ELKHORN SLOUGH
TECHNICAL REPORT SERIES 2010: 3

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and the Elkhorn Slough Foundation

Selected large benthic infaunal invertebrates: factors that control distribution and abundance in Pacific Coast estuaries and a case study of Elkhorn Slough, California

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June 2010

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

This review focuses on Pacific gaper, California butter, Pacific littleneck and jackknife clams, Bay ghost shrimp, and fat innkeeper worm (shown in Figure 1). These are common, large invertebrates in some Pacific US estuaries. As adults, they live buried in soft sediments, suspension or deposit-feeding on tiny particles they trap from the water column -- dinoflagellates, diatoms, other microorgansims, detritus (Haderlie and Abbott 1980, Ricketts et al. 1985). All six species have larvae that spend weeks to months in the plankton before returning to the benthos (seafloor) to settle. These species were not chosen as particularly robust indicators of estuarine habitat quality– tiny crustaceans and polychaetes dwelling in this habitat, collected by cores and identified microscopically, are better suited to this purpose. Instead, they were chosen as key species relevant to the public and coastal decision-makers, for three main reasons: 1) they are common for human harvest, 2) they are food resources for animals important to humans, and 3) they play important roles in structuring estuarine communities.

Human harvest

All six of these species are collected recreationally for food or bait along the Pacific coast (Fitch 1953, Emmett et al. 1991). The recreational fishery is substantial; for instance, an estimated 56,000 gaper clams are taken from Humboldt Bay annually (Moore 2001a). From 2000-2006, the dollar value of the commercial fishery on the Pacific coast of the U.S. ranged from about $77,000 to $275,000/year for Pacific littleneck clams, $70,000-$203,000 for Bay ghost shrimp, $2500-$20,000 for Pacific gaper clams, and $200-$2300 for jackknife clams (National Marine Fisheries Service, http://www.st.nmfs.noaa.gov/st1/index.html).

Food resources for animals important to humans

All of these species except ghost shrimp are known to comprise important food resources to commercially valuable flatfish such as California halibut and starry flounder during their residence in estuaries (Peterson and Quammen 1982, Emmett et al. 1991). These species are also preyed upon by bat rays, leopard sharks, and other elasmobranchs (Haderlie and Abbott 1980, Emmett et al. 1991). Some of the species are known to be eaten by *Cancer* crabs, including commercially harvested species (Peterson 1982, Chew and Ma 1987, Emmett et al. 1991). Jackknife clams are consumed by migratory shorebirds popular with birdwatchers (stilts, godwits, curlews, dowitchers) (Merino 1981); ghost shrimp are also eaten by shorebirds (M. Page, pers. com.). Four of these species are known to be heavily consumed by threatened sea otters (Rice 1980, Kvitek et al. 1988).

Important roles in structuring estuarine communities

All of these species burrow into mudflats and affect the habitat structure of soft sediments for other species. Ghost shrimp have been likened to earthworms of the sea for their role turning over sediments, and have been shown to affect clam densities (MacGinitie 1935, Peterson 1977, Murphy and Kramer 1992). Burrowing invertebrates can also alter physical processes in the estuary. Density of bivalves may affect sediment transport rates more strongly than tidal range, currents, or sediment supply (Wood and Widdows 2002). Some of these species have also been shown to lead to local increases in estuarine biodiversity. Fifty species in ten phyla are known to occur on the siphonal plates of gaper clams (Haderlie and Abbott 1980). Small gobies, crabs, and scale worms share the burrows of ghost shrimp and fat innkeepers (Fisher and MacGinitie 1928, MacGinitie 1934).

General information about each of the species is summarized in Table 1.

B. Trends in distribution and abundance

The distribution of all six of these species along the Pacific coast of the US is very broad. Gaper clams, littleneck clams, and ghost shrimp range from Baja California to Alaska. California butter clams, jackknife clams and fat innkeeper worms have their northern limit at Humboldt Bay, California; their southern limit varies between species from Costa Rica to southern California (Table 1).

Estuaries are very important for all of these species. Jackknife clams and ghost shrimp are almost entirely confined to estuaries. Littleneck clams are common in sheltered coastal areas as well as estuaries. The remaining three species can occur on the open coast, but are most abundant in estuaries, and most of the human harvest of these species is centered there.

Very little is known about coastwide trends in the distribution and abundance of these species. There has been no consistent monitoring for them at a regional scale. All are known to have dense populations in multiple estuaries and no concerns have been raised about range-wide decline for any of them. However, declines in particular areas have been documented for various species since the 1990s. Gaper clams have decreased in Morro Bay (Moore 2001a), butter clams in Morro and Bolinas Bays (Moore 2001b), and littleneck clams have apparently decreased in the northwest (Washington and British Columbia), because landings have decreased while effort has increased (Chew and Ma 1987).

C. Factors affecting estuarine density

As with populations of any organism, multiple factors affect density of adults of the six benthic invertebrate species considered here, and factors may vary in importance between species, time periods, and places. There have been no thorough characterizations of population regulation in any of these six species, but there have been studies of these and similar species identifying particular factors that may play a large role in determining density. These will be reviewed below.

Physical environment

Densities of burrowing invertebrates on the bottom of estuaries are often affected by physical factors. For suspension feeders, both individual growth rates and population densities often increase with tidal velocities. For instance, growth rates of littleneck clams are highest in tidal currents near the mouth of estuaries and decrease with distance from the mouth (Chew and Ma 1987). Growth, fecundity and density of ghost shrimp also are highest near the mouth of estuaries and decrease with distance from the mouth (Dumbauld et al. 1996). In general, strongly flushed estuaries with short residence times can support larger populations of bivalves than those with longer residence times (Dame and Prins 1998). Other physical factors may also affect densities; for example, jackknife density was found to be affected by tidal elevation, water temperature, and sediment characteristics (Merino 1981). Littleneck clam populations may experience high mortality following burial by high sediment deposition (Peterson 1985, T. Moore, pers. com.).

Biogenic habitat modification

The properties of sedimentary environments of estuaries are continually altered by organisms living in them, including grain size distribution, stability, susceptibility to erosion, pore water flux, and chemistry (Woodin 1999). Indeed, physical properties such as sediment transport rates may be affected more strongly by biological factors, such as density of infaunal invertebrates, than by physical factors such as tidal range, currents, or external sediment supply (Wood and Widdows 2002). Densities of benthic invertebrates such as clams may thus be affected by other invertebrate species, mediated through changes in their sedimentary habitat (Murphy and Kramer 1992). All of the species reviewed here have the potential to affect each other. Epifaunal predators such as sharks and rays also affect the physical environment by the pits that result from their excavations of bivalves, and these substrate disturbances may decrease densities of infauna (Wilson 1990). Eelgrass beds often have increased abundance of gaper clams relative to unvegetated areas, perhaps due to sediment stabilization (T. Moore, pers. com.).

Primary producers

As in other ecosystems, there have been controversies about the relative importance of bottom-up (driven by nutrients and primary producers) vs. top-town (driven by predation) control of consumer populations in estuaries; here as elsewhere, both types of forcing factors no doubt are involved, with their importance varying in different times and places. In some cases, certainly, abundance of consumers has been shown to increase as a function of producer abundance, which in turn is driven by concentrations of nutrients (Valiela et al. 2004). On the west coast of the U.S., isotope studies have revealed that invertebrates in tidal flats and channels derive most of their nitrogen from algal sources (consumed live from planktonic microalgae or derived from detritus of benthic micro or macroalgae) rather than from pickleweed marsh or upland-derived sources (Kwak and Zedler 1997, Page 1997). So increases in the density of the six invertebrate species considered here may result from nutrient-enrichment stimulating algal growth.

Negative bottom-up effects have also been documented for estuarine systems – nutrient-stimulated macroalgal canopies may lead to more frequent hypoxic conditions on the seafloor of estuaries (Valiela et al. 2004). Hypoxia is known to have negative impacts on benthic communities (Diaz and Rosenberg 1995). On the east coast of the U.S., abundance of a common clam species was shown to decrease dramatically following hypoxia events, which in turn lead to decreased abundance of an important demersal fish (Powers et al. 2005). Seasonal macroalgal blooms have been shown to decrease clam abundances in a California estuary, likely due to anoxia and high concentrations of sulfide under the algal mats (Everett 1991).

