attributes—measurements of oyster performance in the field, based on our study;
- 2. **Supportive factors**—those factors our field data indicate affect native oyster populations in our region;
- 3. Stressors—one that our field data indicates negatively affects native oysters (salinity range), one that work elsewhere indicates impacts oysters (predation by oyster drills) and three that are measures of how likely sites are to approach threshold levels for the factors our lab experiments indicate are stressful to oysters (high air temperatures, low dissolved oxygen, low salinity). Data for these last three measures were generated from our current project, or from longer-term monitoring efforts (Appendix 4). While sites may not currently reach threshold levels—no sites had average daily air temperatures above 40°C, during our study period, for example—we assumed that sites that already experience high levels of these stressors may be more likely to do so with increasing intensity and frequency in the future under climate change scenarios.

When data are not available for a parameter, no score is entered, and the box is shaded with cross-hatching. Missing data do not affect the overall site score, but the more missing values, the greater uncertainty about the overall score for the site.

PARAMETERS AND SCORING

The parameter column lists the parameters used in the table.

The scoring column shows how raw data were converted into scores. For each parameter, scores range from 0 (lowest) to 100 (highest) in five equal increments (0, 25, 50, 75, 100) or in four increments (0, 33, 67, 100). Note that in some cases, for example for the number of oyster drills, a *high* number translates into a *low* score, as higher predation is obviously not good for sustainable oyster populations. In other cases, such as adult oyster density, high density earns a high score.

Adult oyster density on large hard substrates near mean lower low water. 2.0. Weighted multiplier: 2.0. Omit, along with oyster size and size frequency measures, if no hard substrate exists at site.

Population estimate. Weighted multiplier: 2.0. These order of magnitude estimates were generated by estimating the amount of hard substrate at mean lower low water over a 300 m stretch of shoreline centered over our 30 m transects, and multiplying this by the percentage of cover of oysters in our transects. This score is used in place of adult oyster density to generate a site's conservation value. Sites with no oysters earn a zero score for conservation value.

Adult oyster size. Weighted multiplier: 1.25. This is the mean of the largest oysters (upper quartile) on large hard substrates near mean lower low water. Mean size of the largest oysters incorporates growth and survival; this measure can be used where data on growth and survival are absent, combined with data on the diversity of size classes. Although easy to obtain, this measure should be interpreted with caution and balanced against other known factors, as many factors (such as recruit density) can limit size.

Diversity of size classes. Weighted multiplier: 1.5. Data from transects on hard substrate at mean lower low water made in the fall, after recruitment period. The Gini-Simpson index ranges from 0 (lowest diversity) to 1 (highest diversity) and incorporates measurements of both number of size classes and evenness (or distribution) of individuals among size classes. The score will be higher when multiple size classes are present, indicating successful recruitment and survival. This measure can be used in combination with adult oyster size for a synoptic view of a site, when data on growth and mortality are missing. However, precision

is increased when direct measurements of growth and mortality are included.

Recruit density. Weighted multiplier: 2.0 (1.25 for generating score for restoration to include seeding). Data from settlement plates near mean lower low water, calculated as the number of settlers/m²/day, quarterly averages. Ideally, recruitment calculations should be averaged over multiple years, as recruitment can be highly variable in some locations. A zero score in the parameter results in a zero site score for restoration reliant on natural recruitment; for restoration that includes seeding, this parameter is downweighted. However, sites with no measured recruitment still rank lower than sites with natural recruitment.

Reliable recruitment. Weighted multiplier 1.25 (1.0 for generating score for restoration to include seeding). Data from settlement plates near mean lower low water; coefficient of variation (CV) of recruitment density (above). The CV is the ratio of standard deviation to the mean. Many sites have sporadic very high recruitment while others are moderate but steady. This score balances recruitment rate against variability in recruitment. However, multiple years are needed to calculate this score. Some of the sites that scored well based on our two years of study would have done poorly if data from earlier years were used. Sites that had no recruitment during our study period also received a 0 score for reliability, as they were reliably bad in terms of recruitment!

Larvae exported. Weighted multiplier 1.25 (1.5 for generating site conservation value score). Approximate number of larvae exported per square meter from each site for a subset of sites. Product of adult density (above) × fecundity rate (from field data) × estimated larval production (from literature) × larval exports based on data from shell chemistry analysis.

Survival rate. Weighted multiplier 1.5. Percent alive/day of oysters observed over time, averaged across all quarters. Ideally sites have high survival. Outplanted oysters can be used to determine survival rates at a site with few to no oysters.

Growth rate. Weighted multiplier 1.0 (1.25 for sites with no or low numbers of oysters). Growth measured in mm/day for oysters observed over time, averaged across all quarters. Ideally sites should have high growth of oysters, which may result in oysters being less susceptible to environmental stress and/or predation. Outplanted oysters can be used to determine growth rates at a site with few to no oysters. This measure needs to be treated with caution, as high recruit densities can inhibit growth.

