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Olympia oyster: factors that control distribution and abundance in Pacific Coast estuaries and a case study of Elkhorn Slough, California

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ABOUT THIS DOCUMENT

This document was written by Kerstin Wasson, Elkhorn Slough National Estuarine Research Reserve. The following experts have generously reviewed and greatly improved this document.

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This document is part of a series of reports on key species that use estuarine habitats on the Pacific Coast. Coastal decision-makers are setting habitat and water quality goals for estuaries worldwide and exploring restoration projects to mitigate the major degradation estuarine ecosystems have undergone in the past century. These goals can be informed by an understanding of the needs of key species that use estuarine habitats. To inform on-going restoration planning as a part of ecosystem-based management at Elkhorn Slough, an estuary in central California, we have selected eight species / groups of organisms that are ecologically or economically important to estuaries on the Pacific coast of the United States. The first five sections of each review contain information that should be broadly relevant to coastal managers at Pacific coast estuaries. The final sections of each review focus on Elkhorn Slough.

Kerstin Wasson served as Editor-in-Chief for this series of reports, with editorial and production assistance from Erin McCarthy and Quinn Labadie. They conducted this work as staff of the Elkhorn Slough National Estuarine Research Reserve, owned and managed by the California Department of Fish and Game in partnership with the National Oceanic and Atmospheric Administration (NOAA). Grants from the Packard Foundation, Resources Legacy Fund Foundation, and the Estuarine Reserves Division of NOAA supported this project.

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ABOUT THE ELKHORN SLOUGH TECHNICAL REPORT SERIES

The mission of the Elkhorn Slough Foundation and the Elkhorn Slough National Estuarine Research Reserve is conservation of estuarine ecosystems and watersheds, with particular emphasis on Elkhorn Slough, a small estuary in central California. Both organizations practice science-based management, and strongly support applied conservation research as a tool for improving coastal decision-making and management. The Elkhorn Slough Technical Report Series is a means for archiving and disseminating data sets, curricula, research findings or other information that would be useful to coastal managers, educators, and researchers, yet are unlikely to be published in the primary literature.

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A. Background

Oysters are suspension-feeding bivalve mollusks that live with one valve permanently cemented to hard substrate, usually in protected bays and estuaries. Oyster reefs have declined worldwide as a result of human exploitation and habitat alteration (Kirby 2004). The oyster indigenous to the western United States, the Olympia oyster (*Ostrea lurida*), is our focus here (Figure 1). Various non-native oysters have also been introduced to this region for aquaculture, including the Eastern oyster (*Crassostrea virginica*) from the U.S. Atlantic coast, and especially the Pacific oyster (*Crassostrea gigas*) from Japan. Olympia oysters are smaller (maximum size typically around 7 cm) than their non-native counterparts, but have larger gill ostia, meaning that unlike the other species they cannot capture the smallest component of plankton (nannoplankton) from the water column; they feed on diatoms, flagellates and detritus from marine plant and animal cells (Barrett 1963). Olympia oysters, like most oysters, are hermaphrodites, beginning as males and then frequently alternating genders. Unlike the two non-native species, the individuals functioning as females retain and brood embryos and larvae for about ten days before releasing them into the plankton (Hopkins 1935), where they remain for perhaps another few weeks before settling (Baker 1995). Brooding may increase the chance that larvae are retained within the embayment occupied by their parents, important on this coast with widely spaced, rare estuaries. Indeed, oyster larvae are rarely detected in coastal plankton (Baker 1995). The larvae settle preferentially on the underside of surfaces (Hopkins 1935) and grow to full size in about four years (Baker 1995). Olympia oysters form clumps and aggregated “beds”, but do not typically form extensive reefs such as those built by the two non-native species (Grosholz 2007).

Olympia oysters were chosen as key species relevant to decision-making regarding estuarine ecosystem restoration for the following reasons: 1) they have long been harvested by humans, 2) they provide food resources for other important species, 3) they play significant ecosystem roles.

Human harvest

Olympia oysters have been collected and consumed by humans since prehistoric times, appearing widely in Native American middens (e.g., Jones 2002). After the Gold Rush, they were extensively harvested, particularly to provide familiar fare to recent emigrants in the San Francisco Bay region from the oyster-rich East Coast of the United States. Olympia oysters were commercially harvested from many estuaries on this coast, but most intensively from Washington State (Barrett 1963). Today, most estuaries have such small native oyster populations remaining that commercial harvest is not viable. Puget Sound has the only extensive commercial operations today, with a combination of wild-caught and farmed individuals totaling 1.2-25.8 metric tons of harvest per year (with dollar values of $99,200-$884,800/year) between 2001-2006 (National Marine Fisheries Service, http://www.st.nmfs.noaa.gov/st1/index.html).

Food resources for other important species

Olympia oysters provide food resources to various species important to humans. They are preyed upon by several species of ducks (particularly scoters and scaup) and sharks and rays (particularly leopard sharks and bat rays) (Barrett 1963, Baker 1995), which are popular among those engaged in coastal recreation and wildlife viewing. Olympia oysters can comprise an important component of the diet of commercially harvested (*Cancer* spp.) crabs (Barrett 1963, Baker 1995). Oysters elsewhere have been shown to provide important feeding habitat for various species, including the juveniles of commercially harvested fish (Coen et al. 2007).

Ecosystem role

Olympia oysters have the potential to strongly influence estuarine ecosystems. Oysters can serve as ecosystem engineers, creating refuges and habitat for many species by providing hard, complex structure in soft-sediment systems (Coen et al. 2007). Olympia oyster beds have been shown to increase species richness (Kimbro and Grosholz 2006) or diversity (Ferraro and Cole 2007) of the benthic community in estuaries. Oyster shells and beds provide spawning and nursery habitat for fishes such as gobies in San Francisco Bay (M. McGowan, pers. com.). At high density, oysters also have the potential to improve water quality by removing phytoplankton and thereby decreasing low oxygen conditions resulting from organic enrichment and phytoplankton respiration (Coen et al. 2007).

B. Trends in Distribution and Abundance

The reported range of *Ostrea lurida* is from Cabo San Lucas, Baja California, Mexico to Sitka, Alaska (Baker 1995), although recent reports suggested the northern limit may be northern British Columbia (Gillespie 2009). A closely related species, *Ostrea conchaphila*, occurs from Panama to Baja California; for a time, these two species were synonymized, but recent molecular evidence supports their separation (Polson et al. 2009).

Throughout its range, the Olympia oyster is mostly restricted to bays and estuaries, which are typically isolated and widely spaced (Baker 1995). Most documented populations are intertidal, but this may reflect a bias in search effort rather than the true distribution. Subtidal populations typically go to about 10 m but are known from water as deep as 20 m (Grosholz 2007).

Olympia oysters have a rich fossil record on the Pacific coast of North America dating back to the late Miocene, and apparently were sometimes dominant in coastal communities (reviewed by Baker 1995). They are also widely represented in Native American shell middens (Baker 1995). The distribution of Olympia oysters today is probably fairly similar to what it was prior to human colonization – they are present at the majority of bays and estuaries along the coast (Polson and Zacherl 2009). However, oysters are currently absent from some bays (e.g., Morro Bay, Bolinas Lagoon, CA) where they were reported historically (Polson and Zacherl 2009). Moreover, abundances have apparently declined dramatically at most bays and estuaries over the past 150 years (Barrett 1963, Baker 1995). Declines are attributed to a variety of factors, including overharvesting, decreased water quality, and increased predation by non-native species (see next section).

C. Factors affecting estuarine density

As with populations of any organism, multiple factors affect the density of Olympia oysters, and factors may vary in importance temporally and spatially. We review some of the major factors likely to regulate populations of Olympia oysters below, recognizing that multi-factor experiments are needed to determine which factors (or combinations of factors) are most important currently in different regions.

Human harvest

After European colonization and expansion following the Gold Rush, the pressure on native oyster populations on the Pacific coast increased dramatically in some estuaries, driven primarily by demand by emigrants from the East Coast (Barrett 1963). The expansion and collapse of oyster aquaculture along the western coast of the United States has been considered an example of the unsustainable use of a natural resource (Kirby 2004). Overharvest of Olympia oysters nearly depleted whole populations in many estuaries on the coast, including Willapa Bay, Yaquina Bay, Humboldt Bay and Elkhorn Slough (Barrett 1963, Baker 1995), and continued low abundance in some of the estuaries may be a legacy of overharvest. Willapa and Yaquina Bays in particular supplied the San Francisco Bay region with fresh oysters between 1850-1930 (because local oyster populations were not abundant then), and underwent dramatic declines in oyster abundance during this period (Barrett 1963, Baker 1995, White et al. 2009b).