Predation

Predation by shorebirds and fish has been shown to regulate populations of benthic invertebrates in estuarine systems (Quammen 1984, Wilson 1990, Valiela et al. 2004). The six species considered here are known to be preyed upon by a number of species, including sharks and rays, flatfish, shorebirds, sea otters and humans. In some cases, predation rates for these species have been quantified, for instance for sea otters on gaper clams (Kvitek et al. 1988), California halibut on littleneck clams (Peterson and Quammen 1982), and *Cancer* crabs on various bivalves (Peterson 1982). However, there have been few studies that have demonstrated effects of predation on population density for these species. Indeed, it is difficult to empirically demonstrate effects of predation because the cages typically used in predator-exclusion treatments often fill with sediments in depositional environments and lead to artifacts that can obscure the effects of predation (Hulberg and Oliver 1980). In a correlational study, Jolly (1997) found significant decreases in average size, but not in density, for gaper and butter clams following colonization of Elkhorn Slough by sea otters. There can be important interactions between predation and other physical and biological parameters. For instance, gaper clams face less sea otter predation in soft sediments where they can burrow more deeply than in firmer sediments (Kvitek et al. 1988), and toxins accumulated from harmful algal blooms may reduce sea otter predation on bivalves (Kvitek and Bretz 2004).

Human harvest

All six of the focal species are harvested to varying degrees by humans, with very heavy take in some estuaries. Harvesting has been shown to correlate with decreased abundance of ghost shrimp (Peterson 1975). The effects of human harvest on densities of the other invertebrates has not been characterized. For the four species that occur subtidally as well as intertidally, such as the gaper clam, the lightly harvested subtidal portion of the population may sustain recruitment into the heavily harvested intertidal portion (Moore 2001a). However, declines have been observed in the most heavily harvested of these six species, the littleneck clam (Chew and Ma 1987), and these may be the result of human use.

Recruitment limitation

All six of these invertebrate species have larvae that spend a few weeks in the plankton before returning to the estuarine benthos to settle. The plankton period is likely a time of high mortality, both from predation by planktivorous fish and invertebrates, and from physical limitations in using currents to successfully return to appropriate habitat for settlement. However, very little is known about the larval and recruitment phases of these species. Demographic studies of gaper and littleneck clams revealed that recruitment is highly variable between years and may affect population size (Clark et al. 1975, Emmett et al. 1991). Recruitment limitation may thus contribute heavily to short-term temporal patterns, though it may not account for long-term trends or spatial patterns of density within estuaries (Olafsson et al. 1994). Variation in larval retention within estuaries and larval transport from adjacent waters into estuaries no doubt is one factor influencing abundance.

D. Factors that determine estuarine distribution

The distribution of these large benthic invertebrates is largely determined by the availability of appropriate habitat, which for adults of all six of these species consists of mudflats and tidal channels in sheltered coastal areas. The habitat requirements of these species are fairly broad, as evidenced by their presence in most of the large estuaries within their range on the Pacific coast of the U.S., even though these estuaries vary greatly in terms of freshwater inputs, geomorphology, acreage of marshes, size, and other factors. Nevertheless, these species are often limited to particular regions within estuaries. Three main factors are critical in defining the distribution of these large invertebrates within estuaries: tidal elevation, sediment properties, and water quality.

Tidal elevation

Each species occurs across a limited range of tidal elevations. Ghost shrimp are generally found at the highest tidal elevation of these species and are limited to the intertidal zone (MacGinitie 1935). The other five species occur in both mid-low intertidal mudflats or sandflats to shallow subtidal areas, although littleneck and jackknife clams are found primarily in the intertidal zone (MacGinitie 1935, Fitch 1953, Haderlie and Abbott 1980, Emmett et al. 1991).

Sediment properties

All six species require sufficient unconsolidated soft sediments in which to burrow; they cannot burrow into hard-packed clay or hard substrates. The deeper-burrowing species (e.g., gaper, often burrows 50-100 cm) require a deeper layer of unconsolidated sediments than do the shallow-burrowing ones (e.g., littleneck, typically in top 10 cm). The six species vary in their requirements for sediment size distribution. Jackknife clams are only found in sediments that contain a substantial proportion of fine sediments (silts or clays); these conditions are typically found under low tidal velocities (Merino 1981). On the other extreme, littleneck clams are most abundant in mixed sediments, such as gravel or cobble mixed with mud or sand; these conditions are typically found in high tidal velocities (Haderlie and Abbott 1980, Chew and Ma 1987). Gaper and butter clams are found in firm sandy mud (Fitch 1953, Haderlie and Abbott 1980); such conditions are generally found in the more strongly tidally influenced portions of the estuary near the mouth. Fat innkeepers and ghost shrimp are also found in sandy mud, but do not require as firm packing of the sediments as the clam species (MacGinitie 1935, Haig and Abbott 1980, Rice 1980).

Water quality

Little is known about the water quality tolerances of these six species. They clearly have fairly broad tolerances for temperature and salinity because they are distributed across large estuaries with varying conditions. However, these species are not typically found in small river mouth lagoons or bar-built estuaries, presumably because they cannot tolerate prolonged freshwater or stagnant conditions that occur in these places during periods of mouth closure. Gaper clams in Tomales Bay colonized the upper estuary during a period of drought, but were killed when the drought ended, decreasing salinity in this area (T. Moore, pers. com.). Littleneck clams cannot withstand salinities below 20 ppt, and are highly sensitive to copper and tri-n-butyltin used in boat paints (Emmett et al. 1991). Ghost shrimp are sensitive to pesticides and indeed are intentionally controlled with carbaryl in order to decrease their impacts on oyster aquaculture in some estuaries (Dumbauld et al. 1996; Feldman et al. 2000). Low oxygen conditions are known to affect many similar benthic invertebrate species (Diaz and Rosenberg 1995). No doubt the distributions of all six of these species are bracketed by extremes in water quality conditions, both in naturally varying parameters (salinity, temperature, dissolved oxygen) and in terms of contaminants generated by human activities, but exact tolerance levels remain to be characterized.

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

The estuary-wide abundance of these species is a function of their density and their distribution. Large-scale estuarine restoration projects could modify either densities or distributions. The goals of estuarine restoration often include improvements to water quality and/or increases in threatened habitat types. The types of responses expected from these six invertebrate species to changes in water quality and habitat area as a result of restoration are reviewed below. Since so little is known about population regulation (control of density) in these species, the focus is on changes in distribution (based on changes in appropriate habitat).

Changes to water quality

In general, the tolerance of these species is broad, so human activities that slightly change water quality are unlikely to have significant effects on the estuary-wide abundance of these species. However, dramatic changes in water quality may have significant effects. For instance prolonged freshwater inundation or high pesticide concentrations are likely to significantly decrease estuary-wide abundance, and restoration projects that reverse such levels are likely to result in increases. The effects of changes in nutrient concentrations are difficult to predict. These suspension feeding animals are likely to benefit from stimulation of algal growth in the estuary, but are more likely to face negative impacts from macroalgal mats under eutrophic conditions. Eutrophic conditions are also likely to negatively affect these species by increasing periods of low oxygen concentration (hypoxia).

Changes to habitat extent

The estuary-wide abundance of all of these species is a function of extent of appropriate mudflat habitat. Watershed or hydrodynamic alterations resulting in estuarine progradation or degradation could lead to loss of mudflats, through conversion to marshes and uplands in the former and to deep channels in the latter. Substantial loss of mudflats would almost certainly result in a significant decrease in the estuary-wide populations of the species. Since the definition of appropriate mudflat habitat differs by species, patterns would differ for each species. Ghost shrimp, littleneck clams and jackknife clams are largely limited to the intertidal zone, and would be negatively impacted by conversion of intertidal to subtidal mudflats, but abundance of the other three species might not be affected, since they are abundant in the subtidal zone. Alterations that would increase the proportion of fine sediments on mudflats (slowing of tidal currents or siltation from upland land use) would likely increase the abundance of jackknife clams but decrease the abundance of the other species, which rely on coarser sediments.

