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# Ecological Signatures of Anthropogenically Altered Tidal Exchange in Estuarine Ecosystems

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**Abstract** One of the most conspicuous anthropogenic disturbances to estuaries worldwide has been the alteration of freshwater and tidal influence through the construction of water control structures (dikes, tide gates, culverts). Few studies have rigorously compared the responses of differing groups of organisms that serve as contrasting conservation targets to such anthropogenic disturbances in estuarine ecosystems. Elkhorn Slough in central California includes a spectrum of tidally restricted habitats behind water control structures and habitats experiencing full tidal exchange. To assess community composition for several different taxa in habitats with varying tidal exchange, we employed a variety of field approaches and synthesized results from several different studies. Overall, we found that communities at sites with moderately restricted tidal exchange were fairly similar to those with full tidal exchange, but those with extremely restricted tidal exchange were markedly different from other categories. These differences in community composition are likely the result of several factors, including restricted movement due to physical barriers, differences in water quality characteristics, and differences in habitat structure. Indeed, in this study, we found that water quality characteristics strongly vary with tidal restriction and may strongly influence patterns of species presence or absence. We also found that different conservation targets showed contrasting responses to variation in tidal exchange. Full exchange appears to favor native oysters, commercially valuable flatfish, migratory shorebirds, and site-level biodiversity. Minimal tidal exchange due to water control structures supports a suite of estuarine endemics (including the tidewater goby and California brackish snail) not represented elsewhere and minimizes invasions by non-native marine species. Altogether, our results suggest that total estuary-wide biodiversity may be enhanced with a mosaic of tidal exchange regimes.

**Keywords** Brackish · Ecological indicator · Estuarine · Invasion · Fish nursery · Migratory shorebirds · Salt marsh · Tidal exchange · Water control structure · Wetland restoration

## Introduction

Estuaries are among the most heavily altered ecosystems (Edgar et al. 2000). One of the most widespread human alterations of estuarine ecosystems is restriction of tidal and

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freshwater exchange through construction and maintenance of water control structures (Kennish 2002). Water control structures (e.g., berms, dikes, tidegates, culverts) are typically constructed to reclaim wetlands for human uses, to prevent flooding of adjacent lands, or to impound freshwater for waterfowl hunting or livestock use. In recent decades, estuarine conservation and restoration efforts have attempted to reverse some of these human alterations to tidal and freshwater exchange by removing or altering existing water control structures (Williams and Orr 2002). It is not always possible or desirable to reinstate full tidal exchange, due to constraints from adjacent human activities or due to concern for particular conservation targets that require more limited exchange. A common alternative to the removal of water control structures is to increase tidal exchange by modifying existing structures (e.g., by increasing the number or size of culverts connecting a wetland to unrestricted portions of the estuary; Callaway 2001).

Hydrologic processes are one of the key determinants of estuarine function and species composition (Callaway 2001), but it has proved difficult to accurately predict the abiotic and biotic effects of installation, removal, or modification of water control structures (Sanzone and McElroy 1998). Such predictions are essential for restoration planning. At the project scale, the ability to predict upstream effects of removing or altering water control structures is necessary to set measurable and feasible management objectives. At the whole-estuary scale, understanding the ecological implications of tidal restriction and restoration is critical for regional goal setting and planning, ensuring appropriate representation and distribution of different tidal and freshwater exchange levels, and persistence of the desired conservation targets.

To determine the appropriate levels of water exchange at both the site and estuary-wide level, we need to understand how estuarine ecosystems respond to different levels of tidal exchange (Sanzone and McElroy 1998; Boumans et al. 2002). One approach is to compare estuaries with differing amounts of tidal exchange (i.e., estuaries with a large vs. small opening to the sea). This comparative approach detected differing ecological communities related to physical features including mouth closure, tidal range, and salinity in Tasmanian estuaries (Edgar et al. 2000). A second approach is to evaluate the community structure within a single estuary along a naturally occurring gradient of tidal vs. freshwater influence; studies of invertebrate communities related to salinity gradients provide an example of this method (e.g., Jones et al. 1990; Bulger et al. 1993; Attrill 2002). A third approach is to compare contiguous estuarine habitats with naturally unrestricted vs. artificially restricted water exchange. Using this third approach, significant effects of tidal restriction have been reported, particularly on salt marsh vegetation (e.g., Roman et al. 1984; Burdick et al. 1997; Zedler et al. 2001) and nekton (e.g., Burdick et al. 1997; Raposa and Roman 2003).

Salt marsh vegetation and nekton are two commonly used indicators of estuarine health, although numerous other ecological indicators exist, ranging from ecosystem processes to the extent of different habitats, communities, and species (Fairweather 1999; Vos et al. 2000). Estuarine ecosystems host hundreds of species, but most previous studies of tidal restriction have focused on only a few species. We were interested in determining whether different groups of organisms respond similarly to tidal restriction or whether responses differ across taxa or functional groups. Thus, we sampled a broad variety of taxa, using several field-sampling approaches, and also assessed water quality parameters that are likely to influence some of the observed responses to tidal restriction.

Most previous studies of tidal restriction examined a single pair of restricted and unrestricted exchange sites. Tidally restricted sites, however, are not homogenous; water control structures can permit a gradient from substantial tidal influence to none at all (Sanzone and McElroy 1998). One recent study examined three tidally restricted sites and found that ecological differences between paired restricted and unrestricted sites increased with increasing tidal restriction (Raposa and Roman 2003). To more comprehensively examine this reported trend, we sampled numerous sites with different levels of tidal exchange, varying from completely restricted to full tidal exchange. This allowed us to not only examine variation *between* restricted and unrestricted tidal exchange but also *within* varying degrees of tidal restriction.

We carried out our study in the Elkhorn Slough watershed of central California, an ideal system for this research. Historically, this watershed harbored an integrated estuarine network with five connected arms. Tidal exchange is currently artificially restricted to four of these arms (Bennett Slough, Moro Cojo Slough, Tembladero Slough, the old Salinas River channel) and to portions of the fifth (Elkhorn Slough). Within a relatively small area, the entire spectrum of tidal exchange is represented, from very strong flushing in unrestricted areas to lagoons with moderate tidal range to former tidal wetlands that now have almost no tidal influence. Although research on the estuarine communities occurring in the Elkhorn Slough area is extensive (reviewed in Caffrey et al. 2002), almost all studies have focused on habitats with full tidal exchange. In this investigation, we surveyed wetlands with full tidal exchange and different degrees of tidal restriction (Fig. 1), sampling algae, plants, invertebrates, fishes, birds, and marine mammals. This enabled us to assess the effects of tidal exchange on species richness and composition of a variety of potential conservation targets and thereby inform wetland management strategies.

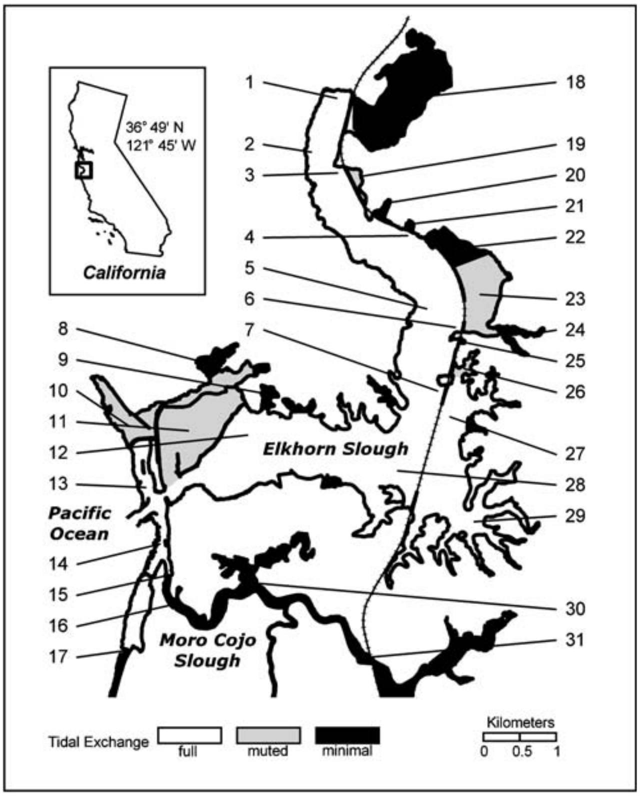

**Fig. 1** Map of estuarine habitats in the Elkhorn Slough area. *Shading* represents the tidal exchange regime. Sites sampled in this study are *numbered*; see Appendix for information about site names and locations

## Methods

### Study System and Definition of Tidal Exchange Categories

Elkhorn Slough (36°48′ N, 121°47′ W) and adjacent tidal wetlands comprise a network of estuarine habitats on the central coast of Monterey Bay in central California. The existing spatial patterns of tidal exchange reflect anthropogenic changes to Elkhorn Slough hydrography (for a historical description of estuarine habitats in Elkhorn Slough and their temporal changes due to natural and anthropogenic disturbances, see Van Dyke and Wasson 2005). At the mouth and throughout most of the main channel of Elkhorn Slough, tidal exchange is unrestricted, with daily tidal range very similar to that found on the adjacent open coast. In contrast, over a third of the original tidal wetlands of this estuarine ecosystem are behind structures that limit tidal exchange (e.g., dikes, levees, culverts, and tide gates).

The initial goal of this investigation was to compare ecological communities under full versus restricted tidal exchange. Subsequent to preliminary data collection, it became clear that differences might exist even among restricted sites with moderate versus minimal exchange. Even though restricted sites spanned a continuum of tidal exchange, we developed arbitrary but explicit and repeatable definitions of two different restricted exchange categories, leading to three different categories of tidal exchange:

- Full tidal exchange: no water control structures present, tidal range similar to adjacent open coast (250 cm max)
- Muted tidal exchange: water control structures present, moderate tidal exchange, as evidenced either by tidal range greater than 30 cm or average rainy season salinity greater than 25 ppt
- Minimal tidal exchange: water control structures present, very little or no tidal exchange, as evidenced either by tidal range less than 3 cm or average rainy season salinity less than 25 ppt

The Elkhorn Slough area currently harbors 892 ha of full, 203 of muted, and 294 of minimal tidal exchange habitat. Sampling sites were distributed throughout each of these tidal exchange categories in Elkhorn Slough area wetlands (Fig. 1; Table 1). Within the minimal exchange category, we only sampled sites that still had some current or recent connectivity with the estuarine system, as evidenced by water salinity significantly greater than freshwater (>5 ppt) at least seasonally.

### Biological Surveys

To broadly examine the effects of tidal exchange on estuarine communities, we synthesized field data from multiple sources. We use the word community to refer to “any assemblage of populations of living organisms in a prescribed area or habitat” (Krebs 1994, p. 431). Three of the components (fishes and crabs, rapid assessment of communities, marsh-upland ecotone plants) were designed specifically to test hypotheses about tidal exchange effects. The other components (fouling communities, invertebrate recruitment patterns, shorebirds) represent portions of larger studies conducted primarily for other purposes, from which we have extracted unpublished data relevant to the tidal exchange investigation. For most of the components, data were originally collected as species abundances. To better compare among studies with differing methods, we converted all data to presence/absence, with frequency (proportion of sites surveyed where the species was present) as the unit of comparison among studies and species. Abundance and presence/absence data showed similar trends for all studies where both were collected. In the descriptions of methods below, we simply list number of sites in each tidal exchange category surveyed; the site identities are provided in Table 1.