Substrate availability and sediment deposition

Since oysters are found frequently in estuarine systems dominated by soft sediments, their densities may be strongly affected by the amount and type of hard substrate to which to attach their lower valve. Olympia oysters can settle even on tiny pieces of hard substrate (broken shells, gravel) as well as on larger rocks and anthropogenic structures such as docks and pilings (Baker 1995). However the hard substrates must provide sufficient clearance above the mud so that the oysters avoid being buried and smothered (MacGinitie 1935). In areas with shallow unconsolidated sediments, attachment may be to tiny pieces of hard substrate, such as gravel or shells, but in areas with deep unconsolidated sediments or unstable, shifting sediments, adults are only found on larger rocks or anthropogenic substrates (Wasson 2010). Olympia oysters may be less abundant and smaller in areas with finer sediments (McGowan and Harris 2007), and their absence from areas with high deposition rates, such as Bolinas Lagoon or Morro Bay has been attributed to sedimentation (Barrett 1963). Likewise, the decline of oysters in San Francisco Bay may have been due to increased sedimentation resulting from hydraulic mining (Barrett 1963). Thus oyster abundances in soft sediment systems may have decreased in many estuaries where human land uses in the watershed have increased sediment deposition rates; in areas where they formerly attached to small gravel or shell bits they now require larger substrates to avoid burial. In contrast, oyster abundances may have increased locally in places where humans have added hard substrates such as armored shorelines, docks and pilings. Oysters are larger on such substrates than on small rocks on sand and mud (Harris 2004, McGowan and Harris 2007).

Tidal elevation

Tidal elevation affects Olympia oyster densities. In Willapa Bay, Washington, any prolonged emergence appears to be harmful to oysters (Trimble et al. 2009), while in California large adults are often found in the mid intertidal zone (30-50 cm above MLLW), though at lower densities than in the low intertidal zone (near MLLW) (Wasson 2010). In both Washington and California, Olympia oysters recruit and survive at greater densities at lower (0-30 cm below MLLW) vs. higher (30-50 cm above MLLW) tidal elevations (Trimble et al. 2009, White et al. 2009a, Wasson 2010).

Water quality

Water quality conditions may also affect oyster densities.

<u>Salinity</u>: Olympia oysters cannot withstand prolonged salinities below about 15-25 ppt (Hopkins 1936) and so density can be affected by freshwater inputs. Low salinities associated with prolonged river outflows resulted in substantial dieoff of oysters at several sites in San Francisco

Bay (Grosholz et al. 2008), and do not survive prolonged periods at 20 ppt (Attoe and Grosholz, unpublished data). Salinity tolerance has not been tested consistently for oysters throughout their range, so while it is clear that oysters are not adapted to habitats strongly influenced by freshwater, their precise tolerance of different salinities for different amount of times is not known.

Temperature: The onset of reproduction is triggered when a particular daily minimum (high tide) temperature is exceeded, for instance 13^0C in Puget Sound (Hopkins 1935), but the particular triggering temperature appears to vary between sites, with reproduction occurring at higher temperatures in the southern part of the range (Seale and Zacherl 2007). Warmer temperatures lead to faster gametogenesis, a longer reproductive period, and more larval production (Baker 1995), so in populations that are limited by recruitment (see below), temperature could affect adult density.

Turbidity: It has been reported that Olympia oysters are particularly vulnerable to turbidity (Barrett 1963), but this has not been further studied to determine whether turbidity affects feeding (valves are closed to avoid taking in sediment) or rather results in high sediment deposition burying oysters.

Dissolved oxygen: Hypoxia is well known to affect benthic invertebrate communities, even at sub-lethal levels (Diaz and Rosenberg 1995), but exact tolerances of Olympia oysters for different oxygen levels are not known. In bays with prolonged low oxygen conditions at the bottom, this might be an important factor controlling oyster densities and distribution.

Contaminants: Dramatic declines in Puget Sound oyster populations in the 1930s have been attributed to contaminants, particularly sulfates, from pulp mills (Baker 1995). The specific tolerance of Olympia oysters to other forms of pollution is not known, but may limit densities in some cases. However, observations of live Olympia oysters in contaminated areas of San Francisco Bay suggests they have fairly broad tolerance for contamination (E. Grosholz, unpubl. data).

Competition with fouling species

In Willapa Bay, non-native fouling species have been shown to limit growth and survival of Olympia oyster recruits (Trimble et al. 2009), although Olympia oysters are considered the competitive dominants on hard substrate in Tomales Bay (Kimbro and Grosholz 2006). In San Francisco Bay, mussels have been observed to overgrow oysters (C. Zabin, pers. com.). Competition with fouling species on hard subtrates may thus limit Olympia oyster densities in some places. Small substrates (such as gravel or shell bits) may provide a refuge from competition, because they are sufficient for oyster attachment but not for colonies of fouling species (Trimble et al. 2009). So the intensity of competition of Olympia oysters with fouling species may vary with substrate size, with large, man-made substrates such as armored shorelines and docks having the highest rates of competition. Competition with fouling species also appears to be reduced at higher tidal elevations (C. Zabin, unpublished data from San Francisco Bay; Wasson 2010 for Elkhorn Slough).

Predation

Predation by shorebirds and fish has been shown to regulate populations of some benthic invertebrates in estuarine systems (Wilson 1990), and may play an important role in oyster populations as well. Bat rays and other rays and sharks are known to be important predators in some estuaries used as nursery grounds from Spring-Fall; commercial growers of non-native oysters typically use low fences to exclude them because impacts on oyster beds can be substantial (Barrett 1963). Various native *Cancer* crabs are known to eat oysters (Barrett 1963, Baker 1995), and Olympia oysters were the favorite of four bivalve prey items offered to non-native European green crabs (Palacios and Ferraro 2003), which may pose a threat to oysters at Tomales Bay (Grosholz and Kimbro 2007). Introduced Atlantic and Japanese oyster drills and a Japanese flatworm are abundant at some estuaries where non-native oysters are cultured, and may pose a risk to Olympia oysters, especially if these are at densities too low to saturate the predators (Barrett 1963, Buhle and Ruesink 2009, Kimbro et al., in review). Selected ducks (scaup, scoters) are also known to prey on oysters (Baker 1995). It is not clear to what extent the density of Olympia oysters is determined by predation by any of these species, and the importance of predation probably varies temporally and spatially.

Recruitment limitation

Reduction of population sizes due to overharvest or pollution may have left insufficient spawning stock for recolonization even after harvesting ceased or water quality improved, so recruitment limitation may interact with the factors reviewed above to limit oyster densities. Recruitment limitation might be especially important in estuaries (or portions of estuaries) with low residence times, where larvae may be advected to the open coast rather than retained within the estuary. Episodic recruitment of larvae into residential lagoons connected to San Francisco Bay result in large temporary populations of native oysters, so larval retention can be important to recruitment (M. McGowan, unpublished data). Modifications to the historic seasonal flows of freshwater may have disrupted estuarine density-driven circulation patterns that retained oyster larvae. However, no studies to date have demonstrated recruitment regulating adult populations of Olympia oysters. Both reproductive output (average number of broods per female) and recruitment show high interannual variability in Olympia oysters (Hopkins 1935). In Willapa Bay, larval densities of Olympia oysters are greater than those of commercially harvested non-native oysters (Trimble et al. 2009). While intertidal oysters are very rare in Willapa Bay, subtidal populations may be more abundant, serving as the source of recruitment (Trimble et al. 2009), and this pattern of subtidal subsidization of intertidal populations may be common in some other estuaries as well.

D. Factors affecting estuarine distribution

While many factors potentially affect the density of Olympia oysters, only a few key factors are known which drive their distribution.

Coastal habitat type

Olympia oysters are generally restricted to sheltered bays and estuaries (Baker 1995). It is not clear what mechanism limits their distribution but no extensive populations are known from the open, wave-swept coast.

Tidal elevation

Across their range, Olympia oysters have a fairly broad elevational distribution. The upper limit is somewhere from the mid to lower intertidal zone (approx. 50 cm above MLLW in California); the lower limit is not known but beds have been reported from 20 m (Baker 1995, Grosholz 2007). Within a particular site, the elevational distribution of Olympia oysters is often much narrower; for instance, they are largely absent from the intertidal zone in Willapa Bay (Polson and Zacherl 2009, Trimble et al. 2009) and largely absent from the subtidal zone in San Francisco Bay (Harris 2004, Grosholz et al. 2008) and Elkhorn Slough (Wasson 2010). The factors behind these site differences are not yet well characterized.

Hard substrate

Since oysters attach to hard substrates, the absence of hard substrates from particular bays or portions thereof can limit their distribution. In systems with high sediment movement or deposition rates, hard substrates must be large enough to prevent settled oysters from becoming buried. Absence of such larger hard substrates may explain the distributional limits of Olympia oysters within many depositional estuarine systems on this coast today.

Salinity

Olympia oysters cannot withstand extended periods of salinities below 15-25 ppt (Baker 1995). They thus do not form stable long-term populations in habitats where salinity is regularly reduced by substantial freshwater inputs, such as the upper reaches of estuaries or river mouth lagoons.

E. Predicted changes in estuary-wide abundance in response to estuarine restoration projects

The total estuary-wide abundance of Olympia oysters is a function of their density and distribution. Large-scale estuarine restoration projects could modify either densities or distributions. The goals of broad ecosystem-level estuarine restoration often focus on improvements to water quality and/or increases in threatened habitat types. The types of responses expected from Olympia oysters to changes in water quality and habitat area as a result of restoration are reviewed below. Single-species, directed restoration efforts of Olympia oysters are also briefly reviewed.