Changes in the abundance of other estuarine habitat types (e.g., extent of salt marsh) as a result of estuarine restoration projects is not likely to have a significant effect on the abundance of these six species, since they derive most of their nitrogen from algal sources.

F. Status and trends of Elkhorn Slough populations

Spatial patterns of distribution and abundance

The abundance of the six focal species in different estuarine habitats of Elkhorn Slough (Figure 2) is summarized in Table 2. Gaper and butter clams show similar patterns. They are both extremely abundant intertidally and subtidally near the mouth of the estuary and in the lower Elkhorn main channel, with the gaper more abundant intertidally and the butter clam the more abundant species subtidally. In the mid-Slough main channel, they become rare intertidally but are still common subtidally. Individuals are only found rarely in other locations. Littleneck clams and fat innkeepers are also most abundant near the mouth, but their abundance tapers more gradually with distance from the mouth. The largest ghost shrimp beds are found near the mouth, but scattered individuals are widespread through the estuary, and a few sizeable beds are found far from the mouth. Scattered jackknife clam individuals are also found throughout the estuary, but populations are only abundant in areas with fine sediments far from the mouth.

Temporal trends in distribution and abundance

Prehistoric records of three of the focal species have been documented from native American middens in the area (Breschini and Haversat 1995, Jones et al. 1996, Jones 2002). Gaper, butter, and littleneck clams are present in virtually all middens encompassing thousands of years of human history and ranging from sites near the Elkhorn mouth to the current Struve Pond area and southeast to the current upper Moro Cojo area. The archeological record thus suggests that there was an extensive estuarine network supporting these estuarine clams fairly continuously for about 7000 years, except for a period around 3000 years ago when the Slough was dominated by freshwater and brackish plant communities, appeared to have little human presence (no middens), and may have been closed to the sea. Littleneck clams are the most abundant shells in the middens, perhaps because they are found much shallower in the mud and thus more easily collected. Gaper clams are more abundant than butter clams; since both of these burrow deeply and are similarly flavorable, this pattern may reflect greater intertidal abundance of gapers vs. butter clams, a pattern still found today.

The middens hold no record of fat innkeepers and ghost shrimp, which is not surprising since these animals have few hard parts that would be preserved – their absence from the middens does not shed light on their prehistoric abundance. In contrast, the absence of jackknife clams from middens may have real significance, although they have relatively thin shells and may not have been preserved as well as the other clams. Jackknife clams are palatable and fairly easily collected. By the 1920s, jackknife clams were common near the head of the Slough (MacGinite 1935). Today they are fairly abundant in restored habitats in the mid-Slough; their absence from middens may suggest that there has been an estuary-wide increase in abundance since prehistoric times.

Since historic times, there have been various studies evaluating populations of the six focal species (Table 2). MacGinitie (1935) characterized invertebrate communities near the mouth. In subsequent decades, various researchers assessed bivalves, especially related to human harvest (Addicott 1952, Eissinger 1970, Spratt 1982, Gardner and Kvitek 1998). Studies were also conducted to assess impacts of sea otters on bivalve populations (Anderson and Kvitek 1987, Kvitek et al. 1988, Jolly 1997). There have also been some more general surveys characterizing Slough habitats (Nybakken et al. 1977, Wasson and Fork, unpublished data).

The most obvious temporal trend in abundance emerging from these studies is a decline in ghost shrimp abundance near the mouth of the estuary. Conducting fieldwork in the 1920s, MacGinitie (1935) found the shrimp to be common at every site he surveyed in the mouth area. By the 1970s abundances had decreased, and remained lower to the 1990s (Gardner and Kvitek 1998). Currently there is one dense bed of ghost shrimp near the mouth, but most sites have very low abundance with widely scattered individuals (Wasson and Fork, unpublished data). However, ghost shrimp colonized formerly diked habitats in the Parson's complex, where mudflats now replace historic salt marshes (Holloway 1994), and new beds have formed along the main channel in the mid-Slough region (Wasson and Fork, unpublished data). While it seems clear that abundance has decreased in the mouth area, it is difficult to assess whether estuary-wide abundance of the species has decreased since the 1920s.

Changes in abundance or distribution of the other species are not evident. There are some differences in reported densities of gaper and butter clams and fat innkeepers between studies, but it is difficult to draw conclusions without a rigorous long-term monitoring program using consistent sampling methods, estimates of abundance, and sites. Since 2002, the Elkhorn Slough National Estuarine Research Reserve has examined densities of distinctive burrow holes at various sites in the Lower Slough using permanent transects and consistent methods (Wasson and Fork, unpublished data). Trends in gaper clam and fat innkeeper abundance from two sites are shown in Figure 3. The large interannual and spatial variation revealed by these analyses suggests that detecting subtle trends would require huge sample sizes, and cannot be done with data from past surveys. However, the existing data certainly are sufficient to rule out dramatic differences in distribution or abundance between periods of study. To the extent that the historic and prehistoric data can reveal broad trends, they suggest that populations of large clams and fat innkeepers have been relatively stable in abundance and distribution in lower Elkhorn Slough, while ghost shrimp have declined near the mouth and jackknife clams may have increased in restored habitats in the mid-Slough.

Factors affecting distribution and abundance at Elkhorn Slough

Major factors that may have influenced the distribution and abundance of the key species at Elkhorn Slough over the past 150 years are reviewed below.

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. Jackknife clams are found in similar abundance in mid-Slough areas with full vs. restricted tidal exchange (Wasson and Fork, unpublished data), but the other five key invertebrate species are largely absent from areas with restricted tidal exchange (Table 2). Midden data (Jones 2002) and fossil clam shells in situ (Wasson, pers. obsv.) suggest that large clams were abundant in areas where they are now absent due to tidal restriction, including the old Salinas river channel, lower Moro Cojo, and Bennett Slough. Restriction of tidal exchange has thus almost certainly decreased the distribution and likely the estuary-wide abundance of five of the six invertebrate species considered here.

One extensive wetland area, the Parsons Slough complex, was diked and drained for decades and then returned to tidal exchange in the 1980s. This area had historically been dominated by marsh, but had subsided below the tidal elevation that supports marsh vegetation and thus converted to intertidal and subtidal mudflats following return of tidal exchange (Van Dyke and Wasson 2005). In this area, there has thus been a net gain of potential mudflat habitat for the key species. It is too far from the mouth to sustain large populations of large clams, but small populations of gaper clams occur in one subtidal channel (Anderson and Kvitek 1987) and low numbers of littleneck clams, ghost shrimp, and fat innkeepers are found in this complex (Table 2). Jackknife clams are fairly abundant in this area where they would have been rare earlier due to dominance of marsh vegetation, so their estuary-wide abundance may have increased as a result of this anthropogenic alteration of the landscape.

Harbor mouth

In 1946, the Army Corps of Engineers created a new, larger mouth to the Elkhorn Slough estuarine system to accommodate Moss Landing Harbor. The effects of harbor construction and mouth maintenance on the six focal invertebrate species are complex. On the one hand, they may have increased the net amount of suitable mudflat habitat for these species. The increased tidal range resulting from the new mouth dramatically increased the area of intertidal mudflats along the main Elkhorn channel (Eissinger 1970), although baseline data on the natural tidal range for the estuary is lacking (by 1945 the tidal prism had been substantially decreased due to sedimentation of the estuary from human land use changes in the watershed and due to extensive diking and draining of portions of the estuarine complex). Changes to tidal inundation patterns resulting from the harbor mouth have also likely contributed to the conversion of salt marshes to mudflats along the main channel of the Slough (Van Dyke and Wasson 2005). Most of the extensive new areas of mudflat are far from the mouth and at a high intertidal elevation, and thus do not represent appropriate mudflat habitat for the six focal species. Eventually however salt marsh conversion to mudflat may create additional appropriate habitat for these species.