#### *Rapid Assessment of Communities*

To broadly characterize algal, invertebrate, bird, and marine mammal communities, we surveyed 15 sites during

**Table 1** Location and survey information for sites in Fig. 1

| Site | Latitude | Longitude | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 36°51′24.5″ | 121°45′19.6″ | X | X | | | X | | X | |
| 2 | 36°51′7.6″ | 121°45′44.9″ | | | | | X | | | |
| 3 | 36°51′3.4″ | 121°45′29.6″ | | | X | X | | | | |
| 4 | 36°50′28.7″ | 121°44′44.0″ | X | X | | X | X | | X | X |
| 5 | 36°50′0.2″ | 121°44′45.0″ | | X | | | X | | | |
| 6 | 36°49′47.3″ | 121°44′22.7″ | X | X | X | | X | | | |
| 7 | 36°49′25.3″ | 121°45′34.5″ | | X | | X | X | | | |
| 8 | 36°49′30.7″ | 121°46′37.4″ | X | X | X | | X | | X | X |
| 9 | 36°49′20.1″ | 121°46′7.1″ | | X | | | | | | X |
| 10 | 36°49′9.7″ | 121°47′11.0″ | X | X | X | | X | X | X | X |
| 11 | 36°49′0.7″ | 121°46′46.5″ | | | | | | X | | |
| 12 | 36°49′0.0″ | 121°46′20.4″ | | | | | | X | | |
| 13 | 36°48′56.0″ | 121°47′14.1″ | X | | | | X | X | X | |
| 14 | 36°48′1.9″ | 121°47′3.8″ | X | | | | | | X | |
| 15 | 36°47′56.6″ | 121°47′5.2″ | X | X | | | | | X | X |
| 16 | 36°47′44.9″ | 121°46′57.3″ | | | | | X | | X | |
| 17 | 36°47′41.3″ | 121°47′20.5″ | | | X | | X | X | | X |
| 18 | 36°51′17.1″ | 121°45′9.4″ | X | X | X | | X | X | X | X |
| 19 | 36°50′53.4″ | 121°45′17.3″ | X | | X | X | | | | X |
| 20 | 36°50′39.5″ | 121°45′4.6″ | | X | | | X | | X | X |
| 21 | 36°50′33.5″ | 121°44′48.8″ | X | X | | | X | | X | X |
| 22 | 36°50′20.1″ | 121°44′22.9″ | | X | X | | X | X | | X |
| 23 | 36°50′8.6″ | 121°44′13.5″ | X | X | X | X | X | X | X | X |
| 24 | 36°49′46.7″ | 121°43′56.4″ | | X | | | | X | | X |
| 25 | 36°49′42.3″ | 121°44′20.8″ | X | X | | | X | | | X |
| 26 | 36°49′28.4″ | 121°44′23.0″ | X | X | X | X | X | | X | X |
| 27 | 36°49′16.0″ | 121°44′22.3″ | | X | | | | X | X | X |
| 28 | 36°48′39.4″ | 121°44′53.4″ | | | X | | X | | | |
| 29 | 36°48′34.4″ | 121°44′11.5″ | | | | | X | X | | |
| 30 | 36°47′56.8″ | 121°46′17.7″ | | X | X | | X | X | | X |
| 31 | 36°47′22.4″ | 121°45′15.9″ | X | | | | | | | X |

Final columns indicate surveys conducted at each site.
*1* Rapid community assessments, *2* fishes and crabs, *3* marsh-upland ecotone plants, *4* fouling community, *5* invertebrate recruitment, *6* shorebirds (more detailed maps in Connors 2003), *7* water quality, *8* tidal range

September–November 2005. We surveyed five full, five muted, and five minimal tidal exchange sites. We spent about 1.5 h per site, during a low tide (water level was 20–50 cm above mean lower low water at the full and muted sites). At each site, we first identified all birds and marine mammals visible in the adjacent estuarine habitats (marshes, mudflats, and standing water), scanning on average 10,000 m$^2$ for 2 min. To search for brackish snails and carry out crude assessments of mudflat infaunal communities, we collected three 12-cm-diameter cores of soft sediments (~5 cm depth) in 20 cm of standing water (shallow subtidal areas of full exchange sites; lagoonal/channel areas of restricted sites). Each core was spatially separated by at least 10 m. In the field, we sieved the sediment through a 0.5-mm mesh and then identified and counted all visible invertebrates in the field. Mollusks were identified to species because they are readily identified and include some species of concern; the remaining invertebrates were mostly identified to higher taxonomic levels. To assess fouling communities, we surveyed a variety of hard substrates (rocks, fence posts, pipes, etc.), excluding the interior surfaces of active culverts (since culverts were not present at all sites and tended to have distinctive communities; the inclusion of these surfaces might have biased the findings). We searched on average 50 m$^2$ of hard substrate per site. We carried out field identifications of the algae and invertebrates present; those requiring microscopic examination for accurate species identification were only keyed to higher taxonomic levels. We also carried out rapid visual surveys of the site to include any other conspicuous species present on the mudflats (e.g., ditch grass) or in the shallow water (e.g., water boatmen) that were missed by the other components of the survey.

### *Fish and Crab Surveys*

We surveyed six full, four muted, and nine minimal tidal exchange sites. We assessed shallow water areas (<2 m depth) at these sites in April and in August of 2005. At each site, we estimated the density of fishes and crabs using three replicates of each of three different methods of collection: seines, small minnow traps, and larger rectangular fish traps. For the seine tows, we manually dragged a 7-m-long by 2-m-deep bag seine, composed of a 3-mm square delta mesh, with each tow lasting about 3 min. The small minnow traps were cylindrical plastic traps 0.43 m long by 0.23 m wide (widest diameter) with 4.8-mm mesh and a 22-mm-diameter entrance hole in each end of the cone. The large rectangular traps were 0.81-m-long by 0.61-m-wide by 0.28-m-deep steel frame traps with a 1.27-cm polyethylene mesh. All traps were deployed for approximately 24 h at each site and were baited with two anchovies prior to deployment. We determined the presence of each species of crab and fish that were collected across all three replicates of each method. To describe the average fish and crab community structure across seasons, we then combined the data across April and August for subsequent analyses.

### *Marsh-upland Ecotone Surveys*

We surveyed four full, four muted, and four minimal tidal exchange sites during April–May 2005. At each site, we surveyed a 100-m transect along the ecotone and parallel to shore. Transects were located haphazardly, as close as possible to the spot where we arrived at the marsh (from upland or water, depending on the site) but well away from any trails or other human structures. We surveyed a 100-m transect, noting all plant species present in the ecotone. In this study, the upper and lower ecotone boundaries were arbitrarily but repeatably defined. The lower (shoreward) boundary of the ecotone was defined as the last place in the marsh where 100% of the vegetation consisted of pickleweed (*Salicornia virginica*). The upper (landward) boundary of the ecotone was defined as the first place where 100% of the vegetation consisted of upland species. Ecotone width was variable, so we tracked its boundaries carefully as we surveyed the 100-m transect, counting only plant species found within the defined ecotone zone.

### *Fouling Community Surveys*

We deployed recruitment plates at three full and three muted exchange sites. Six poly(vinyl chloride) (PVC) plates (5×10 cm) covered in 3M™ Safety Walk were attached to PVC racks and oriented vertically in the water column. Two racks, each containing half of the plates, were deployed at 0 mean lower low water such that the lowest edge of the plates were suspended 10 cm above the benthic substratum and the primary settling surface facing into the current. Plates were deployed in August 2002 after 10 days in a saltwater flow tank to diffuse chemical contaminants and promote biofilm development. Upon retrieval in October 2004 (27 months total soak time), the back and front of each plate were digitally photographed, and all algae and invertebrates attached to the plates were identified down to the lowest taxonomic level possible; in most cases, this was to species (see Heiman 2006 for further detail of methods).

### *Invertebrate Recruitment Surveys*

To sample invertebrate recruitment at the mudflat surface, we deployed recruitment mats just below the marsh edge in September and December 2005 at ten full, four muted, and seven minimal tidal exchange sites. Mats consisted of an Astroturf™ square (20×20 cm) fastened to the mud surface with stainless steel pegs (methods similar to Wolters et al. 2004). On 14 September 2005, one recruitment mat was deployed at each site during low tide and retrieved on 16 September (after four tidal inundations). On December 3 2005, three recruitment mats were deployed at each site during low tide and retrieved 2 days later on 5 December (after four tidal inundations). Upon retrieval, the mats were individually rinsed with freshwater onto a 2-μm sieve, and both the mats and residuals were examined using a dissecting microscope, counting all invertebrates. Organisms were identified to the lowest taxonomic level possible. To describe the presence of recruits for each species across seasons, data were combined for the fall and winter surveys.

### *Shorebird Surveys*

From March 1999 to July 2000, we surveyed ten full, three muted, and four minimal tidal exchange sites, two to three times each month for shorebirds. Full exchange sites consisted of five of the numbered sites indicated in the Table 1 and in Fig. 1, as well as the main channel of Elkhorn Slough divided into five sections from mouth to head. Surveys of each site were conducted within a 6-h period around low tide. We surveyed the main channel of Elkhorn Slough from a motorboat, Moro Cojo Slough from a kayak or on foot (depending on water depth), and all other sites on foot. All shorebirds on mudflats were identified to species and counted. More detail on site locations and survey methods is available in Connors (2003). We averaged data from all seasons and years to compare year-round habitat usage of the different sites.

## Water Quality and Tidal Range Assessments

Since 1988, multiple sites within the Elkhorn Slough watershed have been monitored monthly using standard water quality analysis protocols. We examined data from 2000 to 2005 for those sites where biological data were also collected: five full, three muted, and six minimal exchange sites. Our goal was to characterize how sites vary in water quality conditions and to determine whether our categorization of tidal exchange adequately encompassed variation among groups of sites. Water quality data included measures of daytime temperature (°C), dissolved oxygen (% saturation), pH, turbidity (nephelometric turbidity units, NTU), $NO_x$ (μm), $NH_3$ (μm), $PO_4$ (μm), and salinity (ppt) in both the dry (May–October) and rainy seasons (November–April) at each water quality monitoring site. To assess tidal range at restricted sites, we surveyed five muted and ten minimal exchange sites on 12 December 2005. We manually estimated water level maximum and minimum over an entire tidal cycle using stakes demarcated in increments of 5 cm. For full exchange sites, data from three in situ instruments deployed in different areas of Elkhorn Slough (available from http://www.mbari.org/lobo and http://cdmo.baruch.sc.edu/) revealed that daily tidal range is virtually identical (within 2 cm) in all portions of the Elkhorn Slough wetlands without water control structures. We used these in situ data to obtain an estimate of the tidal range on 12 December 2005 (3 days prior to full moon) for all our full exchange sites.

## Data Analysis

### *Community Patterns—Multivariate Analyses*

To understand how the community patterns documented in each of the above studies varied with tidal exchange, we employed several related multivariate statistical procedures, including nonmetric multidimensional scaling (nMDS), analysis of similarities (ANOSIM), and similarity percentages (SIMPER) with the program Primer v.6 (Clarke and Gorley 2006). Bray–Curtis similarity matrices were employed to construct the resemblance matrices used in the nMDS and ANOSIM (as is recommended for biological data—McCune and Grace 2002). For those data sets where density or relative abundance data were also available, we also compared the above analyses (nMDS, ANOSIM, and SIMPER) on both the density/relative abundance data and the presence/absence data to verify that the trends were similar across data types for each study. For all six studies, the results were very similar irrespective of data type, and for ease of interpretation and comparison across studies, we proceeded with an analysis of presence/absence data. We evaluated species accumulation plots to assess bias due to differences in sampling intensity across tidal exchange categories. For each study, the species accumulation curves were of similar shape for each category, which suggests that comparisons across categories will represent true differences in community structure (even if sampling intensity was not great enough to completely characterize communities). For each nMDS analysis, we report the nMDS ordination stress values for each data set; generally, stress values below 0.20 are considered useful in analyzing patterns among multiple variables (Clarke 1993). ANOSIM was used to determine if sites differentiated statistically among tidal exchange categories by their community structure (Clarke 1993). The *R* statistic values generated by ANOSIM for pairwise comparisons indicate the dissimilarity for sites grouped by tidal exchange category (values near 1 indicate different composition; values near 0 indicate similar composition). We then used SIMPER to determine which species contributed most to the observed dissimilarities among groups (Clarke 1993).