Changes to habitat extent

The goal of many ecosystem-wide restoration projects in estuaries is to increase the area of salt marshes. The effect of marsh restoration on oyster populations has not been well-studied. Under some conditions, marshes might prove beneficial if they trapped sediment that otherwise would deposit in oyster beds, burying them. On the other hand, in some cases marsh restoration would decrease available habitat for oysters, by converting shallow subtidal or low intertidal mudflat habitat to vegetated marsh.

Changes to water quality

Another common ecosystem-wide goal for estuarine restoration is improvement of water quality, particularly decrease in nutrient loading and contaminant inputs. The effects on oysters would be project-specific. In highly polluted systems, oyster populations might respond very significantly to such changes in water quality, because they were previously limited by low oxygen conditions, particular contaminants, or high turbidity. For instance, recovery of populations of Olympia oysters in southern Puget Sound occurred only after cessation of pulp mill sulfate inputs (Baker 1995, White et al. 2009b). In less polluted systems, oyster response to water quality improvements may not be significant, since their tolerances are quite broad and water quality may not be limiting abundances. However, reductions in eutrophication may be helpful because Olympia oysters have large ostia (relative to their Atlantic and Asian counterparts) that are better adapted to filter diatoms characteristic of more pristine marine waters, rather than small green algae and flagellates (M. McGowan, pers. com.). Improvements in water quality would also likely decrease suspended sediments which can interfere with feeding, and burial by sediments.

Directed oyster restoration

In addition to ecosystem-wide restoration efforts, many estuaries are developing specific initiatives to enhance Olympia oyster populations. Southern Puget Sound has a long history of Olympia oyster aquaculture, and currently hosts the largest commercial operations. While these beds are harvested, they can complement native oyster restoration, since larval production from the beds presumably results in recruitment beyond their boundaries. Restoration initiatives are underway in Puget Sound, Netarts Bay, Coos Bay, Humboldt Bay, Tomales Bay and San Francisco Bay. These mostly consist of small scale experimental approaches testing the effects of different types of substrate addition and comparing the success at different sites. Substrate limitation is one important factor potentially limiting the abundance of oysters (White et al. 2009a), but other factors such as sedimentation rates, competition from fouling non-native species and predation from non-native predators (see section C above) and low recruitment rates will also need to be incorporated into restoration strategies.

F. Status and trends of Elkhorn Slough populations

Current distribution, abundance, growth and recruitment

The first surveys for Olympia oyster populations at Elkhorn Slough occurred very recently. Heiman (2006) searched 125 intertidal sites using a rapid assessment survey approach. She reported occasional Olympia oysters in the North and South Harbor areas near the mouth of the estuary but found no oysters in the lower Elkhorn channel. The most abundant oyster populations were found in the mid Elkhorn channel near Kirby Park, with oysters present throughout the mid-upper Slough and in the Parsons complex. Another survey (Ritter et al. 2008) found similar results, although the oysters in the North and South Harbor areas were dead; live oysters were only found in the mid-upper Elkhorn area. The researchers in this second study also examined numerous sites with artificial tidal restriction and found oysters to be absent from sites with minimal tidal exchange (e.g., Moro Cojo Slough, Struve Pond, Porter Marsh), although they were present in restricted areas with more moderate exchange (Whistlestop Lagoon, North Marsh, North Azevedo Pond). More recently, surveys were conducted for oysters at water monitoring stations and along the Elkhorn main channel (Wasson 2010). Similarly to the above studies, oysters were found to be absent from sites with very restricted tidal exchange and from any sites without artificial hard substrates (Figure 2). No targeted oyster surveys of the subtidal have been conducted at Elkhorn Slough, but oysters have never been observed by divers in the Slough working on other projects (R. Kvitek, pers. com, J. Oliver, pers. com.), and recent thorough ROV surveys of the portion of the main channel with most abundant intertidal populations (the stretch from Parsons to Kirby) have not detected any live subtidal oysters (K. Gomez and R. Kvitek, unpubl. data).

The low abundance of oysters in the harbor area and sites with artificially restricted, minimal tidal exchange may be due to freshwater inputs; water quality data indicate that salinities of below 20 ppt can persist in these areas. The apparent absence (or low abundance) of oysters in the lower main channel of Elkhorn Slough may be due to lack of hard substrates of sufficient size to keep oysters from being buried in rapidly shifting sediments; all known populations in fully tidal areas of the Slough occur on larger artificial hard substrates, such as rocks used to armor banks, bridges, and pilings. Lack of larval retention in areas with low residence time may also be an issue. In the region of the Slough where oysters are abundant intertidally but absent subtidally, there is ample shell hash in the subtidal channel, but this is largely overgrown by non-native sponges, tunicates and bryozoans (K. Gomez and R. Kvitek, unpubl. data). These non-native fouling species may prevent oysters from growing in the subtidal.

Recently, we have set up permanent monitoring transects at three intertidal sites with full tidal exchange with the highest known densities of Olympia oysters in Elkhorn Slough, and at three nearby sites with artificially restricted tidal exchange. Density at the three full tidal sites in the low intertidal (about 15 cm above MLLW) averaged about 26/m^2; in the mid intertidal (about 45 cm above MLLW) averaged about 6/m^2; density in the tidally restricted sites averaged about 10/m^2. Size distributions differed by site (Figure 3). At all three of the fully tidal sites, small classes were not very well represented. At one of the artificially tidally restricted sites (North Azevedo), small classes were very well represented but large ones were not. At another tidally restricted site (North Marsh), only a few large individuals were present. Based on these recent surveys of distribution and abundance, we estimate that perhaps 5000-10,000 adult oysters are alive in the estuary today.

Growth rates of marked individuals tracked from summer-fall 2007 revealed an average growth rate of 4.7 mm/year in the low intertidal, and 2.6 mm/year in the mid intertidal. There was a decline in growth rate with size; for individuals larger than about 50 mm growth was less than measurement error (Figure 4). Recruitment as assessed at these sites on bricks deployed in summer and retrieved in fall 2007 was variable, over 400/m^2 at some sites and under 10/m2 at others. Recruitment was higher in full than restricted tidal exchange, and higher in the low vs. mid intertidal zone of fully tidal sites. However, a few years earlier, extremely low recruitment was documented on settlement plates by Heiman (2006), and low recruitment was also observed in 2008 (Wasson, unpublished data).

Experimental studies are underway to determine what limits survival and growth of oysters in mid-upper Elkhorn Slough (K. Wasson, unpublished). Burial by sediments and overgrowth by non-native fouling species appear to pose major challenges (Figure 5).

Temporal trends in distribution and abundance

Paleoecological data indicate that oysters dominated benthic communities in the lower estuary from 10,000-4000 years ago, in Bennett Slough, lower Elkhorn Slough, and lower Moro Cojo Slough (Hornberger 1991). Oysters were not found in cores in the upper reaches of Elkhorn Slough or Moro Cojo, possibly because these areas had salinities that were seasonally too low.

In the lower estuary, oysters disappeared from cores about 4000 years before present. Hornberger attributes this to a conversion from shallow subtidal habitat to vegetated intertidal salt marsh habitat at the site of the core (no core was taken in current channel habitat). The lack of oysters thus probably represents a decrease in distribution, as channel habitat narrowed, not a true absence from the system.

Another source of data is from Native American middens (summarized by Jones 2002). Oystershells were found in all five major middens distributed around different portions of the estuarine system, from Bennett Slough to Elkhorn Slough to Moro Cojo to Moss Landing. They were present at the estuary in all periods represented, from about 8000-300 years before present. However, they never account for a very substantial portion of the shells in the middens – mussels and clams always dominated, one to two orders of magnitude more abundant than oysters by weight. Midden abundance of course cannot be translated directly into estuary-wide abundance – oysters are more difficult to harvest, slower growing, and have less meat than a mussel or a clam, so even at equal field abundance one would expect oysters to be much rarer in middens. Still, these data suggest that oysters were not the dominant bivalve in the system, or they would have been better represented in midden records.

In 1904 and 1912, there are county records of claims made by local residents to estuarine habitats for the purpose of oyster cultivation. These residents recorded their intent to plant and cultivate oysters in staked and marked oyster beds in portions of the Salinas river channel, the lower Elkhorn channel, Moro Cojo Slough and Tembladero Slough. No further information is available about these claims, but these records suggest that Olympia oysters were present in these areas in this period, because presumably the residents would have ascertained this before staking claims to these areas for oyster cultivation. Olympia oysters are today absent from the Salinas channel, Moro Cojo Slough, and Tembladero Slough and are very rare in the harbor area and lower Slough.