Conversely, the harbor may also have led to decrease in suitable habitat for these focal species. The harbor was constructed in areas that formerly hosted abundant populations of invertebrates in intertidal mudflats and shallow subtidal mudflats and eelgrass beds (MacGinitie 1935). There was thus substantial loss of habitat as harbor structures replaced these natural habitats. In portions of the subtidal of the main channel of Elkhorn Slough rapid tidal velocities related to the artificially large estuarine mouth have scoured unconsolidated soft substrate, resulting in conversion of habitat formerly occupied by gaper and butter clams to hard clay suitable for pholad boring clams (J. Oliver, pers. com.). However, currently butter clams are very abundant in the mid estuary (Seal bend to Parsons entrance) in areas where shell hash appears to be armoring the thalweg from further scour (R. Kvitek, pers. com.).

In summary, it is unknown whether there has been a net gain or loss of suitable habitat and thus of estuary-wide abundance of these focal species resulting from the construction and maintenance of the harbor mouth.

Water quality

Freshwater inputs to Elkhorn Slough have decreased over the past century, with diversion of rivers and decrease in groundwater due to heavy agricultural usage (Caffrey and Broenkow 2002). Rainy season salinity has thus likely increased significantly in the estuary. The shift to more marine salinities year-round may have increased the distribution of the six invertebrate species in the estuary, which cannot tolerate extended periods of low salinity.

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). Ghost shrimp are known to be sensitive to pesticides (Dumbauld et al. 2006) and it has been suggested that population decline in the North Harbor area may be a result of agricultural pollutants (Gardner and Kvitek 1998, Wasson et al. 2002).

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 entrainment on the clams, worms, and shrimp that are our focus here, but it is possible that there could be population level effects if a large proportion of larvae were entrained, limiting recruitment (Wasson et al. 2002).

Invasions by non-native species

Non-native species account for about 21% of species richness and 23% of abundance in soft-sediment cores in Elkhorn Slough (Wasson et al. 2005). The key species considered here could be affected by competition from non-native infaunal species. In the subtidal main channel from Parsons to Kirby, cover by non-native fouling species (sponges, tunicates, bryozoans) is as high as 50-100% on shell hash, where butter clam siphons are also visble (K. Gomez and R. Kvitek, unpubl. data). These non-native species may be competing with clams for space or food.

Human harvest

Elkhorn Slough represents the most popular clamming area between San Francisco and Morro Bay (Spratt 1982). All six of the species considered here are collected either as food or for bait. In the 1960s, up to 150 people could be seen out on a low tide; by the late 1970s, a dozen people digging were more typical (Spratt 1982), and today only a few individuals at a time are observed on the mudflats at low tide (Wasson, pers. obsv.). Individuals in both 1969 and 1978 harvested about 5 clams per day, with 84-89% of the catch comprised of gapers and 11-16% butter clams (Spratt 1982). For both species, there was a marked increase in size with decreasing tidal elevation, and the largest clams were collected on the very lowest tides of the year (Spratt 1982); this pattern may be the result of higher mortality rates due to human harvesting in the higher intertidal zone. A dramatic decline in the largest ghost shrimp bed in the North Harbor area was observed in the 1980s after bait fishermen began using suction pumps to collect shrimp (J. Oliver, pers. com.) A study of gaper clams, fat innkeepers, and ghost shrimp in mouth area mudflats at Elkhorn Slough temporarily designated as no-take areas found no population recovery after two years (Gardner and

Kvitek 1998). More studies are needed to determine whether human harvest affects population abundance or size structure of these key species at Elkhorn Slough, but in any case for those species with subtidal populations (Table 1), there is a refuge from human harvest.

Sea otters

Sea otters have been found in Slough area middens throughout prehistoric times (Jones 2002), but had been absent in recent history until 1984, when a group of males began seasonally occupying the Slough (Kvitek et al. 1988). For the first decade, about fifteen otters at a time were found in the Slough, with no detectable impact on abundance or size distribution of bivalve prey (Kvitek et al. 1988). In 1995, a large group of young males colonized the Slough and remained year-round, with up to 54 individuals present at a time (1997). Subtidal surveys repeating protocols from a decade earlier found densities of clams and fat innkeepers had not decreased, but average size had. Sea otters have remained abundant and may now be affecting densities as well as size structure. Kao (2000) found that diet of large leopard sharks was comprised largely by fat innkeepers in the late 1990s, with far fewer clams than in the 1970s, and suggests that this difference may be the result of sea otters decreasing the availability of large clam prey.

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). In order 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 3). 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 over 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.

The mudflat invertebrates considered here were divided into two groups. For those with extensive, abundant subtidal populations at Elkhorn Slough (gaper and butter clams, fat innkeeper worms), we used "total mud" area (intertidal mudflat plus shallow and deep subtidal, part E of Table 3) to make these predictions. For those species limited mostly or entirely to intertidal mudflats (littleneck and jackknife clams, ghost shrimp), we used intertidal mudflat area from the habitat predictions (part C of Table 3). The predictions based on habitat extent alone are indicated with "H" and shown in blue in Figure 4. For these mudflat invertebrate species, there probably is a significant positive correlation between population size and extent of habitat of the appropriate tidal elevation, so using habitat-based estimates is a reasonable starting point for predicting response to management alternatives.

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 these species. 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 4. 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.

All of these species except jackknife clams are most abundant in strongly marine influenced areas with significant sandy components to the sediments, at Elkhorn Slough and other estuaries (see section D above). The larger sediment sizes may directly affect abundance (e.g., burrows may be more stable in harder packed sediments) and/or may simply be correlated (e.g., feeding rates may be higher in areas with strong tidal currents that also have sandier sediments). Predictions are not available for how the alternatives will alter gradients of tidal energy or sediment size distribution. However it seems plausible that under Alternative 1 (and Alternative 4, which is fairly similar for the lower estuary), the proportion of the estuary which has strong tidal flushing and sandy sediments is likely to increase in years 10 and 50 as a result of continued increase in tidal prism. This may lead to increases in estuary-wide abundance of all of these invertebrates except jackknife clams, which would be expected to decrease, since they are most abundant in areas with lower tidal energy and fine sediment sizes. (These scenarios are marked with "+m" for "increased extent of marine-influenced, sandy habitats" in Figure 4.) Conversely, it is likely that under Alternatives 2-3 the proportion of the estuary which has strong tidal flushing and sandy sediments will decrease, in all years, due to decrease in tidal prism. This may lead to decreases in estuary-wide abundance of all of the invertebrates except jackknife clams, which would be expected to increase (such scenarios are marked with "-m" for "decreased extent of marine-influenced, sandy habitats" in Figure 4).

All of these invertebrates except for littleneck clams require deep unconsolidated sediments for burrowing. Observations over the past decades suggest that there has been extensive loss of fine sediments from the subtidal zone near the mouth of the estuary as a result of tidal scour – the depth of unconsolidated sediments has been decreased to near zero for some areas of the lower main channel. The burrowing species with extensive subtidal populations (gaper and butter clams and fat innkeepers) have decreased in abundance in these highly scoured areas, while boring pholad clams have replaced them (J. Oliver, pers. com.). No predictions are available for depth of unconsolidated sediments under the management alternatives, but it seems likely that tidal scour will continue to export fine sediments from the channel, thus making some areas that currently have deep enough unconsolidated sediments for burrowing unavailable in the future. So this factor might lead to a decrease in the three subtidal species under Alternative 1 (and similar Alternative 4). (These scenarios are marked with "-d" for decreased depth of unconsolidated sediments in Figure 4.) Conversely, Alternatives 2-3 should allow for more fine sediments to accumulate in the main channel, restoring areas that are now scoured to appropriate habitat for burrowing species. This could lead to increases in these three subtidal species. (These scenarios are marked with "+d" in Figure 4.)