### *Species Richness Patterns*

To determine whether the number of non-native species varied with tidal exchange, we indicated all species that were definitely non-native to California in our summary database (Table 3). These designations were based primarily on the key regional field guides used for identification (birds: Sibley 2000; marine invertebrates: Smith and Carlton 1975; insects: Powell and Hogue 1979; White 1998; Borror and White 1998; Triplehorn and Johnson 2005; fishes: Miller and Lea 1972; plants: Hickman 1993) and by web-based literature searches. For some species complexes (i.e., groups of species difficult to differentiate), at least one member of the complex is known to be non-native. Since field identification could not determine which species was present, we categorized these complexes as native. Therefore, our assessments of proportions of non-native species in the communities surveyed are likely underestimates.

To determine whether the representation of characteristic estuarine species varied as a function of tidal exchange, all species were placed into one of three habitat affiliations according to the following definitions (using the same field guides and web-based literature searches as mentioned above): E, species typically found in estuarine or brackish habitats, although they may rarely occur in other ecosystems; M, species broadly distributed in marine or coastal habitats, including estuaries; T, species broadly distributed in terrestrial or freshwater habitats, including the margins of estuaries. In most cases, these designations were easily applied to each species; in some instances, arbitrary decisions were made to classify the more ubiquitous species (e.g., migratory birds that use a variety of wetland types and could be considered either M or T). The key category of interest—E for characteristic estuarine species—is robust because we were conservative in only placing species typical of estuarine or brackish habitats in this category. Although direct comparisons of species richness patterns across taxa may not be reliable since taxonomic groups were not all sampled with equivalent intensity/effort, comparisons of species richness patterns among tidal exchange categories within taxonomic groups are reliable (based on the similarity of species accumulation plots across categories as mentioned above).

### *Water Quality Assessment*

To determine how water quality parameters varied across many of our study sites, we used nMDS (we employed nMDS instead of the more traditional principal components analysis due to nonlinear relationships between some of the variables). Prior to analysis, the dataset was normalized, and the Euclidean distance matrix was employed to construct the resemblance matrices used in the nMDS (as is recommended for environmental data—McCune and Grace 2002). We used SIMPER analysis to determine which water quality parameters most strongly differentiated tidal exchange categories. We conducted a multivariate analysis of variance (MANOVA) to assess the variation among categories across all water quality factors and to generate univariate analyses of variance testing whether each water quality factor varied significantly among categories (however, since not all water quality factors are independent, the univariate *F* tests may be misleading). For each water quality factor, we visually assessed boxplots for normality and for homogeneity of spread of samples (side-by-side boxplots for multiple groups) and transformed variables when necessary to meet the normality and homoscedasticity assumptions of MANOVA (square-root transforms of temperature and dissolved oxygen, natural log transformation of turbidity, $NO_x$, and $NH_3$).

## Results

### Community Patterns

Multivariate analyses of each of the six study components revealed differences in community composition among the tidal exchange categories (Figure 2, Table 2). The rapid assessment of mammal, bird, algal, and invertebrate communities and the fish and crab surveys revealed significant differences between the minimal vs. both full and muted tidal exchange categories but no significant differences between these latter two categories. In contrast, plant community structure in the marsh-upland ecotone was marginally different between the muted tidal exchange category vs. both the minimal and full tidal exchange categories, but the latter two categories were not significantly different. The fouling community survey detected a marginal difference between the full and muted tidal exchange categories (no minimal sites were examined in this component). The invertebrate recruitment survey detected significant differences between minimal vs. both full and muted tidal exchange categories and a marginal difference between full and muted tidal exchange categories. The shorebird surveys detected significant differences between the full and minimal tidal exchange categories but did not detect significant differences between the muted and the other tidal exchange categories.

The SIMPER analyses revealed which species were most important in contributing to differences in community structure among categories (species marked with several asterisks in Table 3; note that frequency indicates the proportion of sites for which a given species was present within each tidal exchange category). Those species that contributed the most to distinguishing full vs. muted tidal exchange included Western/least sandpipers, willets, sanderlings, Olympia oysters, salt grass, and alkali heath (more frequent in full) and three-spined sticklebacks, long-jaw

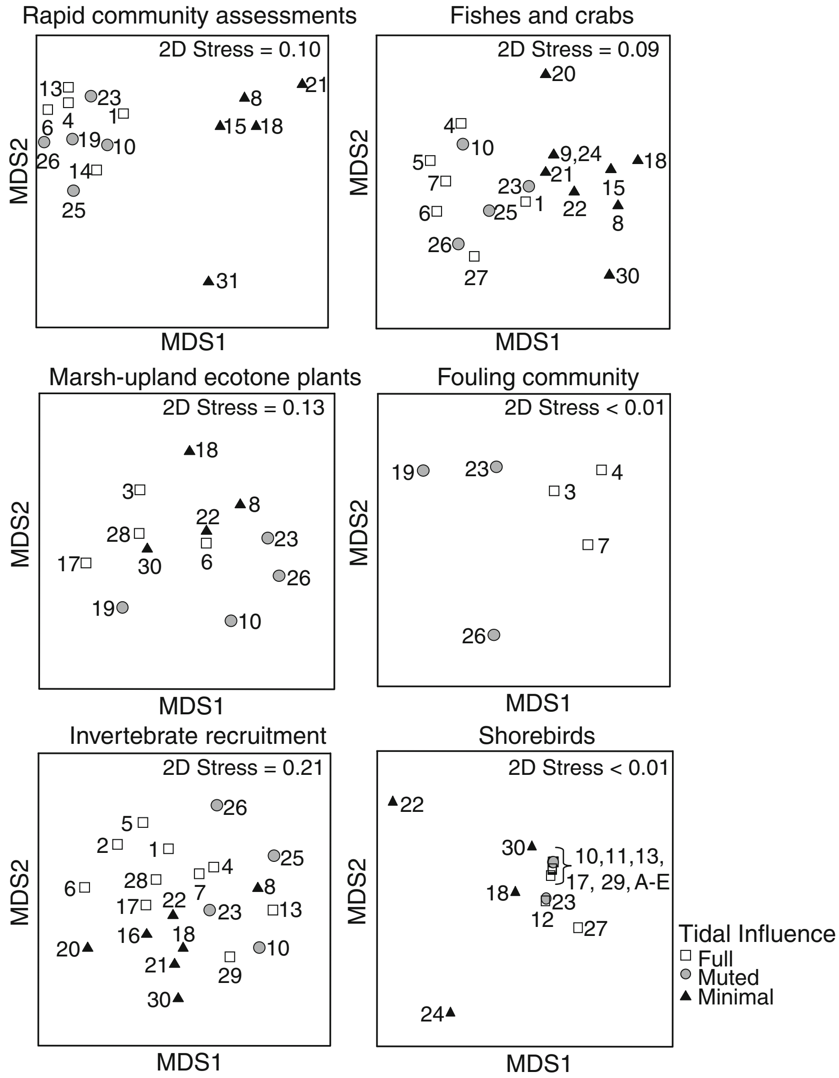

**Fig. 2** nMDS ordinations of community composition. Survey type: rapid assessment of communities, fishes and crabs, marsh-upland ecotone plants, fouling community, invertebrate recruitment, and shorebirds. *Shading* indicates the tidal exchange regime

**Table 2** ANOSIM and SIMPER results for each study

| Study | Test | Statistic | Global | Full vs. muted | Full vs. minimal | Muted vs. minimal |
|---|---|---|---|---|---|---|
| (1) Rapid assessment of communities | ANOSIM | *R* statistic | 0.664*** | 0.192 | 0.852*** | 0.828*** |
| | SIMPER | Dissimilarity | | 57.5 | 87.44 | 86.26 |
| (2) Fishes and crab surveys | ANOSIM | *R* statistic | 0.499*** | −0.121 | 0.759*** | 0.522*** |
| | SIMPER | Dissimilarity | | 33.36 | 64.56 | 53.72 |
| (3) Marsh-upland ecotone surveys | ANOSIM | *R* statistic | 0.295** | 0.391* | 0.161 | 0.286* |
| | SIMPER | Dissimilarity | | 59.76 | 48.06 | 56.56 |
| (4) Fouling community surveys | ANOSIM | *R* statistic | | 0.648* | | |
| | SIMPER | Dissimilarity | | 70.47 | | |
| (5) Invertebrate recruitment surveys | ANOSIM | *R* statistic | 0.270*** | 0.193* | 0.268*** | 0.389** |
| | SIMPER | Dissimilarity | | 62.73 | 62.27 | 66.40 |
| (6) Shorebird surveys | ANOSIM | *R* statistic | 0.333** | 0.083 | 0.471** | −0.209 |
| | SIMPER | Dissimilarity | | 2.91 | 18.77 | 17.87 |

ANOSIM results include the global test for whether tidal exchange regimes vary in their community structure based on the presence/absence data provided by each study. ANOSIM and SIMPER results include pairwise comparisons of the community structure (ANOSIM) and the average dissimilarity (SIMPER) of each tidal exchange regime. Associated ANOSIM *p* values are denoted as: *0.05–0.1, **0.01–0.05, ***<0.01

mudsuckers, and poison hemlock (more frequent in muted). Those species that contributed the most to distinguishing full vs. minimal exchange included willets, gulls, long-billed curlews, Japanese mud snails, amethyst gem clams, European and yellow shore crabs and fleshy jaumea (more frequent in full) and California brackish snails, water boatmen, and poison hemlock (more frequent in minimal). Those species that contributed most to distinguishing muted vs. minimal tidal exchange included long-billed curlews, staghorn sculpins, Japanese mud snails, European and yellow shore crabs (more frequent in muted) and water boatmen, soft chess, salt grass, alkali heath, and curley dock (more frequent in minimal).

## Species/Taxa Richness Patterns

For all surveys combined, we detected a minimum of 186 species in the shallow estuarine habitats of the Elkhorn Slough area (Table 3). The subsequent analysis of richness was conducted considering each distinct taxonomic entry in Table 3 as a species, but we caution that the species richness numbers we report are likely underestimates for those taxa where identifications were to higher units. Species richness across all taxa was highest in full exchange (140 species), lower in muted exchange (107 species), and lowest in minimal exchange (96 species). A detailed summary of species richness patterns by higher taxon, habitat affiliation, and occurrence of non-natives is shown in Fig. 3.

### *Richness Patterns by Taxon*

Richness of primary producers (70 species) and invertebrates (70 species) was much higher across all three estuarine habitats than that of fishes (18 species) and birds (26 species). Each taxon showed a different pattern of richness across tidal exchange categories. Among primary producers (plants and algae combined), species richness in the full and minimal exchange sites was similar and higher than in the muted exchange. Among invertebrates, there was a decline in richness with decreasing tidal exchange. For fishes, species richness in the full and muted exchange sites was similar but higher than in the minimal exchange sites. Bird richness was highest in the muted exchange site and slightly lower in the minimal and full exchange sites.

### *Richness Patterns by Habitat Affiliation*

We identified 77 freshwater/terrestrial species (41.4% of the total species detected). Freshwater/terrestrial species richness was highest in minimal exchange (56 species), lower in full exchange (47 species), and lowest in muted exchange (37 species). Freshwater/terrestrial species accounted for the majority of the species found among primary producers (mostly upland plants), about half of the species among birds, and a minority of the richness among both invertebrates and fishes.