In the late 1920s, MacGinitie (1935) conducted extensive surveys of Elkhorn Slough, mostly focusing on the invertebrate communities of mudflats near the mouth. He reported that the Olympia oyster was “very plentiful in all parts of the slough where there are rocks or pilings to which it can attach”, and mentioned various sites in the mouth area as well as a railroad bridge five miles up the Slough (presumably at North Marsh) having especially abundant populations (MacGinitie 1935). In 1926, oystermen from San Francisco Bay heavily harvested the Slough’s oyster populations (Barrett 1963); this implies oyster abundance was sufficient to make harvesting worthwhile. There are no known records of subsequent commercial harvest of Olympia oysters from Elkhorn Slough. Instead, various non-native oyster species were introduced and grown in the Slough in the 1920s-1970s. None of these species reproduced in Elkhorn Slough, and most of the oyster operations were short-lived and ultimately not very successful (Barrett 1963), so these non-native oysters probably never reached densities that posed a problem for Olympia oysters. However, non-native fouling species accidentally introduced with the non-native oysters did become established in Elkhorn Slough (Wasson et al. 2001) and may pose a threat to Olympia oyster populations (see below).

We know of no surveys for oysters conducted until recently, so the status of Olympia oysters from the 1930s-2005 is unknown. Browning (1972) suggests that Olympia oysters had disappeared from the Slough, so presumably they were at least fairly rare, but no indication is given in this report of search effort or locations.

In summary, Olympia oysters have clearly been a part of benthic communities at Elkhorn Slough in most periods from 10,000 years ago to the present. Native American midden data suggest they were not the dominant mollusks in the system, but beyond that data on their abundance is lacking. Records from 1904 and 1912 suggest oysters were present in areas of the lower estuary where they are largely absent today. Observations in the 1920s (MacGinitie 1935) as well as a brief episode of intense commercial harvest suggest that oysters were abundant in this period. Today Olympia oysters are rare in the Elkhorn Slough estuary, mostly limited to larger artificial hard substrates in the intertidal zone of the mid-upper main channel of the slough. Even sites with the most abundant populations are limited in extent and have relatively low densities, especially of small adult oysters. So Olympia oysters have certainly undergone a decline in the past century; it is unknown how current population sizes compare to those typical over the past few thousand years.

Factors affecting distribution and abundance at Elkhorn Slough

Major factors that may have led to the decline of oyster populations over the past 90 years are described below. Table 1 summarizes site differences in factors most likely to limit oyster abundance at Elkhorn Slough.

Burial by sediments

Oysters are absent from much of the main channel of Elkhorn Slough because the tiny hard substrates that are present there (i.e., bits of broken shell or gravel) are not sufficiently large to allow oysters to avoid burial by sediments (Wasson 2010). Oysters only survive on tiny hard substrates in a few sites in the Slough where there are rapid currents over gravel bars that remove fine sediments (channel just outside of North Marsh, just inside of North Azevedo Pond, and just inside of Rookery Lagoon). Elsewhere in the estuary they occur only on large artificial substrates that prevent burial by shifting sediments.

Water quality

Water quality in the estuarine habitats of Elkhorn Slough has decreased over time as a result of changes in human land use. In particular, high concentrations of pesticides and nutrients occur during the rainy season, especially in southwestern portion of the estuary and near the mouth (Caffrey 2002, Phillips et al. 2002, Caffrey et al. 2007). Declines in water quality might have had negative impacts on oyster populations. An investigation of oyster distribution at 24 water quality stations in Elkhorn Slough revealed that water quality strongly predicted the difference between sites with high abundance of oysters vs. sites without oysters (Wasson 2010). The key parameters contributing to this dissimilarity were turbidity and nutrient concentrations, both higher at sites without oysters. Oyster beds also are sometimes covered by thick algal mats which might reduce feeding currents.

Restriction of tidal exchange

More than 50% of Elkhorn Slough's estuarine habitats were diked and removed from natural tidal influence to support human land uses over the past 150 years (Van Dyke and Wasson 2005). Tidal exchange has been restored to some of these areas, but about a third of estuarine habitats still remain behind water control structures. Oysters are generally absent in tidally restricted habitats in Elkhorn Slough (Ritter et al. 2008); they are found in only three tidally restricted sites (Whistlestop Lagoon, North Marsh, North Azevedo Pond). Paleocore (Hornberger 1991) and midden data (Jones 2002) suggest that oysters were present in areas where they are now absent, likely due to tidal restriction, including the old Salinas river channel, lower Moro Cojo, and Bennett Slough. All of these restricted areas undergo prolonged periods of rainy season hyposalinity (due to freshwater inputs not diluted by tidal exchange) inappropriate for oysters. Restriction of tidal exchange has thus almost certainly decreased the distribution and likely the estuary-wide abundance of oysters.

Artificial harbor mouth

In 1946, the Army Corps of Engineers opened a new deeper, wider mouth to the estuary in line with the main channel of Elkhorn Slough and the Monterey Submarine Canyon, in order to accommodate the newly created Moss Landing Harbor (Caffrey et al. 2002). This led to an increase in tidal prism and velocities in the estuary, and may have affected oyster populations. The strong tidal currents have resulted in tidal scour – sediment movement and export from the main channel – which may have made oysters more prone to burial by sediments. Another change resulting from the harbor was to residence time of water in the Slough. Residence time in the lower Slough is currently only about one day (S. Monosmith, pers. com.). It is possible that the absence of larvae from most of the lower Slough and mouth area is at least partly a result of lack of retention of oyster larvae in these areas. Increased connectivity with the adjacent marine environment may also have increased predation by marine species (crabs, snails, sharks) in the lower estuary. Cool temperatures in the lower estuary due to strong tidal flushing may also decrease oyster reproduction. Regardless of the mechanism, it seems likely that the artificial harbor mouth is responsible for the absence of oysters from the lower estuary where they were formerly reported to be abundant.

Power plant entrainment

A large power plant operates near the mouth the estuary, with intake pipes in the harbor taking in a volume of water equivalent to about a third of the volume of Elkhorn Slough per day when operating at maximum capacity. There have been no studies of this entrainment on bivalves, but it is possible that there could be population level effects on oysters if a large proportion of larvae were entrained, limiting recruitment.

Invasions by non-native species

Non-native species account for 77% of species richness and 84% of cover of sessile species on hard substrates in Elkhorn Slough (Wasson et al. 2005). Abundance of oysters may have been reduced over the past decades as these non-native species were introduced and became abundant, especially in the upper estuary. In particular, oysters sometimes appear to be overgrown by a non-native sponge (*Hymeniacidon sinapium*) in the very low intertidal zone and a reef-forming worm (*Ficopomatus enigmaticus*) in the mid intertidal zone (Figure 5). Non-native oyster drills which pose a threat in other Pacific estuaries are not currently established in Elkhorn Slough.

Human harvest

It is reported that in 1926, oystermen from San Francisco Bay heavily harvested Olympia oysters at Elkhorn Slough, leading to near local extinction of the population there (Barrett 1963).

Overharvest can lead to long-term decline of oyster populations (Kirby 2004) and it is possible that the legacy of this harvesting persisted for many decades.

G. Predictions for Elkhorn Slough under different management alternatives

Overview

Four large-scale management alternatives for Elkhorn Slough were developed with the goal of decreasing rapid rates of subtidal channel scour and salt marsh conversion to mudflat habitat that have been documented over the past decades (Williams et al. 2008, Largay and McCarthy 2009). Changes to physical processes and water quality in response to these management alternatives vs. a "no action" alternative have been modeled and summarized (Williams et al. 2008, Largay and McCarthy 2009). To determine which management alternative best optimizes estuarine ecosystem health, the coastal decision-makers involved in this process of wetland restoration planning require at minimum some basic information about how species that play major ecological or economic roles are likely to respond to the different management alternatives. In the absence of detailed demographic data and rigorous quantitative modeling, it is impossible to obtain robust quantitative predictions about response of these key species. Instead, the goal of the preceding review of factors affecting density and distribution of the species across their range and the evaluation of trends at Elkhorn Slough is to provide sufficient information to support qualitative predictions based on professional judgment of experts. These predictions represent informed guesses and involve a high degree of uncertainty. Nevertheless, for these species the consensus of an expert panel constitutes the best information available for decision-making.

Biological predictions based on habitat extent

Our assessment of the management alternatives has multiple components. First, we predict how population sizes will respond to alternatives based only on extent of habitat of the appropriate tidal elevation. This assessment was based on the predictions of habitat extent at Year 0, 10, and 50 under the five alternatives (as summarized in Largay and McCarthy 2009 and shown in Table 2). Note that all alternatives involve major loss of salt marsh and concurrent gain of other habitat types at year 50; this is due to an assumption of 30 cm of sea level rise after 50 years, which largely overshadows effects of the alternatives. A significant change in habitat area was defined as an increase or decrease of 20% or greater over year 0, No Action (Alternative 1) acreages. Likewise, a significant change in population size of the species was defined as an increase or decrease of 20% or greater over the average population size of the past decade (1999-2008). For the habitat and species predictions, the geographic boundaries are all the fully tidal estuarine habitats of Elkhorn Slough excluding the Parsons complex (predictions do not include tidally restricted areas). For this first component, we made a very simplified assumption that population size is a linear function of area of habitat of appropriate tidal elevation. Thus for example a significant increase in habitat extent translates directly into a significant increase in population size.