Water quality predictions (by K. Johnson, summarized by Largay and McCarthy 2009) did not suggest that hypoxia would be common under any alternative. However, the modeling assumed good mixing in the water column. It is possible that stratification could occur under Alternatives 2-3, and these invertebrates might be subject to prolonged hypoxia, which would decrease abundance. For instance, high numbers of recently dead jackknife clams with intact shells were found in the Parsons Complex in 2009 following a period of unusually low dissolved oxygen (Wasson, unpubl. data). With reduced tidal exchange under Alternatives 2-3, macroalgal mats might also become significantly more abundant. Thick, extensive algal mats are known to accumulate currently in areas of the estuary with muted tidal exchange (e.g., Bennett Slough, Whistlestop Lagoon), and benthic infauna, including the species highlighted here, are very much reduced in abundance under such mats. Increased stratification and eutrophic symptoms (hypoxia or algal cover) might thus lead to decreases in all the species under Alternatives 2-3. (These scenarios are marked with "+e" for increased eutrophication in Figure 4.)

Sea otters can dramatically alter average size and abundance of their preferred prey species. It is possible that fewer sea otters would forage in the Slough as a result of Alternatives 2-3. Alternative 2 (the mouth re-route) has a complete dam between the area most heavily populated by otters currently and the Slough. Alternative 3 (sill) might entail navigational challenges for passage over high velocity areas between the harbor area and the Slough. If numbers of foraging sea otters decreased as a result of such barriers to movement, population sizes of gaper and butter clams and fat innkeepers might increase. (This scenario is marked with "+b" for barrier to movement of mammals and fish in Figure 4.)

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 4, 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 4, 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 for any of the species in Year 0. Based on habitat extent changes alone, we predict no change in any of the species at Year 10, because acreage of mudflat habitat does not change significantly. At Year 50, we predict significant increases for all species, because intertidal and total mudflat habitat extent increases significantly.

In the best case scenario, estuary-wide populations of all species except jackknife clams might increase sooner or more than expected (arrows marked with "+m" in Figure 4), because extent of optimal habitat for these species, resembling areas currently found near the mouth in the lower Slough, with strong tidal influence and sandy sediments, might expand up the estuarine gradient. Jackknife clams thrive in areas with weaker tidal influence and fine sediments, so they could decrease due to this factor.

In the worse case species, tidal scour could decrease the extent of areas with sufficient depth of unconsolidated sediments to allow for burrowing. Some areas of the lower main channel that used to have large clams and worms now are dominated by pholad boring clams because of tidal scour (J. Oliver, pers. com.) Further tidal scour could lead to decreases of the species with extensive subtidal distributions near the mouth (gaper and butter clams, fat innkeepers), as the subtidal lower main channel becomes further scoured (arrows marked with "-d" in Figure 4). This worst case scenario could perhaps be mitigated by addition of sediments to scoured areas of the main channel. This might prove especially effective in later decades when tidal velocities in the main channel are predicted to slow significantly, such that added sediments might be retained rather than exported (Largay and McCarthy 2009).

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

Based on habitat extent changes alone, we predict that the three species with extensive subtidal populations will not undergo any significant changes in population size in any of the three periods, because total soft sediment area (intertidal mudflat plus subtidal) is not predicted to change significantly (relative to year 0, Alternative 1). However, intertidal mudflat area is predicted to be significantly decreased in all years, so based on habitat alone we predict that the three species with primarily intertidal distributions (littleneck and jackknife clams and ghost shrimp) will be significantly decreased in all periods.

In the best case scenario, species that are abundant in the subtidal (gaper and butter clams and fat innkeepers) may increase beyond what is predicted above due decreased tidal velocities permitting accumulation of sediments in areas of the main channel that have in the past lost soft sediments due to scour; this increased depth of unconsolidated sediments would lead to return of large clams and fat innkeepers to areas that now are dominated by pholad boring clams (arrows marked with "+d in Figure 4). If sea otters became less abundant in the Slough in this alternative (because of the barrier separating the primary rafting area in the harbor from the Slough), populations of these three species, which are important prey items for sea otters in the Slough, might also increase (arrows marked with "+b" in Figure 4). As the extent of mudflat habitats with strong tidal flushing and sandy sediments decreased in this alternative, Jackknife clams might expand their distribution and abundance (arrow marked with "-m" in Figure 4).

In the worst case scenario, populations of all the species other than Jackknife clams might decrease under this alternative (arrows marked with "-m" in Figure 4), because extent of habitat with strong tidal flushing and sandy sediments such as the lower estuary areas where they are currently most abundant would decrease. If duration of hypoxia increases or if export of algal mats is inhibited by the new mouth configuration and algae accumulate to a much greater extent than currently in the main channel, all these species would likely decrease in abundance. Potential decreases of these three species associated with increased expression of such symptoms of eutrophication (hypoxia, macroalgal cover) are shown with arrows marked "+e" in Figure 4. Design refinements of this alternative that would prevent water column stratification and algal mat accumulation would help support these species.

<u>Alternative 3a – Low sill under Highway 1 bridge to slightly decrease tidal prism</u>

Based on habitat extent changes alone, we predict no significant change in any of the species at Year 0 or Year 10, as there are no significant changes in mudflat area relative to Year 0 of the No Action alternative. At Year 50, there is still no significant difference in intertidal mudflat habitat, so the three species limited largely to the intertidal zone (jackknife and littleneck clams, ghost shrimp) are not predicted to change significantly. However there are predicted increases to subtidal habitat, so we predict significant increases in those species that are abundant subtidally (gaper and butter clams, fat innkeepers) at 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.

<u>Alternative 3b – High sill under Highway 1 bridge to strongly decrease tidal prism</u>

Based on habitat extent changes alone, we predict no significant change in the three species with extensive subtidal populations (gaper and butter clams, fat innkeepers) in any of the periods, because total mudflat (intertidal + subtidal) area is not predicted to change significantly. However, for the species with primarily intertidal distributions (littleneck and jackknife clams, ghost shrimp), we predict decreased population sizes in years 0 and 10, because a significant decrease in intertidal mudflat area is predicted in those periods. By year 50, intertidal mudflat area is no longer significantly different than in year 0 of Alternative 1, so we predict population sizes of these species will not be significantly different either.

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 for ghost shrimp, littleneck and jackknife clams. 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 for these three species show no significant change at Year 50 for Alternative 4 (while they show an increase for Alternative 1).

The potential increases and decreases that might occur beyond these habitat-based changes are the same as described for Alternative 1. Likewise, the suggestions for mitigating the worse case scenarios are the same.

Synthesis: ranking management alternatives for this taxon

For this suite of mudflat invertebrates, the most favorable alternative in terms of habitat extent is Alternative 1, the "no action" alternative. This is also the best scenario in terms of habitat quality for most of these species, with exception of potential concerns for scour of fine sediments affecting subtidal populations and jackknife clams. Nevertheless, with the gain in intertidal mudflat seen under Alternative 1, it appears likely that there will be a net gain in new mudflats with sufficient unconsolidated sediment for burrowing, even if some existing areas hosting these species become too scoured to support them. The concerns about increased marine influence are overshadowed by concerns over eutrophication in some of the other alternatives. Alternative 4 (Parsons) has no gain in intertidal habitat, but may have better retention of fine sediments in the lower main channel, and so should also be quite favorable to these species also. Alternative 3a (low sill) has similar habitat patterns, but some concerns associated with eutrophication. Alternative 3b and 2 rank last, respectively, due to their decreases in intertidal mudflat area coupled with potential concerns with decreased water quality and increased algal mats. So from the perspective of these focal species taken together, the ranking is:
Alternative 1 > 4> 3a > 3b > 2.

External factors affecting population trends and importance relative to management alternatives

In addition to changes induced by the above management alternatives, populations of these mudflat invertebrate species may be significantly affected by other factors over the next decades. For instance, significant changes in sea otter or shark and ray populations unrelated to the management alternatives could translate into changes in population sizes of the large clams and fat innkeeper worms. Demographic trends for these predators are too uncertain to predict whether this will be an important factor relative to habitat changes. Another potential factor is acidification of coastal waters resulting from global climate change. This could negatively affect all the clam species, 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 habitat changes resulting from the management alternatives, though this possibility cannot be ruled out.