We documented 30 estuarine species (16.1% of the total), with the most species found in full exchange (24 species) and followed by muted (20 species) and minimal exchange (15 species). Patterns of richness for estuarine species differed across higher taxa. Among estuarine primary producers, richness was marginally higher in full and minimal vs. muted exchange sites. Among estuarine invertebrates, species richness was highest in the full and muted exchange sites, while for estuarine fishes species, richness was highest in the minimal exchange site. We found no bird species that appeared to be typical only of estuaries.

We found 79 coastal/marine species (42.5% of the total), with the highest number in full exchange (68 species), followed by muted (50 species), and then minimal

**Table 3** Frequency and contribution to dissimilarity between tidal regimes of all species found in estuarine surveys

| | | | | | | **Frequency** | | | **Dissimilarity** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Scientific Name** | **Common name** | **Group** | **Study** | **Habitat** | **full** | **muted** | **minimal** | **full vs. muted** | **full vs. minimal** | **muted vs. minimal** |
| | **Alga** | | | | | | | | | | |
| * | *Caulacanthus ustulatus* | red turf alga | Rhodophyta | 1 | M | 0.40 | 0.80 | 0.00 | * | | ** |
| | *Gracilaria / Gracilariopsis* sp. | graceful red alga | Rhodophyta | 1 | M | 0.40 | 0.60 | 0.00 | * | * | ** |
| | *Ulothrix* sp. | blue-green alga | Chlorophyta | 1 | M | 0.20 | 0.40 | 0.00 | * | | * |
| | *Ulva* spp. | sea lettuce | Chlorophyta | 1 | M | 1.00 | 1.00 | 0.80 | | | |
| * | *Caulacanthus ustulatus* | red turf alga | Rhodophyta | 4 | M | 0.67 | 0.00 | - | * | | |
| | *Ulva linza* | ribbon sea lettuce | Chlorophyta | 4 | M | 0.67 | 0.00 | - | ** | | |
| | unidentified rhodophyte | filamentous red alga | Rhodophyta | 4 | M | 0.20 | 0.00 | 0.00 | | | |
| | **Bird** | | | | | | | | | | |
| | *Agelaius phoeniceus* | red-winged blackbird | Emberizidae | 1 | T | 0.00 | 0.00 | 0.20 | | | |
| | *Anas platyrhyncos* | mallard | Anatidae | 1 | T | 0.00 | 0.20 | 0.40 | | * | * |
| | *Ardea herodias* | great blue heron | Ardeidae | 1 | T | 0.20 | 0.40 | 0.20 | * | | * |
| | *Bucephala clangula* | common goldeneye | Anatidae | 1 | T | 0.00 | 0.20 | 0.00 | | | |
| | *Calidris mauri/ minutilla* | Western/ least Sandpiper | Scolopacidae | 1 | M | 0.80 | 0.20 | 0.20 | ** | * | * |
| | *Casmerodius albus* | great egret | Ardeidae | 1 | T | 0.40 | 0.40 | 0.20 | * | * | * |
| | *Catoptrophorus semipalmatus* | willet | Scolopacidae | 1 | M | 0.80 | 0.20 | 0.00 | ** | ** | |
| | *Egretta thula* | snowy egret | Ardeidae | 1 | T | 0.40 | 0.20 | 0.20 | * | * | |
| | *Fulica americana* | American coot | Rallidae | 1 | T | 0.20 | 0.00 | 0.00 | | | |
| | *Gavia immer* | common loon | Gaviidae | 1 | T | 0.20 | 0.00 | 0.00 | | | |
| | *Himantopus mexicanus* | black-necked stilt | Recurvirostradae | 1 | T | 0.20 | 0.40 | 0.80 | * | * | ** |
| | *Limnodromus griseus/ scolopaceus* | short-/long-billed dowitcher | Scolopacidae | 1 | M | 0.40 | 0.00 | 0.20 | | * | |
| | *Limosa fedoa* | marbled godwit | Scolopacidae | 1 | M | 0.20 | 0.00 | 0.00 | | | |
| | *Lophodytes cucullatus* | hooded merganser | Anatidae | 1 | T | 0.00 | 0.20 | 0.00 | | | |
| | *Numenius americanus* | long-billed curlew | Scolopacidae | 1 | M | 0.60 | 0.00 | 0.00 | * | * | |
| | *Nycticorax nycticorax* | black-crowned night heron | Ardeidae | 1 | T | 0.00 | 0.20 | 0.00 | | | |
| | *Pelecanus erythrorhynchos* | white pelican | Pelecanidae | 1 | T | 0.00 | 0.20 | 0.00 | | | |
| | *Pelecanus occidentalis* | brown pelican | Pelecanidae | 1 | M | 0.60 | 0.20 | 0.00 | * | * | |
| | *Podilymbus podiceps* | pied-billed grebe | Podicipedidae | 1 | T | 0.20 | 0.40 | 0.20 | * | | * |
| | *Tringa flavipes/ melanoleuca* | lesser/greater Yellowlegs | Scolopacidae | 1 | M | 0.20 | 0.20 | 0.20 | * | * | * |
| | *unidentified species* | gull | Laridae | 1 | M | 0.80 | 0.40 | 0.00 | * | ** | * |
| | *Calidris alba* | sanderling | Scolopacidae | 6 | M | 0.80 | 0.50 | 0.40 | *** | * | * |
| | *Calidris alpina* | dunlin | Scolopacidae | 6 | M | 1.00 | 1.00 | 0.60 | | * | * |
| | *Calidris mauri* | Western sandpiper | Scolopacidae | 6 | M | 1.00 | 1.00 | 0.80 | | | |
| | *Calidris minutilla* | least sandpiper | Scolopacidae | 6 | M | 1.00 | 1.00 | 1.00 | | | |
| | *Catoptrophorus semipalmatus* | willet | Scolopacidae | 6 | M | 1.00 | 1.00 | 0.80 | | | |
| | *Himantopus mexicanus* | black-necked stilt | Recurvirostradae | 6 | T | 0.90 | 1.00 | 1.00 | ** | | |
| | *Limnodromus griseus/ scolopaceus* | short-/long-billed dowitcher | Scolopacidae | 6 | M | 1.00 | 1.00 | 0.80 | | | |
| | *Limosa fedoa* | marbled godwit | Scolopacidae | 6 | M | 1.00 | 1.00 | 0.80 | | | |
| | *Numenius americanus* | long-billed curlew | Scolopacidae | 6 | M | 1.00 | 1.00 | 0.20 | | ** | ** |
| | *Pluvialis squatarola* | black-bellied plover | Charadriidae | 6 | M | 1.00 | 1.00 | 0.60 | | * | * |
| | *Recurvirostra americana* | American avocet | Recurvirostradae | 6 | T | 1.00 | 1.00 | 1.00 | | | |
| | **Fish** | | | | | | | | | | |
| | *Atherinops affinis* | topsmelt | Atherinidae | 2 | M | 1.00 | 1.00 | 0.56 | | * | * |
| | *Citharicthys stigmaeus* | speckled sandab | Bothidae | 2 | M | 0.33 | 0.00 | 0.00 | * | | |
| | *Clevelandia ios Lepidogobius lepidus* | arrow goby/bay goby | Gobiidae | 2 | E | 0.83 | 1.00 | 0.56 | | * | * |
| | *Clupea harengus pallasii* | Pacific herring | Clupeidae | 2 | M | 0.00 | 0.25 | 0.11 | * | | * |
| | *Cymatogaster aggregata* | shiner surfperch | Embioticidae | 2 | M | 0.50 | 0.00 | 0.00 | * | * | |
| | *Engraulis mordax* | Northern anchovy | Engraulididae | 2 | M | 0.00 | 0.25 | 0.00 | | | |
| | *Eucyclogobius newberryi* | tidewater goby | Gobiidae | 2 | E | 0.00 | 0.00 | 0.22 | | | |
| * | *Gambusia holbrooki* | mosquitofish | Poeciliidae | 2 | T | 0.00 | 0.00 | 0.22 | | | |
| | *Gasterosteus aculeatus* | threespine stickleback | Gaterosteidae | 2 | T | 0.33 | 0.50 | 1.00 | ** | * | * |
| | *Gillicthys mirabilis* | longjaw mudsucker | Gobiidae | 2 | E | 0.33 | 0.75 | 0.89 | ** | * | |
| | *Girella nigricans* | opaleye | Girellidae | 2 | M | 0.00 | 0.25 | 0.00 | | | |
| | *Leptocottus armatus* | staghorn sculpin | Cottidae | 2 | M | 1.00 | 1.00 | 0.33 | | * | ** |
| | *Paralichthys californicus* | California halibut | Bothidae | 2 | M | 0.33 | 0.25 | 0.00 | * | | |
| | *Platichthys stellatus* | starry flounder | Pleuronectidae | 2 | M | 0.17 | 0.00 | 0.00 | | | |
| | *Platyrhinoidis triseriata* | thornback | Plathyrinidae | 2 | M | 0.17 | 0.00 | 0.00 | | | |
| | *Porichthys notatus* | plain-fin midshipman | Batrachoididae | 2 | M | 0.17 | 0.25 | 0.00 | * | | |
| | *Sygnathus leptorhyncus* | bay pipefish | Sygnathidae | 2 | M | 0.17 | 0.25 | 0.00 | * | | |
| | *Xystreurys liolepis* | fantail sole | Bothidae | 2 | M | 0.00 | 0.25 | 0.00 | | | |
| | **Invertebrate** | | | | | | | | | | |
| * | *Amathia vidovici* | gelatinous bryozoan | Bryozoa | 1 | M | 0.20 | 0.20 | 0.00 | | | |
| | *Ammothea hilgendorfi* | Japanese sea spider | Arthropoda-Chelicerata | 1 | M | 0.00 | 0.40 | 0.00 | * | | * |
| | *Anthopleura sola* | solitary anemone | Cnidaria-Anthozoa | 1 | M | 0.20 | 0.00 | 0.00 | | | |
| | *Balanus glandula* | acorn barnacle | Arthropoda-Crustacea | 1 | M | 0.80 | 0.80 | 0.00 | * | ** | ** |
| * | *Batillaria attramentaria* | Japanese mud snail | Mollusca-Gastropoda | 1 | E | 0.80 | 1.00 | 0.00 | | ** | *** |
| * | *Bugula neritina* | brown bryozoan | Bryozoa | 1 | M | 0.60 | 0.40 | 0.00 | * | * | * |
| | *Chthamalus sp.* | tiny acorn barnacle | Arthropoda-Crustacea | 1 | M | 0.40 | 0.20 | 0.00 | * | | |
| * | *Conopeum tenuissum* | lacy crust bryozoan | Bryozoa | 1 | E | 0.00 | 0.40 | 0.00 | * | | * |
| * | *Diadumene* spp. | small anemone | Cnidaria-Anthozoa | 1 | E | 0.40 | 0.80 | 0.00 | * | * | ** |
| * | *Ectopleura crocea* | pink mouth hydroid | Cnidaria-Hydrozoa | 1 | E | 0.40 | 0.20 | 0.00 | * | | |
| * | *Ficopomatus enigmaticus* | gregarious tube worm | Annelida | 1 | E | 0.40 | 0.20 | 0.20 | * | * | * |
| | *Flabellina trilineata* | three-lined nudibranch | Mollusca-Gastropoda | 1 | M | 0.20 | 0.00 | 0.00 | | | |
| * | *Gemma gemma* | amethyst gem clam | Mollusca-Bivalvia | 1 | E | 1.00 | 0.40 | 0.00 | * | *** | * |
| | *Hymeniacidon sinapium* | orange sponge | Porifera | 1 | E | 0.40 | 0.60 | 0.00 | | | |