Olympia oysters at Elkhorn Slough occur on hard substrates on intertidal mudflats, so we used habitat predictions for intertidal mudflat area (part C of Table 2). The predictions based on habitat extent alone are indicated with "H" and shown in blue in Figure 6. At the scale of a whole estuary, there is probably only a very weak correlation between aerial extent of intertidal mud and oyster abundance; at Elkhorn Slough oysters are absent from large areas of the intertidal zone due to lack of hard substrates of sufficient size to prevent burial in sediments, as well as due to absences attributed to water quality issues or lack or larval retention. However, at the scale of single sites that host extensive oyster populations, there probably is a robust correlation between oyster population size and extent of habitat area of appropriate tidal elevation. For instance, consider the site with highest numbers of oysters currently in the estuary, Kirby Park. Here there are large rocks from about 20 cm below mean lower low water (MLLW) to about 120 cm above MLLW, positioned to protect a parking lot from bank erosion. Oysters are found on the rocks from about MLLW to 50 cm above MLLW. Below this, they appear to be outcompeted by non-native fouling species; above this, they appear to suffer from desiccation. In management alternatives 2 and 3, where the tidal range decreases, the area of rocks within the appropriate tidal range for oysters would shrink, and thus numbers of oysters would likely decrease.

Factors other than habitat extent that may be altered by management alternatives

Clearly the assumption of a strictly linear correlation between population size and extent of habitat of appropriate tidal elevation is overly simplistic and unlikely to accurately describe population response to the alternatives. Habitat quality or environmental conditions other than habitat extent are also important drivers of estuary-wide population size. Unfortunately, we lacked quantitative predictions for most parameters relevant to habitat quality for oysters. In order to address this short-coming, we attempted to identify key aspects of each management alternative that might affect habitat quality or critical environmental conditions. Consideration of these aspects led to characterization of “best case” and “worst case” scenarios for each alternative, indicated by arrows in Figure 6. These arrows represent qualitative assessments; the exact length or location of the arrow has no quantitative significance. Each arrow is marked with a letter; abbreviations are described below. The description of the range of possible outcomes may be as important for decision-makers as the rough predictions of changes to population sizes based on habitat extent. Moreover, we indicate what sort of measures might be taken to avoid or mitigate the worst case scenario. This information will provide important guidance on future design or refinement of management alternatives. Identification of important parameters other than habitat extent which may be altered by the management alternatives may also lead to future physical modeling and predictions of these parameters, funding permitting, which would enable more robust biological predictions to be made in future iterations of this process, as management alternatives are refined. Here we review the factors invoked in the development of worst and best case scenarios for each of the alternatives.

Water quality has been shown to correlate strongly with oyster distribution in Elkhorn Slough, with oysters absent from sites mostly strongly expressing symptoms of eutrophication, with especially high nutrient and turbidity concentrations and high daytime dissolved oxygen, corresponding to nighttime hypoxia (Wasson 2010). Predicted changes to dissolved oxygen concentrations under the management alternatives (Johnson in Largay and McCarthy 2009) are relatively minor, because oxygen production and consumption are largely locally driven. However, it seems possible that expression of symptoms of eutrophication may increase under Alternatives 2 and 3 due to decreased tidal flushing and depth; this potential factor is indicated with a “+e” for increased eutrophication in Figure 6.

While strong tidal flushing can benefit oysters by increasing water quality, it may pose a challenge by reducing larval retention in the estuary. Absence of native oysters from hard substrates nearest to the mouth of the estuary may be due to the very low residence time of these strongly marine-influenced areas (though other factors such as predation by marine species cannot be ruled out without experimental tests). Residence time may gradually decrease in the estuary under Alternatives 1 and 4 in areas where oysters are now abundant, leading to problems with larval retention. Strong tidal flushing may also decrease the length of time that temperatures are warm enough for oyster reproduction. This potential factor is indicated with a "+m" for increased marine influence in Figure 6. Conversely, residence time may increase, allowing for more larval retention and warmer temperatures, under Alternatives 2-3; this potential factor is indicated with a "-m" for decreased marine influence in Figure 6. High interannual variation in recruitment, with almost complete absence of recruitment in some years, combined with low numbers of small individuals detected in surveys, suggests that larval retention and recruitment limitation may be important factors affecting population size.

Burial by unconsolidated sediments appears to limit oysters to large artificial hard substrates in many portions of the estuary. In a few sites where depth of unconsolidated sediments is low, oysters survive on small, natural hard substrates such as broken clam and snail shells. If depth of unconsolidated sediments decreased significantly on intertidal mudflats, this would lead to an extensive increase in the distribution of oysters. No predictions are available for depth of unconsolidated sediments under the management alternatives. Predicted tidal velocities in the subtidal zone suggest fine sediments will continue to be lost at higher rates from the lower main channel in Alternatives 1 and 4 than in Alternatives 2-3. However no predictions of changes to deposition rates have been made for the intertidal zone. Such changes would likely be most pronounced in the lower estuary, where oysters are largely absent, perhaps due to lack of larval retention. So sedimentation rate changes under the different management scenarios are not included in our characterization of the alternatives, because they are too uncertain in the intertidal zone and because they appear unlikely to strongly affect the portion of the estuary where oysters are most abundant.

Oysters appear to be outcompeted in the low intertidal by non-native fouling species. Non-native species cover is much higher currently in the upper Slough than the lower Slough (Wasson et al. 2005). It is possible that the increased residence time or temperature associated with Alternatives 2 and 3 would increase cover of non-native fouling species, with direct negative impacts to oysters, but uncertainty is too great to include this mechanism in the predictions.

Predictions for key species under different management alternatives

Each alternative is evaluated below. The assessment for each includes a) predictions based on extent of habitat of appropriate tidal elevation alone, summarized by the "H" and blue font in Figure 6, b) consideration of other factors (habitat quality, environmental conditions) related to the management alternatives that might alter these predictions, leading to "best" and "worst" case scenarios shown by arrows in Figure 6, and c) suggestions for how worst case scenarios could be avoided or mitigated.

Alternative 1 – No action

By definition, there will be no significant change in Year 0. Based on habitat extent changes alone, we predict no change at Year 10, because acreage of intertidal mudflat habitat does not change significantly. At Year 50, we predict a significant increase because extent of habitat of appropriate tidal elevation increases significantly. These habitat based trends are supported by trends over the past decades, which may serve as a proxy for “no action” trends in the future. There appears to have been a gradual increase in oysters in Elkhorn Slough over the past decades, since they were considered locally extinct in the 1970s (Browning 1972) and now are certainly visibly present, if rare.

In the worst case scenario, increased marine influence might reduce residence time or temperature in the mid-estuary, reducing oyster recruitment and thus estuary-wide population size (arrows marked “+m” in Figure 6). There are no clear strategies to increase larval retention or temperature and mitigate this worst case scenario.

Alternative 2 – Re-route of estuary mouth to create new inlet and decrease tidal prism

Based on habitat extent changes alone, we predict that oyster populations will decline significantly at Years 0, 10, and 50. For instance, the largest number of oysters in the estuary are found at Kirby Park on rocks protecting the parking lot from erosion. Oyster numbers there may decline as the amount of rocks at the appropriate tidal elevation shrink; most significantly, some currently intertidal ones will become subtidal, and oysters appear to be outcompeted by sponges and other fouling animals in the subtidal at Elkhorn. This could of course be mitigated by adding additional rocks horizontally in the appropriate tidal range at this site (i.e., beyond the extent of the parking lot), so total amount of hard substrate at the appropriate tidal elevation remains constant.

In the best case scenario, oyster populations might increase beyond what is predicted by habitat area alone, because decreased marine influence might increase larval retention and water temperature and thus increase recruitment and adult density (arrows marked “-m” in Figure 6). In the worst case scenario, decreased tidal flushing might increase symptoms of eutrophication, such as nutrient concentrations, turbidity and hypoxia, leading to decreases in oyster populations beyond what is projected based on habitat area alone (arrows marked “+e” in Figure 6). Oyster populations have been shown to be negatively correlated with these eutrophication indicators in Elkhorn Slough. This worst case scenario could potentially be decreased if measures to improve water quality by decreasing agricultural inputs were implemented concurrently with the hydrological changes.

Alternative 3a – Low sill under Highway 1 bridge to slightly decrease tidal prism

Based on habitat extent changes alone, we predict no significant change in oyster populations in any year. The factors that lead to best and worst case scenarios deviating from the above predictions, and the potential ways of mitigating the worst case scenarios, are the same as described for Alternative 2.

Alternative 3b – High sill under Highway 1 bridge to strongly decrease tidal prism

Based on habitat extent changes alone, we predict significant decreases in oyster populations in Years 0 and 10, but no significant change (from Year 0 in the No Action scenario) in Year 50.

The factors that lead to best and worst case scenarios deviating from the above predictions, and the potential ways of mitigating the worst case scenarios, are the same as described for Alternative 2.

Alternative 4 – Decreased tidal prism in Parsons Complex

The predictions for this alternative are very similar to those for Alternative 1. Only the predictions based on habitat extent alone differ at Year 50. While there is a significant increase in intertidal mudflat area at Year 50 for Alternative 1, it is (just barely) not significant for Alternative 4. So habitat-based predictions show no significant change at Year 50 for Alternative 4 (while they show an increase for Alternative 1).