Water temperature. Weighted multiplier 1.25. Water temperatures sampled near mean lower low water. Warmer water temperatures were correlated with positive oyster performance in the field for the range of temperatures measured at our sites (Appendix 4).

Chlorophyll. Weighted multiplier 1.25. Average concentration spring through fall near our study sites, spot samples. Oyster performance in the field was positively correlated with higher chlorophyll at our study sites over the range of chlorophyll *a* measured at our sites (Appendix 4).

Salinity range. Weighted multiplier 1.5. Data from continuous salinity loggers. Oyster performance in the field was positively correlated with higher salinity at our study sites over the range of salinity measured at our sites (Appendix 4).

Drill predation. Weight multiplier 1.25. This risk factor is estimated by the number of Atlantic oyster drills (*Urosalpinx cinerea*) counted along our study transects; no other species of drills were found. The non-native drills are not present in Elkhorn Slough or at most of our study sites in San Francisco Bay.

Risk of high air temperature. Weighted multiplier 1.25. This risk factor is estimated by the percentage of days with daily maximum temperatures >30°C at mean lower low water, measured during our study period (Appendix 4). Laboratory experiments indicate very high air temperatures are negatively correlated with oyster performance (Appendix 3); we assumed that sites that are warmer now are more vulnerable to experiencing higher temperatures under global climate change.

Low dissolved oxygen. Weighted multiplier 1.25. This risk factor is estimated by the average deviation from an acceptable range that sites currently experience (Appendix 4). Laboratory experiments indicate low oyster performance in hypoxic conditions, although effects can be partially offset by warmer water temperatures (Appendix 3).

Risk of low salinity events. Weighted multiplier 1.5. This risk factor is estimated using the percentage of years during which at least one low salinity event of 4 consecutive days of salinity <5 ppt occurred. Data from long-term records; length of record varies by site (Appendix 4). Laboratory experiments show oyster mortality increases under very low salinity conditions, such as those experienced in some parts of SF Bay during heavy winter-spring rains.

Overall scores

Oyster restoration score, restoration reliant on natural recruitment. If recruitment was zero, then score is zero. Otherwise all parameters are used except for the site population estimate and are weighted as noted above.

Oyster restoration score, restoration to include seeding. This score uses all parameters except for the site population estimate. Recruitment density and recruitment CV are downweighted as indicated.

Conservation value for oysters. Uses all parameters but weights larvae exported higher, and substitutes population estimate for adult oyster density. If population is zero, then the score is zero.

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Appendices

The appendices are available as pdfs on-line, at www.oysters-and-climate.org.

Appendix 1. Supplemental information about project funding and team composition.

Appendix 2. Field monitoring: methods and results.

Appendix 3. Laboratory experiments: methods and results.

Appendix 4. Site evaluation table: detailed explanation.

Image Credits

Abbreviations: t (top), m (middle), b (bottom), l (left), c (center), r (right)

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PAGE 7: Anna Deck

PAGE 8: Marilyn Latta

Figure 1: Olympia Oyster Life Cycle by Julia C. Blum is licensed under the Creative Commons Attribution—NonCommercial 4.0 International License. To view a copy of this license, visit http://creativecommons.org/licenses/by-nc/4.0/. Image source: http://www.flickr.com/photos/juliacblum/13316182434/.

PAGE 9: TL Anna Deck, BR Brian Cheng

PAGE 10: Anna Deck

PAGES 11-12, Figures 2 and 3: Stillwater Sciences

РАGE 13 T Stephanie Kiriakopolos, м Kerstin Wasson, в Anna Deck

РАGE 14: Т Marilyn Latta, м Anna Deck, в Marilyn Latta

PAGE 16: T, M, R Anna Deck

PAGE 17: Seventeenth Street Studios based on Ferner et al 2014

PAGE 18: T Kerstin Wasson, B Stephanie Kiriakopolos

РАGE 20: т Kerstin Wasson, в Anna Deck

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PAGE 22: T AND B Kerstin Wasson

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PAGE 24: L Bruce Lyon, м AND в Stephanie Kiriakopolos

PAGE 25: Brian Cheng

PAGE 26: T Anna Deck, BL US Army Corps of Engineers,

вк Keith Ellenbogen

РАGE 28: В Kerstin Wasson, м Christopher Lim, в Andy Chang

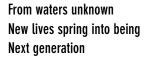
PAGE 29: Marilyn Latta

PAGE 30: Christopher Lim

PAGE 31: T Anna Deck, B Kerstin Wasson

PAGE 43: Anna Deck

PAGE 43: Chela Zabin



Haikus: These originated as a joking response to a request to reduce our research into short, succinct paragraphs. It turned out they were fun to do.