**Table 3** (continued)

| | | | | | | Frequency | | | Dissimilarity | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Scientific Name** | **Common name** | **Group** | **Study** | **Habitat** | **full** | **muted** | **minimal** | **full vs. muted** | **full vs. minimal** | **muted vs. minimal** |
| * | *Littorina sp.* | periwinkle snail | Mollusca-Gastropoda | 1 | M | 0.40 | 0.40 | 0.00 | * | * | * |
| | *Lottia sp.* | limpet | Mollusca-Gastropoda | 1 | M | 0.40 | 0.00 | 0.00 | * | * | |
| | *Macclintockia scabra* | rough limpet | Mollusca-Gastropoda | 1 | M | 0.20 | 0.00 | 0.00 | | | |
| | *Macoma nasuta* | bent-nose clam | Mollusca-Bivalvia | 1 | E | 0.20 | 0.00 | 0.00 | | | |
| | *Megabalanus californicus* | red-striped barnacle | Arthropoda-Crustacea | 1 | M | 0.20 | 0.00 | | | | |
| | *Mytilus californianus* | California mussel | Mollusca-Bivalvia | 1 | M | 0.40 | 0.00 | 0.00 | * | * | |
| | *Mytilus galloprovincialis / trossulus* | bay mussel | Mollusca-Bivalvia | 1 | E | 0.80 | 0.40 | 0.00 | * | ** | * |
| * | *Nematostella vectensis* | starlet sea anemone | Cnidaria-Anthozoa | 1 | E | 0.00 | 0.20 | 0.00 | | | |
| | *Nemertean* | ribbon worm | Nemertea | 1 | M | 0.00 | 0.80 | 0.00 | ** | | ** |
| | *Nucella emarginata* | emarginate dogwhelk | Mollusca-Gastropoda | 1 | M | 0.20 | 0.00 | 0.00 | | | |
| | *Ostreola conchaphila* | Olympia oyster | Mollusca-Bivalvia | 1 | E | 0.60 | 0.40 | 0.00 | * | * | * |
| | *Pagurus sp.* | hermit crab | Arthropoda-Crustacea | 1 | M | 0.20 | 0.20 | 0.00 | | | |
| | *Physa* sp. | sinestral snail | Mollusca-Gastropoda | 1 | T | 0.00 | 0.00 | 0.20 | | | |
| | *Protothaca staminea / Venerupis* | Pacific/ Japanese littleneck | Mollusca-Bivalvia | 1 | M | 0.60 | 0.00 | 0.00 | | * | |
| * | *Schizoporella unicornis* | single horn bryozoan | Bryozoa | 1 | M | 0.00 | 0.20 | 0.00 | | | |
| | *Siliqua lucida* | transparent razor clam | Mollusca-Bivalvia | 1 | E | 0.00 | 0.20 | 0.00 | | | |
| | *Tryonia imitator* | California brackish snail | Mollusca-Gastropoda | 1 | E | 0.00 | 0.00 | 0.80 | | ** | ** |
| | unidentified amphipod | beach hopper | Arthropoda-Crustacea | 1 | M | 1.00 | 1.00 | 0.20 | | ** | ** |
| * | unidentified botryllid | slimy sea squirt | Chordata-Tunicata | 1 | M | 0.20 | 0.00 | 0.00 | | | |
| | unidentified chironomid | midge larva | Arthropoda-Insecta | 1 | T | 0.00 | 0.00 | 0.20 | | | |
| | unidentified coroxid | water boatman | Arthropoda-Insecta | 1 | T | 0.00 | 0.00 | 0.80 | | ** | ** |
| | unidentified insect | insect | Arthropoda-Insecta | 1 | T | 0.00 | 0.20 | 0.00 | | | |
| | unidentified oligochaete | freshwater worm | Annelida | 1 | T | 0.00 | 0.00 | 0.20 | | | |
| | unidentified polychaete | segmented bristle worm | Annelida | 1 | M | 1.00 | 0.80 | 0.00 | | *** | ** |
| | unidentified poriferan | yellow sponge | Porifera | 1 | M | 0.40 | 0.60 | 0.00 | * | | * |
| | unidentified spirorbid | spiral tube worm | Annelida | 1 | M | 0.20 | 0.00 | 0.00 | | | |
| | unidentified tanaid | tanaid | Arthropoda-Crustacea | 1 | M | 0.20 | 0.00 | 0.00 | | | |
| * | *Watersipora sp.* | fluted red bryozoan | Bryozoa | 1 | M | 0.40 | 0.20 | 0.00 | * | | |
| | *Cancer antennarius* | Pacific rock crab | Arthropoda-Crustacea | 2 | M | 0.50 | 0.50 | 0.00 | ** | * | * |
| * | *Carcinus maenus* | European green crab | Arthropoda-Crustacea | 2 | E | 0.83 | 0.75 | 0.00 | * | ** | ** |
| | *Hemigrapsus oregonensis* | yellow shore crab | Arthropoda-Crustacea | 2 | M | 1.00 | 1.00 | 0.11 | | ** | ** |
| * | *Amathia vidovici* | gelatinous bryozoan | Bryozoa | 4 | M | 1.00 | 0.67 | - | * | | |
| | *Balanus glandula* | acorn barnacle | Arthropoda-Crustacea | 4 | M | 1.00 | 0.67 | - | | | |
| * | *Bowerbankia gracilis* | creeping bryozoan | Bryozoa | 4 | M | 0.67 | 0.00 | - | * | | |
| * | *Bugula neritina* | brown bryozoan | Bryozoa | 4 | M | 0.67 | 0.33 | - | * | | |
| * | *Bugula stolonifera* | beige bryozoan | Bryozoa | 4 | M | 0.00 | 0.33 | - | | | |
| | *Chthamalus sp.* | tiny acorn barnacle | Arthropoda-Crustacea | 4 | M | 0.33 | 0.33 | - | * | | |
| | *Conopeum osburni* | boxy bryozoan | Bryozoa | 4 | E | 1.00 | 0.33 | - | * | | |
| * | *Cryptosula pallasiana* | white bryozoan | Bryozoa | 4 | M | 0.00 | 0.33 | - | ** | | |
| * | *Diadumene franciscana* | San Francisco anemone | Cnidaria-Anthozoa | 4 | E | 0.00 | 0.33 | - | | | |
| * | *Diadumene lineata* | orange-striped green anemon | Cnidaria-Anthozoa | 4 | E | 0.33 | 1.00 | - | ** | | |
| * | *Ectopleura crocea* | pink mouth hydroid | Cnidaria-Anthozoa | 4 | E | 0.33 | 0.00 | - | | | |
| * | *Ficopomatus enigmaticus* | gregarious tube worm | Annelida | 4 | E | 0.69 | 0.00 | - | * | | |
| * | *Halichondria bowerbanki* | Bowerbank's bread sponge | Porifera | 4 | M | 1.00 | 0.00 | - | ** | | |
| | *Haliclona sp.* | yellow sponge | Porifera | 4 | M | 0.33 | 0.33 | - | * | | |
| * | *Hymeniacidon sinapium* | orange sponge | Porifera | 4 | E | 0.00 | 0.33 | - | | | |
| | *Mytilus galloprovincialis / trossulus* | bay mussel | Mollusca-Bivalvia | 4 | E | 0.33 | 0.00 | - | | | |
| | *Ostreola conchaphila* | Olympia oyster | Mollusca-Bivalvia | 4 | E | 1.00 | 0.00 | - | ** | | |
| | unidentified poriferan | yellow sponge | Porifera | 4 | M | 0.33 | 0.00 | - | | | |
| | unidentified spirorbid | spiral tube worm | Annelida | 4 | M | 0.33 | 0.00 | - | * | | |
| * | *Watersipora subtorquata* | fluted red bryozoan | Bryozoa | 4 | M | 0.49 | 0.00 | - | | | |
| | *Allorchestes angusta* | herbivorous amphipod | Arthropoda-Crustacea | 5 | E | 0.90 | 1.00 | 0.71 | | * | * |
| | *Anisogammarus confervicolus* | coastal amphipod | Arthropoda-Crustacea | 5 | M | 0.00 | 0.00 | 0.14 | | | |
| | *Tryonia imitator* | California brackish snail | Mollusca-Gastropoda | 5 | E | 0.00 | 0.00 | 0.57 | | * | * |
| * | *Batillaria attramentaria* | Japanese mud snail | Mollusca-Gastropoda | 5 | E | 0.40 | 0.50 | 0.14 | * | * | * |
| | *Capitella sp.* | spaghetti worm | Annelida | 5 | E | 0.30 | 0.00 | 0.43 | | * | * |
| | *Cumella vulgaris* | tiny cumacean | Arthropoda-Crustacea | 5 | E | 0.20 | 0.00 | 0.00 | | | |
| | *Exosphaeroma octoneum* | shore isopod | Arthropoda-Crustacea | 5 | M | 0.20 | 0.00 | 0.00 | | | |
| * | *Gemma gemma* | amethyst gem clam | Mollusca-Bivalvia | 5 | M | 0.50 | 0.00 | 0.00 | * | * | |
| | *Hemigrapsus oregonensis* | yellow shore crab | Arthropoda-Chelicerata | 5 | M | 0.10 | 0.00 | 0.00 | | | |
| | *Myosotella myosotis* | mouse-ear marsh snail | Mollusca-Gastropoda | 5 | E | 0.30 | 0.25 | 0.29 | * | * | * |
| | *Stenamma* sp. | ant | Arthropoda-Insecta | 5 | T | 0.20 | 0.00 | 0.14 | | | |
| | *Traskorchestia traskiana* | beach hopper | Arthropoda-Crustacea | 5 | E | 0.80 | 0.50 | 0.29 | * | * | * |
| | unidentified arachnid | spiders | Arthropoda-Chelicerata | 5 | T | 0.60 | 0.50 | 0.57 | * | * | * |
| | unidentified brachycera | brachycera fly | Arthropoda-Insecta | 5 | T | 0.40 | 0.50 | 0.86 | * | * | * |
| | unidentified chironomid | midge larva | Arthropoda-Insecta | 5 | T | 0.10 | 0.00 | 0.00 | | | |
| | unidentified coroxid | water boatman | Arthropoda-Insecta | 5 | T | 0.40 | 0.00 | 0.86 | * | * | ** |
| | unidentified dipteran | true fly | Arthropoda-Insecta | 5 | T | 0.30 | 0.00 | 0.43 | | * | * |
| | unidentified ephydrid | brine fly | Arthropoda-Insecta | 5 | M | 0.30 | 0.50 | 0.57 | * | * | * |
| | unidentified hydraenid | water beetle | Arthropoda-Insecta | 5 | T | 0.10 | 0.00 | 0.43 | | * | * |
| | unidentified hypogastrurid | springtail | Arthropoda-Insecta | 5 | T | 0.40 | 0.00 | 0.00 | * | | |
| | unidentified podocopid ostracod | ostracod | Arthropoda-Crustacea | 5 | M | 0.50 | 0.00 | 0.57 | * | * | * |
| | unidentified psocopteran | book/barklice | Arthropoda-Insecta | 5 | T | 0.00 | 0.25 | 0.14 | | | |
| | unidentified saldid | shore bug/water beetle | Arthropoda-Insecta | 5 | T | 0.40 | 0.00 | 0.14 | * | * | |
| | unidentified terebrantian | thrip | Arthropoda-Insecta | 5 | T | 0.20 | 0.50 | 0.14 | * | | * |
| | *Zeuxo normani* | tanaid | Arthropoda-Crustacea | 5 | M | 0.00 | 0.25 | 0.00 | | | |
| | **Mammal** | | | | | | | | | | |
| | *Enhydra lutris* | California sea otter | Carnivora-Mustelidae | 1 | M | 0.20 | 0.40 | 0.00 | * | | * |
| | *Phoca vitulina* | harbor seal | Pinnipedia-Phocidae | 1 | M | 0.20 | 0.00 | 0.00 | | | |