The potential decreases that might occur beyond these habitat-based changes are the same as described for Alternative 1.

Synthesis: ranking management alternatives for this taxon

It is difficult to weigh the contrasting predictions of habitat quality and habitat extent, and to make overarching predictions of which management alternatives are optimal for oysters in the face of many sources of uncertainty. In terms of habitat extent alone, Alternative 1 (no action) might be best. However habitat extent alone is a poor predictor of total oyster abundance in the estuary, since most sites of appropriate tidal elevation lack oysters, presumably for other reasons such as problems with larval retention (at sites with low residence time) or water quality (at sites with high residence time). Currently, oysters are only abundant at sites in the upper estuary. So management scenarios that would increase the proportion of the estuary with conditions like the present upper estuary would likely favor oysters. Overall, we suggest that Alternative 3a might represent the optimal scenario for oysters, because extent of habitat of appropriate tidal elevation remains unchanged relative to the present, tidal flushing is sufficient to prevent major changes in water quality, but marine influence is somewhat reduced, making conditions in the lower estuary somewhat more like the upper estuary. Alternatives 3b and 2 are next in the ranking; they involve loss of habitat of the appropriate tidal elevation (a narrowing of the intertidal band occupied by oysters), but again might make a larger proportion of the estuary resemble conditions found today in the upper estuary. Alternatives 4 and 1 are ranked lowest. While they have stable or increasing habitat of appropriate tidal elevation, oyster populations are expected to remain limited to the upper estuary as under current conditions. Thus the ranking of alternatives from the perspective of oysters is:
Alternative 3a > 3b > 2 > 4 > 1.

External factors affecting population trends and importance relative to management alternatives

In addition to changes induced by the above management alternatives, populations of oysters might be significantly affected by other factors over the next decades. For instance, non-native oyster drills could become established and prey on native oysters. Or shark and ray populations could change in population size, affecting oyster abundance through predation. Competition from non-native fouling species such as the Australian tubeworm Ficopomatus and various sponges and bryozoans might increase as a result of temperature increases from global warming, since many of these species originate from warmer waters. Another potential factor is acidification of coastal waters resulting from global climate change. This could negatively affect oysters, but uncertainty about the timing and local intensity of this phenomenon is still very high. There are thus no factors that are clearly likely to overshadow the changes resulting from the management alternatives, though this possibility cannot be ruled out.

Targeted restoration actions for these species at Elkhorn Slough

Targeted restoration could be undertaken to increase oyster populations in the estuary. Virtually all sites without artificial substrates lack oysters, although nearby sites with rip rap or pilings have them, indicating water quality conditions and recruitment are adequate. Thus addition of hard substrates to such soft sediment areas with nearby live oyster populations would probably increase the estuary-wide population size. Addition of artificial hard substrates to a system naturally dominated by soft sediments may not be a desirable goal for decision-makers wanting to restore more natural processes to the estuary. One option would be to use large clam shells collected at the mouth of the estuary (where they are generated in abundance due to sea otter foraging) to build small reefs in the mid-upper estuary. Use of naturally occurring hard substrates might meet with greater support among stakeholders. Such clam-shell reefs could also serve as living shorelines, protecting eroding banks near human infrastructure (trails, railroad embankments, etc.). Restoration planning should recognize that any hard substrates added would likely end up supporting non-native fouling species as well as oysters.

Another potential approach would be to increase tidal exchange to areas behind water control structures. Oysters are currently present in the tidally restricted sites with some of the greatest tidal exchange (e.g., North Azevedo, Whistlestop Lagoon), but they are currently absent from sites with very limited tidal exchange (e.g., Struve Pond, Moro Cojo) where they were historically abundant (based on paleoecological and midden data). Increasing tidal exchange to these restricted sites would likely increase estuary-wide populations of oysters. However, such increase in tidal exchange may not be desirable due adjacent land uses that could be negatively affected and potential increases to tidal erosion through increase of the tidal prism of the whole estuary. Furthermore, local management decisions have been made to manage some of these historically estuarine wetlands as freshwater habitats.

As general ecosystem-level strategies, improvements to water quality and prevention of introduction or establishment of additional non-native fouling species would also support oyster conservation and restoration in the estuary.

Importance of Elkhorn Slough population sizes

Currently, the majority of the estuary's Olympia oyster population (estimated at 5000-10,000 individuals) is confined to areas of extensive artificial hard substrate in the upper Slough (in the main channel from Parsons to Hudson's landing, and within the Parsons complex). The population may have gradually expanded over the last decades; in the 1970s the Olympia oyster was considered locally extinct (Browning 1972), although it is not clear whether extensive searches were made. Even if there has been a slight recovery, the population size today is low enough to make local extinction a real possibility, if conditions become less favorable for the oyster. To the south, the next known Olympia oyster population is in Mugu Lagoon (the population in Morro Bay went locally extinct some time ago); to the north, the next population is in San Francisco Bay. Conservation of the Elkhorn Slough population is important to ensure continued representation of this key estuarine species in an estuary it has occupied for 10,000 years, and to provide connectivity between northern and southern California populations of Olympia oysters.

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Figure 1. Olympia oyster. Upper left: close-up of oysters in Elkhorn Slough, California [K. Wasson]; Upper right and bottom: dense oyster populations in San Quentin Bay, Baja California [M. Polsen].

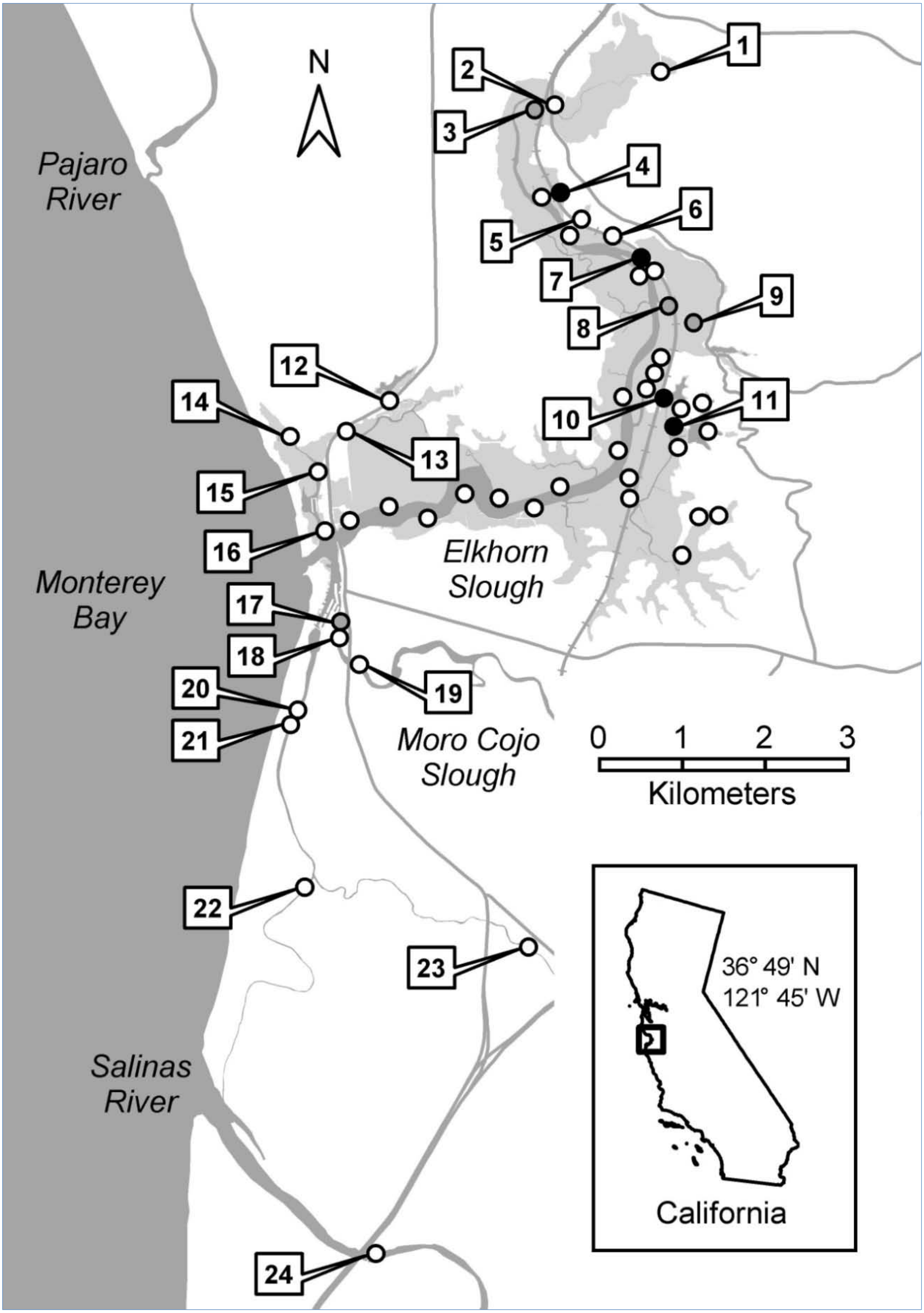

Figure 2. Oyster distribution in Elkhorn Slough. The numbered sites represent water monitoring sites, with hard substrate present, that were surveyed for oysters. Empty circles = sites without oysters, gray shaded circles = sites with low abundance of oysters, darkly shaded circles = sites with high abundance. Sites 4, 7, 8, 9, 10, and 11 were the locations of transects and recruitment studies. The unnumbered sites in Elkhorn Slough are sites dominated by soft sediments, none of which had oysters present.