Targeted restoration actions for these species at Elkhorn Slough

Targeted restoration actions could be undertaken to enhance populations of these species, regardless of which management alternative is implemented. One such action would be addition of sediment to scoured subtidal areas of the lower main channel. If this sediment could be retained in areas that now have hard-packed clay, density of pholad boring clams would likely decline and density of gaper and butter clams and fat innkeepers would increase.

Another potential approach would be to increase tidal exchange to areas behind water control structures. These species are currently present at low abundance in the tidally restricted sites with some of the greatest tidal exchange (e.g., Bennett Slough, 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 these mudflat invertebrate species. 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.

Importance of Elkhorn Slough population sizes

Elkhorn Slough hosts one of the most extensive and accessible populations of fat innkeeper worms in the state of California. For all of the other species, the extensive mudflats of this estuary provide one of the major habitat areas in the state (J. Nybakken, pers. com.). The large clam and worm species comprise an important part of the diet of threatened sea otters that forage in the estuary. These species also sustain estuarine populations of commercially harvested flatfish species as well as of sharks and rays that use the estuary as a nursery. The large clams have been harvested by humans from 8000 years ago to the present at Elkhorn Slough, and thus represent an ancient link between estuarine resources and people. Based on all of the above, significant declines in these species are a cause for concern and should be avoided if possible.

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Bay ghost shrimp

California butter clam

Pacific littleneck clam

Jackknife clam

Bay ghost shrimp

Fat innkeeper worm

Figure 1. Photographs of selected key species of benthic invertebrates of estuarine soft sediments. Pacific littleneck clam photo is by P. J. Bryant; jackknife clam photo is by K. Wasson; ghost shrimp photo is by W. Jorgensen; remaining photos are by G. Anderson.

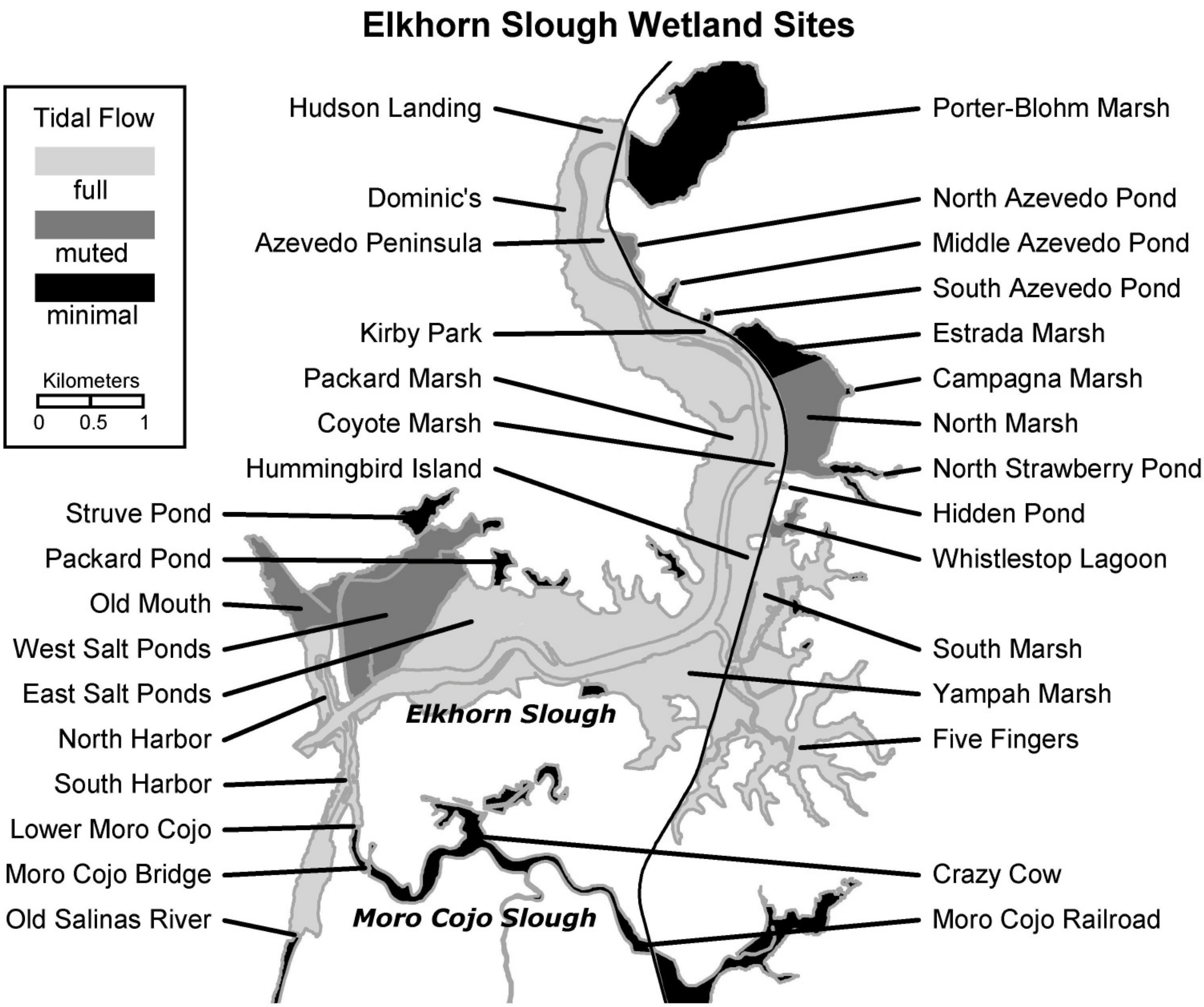


Figure 2. Map of Elkhorn Slough.