**Table 3** (continued)

| | | | | | | Frequency | | | Dissimilarity | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Scientific Name** | **Common name** | **Group** | **Study** | **Habitat** | **full** | **muted** | **minimal** | **full vs. muted** | **full vs. minimal** | **muted vs. minimal** |
| | **Plant** | | | | | | | | | | |
| | *Ruppia maritima* | ditchgrass | Zosteraceae | 1 | E | 0.00 | 0.00 | 0.40 | | * | * |
| | *Ambrosia chamissonis* | beach bur | Asteraceae | 3 | M | 0.25 | 0.00 | 0.00 | | | |
| * | *Anagallis arvensis* | scarlet pimpernel | Primulaceae | 3 | T | 1.00 | 0.75 | 0.50 | | * | * |
| * | *Anthemis cotula* | dog fennel | Asteraceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| * | *Anthriscus caucalis* | bur chervil | Apiaceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| | *Atriplex californica* | California saltbush | Chenopodiaceae | 3 | M | 0.25 | 0.00 | 0.00 | | | |
| | *Atriplex triangularis* | spearscale | Chenopodiaceae | 3 | M | 1.00 | 1.00 | 1.00 | | | |
| * | *Avena barbata* | slender wild oat | Poaceae (Aveneae) | 3 | T | 0.25 | 0.00 | 0.00 | | | |
| * | *Avena fatua* | wild oat | Poaceae (Aveneae) | 3 | T | 0.25 | 0.00 | 0.00 | | | |
| | *Baccharis pilularis* | coyote brush | Asteraceae | 3 | M | 0.75 | 0.50 | 0.50 | * | * | * |
| * | *Brassica nigra/rapa* | black/field mustard | Brassicaceae | 3 | T | 0.25 | 0.75 | 0.25 | ** | * | ** |
| * | *Bromus diandrus* | ripgut grass | Poaceae (Festuceae) | 3 | T | 0.75 | 0.25 | 0.25 | ** | ** | * |
| * | *Bromus hordeaceus* | soft chess | Poaceae (Festuceae) | 3 | T | 1.00 | 0.25 | 0.75 | ** | * | ** |
| * | *Bromus japonicus* | Japanese brome | Poaceae (Festuceae) | 3 | T | 0.25 | 0.00 | 0.00 | | | |
| | *Camissonia ovata* | suncups | Onagraceae | 3 | T | 0.25 | 0.00 | 0.00 | | | |
| * | *Carduus pycnocephalus* | Italian thistle | Asteraceae | 3 | T | 0.00 | 0.50 | 0.50 | * | * | * |
| * | *Carpobrotus edulis* | ice plant | Aizoaceae | 3 | M | 0.25 | 0.00 | 0.25 | | * | * |
| | *Chlorogalum pomeridianum* | wavy-leaved soap plant | Liliaceae | 3 | T | 0.50 | 0.00 | 0.00 | * | * | |
| * | *Cirsium vulgare* | bull thistle | Asteraceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| | *Claytonia perfoliata* | miner's lettuce | Portulacaceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| * | *Conium maculatum* | poison hemlock | Apiaceae | 3 | T | 0.25 | 0.75 | 1.00 | ** | ** | |
| * | *Cotula coronopifolia* | brass buttons | Asteraceae | 3 | M | 0.00 | 0.00 | 0.25 | | | * |
| | *Cuscuta salina* | salt marsh dodder | Cuscutaceae | 3 | E | 0.50 | 0.00 | 0.25 | * | * | |
| | *Distichlis spicata* | salt grass | Poaceae (Festuceae) | 3 | M | 1.00 | 0.00 | 0.75 | *** | * | ** |
| * | *Erodium moschatum* | white-stemmed filaree | Geraniaceae | 3 | T | 0.00 | 0.25 | 0.25 | | | * |
| | *Frankenia salina* | alkali heath | Frankeniaceae | 3 | E | 1.00 | 0.00 | 1.00 | *** | | *** |
| | *Galium aparine* | goose grass | Rubiaceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| * | *Geranium dissectum* | cut-leaved geranium | Geraniaceae | 3 | T | 0.50 | 0.25 | 0.75 | * | * | ** |
| | *Grindelia stricta* | coastal gum plant | Asteraceae | 3 | M | 0.25 | 0.00 | 0.00 | | | |
| | *Heliotropium curassavicum* | seaside heliotrope | Boraginaceae | 3 | T | 0.25 | 0.00 | 0.00 | | | |
| | *Hordeum brachyantherum* | meadow barley | Poaceae (Hordeae) | 3 | T | 0.25 | 0.00 | 0.50 | | * | * |
| * | *Hordeum marinum* | Mediterannean barley | Poaceae (Hordeae) | 3 | T | 0.50 | 0.25 | 0.25 | * | * | * |
| | *Horkelia californica* | California horkelia | Rosaceae | 3 | T | 0.25 | 0.00 | 0.00 | | | |
| | *Jaumea carnosa* | fleshy jaumea | Asteraceae | 3 | E | 0.75 | 0.25 | 0.00 | ** | ** | |
| | *Juncus bufonius* | common toad rush | Juncaceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| | *Juncus sp.* | unidentified rush | Juncaceae | 3 | T | 0.25 | 0.50 | 0.75 | * | ** | * |
| * | *Lavatera cretica* | Cretan mallow | Malvaceae | 3 | M | 0.00 | 0.25 | 0.00 | | | |
| | *Leymus sp.* | creeping wild rye | Poaceae (Hordeae) | 3 | M | 0.25 | 0.00 | 0.50 | * | * | * |
| * | *Lolium multiflorum* | Italian ryegrass | Poaceae (Hordeae) | 3 | T | 0.75 | 0.25 | 0.25 | ** | ** | * |
| * | *Lythrum hyssopifolia* | grass poly | Lythraceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| * | *Medicago polymorpha* | bur clover | Fabaceae | 3 | T | 0.50 | 0.25 | 0.25 | * | * | * |
| * | *Melilotus indicus* | Indian melilot | Fabaceae | 3 | T | 0.25 | 0.25 | 0.00 | * | | |
| * | *Parapholis incurva* | sickle grass | Poaceae (Hordeae) | 3 | E | 0.50 | 0.25 | 0.25 | * | * | * |
| | *Pentagramma triangularis* | golden fern | Pteridaceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| | *Perideridia kelloggii* | Kellogg's yampah | Apiaceae | 3 | T | 0.25 | 0.00 | 0.00 | | | |
| * | *Picris echioides* | bristly oxtongue | Asteraceae | 3 | T | 0.00 | 0.00 | 0.50 | | * | * |
| * | *Plantago coronopus* | cut-leaved plantain | Plantaginaceae | 3 | T | 0.50 | 0.00 | 0.00 | * | * | |
| * | *Plantago lanceolata* | English plantain | Plantaginaceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| * | *Polypogon monspeliensis* | rabbitfoot grass | Poaceae (Agrostideae) | 3 | T | 0.50 | 1.00 | 0.75 | * | * | |
| * | *Raphanus raphanistrum/sativus* | jointed charlock/wild radish | Brassicaceae | 3 | T | 0.25 | 0.50 | 0.25 | * | * | * |
| | *Rubus ursinus* | California blackberry | Rosaceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| * | *Rumex acetosella* | sheep sorrel | Polygonaceae | 3 | T | 0.25 | 0.00 | 0.25 | | * | |
| * | *Rumex crispus* | curly dock | Polygonaceae | 3 | T | 1.00 | 0.25 | 1.00 | ** | | ** |
| | *Salicornia virginica* | pickleweed | Chenopodiaceae | 3 | E | 1.00 | 1.00 | 1.00 | | | |
| | *Salix sp.* | unidentified willow | Salicaceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| | *Sanicula crassicaulis* | gambleweed | Apiaceae | 3 | T | 0.00 | 0.25 | 0.00 | | | |
| | *Scirpus americanus* | three square | Cyperaceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| * | *Silybum marianum* | milk thistle | Asteraceae | 3 | T | 0.00 | 0.25 | 0.25 | | | * |
| * | *Sonchus asper/oleraceus* | prickly/common sowthistle | Asteraceae | 3 | T | 1.00 | 0.50 | 1.00 | * | | * |
| * | *Spergularia bocconii* | Bocconi's sand spurry | Caryophyllaceae | 3 | E | 0.25 | 0.00 | 0.00 | | | |
| | *Spergularia marina* | salt marsh sand spurry | Caryophyllaceae | 3 | T | 0.00 | 0.25 | 0.00 | | | |
| * | *Tetragonia tetragonioides* | New Zealand spinach | Aizoaceae | 3 | M | 0.25 | 0.25 | 0.00 | * | | |
| | *Urtica dioica* | stinging nettle | Urticaceae | 3 | T | 0.00 | 0.00 | 0.25 | | | |
| * | *Vicia sativa* | spring vetch | Fabaceae | 3 | T | 0.25 | 0.00 | 0.00 | | | |
| * | *Vulpia bromoides/myuros* | unidentified fescue | Poaceae (Festuceae) | 3 | T | 0.75 | 0.25 | 1.00 | ** | | ** |

Species that are considered **non-native** to California in the published literature are marked with an asterisk before their scientific names; some of the species not marked by an asterisk may also be non-natives, but insufficient taxonomic or geographic analysis was available to firmly reach this conclusion.

**Studies:** *1* rapid assessment of communities, *2* fish and crab surveys, *3* marsh-upland ecotone surveys, *4* fouling community surveys, *5* invertebrate recruitment surveys, *6* shorebird surveys; **Habitat designation**: *E* species typically found in estuarine or brackish habitats, although they may rarely occur in other ecosystems; *M* species broadly distributed in marine or coastal habitats, including estuaries; *T* species broadly distributed in terrestrial or freshwater habitats, including the margins of estuaries. **Frequency** in each tidal exchange regime (full, muted, minimal) is the proportion of sampled sites in which the species was detected. **Dissimilarity:** contribution of each species to dissimilarity between tidal regimes, based on SIMPER analysis.

[*] The contribution is greater than would be expected if all species were contributing to differences equally but less than twice expected.

[**] The contribution is twice (or more, but less than three times) what would be expected if all species were contributing equally (these species are lightly shaded).

[***] The contribution is three times or more than what would be expected if all species were contributing equally (these species are darkly shaded).