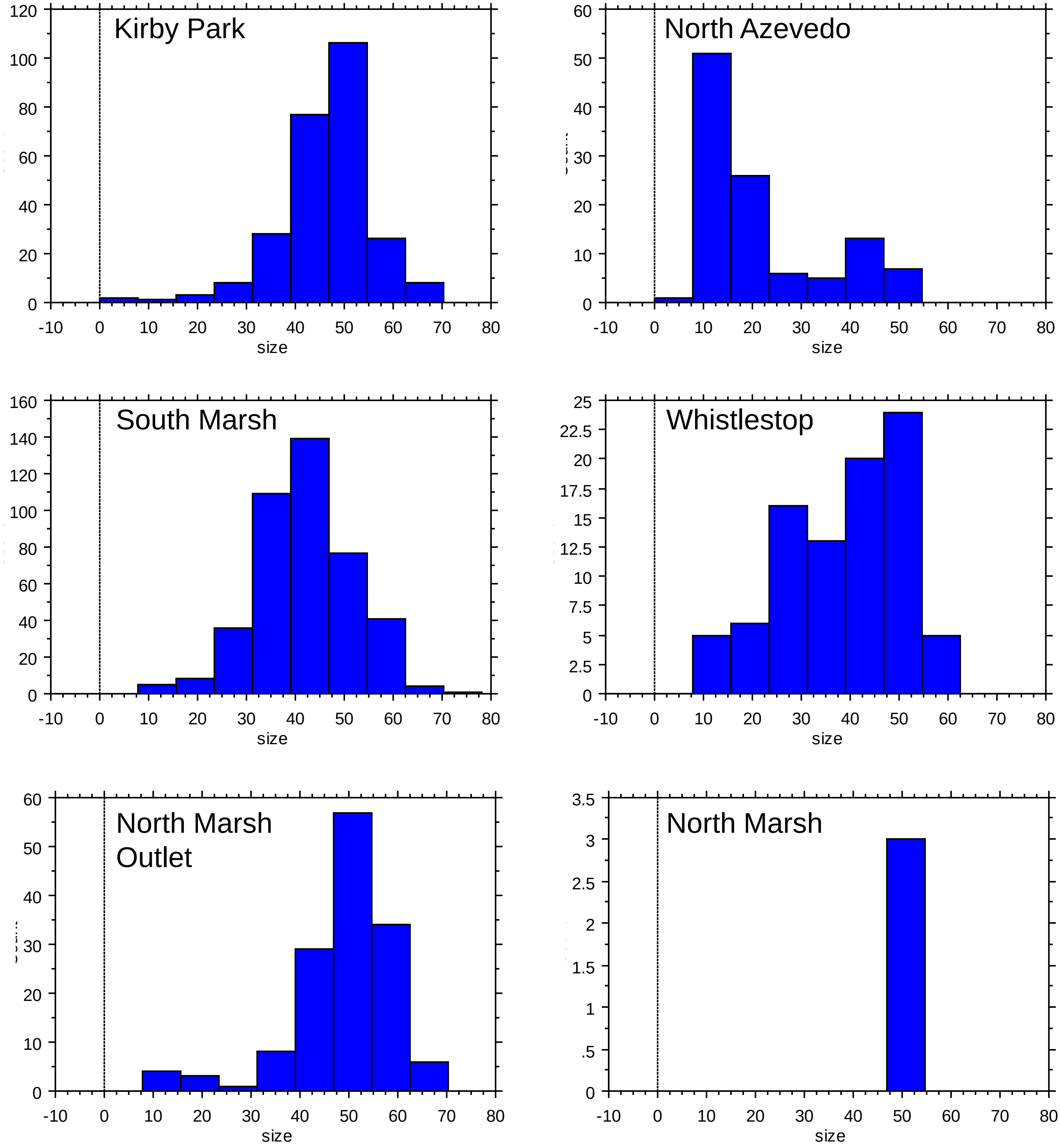

Figure 3. Size distribution of oysters in Elkhorn Slough. Three fully tidal sites are shown on the left; three sites with artificially restricted tidal exchange are shown on the right.

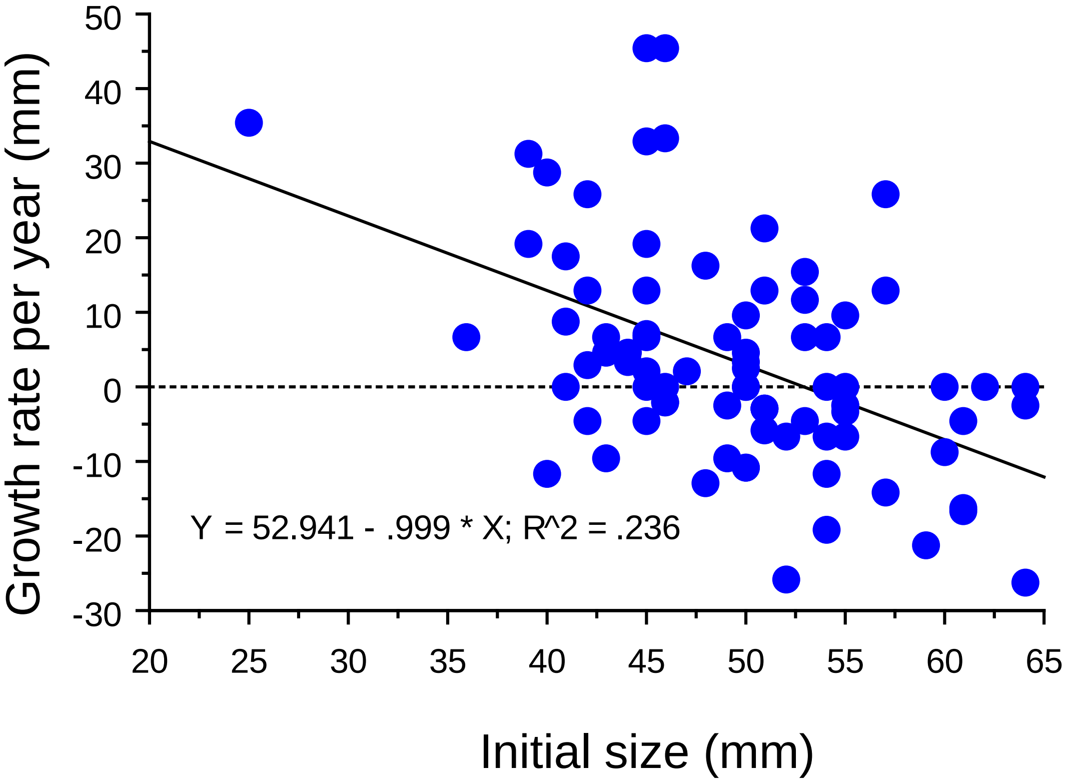

Figure 4. Decrease in oyster growth rate with size at Elkhorn Slough. Data were generated by plotting initial size (maximum length in any axis) of tagged oysters (Summer 07) vs. annual growth rate (calculated by dividing difference in Fall vs. Summer 07 size by number of days since the measurement occurred and multiplying this by 365). The frequency of negative growth rates is a function of the difficulty of determining the exact location of the end of flat extensions of the shell. Despite this inaccuracy, there appears to be a significant trend of decreased growth rate with size. (Data from an unpublished study by K. Wasson).