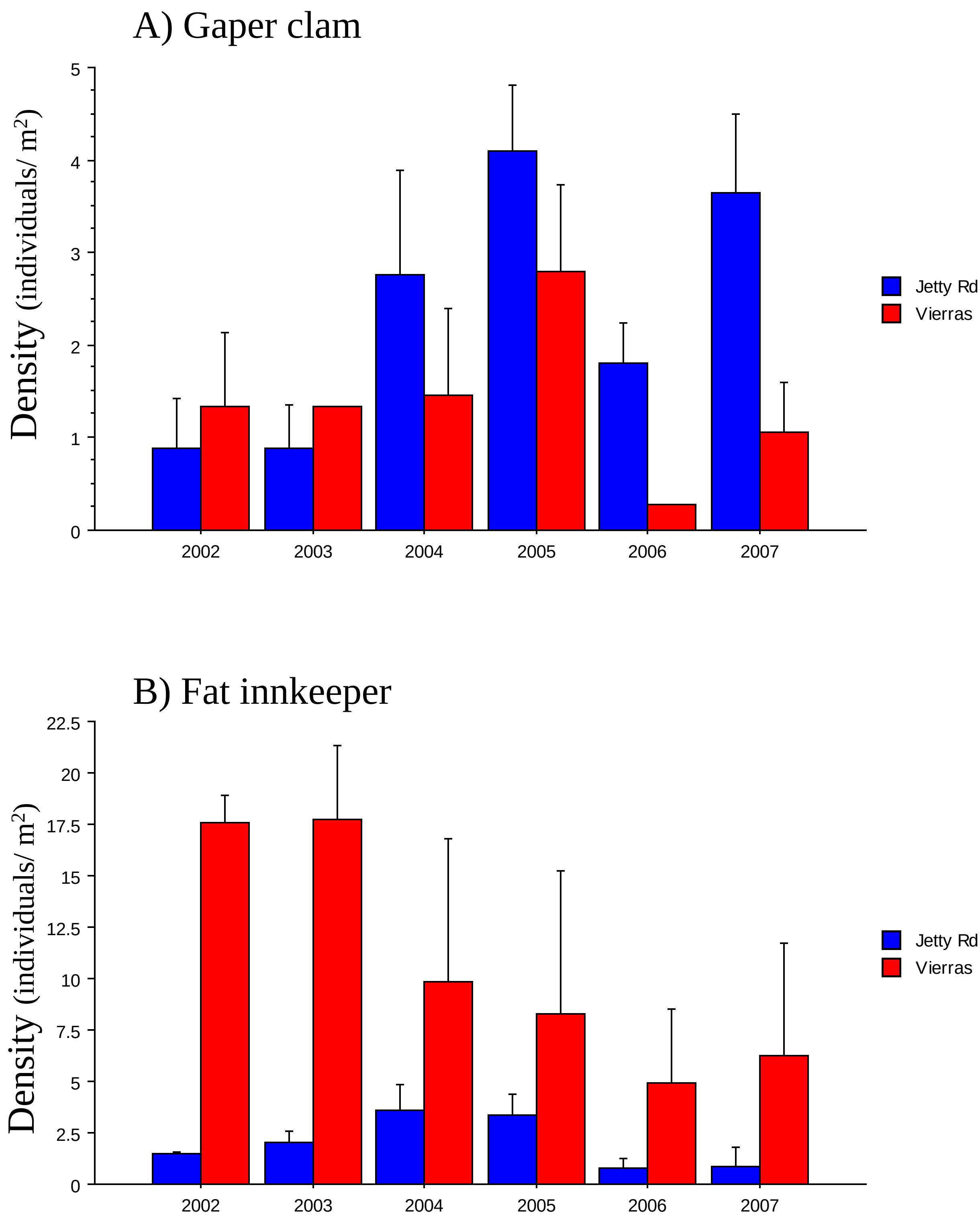
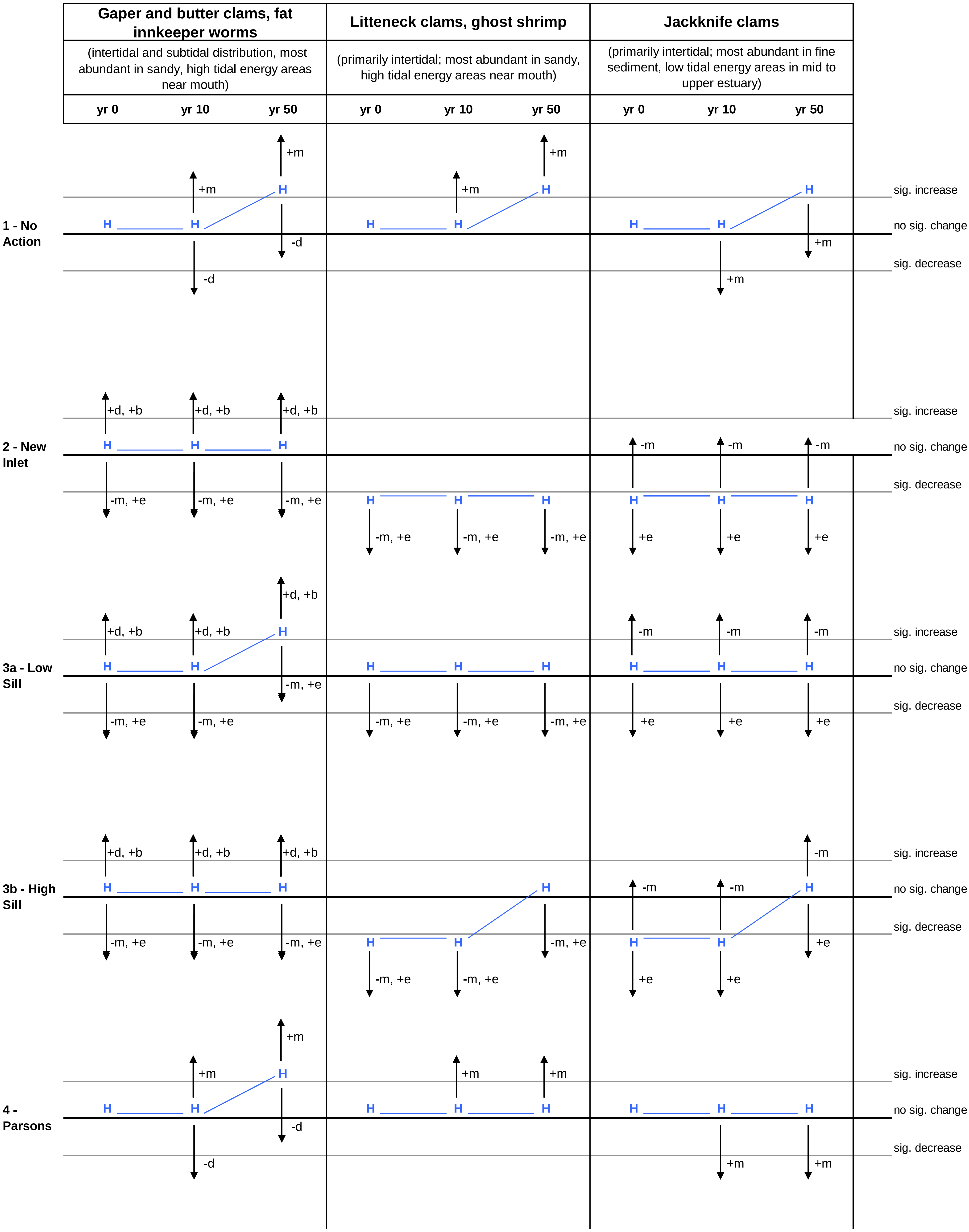


Figure 3. Density of gaper clams and fat innkeepers at a site near the estuary mouth (Jetty Rd) and in the lower main channel of Elkhorn Slough (Vierras). Data are collected at permanent transects. For both species, there is substantial variation between years and between sites. (Elkhorn Slough National Estuarine Research Reserve data provided by S. Fork and K. Wasson).

Figure 4. Predicted response of key mudflat species to management alternatives.



Legend for Figure 4

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 gaper and butter clams and fat innkeeper worms, total mudflat (intertidal mudflats + subtidal) were used as the basis for predictions; for the other three species, 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

"-d" DEPTH OF UNCONSOLIDATED SEDIMENT AND SEDIMENT DEPOSITION RATE decreases as a result of increased tidal energy

"+d" DEPTH OF UNCONSOLIDATED SEDIMENT AND SEDIMENT DEPOSITION RATE increases as a result of decreased tidal energy

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

"+b" BARRIER TO PASSAGE FROM OCEAN OR HARBOR TO SLOUGH might decrease movement of marine mammals or fish

Table 1. Summary of attributes of six large benthic invertebrates important in estuaries. Page 1

Common name	**Pacific gaper clam**	**California butter clam**	**Pacific littleneck clam**	**Jackknife clam**	**Bay ghost shrimp**	**Fat innkeeper worm**
Scientific name	*Tresus nutallii*	*Saxidomus nuttalli*	*Leukoma staminea* (formerly *Protothaca staminea*)	*Tagelus californianus*	*Neotrypaea californiensis* (formerly *Callianassa californiensis*)	*Urechis caupo*
Taxonomy	Mactridae, Bivalvia, Mollusca	Veneridae, Bivalvia, Mollusca	Veneridae, Bivalvia, Mollusca	Solecurtidae, Bilvalvia, Mollusca	Thalassindea, Decapoda, Crustacea, Arthropoda	Echiura
Description	very large clam, to 20 cm, with valves not closing entirely over siphon, which is protected by hard plates	large clam, to 15 cm, with strong concentric ridges and purple on interior of shell	medium-sized clam, to 7 cm, with weak concentric ridges crossed by radial ribbing	medium-sized clam, to 10 cm, with elongate, flattened valves	burrowing shrimp, to 8 cm, yellowish, with one cheliped enlarged	burrowing worm, to 50 cm, with pink, sausage-like body
Range	Baja California (Bahia Magdalena) to Alaska (Kodiak Island)	Baja California (Punta Rompiente) to California (Humboldt Bay)	Baja California (Cabo San Lucas) to Alaska (Attu Island)	Costa Rica (Playa Naranjo) to California (Humboldt Bay)	Baja California (Punta Banda) to Alaska	California (Tijuana Slough to Humboldt Bay)
Coastal habitat distribution	mostly in estuaries and quiet bays, but also in sheltered areas on open coast	mostly in estuaries and quiet bays, but also in sheltered areas on open coast	both in estuaries and protected waters of open coast	estuaries, lagoons, quiet bays	estuaries and quiet bays	estuaries, quiet bays, and on continental shelf along open coast
Ecological highlights	burrows 50-100 cm into soft sediments; squirts distinctive spouts of water when retracting; hosts 50 species from 10 phyla on hard siphonal plates	burrows 30-40 cm into soft sediments	burrows 5-20 cm into soft sediments, but usually are found very close to the surface; no permanent burrows	burrows 10-50 cm into soft sediments, and uses powerful foot to move up and down in burrow	burrows to 50 cm in soft sediment, actively digging and maintaining extensive galleries and thereby disturbing sediments; burrows host scale worm, pea crab, clam and copepod	forms U-shaped burrow 10-50 cm in soft sediments; hosts scale worm, pea crab, and goby
Human use	collected as food, difficult to store because of gape; subject of heavy recreational fishery (e.g., 35,000 clams taken annually from Tomales Bay); commercially taken in OR and WA	collected as food, subject of heavy recreational fishery (e.g., accounting for 30-40% of clam take in Bodega Bay)	collected as food, taken extensively recreationally; commrcially taken in OR, WA and AK; marketed fresh in shell as well as frozen and canned	edible but mostly taken as bait, recreationally and commercially in CA	collected recreationally and commercially in CA and OR as bait	collected recreationally as bait