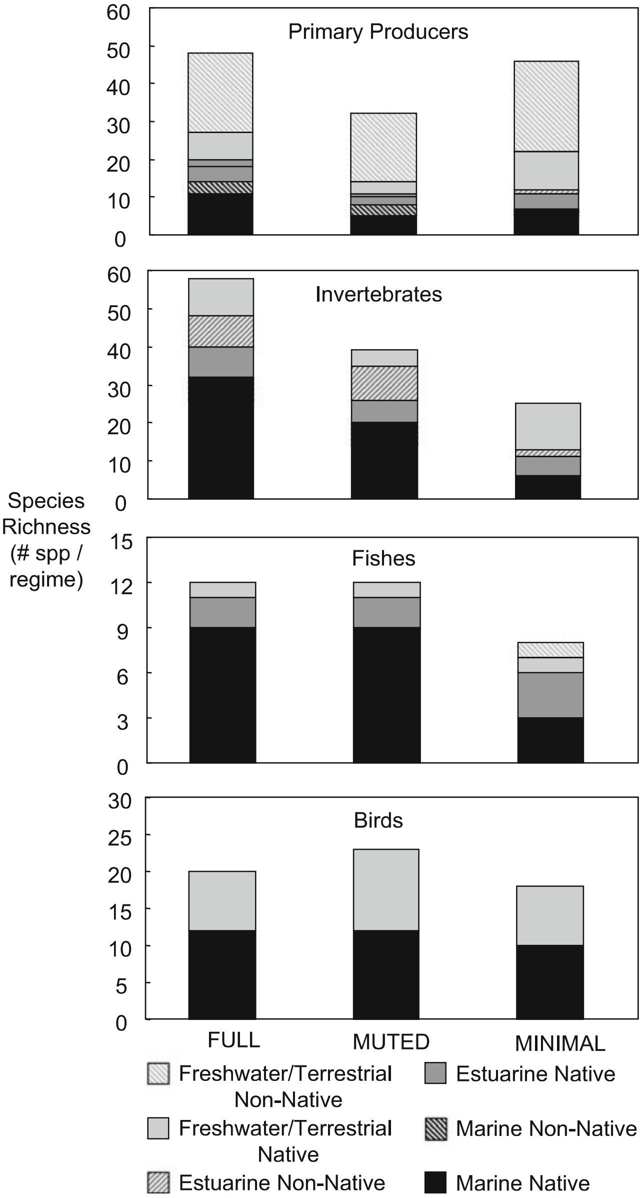

**Fig. 3** Species richness for several taxonomic groups across the three tidal exchange regimes. *Shading* indicates what type of habitat each species is usually found in and whether each species is a definite non-native (*striped shading*) or a likely native or part of a native/non-native species complex (*solid shading*)

exchange (25 species). The paucity of coastal/marine species in the minimal tidal exchange site was particularly pronounced for invertebrates and fishes. Coastal/marine species comprised a clear majority of the fishes, about half of the invertebrates and birds, and about a third of the primary producers.

### *Non-native Richness*

Fifty-six of the total 186 species (30.1%) across all five higher taxa surveyed were clearly documented non-native species, though more were likely present among the taxa not identified to species. There were no strong differences in richness across the full (39 species), muted (36 species), and minimal (30 species) tidal exchange categories. There were strong differences among taxa in the number of non-native species detected. The majority of primary producers documented were non-natives (due mostly to upland weed invasions of the marsh ecotone), and this was true across tidal exchange categories. Many invertebrates were non-native, with the majority of these being estuarine species found in full and muted exchange sites. Among fishes, only one non-native was detected, a freshwater species found in minimal exchange. No non-native birds were detected in our surveys.

### Water Quality Assessment

The nMDS of water quality factors revealed substantial differences across tidal exchange categories (Fig. 4). A superimposition of the tidal exchange categories we defined (see "Methods") on the nMDS ordination demonstrates that these categories based only on tidal range and rainy season salinity adequately encompass the separation among sites (Fig. 4). The SIMPER analyses also indicated which water quality factors were most important in contributing to differences among categories (i.e., the contribution is greater than expected if all factors were contributing to differences equally). Those factors that contributed the most to distinguishing full vs. muted tidal exchange categories included tidal range (greater in full), as well as temperature, pH, dissolved oxygen, and dry season salinity (greater in muted). Those factors that contributed the most to distinguishing full vs. minimal exchange categories included tidal range and rainy season salinity (greater in full) and phosphates (greater in minimal). Those factors that contributed most to distinguishing muted vs. minimal tidal

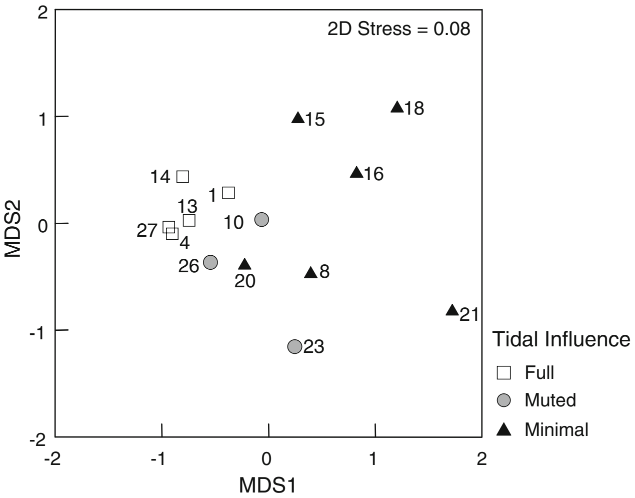

**Fig. 4** nMDS ordination of water quality data showing variation between sites. *Shading* indicates the amount of tidal exchange regime

exchange categories included rainy season salinity (greater in muted), as well as phosphates, ammonia, and turbidity (greater in minimal).

Average water quality characteristics varied significantly among full, muted, and minimal tidal exchange categories (Table 4—multivariate result). Because we used tidal range and rainy season salinity to define each of the tidal regime categories, tidal range and rainy season salinity were therefore significantly different among the categories (Table 4—univariate results). Other water quality characteristics that varied significantly among categories included pH and phosphates, both of which were higher on average in the minimal tidal exchange category relative to the other two. Multivariate and univariate analyses suggest that minimal exchange sites are most distinct, whereas muted and full exchange sites have somewhat similar water quality characteristics.

## Discussion

### Distinctive Ecological Signatures of Tidal Exchange Categories

Tidal restriction affects estuarine species composition at Elkhorn Slough, California. Five of six components of our investigation demonstrated a statistically significant effect of tidal exchange on species composition (Table 2), and nMDS analyses clearly reveal dissimilarity among tidal exchange categories, despite strong site variation within categories (Fig. 2). Effects of natural tidal restriction (by sandbars that reduce tidal exchange) have been reported for fish and invertebrate communities (Young et al. 1997; Edgar et al. 2000). Effects of artificial tidal restriction (through water control structures) on salt marsh vegetation composition and zonation have been reported globally, including the US East coast (Roman et al. 1984; Burdick et al. 1997), the US West coast (Zedler et al. 2001), The Netherlands (de Leeuw et al. 1994), and China (Sun et al. 2003). Responses by invertebrates and fishes to artificial restriction have also been documented on the US East coast (e.g., Burdick et al. 1997; Roman et al. 2002; Stocks and Grassle 2003). Most of these previous studies evaluated only a few restricted vs. unrestricted sites and focused on marsh and/or nekton as indicators. One of the most extensive previous studies (Raposa and Roman 2003) examined three restricted sites and, based on variation found among these sites, suggested that the ecological effects of restriction on nekton communities were increasingly more extreme as tidal exchange was reduced. By including numerous sites and using multiple biological indicators, we were able to thoroughly examine such variation within three levels of tidal restriction, as well as between the extremes of minimal and full exchanges. Different components of the investigation revealed different patterns (Fig. 2), but one common result was marked dissimilarity between tidally restricted sites with muted vs. minimal tidal exchanges, as well as between full vs. minimal exchanges. Separating tidally restricted sites into two categories (muted and minimal), as we did in this study, is more ecologically meaningful than the simple division of sites into those with and without water control structures.

### Potential Mechanisms Explaining Differences Among Tidal Exchange Levels

There are two conceptually different but not mutually exclusive explanations for the differences in species composition we documented among tidal exchange categories. The first is that the physical barrier presented by the water control structure itself may restrict the movement of organisms that disperse through the water. For algae, invertebrates, and fishes, we observed a few differences between full and muted

**Table 4** The average (±standard deviation) water quality conditions in each tidal exchange regime

| Water quality factor (average±Std Dev) | Full | Muted | Minimal | *F* ratio |
|---|---|---|---|---|
| Tidal range (cm) | 200.4±0.89$^{a}$ | 43±40.63$^{b}$ | 4.5±6.16$^{c}$ | 174.20** |
| Salinity—rainy season (ppt) | 24.42±3.82$^{a}$ | 26.82±3.05$^{a}$ | 15.55±4.25$^{b}$ | 11.12** |
| Salinity—dry season (ppt) | 29.09±3.96 | 34.63±8.84 | 33.53±8.65 | 0.72 |
| Temperature (°C)—$\sqrt{x}$ | 4.19±0.11 | 4.36±0.19 | 4.36±0.15 | 2.25 |
| Dissolved Oxygen Saturation (%)—$\sqrt{x}$ | 10.20±0.30 | 10.97±0.52 | 10.94±0.74 | 2.80 |
| pH | 8.22±0.05$^{a}$ | 8.49±0.27$^{ab}$ | 8.52±0.19$^{b}$ | 4.49* |
| Turbidity (NTU)—ln($x$) | 2.84±0.35 | 2.33±1.81 | 3.91±0.64 | 3.60 |
| $NO_X$ (μm)—ln($x$) | 4.45±1.05 | 3.57±0.65 | 4.45±0.95 | 1.04 |
| $NH_3$ (μm)—ln($x$) | 2.26±0.21 | 2.17±0.47 | 2.68±0.64 | 1.47 |
| $PO_4$ (μm) | 5.44±1.67$^{a}$ | 5.41±3.58$^{a}$ | 13.19±4.95$^{b}$ | 7.14* |
| Multivariate Wilk's Lambda | | | | 45.98* |

Values were calculated from monthly data collections from 2000–2005, except for tidal range measured on one spring tide only. Associated *p* values are denoted as: *0.01–0.05, **<0.01, and pairwise comparisons that were significantly different are denoted by subscripts.

exchange sites, suggesting that the relatively large culverts that create muted exchange allow for colonization of muted habitats by these aquatic organisms. However, the communities in minimal exchange sites were distinct from those of the full or muted exchange sites, perhaps in part due to limited dispersal. Minimal exchange sites were typically separated from full exchange sites by tide gates, which are known to inhibit migratory fish passage, especially when water velocity is high (Sanzone and McElroy 1998; Raposa 2002; Giannico and Souder 2004).

The second explanation for the differences in species composition we documented among tidal exchange categories is that they are the result of differing environmental conditions. This explanation likely applies to the differences we observed in bird and upland plant communities, since water control structures do not pose barriers to their movement, and may apply as well to many of the differences we documented in other taxa. Previous investigations of ecological responses to artificial tidal restriction in estuaries have primarily attributed them largely to altered environmental conditions upstream of water control structures rather than to restricted movement of the organisms through the structures (salt marsh responses: Roman et al. 1984; de Leeuw et al. 1994; Burdick et al. 1997; Zedler et al. 2001; Boumans et al. 2002; Roman et al. 2002; Sun et al. 2003; nekton responses: Young et al. 1997; Raposa 2002). Tidal restriction has been described as accentuating the natural sea-to-land gradient of key physical factors (Raposa and Roman 2003).

Tidal restriction may affect environmental conditions by leading to differences in habitat structure as well as water quality characteristics. For instance, due to their dramatically decreased tidal range, our restricted sites had far less area of intertidal mudflats than did the full exchange sites. This difference may contribute to the lower frequency of most shorebird species in restricted (both minimal and muted exchange) vs. full tidal exchange sites. Furthermore, tidal restriction is well known to affect water quality; water quality upstream of estuarine water control structures often involves lower salinity, higher temperature, and higher nutrient and suspended heavy metal concentrations (Sanzone and McElroy 1998; Giannico and Souder 2004). Salinity in particular has long been identified as one of the key determinants of estuarine community composition worldwide, and various contrasting salinity classifications have been developed to capture the importance of this environmental forcing factor (Remane 1934; Barnes 1989; Jones et al. 1990; Bulger et al. 1993; Attrill 2002). The most restricted (i.e., minimal exchange) sites we studied varied in their rainy season salinity depending on the amount of freshwater input they received but were on average much fresher than the muted or full exchange sites because the water control structures served as partial freshwater impoundments. No doubt, the presence of some freshwater species (e.g., midge larvae, sinistral snails) found only in minimal exchange sites is a direct function of salinity, as is the absence of most marine algae and invertebrates, which cannot tolerate freshwater for extended periods. Conversely, the similarity we observed in algal, invertebrate, and fish species composition between full and muted sites may be a function of their overall similarity in water quality.