Figure 5. Threats to Olympia oysters at Elkhorn Slough. Populations in the mid-upper Slough are often covered with algae, overgrown by reef forming tubeworms (left), or orange sponges (right). (Photos by K. Wasson)

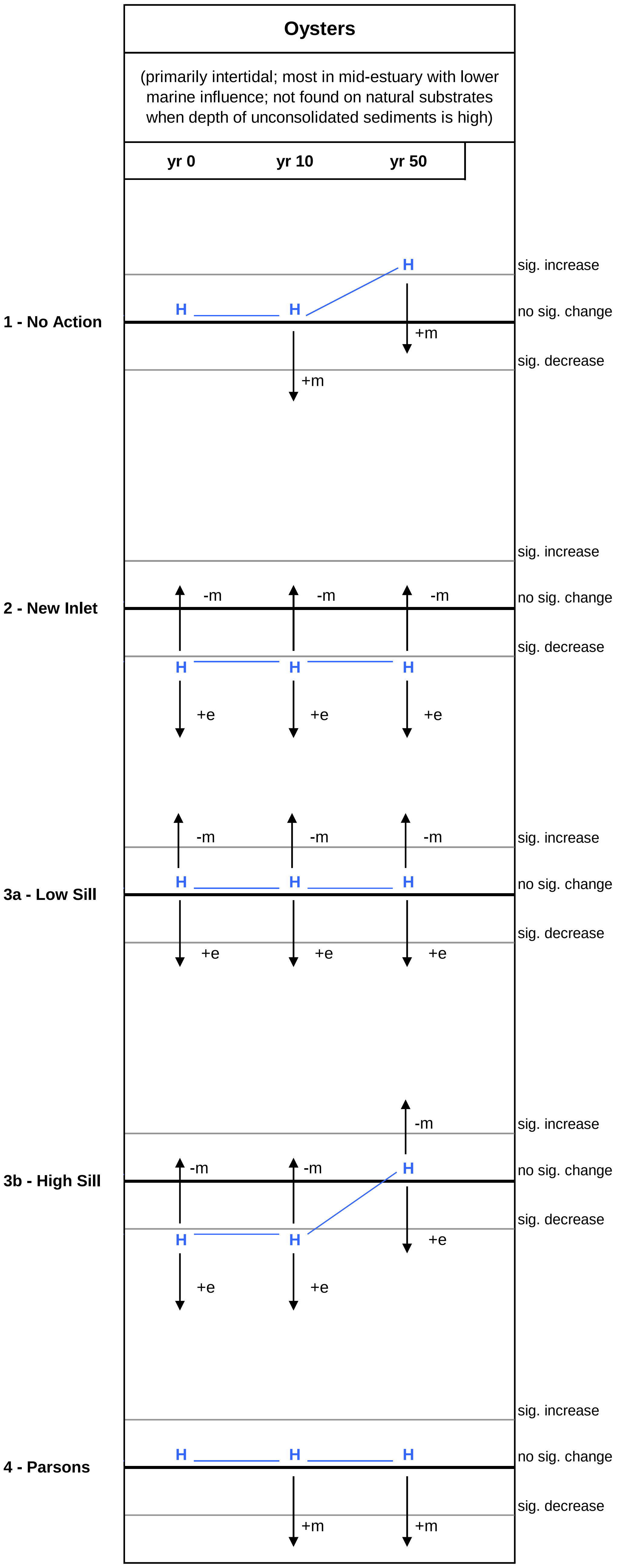

Figure 6. Predicted response of oysters to management alternatives.

Legend for Figure 6

For each group of species, predictions made solely based on habitat extent are shown with a blue "H". These predictions make the simplified assumption of a linear relationship between estuary-wide population size and aerial extent of habitat of the appropriate tidal elevation. Thus a significant increase or decrease in habitat area translates to a significant change in population size.

The habitat predictions summarized in Largay & McCarthy 2009 were used for these projections. For oysters, intertidal mudflat area was used.

A significant change in habitat area was defined as an increase or decrease of 20% or greater over year 0, No Action (Alternative 1) acreages. Likewise, a significant change in population size of the species was defined as an increase or decrease of 20% or greater over the average population size over the past decade (1999-2008).

For the habitat and species predictions, the geographic boundaries are all the fully tidal estuarine habitats of Elkhorn Slough excluding the Parsons complex (predictions do not include tidally restricted areas).

In addition to the habitat-based predictions, we illustrate a range of worst case and best case scenarios using arrows. These represent qualitative assessments of potential factors related to the management alternatives that might increase or decrease populations in ways other than predicted based on habitat extent alone; the exact length or location of the arrow has no quantitative significance. Each arrow is marked with a letter; legend for letters below. See text for more detail.

"+m" MARINE-INFLUENCED, SANDY HABITAT EXTENT WITH LOW RESIDENCE TIME increases as a result of increased tidal prism

"-m" MARINE-INFLUENCED, SANDY HABITAT EXTENT WITH LOW RESIDENCE TIME decreases as a result of decreased tidal prism

"+e" EUTROPHICATION symptoms such as hypoxia, water column chloropyll and macroalgal accumulation increase as result of lower tidal energy

Table 1. Status of oysters and factors likely to limit abundance at sites in the Elkhorn Slough estuarine complex

		main factors limiting oysters				
	STATUS OF OYSTERS	**WATER QUALITY**	**SEDIMENTATION**	**RECRUITMENT**	**COMPETITION**	**COMMENTS ON FACTORS LIKELY TO LIMIT ABUNDANCE**
FULLY TIDAL SITES						
Harbor (north and south)	very rare	XXX	X	XX	X	sites near Salinas channel probably too fresh and too turbid during heavy rains; sites near harbor mouth may not have sufficient larval retention or may have competition from marine species
Lower Elkhorn Slough (Hwy 1 to Parsons)	very rare		XXX	X		no large hard substrates sufficient to prevent burial in fine sediments; maybe some problems with larval retention due to strong tidal flushing
Upper Elkhorn Slough (Parsons to Hudson)	moderately abundant		XXX		XX	oysters only occur in areas where high currents remove fine sediments, or on large hard substrates that prevent siltation; in very low intertidal, overgrowth by fouling species
Parsons Complex	moderately abundant		XXX		XX	oysters only occur in areas where high currents remove fine sediments, or on large hard substrates that prevent siltation; in very low intertidal, overgrowth by fouling species
MUTED EXCHANGE SITES						
Bennett Slough	absent	XXX				in wet years, low salinity conditions persist
Whistlestop Lagoon	moderately abundant			XX	X	limited recruitment compared to adjacent fully tidal site: larvae may not travel through culverts?
North Marsh	very rare	XXX	X	XX	XX	water quality poor except right near tide gates (where only live oysters are found); very low recruitment observed; also high siltation and very high percent cover by fouling species
North Azevedo	moderately abundant				XX	high cover by fouling species on hard substrates
Hidden Pond	absent		XX	XX		not much hard substrate to prevent burial in mud, and perhaps limited larval transport through narrow culvert
MINIMAL EXCHANGE SITES						
Struve Pond	absent	XXX				seasonally too fresh, and also with high levels of agricultural pollution
Moro Cojo	absent	XXX				"
Tembladero Slough	absent	XXX				"
old Salinas Channel (south of Potrero Road)	absent	XXX				"
Strawberry Lagoon	absent	XXX				seasonally too fresh and then too hypersaline, very stagnant water
Estrada Marsh	absent	XXX				"
South Azevedo Pond	absent	XXX				"
Middle Azevedo Pond	absent	XXX				"
Porter Marsh	absent	XXX				seasonally too fresh, and also with high levels of agricultural pollution

Factors limiting oysters are coded, X= may contribute, XX=likely to be important, XXX=likely to be main factor limiting abundance

TABLE 2. Predicted habitat extent under management alternatives.

The numbers represent percent change from baseline conditions (Year 0, No Action alternative) as predicted by H.T. Harvey and Associates and summarized in Largay and McCarthy 2009. Habitats were defined based tidal elevation zones. The area of habitat considered excludes the Parsons Slough complex and all wetlands behind water control structures.

To facilitate perusal of trends, significant increases are coded with warm colors (20% or greater = orange, 50% or greater = red). Significant decreases are coded with cool colors (20% or greater = light blue, 50% or greater = dark blue).

HABITAT PREDICTIONS FOR SINGLE HABITAT TYPES

	A. Deep (>2 m) subtidal			B. Shallow subtidal			C. Intertidal mudflat			D. Salt marsh		
ALTERNATIVE	**yr 0**	**yr 10**	**yr 50**	**yr 0**	**yr 10**	**yr 50**	**yr 0**	**yr 10**	**yr 50**	**yr 0**	**yr 10**	**yr 50**
1 - No Action	0%	9%	42%	0%	8%	15%	0%	3%	22%	0%	-7%	-65%
2 - New Inlet	54%	65%	105%	53%	70%	108%	-39%	-36%	-32%	18%	6%	-40%
3a - Low Sill	9%	12%	20%	8%	22%	72%	-10%	-3%	14%	9%	0%	-55%
3b - High Sill	39%	28%	6%	39%	75%	182%	-34%	-28%	-16%	22%	18%	-36%
4 - Parsons	1%	6%	38%	0%	5%	10%	0%	3%	19%	-1%	-6%	-61%

HABITAT PREDICTIONS FOR COMBINED HABITAT TYPES

	E. Total mud (A+B+C)			F. Shallow mud (B+C)			G. Subtidal (A+B)			H. Intertidal (C+D)		
ALTERNATIVE	**yr 0**	**yr 10**	**yr 50**	**yr 0**	**yr 10**	**yr 50**	**yr 0**	**yr 10**	**yr 50**	**yr 0**	**yr 10**	**yr 50**
1 - No Action	0%	5%	25%	0%	4%	21%	0%	8%	32%	0%	-1%	-12%
2 - New Inlet	-8%	-1%	15%	-24%	-19%	-9%	53%	67%	106%	-17%	-20%	-35%
3a - Low Sill	-4%	3%	23%	-7%	1%	23%	8%	16%	40%	-2%	-2%	-13%
3b - High Sill	-9%	-3%	14%	-22%	-11%	16%	39%	45%	72%	-12%	-10%	-24%
4 - Parsons	0%	4%	22%	0%	4%	18%	1%	6%	27%	0%	0%	-12%