Table 1. Summary of attributes of six large benthic invertebrates important in estuaries. Page 2

Common name	**Pacific gaper clam**	**California butter clam**	**Pacific littleneck clam**	**Jackknife clam**	**Bay ghost shrimp**	**Fat innkeeper worm**
Trends in abundance	No known coastwide trends; Morro Bay populations have decreased since 1990s	No known coastwide trends; Bolinas and Morro Bay populations have declined since 1990s	In Pacific Northwest, commercial landings have decreased while effort has increased, since 1990s	No known coastwide trends	No known coastwide trends	No known coastwide trends
Food resource for…						
Flatfish	Yes (California halibut, starry flounder)	Yes?	Yes (California halibut, diamond turbot)	Yes (diamond turbot)		Yes (starry flounder, California halibut)
Sharks and rays	Yes (bat ray, leopard shark)	Yes (bat ray)	Yes (bat ray)	Yes (sting ray, other rays)	Yes (bat ray, leopard shark)	Yes (bat ray, leopard shark)
Sea otters	Yes	Yes	Yes			Yes
Birds			Yes (ducks)	Yes (stilts, godwits, curlews, dowitchers)	Yes (shorebirds)	
Gastropods	Yes (moon snail)	Yes (moon snail)	Yes (moon snail, oyster drill)			
Crabs	Yes *(Cancer* spp.)	Yes?	Yes *(Cancer* spp.)		Yes *(Cancer* spp.)	
Tidal range	low intertidal to 30 m	mid-intertidal to subtidal	mid-intertidal to 37 m, but usually in low intertidal	mostly mid to low intertidal, but can extend to shallow subtidal	mid-intertidal	low intertidal and shallow subtidal
Sedimentary habitat	firm sand or sandy mud	firm mud, sandy mud, or sand	sand, mud or clay mixed with gravel, shells or cobble	fine sediments with a high proportion of silt or clay	sandy mud	sandy mud
Other physical parameters known	Freezing may limit northern distribution		Highly sensitive to copper and tri-n-butyltin; cannot withstand salinity below about 20 ppt; growth is enhanced by strong tidal currents		growth and fecundity highest near mouth of estuary	
Key references	3, 4, 5, 6, 10, 12, 13, 15	4, 6, 10, 16	4, 6, 10, 11, 13, 17	4, 6, 9, 10, 13	2, 3, 7, 10, 14	1, 3, 8, 10
Abbrevi-ations	1=Fisher & MacGinitie 1928, 2=MacGinitie 1934, 3=MacGinitie 1935, 4=Fitch 1953, 5=Clark et al. 1975, 6=Haderlie & Abbott 1980, 7=Haig & Abbott 1980, 8=Rice 1980, 9=Merino 1981, 10=Ricketts et al. 1985, 11=Chew & Ma 1987, 12=Kvitek et al. 1888, 13=Emmett et al. 1991, 14= Dumbauld et al. 1996, 15=Moore 2001a, 16=Moore 2001b, 17=Reilly 2001; taxonomy and common names for all species based on Carlton 2007; ranges for bivalves from Coan et al. 2000					

Table 2. Abundance of key invertebrate species in different estuarine habitats of the Elkhorn Slough watershed

Common name	Pacific gaper clam	California butter clam	Pacific littleneck clam	Jackknife clam	Bay ghost shrimp	Fat innkeeper worm
Mouth area (all undiked areas west of Hwy 1 including harbors)						
Intertidal	**high** (1, 3, 5, 11)	**medium** (1, 3, 5, 11)	**high** (1, 3, 11)	**absent** (1) to **very low** (11)	**high** (1) to **medium** (3, 10) to **low** (11)	**high** (1, 3, 11)
Subtidal	**very high** (4, 6, 7)	**very high** (6) to **high** (7)				**very high** (4)
Lower Elkhorn Slough (Main channel from Hwy 1 to Seal Bend)						
Intertidal	**high** (2, 3, 10, 11)	**medium** (3, 11)	**high** (3, 11)	**very low** (11)	**low** (3, 11)	**high** (3, 10, 11)
Subtidal	**very high** (6, 9)	**very high** (6, 9)				**very high** (9)
Mid Elkhorn Slough (Main channel from Seal Bend to Parsons Slough)						
Intertidal	**low** (11)	**low** (11)	**low** (11)	**very low** (11)	**very low** (11)	**very low** (11)
Subtidal	**high** (6)	**very high** (6)				
Upper Elkhorn Slough (Main channel from Parsons Slough to Hudson Landing)						
Intertidal	**very low** (11)	**very low** (11)	**low** (11)	**medium** (1, 11)	**low** (11)	**low** (11)
Subtidal	**very low** (4) to **absent** (6)	**very low** (4) to **absent** (6)				
Parsons Complex (Parsons, Five Fingers, South Marsh)						
Intertidal	**absent** (11)	**absent** (11)	**low** (11)	**medium** (11)	**low** (8, 11)	**low** (11)
Subtidal	**very low** (6)	**absent** (6)				
Tidally restricted areas wetlands (areas behind water control structures)						
Intertidal and Subtidal	**low** in Bennett Slough, **absent** in all other muted and minimal sites (11)	**low** in Bennett Slough and Whistlestop Lagoon, **absent** in all other muted and minimal sites (11)	**low** in Bennett Slough and Whistlestop Lagoon, **absent** in all other muted and minimal sites (11)	**medium** in North Marsh and Whistlestop Lagoon, **absent** in all other muted and minimal sites (11)	**low** in Bennett Slough, **absent** in all other muted and minimal sites (11)	**absent** (11)

REFERENCES: 1=MacGinitie 1935, **2**=Addicott 1952, **3**=Eissinger 1970, **4**=Nybakken et al. 1977, **5**=Spratt 1982, **6**=Anderson & Kvitek 1987, **7**=Kvitek et al. 1988, **8**=Holloway 1994, **9**=Jolly 1997, **10**=Gardner & Kvitek 1998, **11**=K. Wasson & S. Fork, unpublished data from Elkhorn Slough National Estuarine Research Reserve monitoring programs

blank cells represent areas where no data is available

abundance is an index of density across intertidal/subtidal mudflats, representing roughly:

	absent: not found despite targetted searching; may be present in numbers too low to have been detected
	very low: < .01 individual/m^2
	low: > .01 individual/m^2
	medium: > .1 individual/m^2
	high: > 1 individual/m^2
	very high: >10 individuals/m^2

applying these definitions involved some guesswork, because some authors only used qualitative assessments, while other only quantified density within zone of maximum abundance, not average density across the intertidal or subtidal zone

TABLE 3. 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%