In addition to differences in salinity, we found that water quality (as assessed by multiple parameters) differed substantially among all three tidal exchange categories, with minimal exchange sites having the most distinct water quality conditions. The tidal exchange categories differ not only in their average values for water quality parameters but also in variance. Water quality studies at Elkhorn Slough suggest that muted exchange sites exhibit substantial daily variation in temperature, salinity, and dissolved oxygen relative to full exchange sites (John Haskins, Elkhorn Slough National Estuarine Research Reserve, unpublished data) and undergo extreme diel biogeochemical cycling (including cycling between supersaturated oxygen and hypoxic conditions—Beck and Bruland 2000). No comparable continuous in situ monitoring of minimal exchange sites has been conducted in the Elkhorn Slough area, but it is likely that short-term variation in temperature and oxygen is even more extreme at these sites. Hypoxia is known to affect estuarine communities, particularly invertebrates and fishes (Powers et al. 2005), and increased hypoxia in restricted tidal conditions could explain the absence of many fish species from these sites.

## Evaluating Tidal Restriction with Regard to Varying Conservation Targets

Our investigation revealed significant differences among tidal exchange categories, but how do these differences inform decision making and restoration planning by coastal managers? Conservation and management targets may include maximizing biodiversity, emphasizing particularly threatened or economically valuable taxa, restoring historical conditions, or supporting regional needs (Fairweather 1999; Groves et al. 2002; Redford et al. 2003). In addition, different taxa may not necessarily have congruent conservation needs (Grenyer et al. 2006). In this study, we interpret our results in a broader ecological and conservation context, discussing the patterns we detected with regard to four different conservation targets.

### *Total Species Richness*

Maximizing biodiversity—for instance as simply assessed by total species richness—is one commonly stated goal for conservation efforts (Redford et al. 2003) and an ecological indicator of ecosystem health (Vos et al. 2000; Zedler et al. 2001). While we found the *site-level* species richness was lowest in minimal tidal exchange, we found that *estuary-wide* richness was maximized by having at least some representation of minimal tidal exchange, since some species are found only in this category. In addition, our results support models and data from elsewhere (e.g., Remane 1934; Barnes 1989) for estuarine invertebrates that show a decline in species richness in a gradient from marine to brackish salinity. Variability in salinity may be more stressful than actual low salinity and may lead to low species richness (Attrill 2002). We found the lowest total species richness (<50% of average at full exchange sites) at those minimal exchange sites that showed the greatest variation between wet and dry season salinity averages, with dry season maxima in salinity well more than 50 ppt. Species richness would almost certainly be increased at these hypersaline sites if tidal range were increased even slightly, as this would lower average salinity to levels associated with greater species numbers.

### *Minimizing Invasions by Non-natives*

Estuarine habitats in California are highly invaded (Cohen and Carlton 1995; Grosholz 2002), and those of Elkhorn Slough are no exception (Wasson et al. 2001, 2005). Invasions are of particular concern for truly estuarine (vs. marine or freshwater) components of the community—about half of the species categorized as estuarine in this study (Table 3) are non-natives. Once non-native species are widespread and abundant, they are virtually impossible to eradicate. When possible, it may be desirable to manage for invasions at the ecosystem level, by enhancing conditions that favor native species over non-natives (Zavaleta et al. 2001).

Overall, we found no clear differences among the tidal exchange categories in terms of proportions of non-natives: About one quarter of species we documented were non-native across categories. The patterns differed for invaders of terrestrial and marine origin. The absolute number of terrestrial invaders (upland plants in the upper marsh and ecotone) was lowest in muted exchange sites, but due to lower overall species richness, the proportion of non-native plants was greatest in this category. Thus, no overarching recommendations with regard to tidal exchange emerge from an assessment of terrestrial invaders.

For invaders of marine origin (algae, invertebrates), both absolute numbers and proportions of the community were higher in full and muted than minimal exchange sites. The lack of an extensive non-native invertebrate community in minimal exchange sites is puzzling, since, in Europe, the majority of non-native invertebrate species are found in low salinity habitats (5–20 ppt in an estuary in The Netherlands : Wolff 1999; 0–10 ppt in brackish inland seas of Europe: Paavola et al. 2005), and low salinity habitats in nearby San Francisco Bay support extensive non-native communities (Cohen and Carlton 1995). While the underlying mechanism is unclear, it appears that invasions are somehow reduced in minimal exchange sites at Elkhorn Slough. This is true across all minimal exchange sites we examined, so slightly increasing tidal range at the sites that become extremely hypersaline in the dry season (while still maintaining them in the minimal exchange category) would likely increase native richness without increasing non-native richness.

### *Native Estuarine Residents*

Estuarine residents are those species that typically spend their entire lives in estuaries or brackish waters and would rarely be found outside such habitats. Because they are dependent on and unique to particular estuaries, native estuarine residents are most likely to go extinct as estuarine habitats become further degraded. In California, estuaries are naturally rare, and now many are highly degraded, so this is a very real concern (Emmett et al. 2000). Native estuarine residents thus comprise another viable conservation target for estuaries and another metric by which tidal exchange categories can be evaluated. The majority of the species we documented in estuarine habitats are not solely estuarine residents (Table 3). Only 30 of 186 species we observed were categorized as estuarine, and of these, only 19 are native to the Pacific coast. There was no striking difference between tidal exchange categories in total numbers of estuarine natives. This result might suggest that estuarine endemics are not affected by the amount of tidal exchange. Closer examination of individual species reveals that this is not the case: The overall pattern is that some species occur mainly in full and muted exchange sites, while others occur mainly in minimal exchange sites.

Some estuarine endemics appear to require significant tidal flushing and thus are absent from minimal exchange sites. Olympia oysters and bay mussels, both considered important ecosystem engineers in estuarine systems for the hard substrates and structural complexity they generate (Coleman and Williams 2002), were found only in full and muted exchange sites and were more common in the former site. Oysters are a key estuarine conservation target, since temperate reef systems worldwide have undergone dramatic declines (Kirby 2004). Other estuarine bivalves, such as large clam species (*Saxidomus nutalli*, *Tresus nutallii*), were not detected by our survey methods (small shallow cores) but appear to occur only in full exchange areas at Elkhorn Slough (K. Wasson, personal observation). Another key estuarine conservation target, eelgrass (*Zostera marina*), occurs at this estuary only in full exchange areas (K. Wasson, personal observation). Thus, for this suite of estuarine residents, a minimal tidal exchange site does not provide a viable habitat and a full exchange site appears superior to a muted site.

In contrast, another suite of estuarine endemics does not occur in sites with significant tidal flushing. Two rare animal species associated with brackish water were found only in minimal exchange sites: the tidewater goby (a federal endangered species) and the brackish snail (an earlier candidate for federal listing). Both the goby and snail are California endemics reported almost entirely from low tidal energy portions of estuaries, lagoons, and river mouths. The tidewater goby is currently known from under 100 sites (Swift et al. 1989) and the brackish snail from only about a dozen (Kellogg 1985). In addition to these rare species, another brackish species, ditchgrass, was found only at minimal exchange sites. Another estuarine resident, the long-jawed mudsucker, increased in frequency with decreasing tidal exchange (from full to muted to minimal exchange). For this suite of estuarine species that are tolerant of a wide range of salinity conditions, minimal tidal exchange may provide a refuge from predation or competition from either fully marine or freshwater species (Kellogg 1985). While minimal exchange sites at Elkhorn Slough are all currently the result of artificial modifications, the conditions there may approximate those in natural coastal lagoons or in uppermost reaches of larger estuaries and certainly lead to representation of at least a few different and some rare brackish estuarine species native to California.

### *Important Estuarine Visitors*

In addition to the native estuarine species described above, which by definition are full-time residents, there are other part-time residents that have been identified as important conservation targets. Migratory shorebirds are one such group that use Elkhorn Slough, which has been designated a globally important bird area by the American Bird Conservancy, recognizing its important role as a stopover on the Pacific flyway. Elkhorn Slough represents a valuable foraging and resting place for migratory species, especially since California has lost 90% of its coastal and freshwater wetlands (Larson 2001). We found that many shorebird species (e.g., willets, long-billed curlews, marbled godwits) were more frequently found in full tidal exchange sites than in the other categories when surveys of both were taken at low tide (as shown by our rapid community assessment results) but that muted exchange sites were used at high tide (as shown by our focused shorebird surveys and Connors 2003). Most of these shorebirds forage on mudflats, and since intertidal mudflats are much more extensive in areas with a broad tidal range, it is not surprising that they are found more frequently in full tidal exchange habitats. One shorebird species (black-necked stilt) showed the inverse pattern, increasing in frequency with decreasing tidal exchange.

Another recognized conservation target for estuaries is marine fishes that may use these areas as nurseries, which include commercially valuable flatfish species. Many such fish are considered estuarine dependent, though data support this to varying degrees for different species (Able 2005). Sixteen marine fishes have been reported to use Elkhorn Slough as a nursery ground (Yoklavich et al. 2002; Brown 2006). Because our sampling of full exchange sites was limited to seining and trapping of shallow areas comparable to the restricted ones, we did not detect many flatfish (which are typically collected in deeper subtidal channels by dredging). Those flatfish that we did detect occurred only in full and muted exchange sites. Eelgrass beds have been reported to support higher fish densities than unvegetated areas (Beck et al. 2001), so we speculate that full exchange conditions (to which eelgrass beds are limited at Elkhorn Slough) are generally better for supporting fish nurseries. However, Pacific herring and northern anchovy were found in restricted exchange sites and not detected in full exchange sites, perhaps suggesting that restricted exchange sites provide valuable habitat for these species. Migration back to the sea is of course critical for these species that use estuaries as a nursery, so further studies are necessary to determine the rate at which individuals successfully return to the open sea through water control structures. Other studies have found that unrestricted tidal exchange habitats are more valuable for commercially fished migratory nekton species than adjacent restricted exchange areas (Rozas and Minello 1999).

Other important visitors to Elkhorn Slough detected in this study include three protected marine species. We found sea otters and brown pelicans in full and muted exchange sites and harbor seals in only full exchange sites. The limited and shallow water of minimal tidal exchange sites is probably not an appropriate habitat for these species typical of deeper coastal waters. For sea otters, the minimal exchange areas lack large invertebrate prey such as bivalves and crabs, upon which they forage actively in muted and full exchange sites.

## *Conclusions*

The evaluation of full vs. muted vs. minimal tidal exchange categories with regard to varying conservation targets yields contrasting results. Certain conservation targets are maximized with increasing tidal exchange, including native oysters, flatfishes, most shorebirds, sea otters, brown pelicans, and total site-level species richness. Other conservation targets are maximized in minimal tidal exchange conditions: threatened tidewater gobies and rare brackish snails were found only in minimal exchange sites, and invasions by marine algae and invertebrates were greatly reduced in these areas. The needs of differing conservation targets may thus be best balanced by ensuring that estuarine ecosystems have representation of a spectrum of different tidal exchange regimes, ideally through natural mechanisms. A mosaic of tidal exchange levels also maximizes estuary-wide species richness and provides a refuge for a unique suite of species, including rare estuarine endemics found only in minimal exchange conditions.

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