

Benthic macrofaunal assemblages of the San Francisco Estuary and Delta, USA

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Abstract The spatial and temporal distribution of macrobenthic assemblages in the San Francisco Estuary and Sacramento–San Joaquin River Delta were identified using hierarchical cluster analysis of 501 samples collected between 1994 and 2008. Five benthic assemblages were identified that were distributed primarily along the salinity gradient: (1) a polyhaline assemblage that inhabits the Central Bay, (2) a mesohaline assemblage that inhabits South Bay and San Pablo Bay, (3) a low-diversity oligohaline assemblage primarily in Suisun Bay, (4) a low-diversity sand assemblage that occurs at various locations throughout the Estuary, and (5) a tidal freshwater assemblage in the Delta. Most sites were classified within the same assemblage in different seasons and years, but a few sites switched assemblage designations in response to seasonal changes in salinity from freshwater inflows.

Keywords Benthos · Macrofauna · San Francisco Bay · Estuary · Delta

Introduction

Benthic macrofauna have been studied extensively in San Francisco Bay (summarized by Nichols 1973 and Thompson et al. 2000) and are well known. Individual benthic organisms may be distributed in complex ways along environmental gradients, but, when all taxa are analyzed together in a set of monitoring samples, they usually form identifiable assemblages. Such assemblages have been identified and described in many US estuaries, including Chesapeake Bay (Dauer et al. 1984), Virginia (Boesch 1973; Diaz 1989), North Carolina, (Hyland et al. 2004), Gulf of Mexico (Engle et al. 1994), and Puget Sound (Llansó et al. 1998). In most cases, differences in species composition among assemblages of a region were found to be structured primarily by salinity and sediment-type.

The San Francisco Bay and the Sacramento–San Joaquin River Delta system forms the largest estuary on the west coast of the US, with a complex salinity gradient that is greatly affected by seasonal patterns of freshwater input (Conomos et al. 1985), among other factors (Moyle et al. 2010). Thompson et al. (2000) previously described the assemblages of this system, but their data were limited to fixed monitoring sites. More recently, Ranasinghe et al. (2012) included

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samples from San Francisco Estuary in a description of benthic assemblages along the US west coast, but they had low sample density in the low-salinity portions of the Estuary, and the large latitudinal gradient they studied may not have defined the assemblage patterns within the Estuary in detail. Thus, there has been no formally published description of the benthic assemblages of the San Francisco Estuary and Delta. The objectives of this paper are to describe the macrobenthic assemblages of the San Francisco Estuary and the Sacramento–San Joaquin River Delta and their variation in space and time, and to identify key environmental factors that may structure the assemblages.

The identification of benthic assemblages has taken on increased importance as regulatory frameworks in both the United States and Europe are increasingly relying on biocriteria. Biological assessments require definition of reference condition, which typically are established independently for each habitat-related assemblage because species composition and abundance vary among habitats (Weisberg et al. 1997; Van Dolah et al. 1999; de Paz et al. 2008; Pinto et al. 2009; Ranasinghe et al. 2009).

Methods

Hierarchical cluster analysis of macrobenthic species abundance data was used to identify the benthic assemblages that occur in the San Francisco Estuary and Delta (Figs. 1 and 2). The analysis was based on 501 samples collected from 365 sites by eight studies conducted between 1994 and 2008 (Table 1). Data were limited to samples collected using 0.044–0.05 m² grab samplers with nominal sample penetration depth of 10 cm and sieved through 0.5–0.595 mm screens. Taxonomy was standardized following SCAMIT (2008) nomenclature, with some species-level identifications elevated to a higher taxon level when data were limited to higher taxonomic levels in several studies. Taxa that occurred in only one sample were eliminated.

Most of the contributing studies collected ancillary sediment and water quality data, including salinity or specific conductivity, percent (dry weight) total organic carbon (TOC), and percent (dry weight) fine sediments (<62 μ m). Specific conductivity was not reported for the DWR or SQO Delta studies, but a review of the monthly water quality monitoring data from DWR over several years indicated that chloride

concentrations in the tidal freshwater reaches of the Delta do not exceed 300 mg/L, which equates to a salinity of \sim 0.5 psu (DWR 2006).

Classification analysis consisted of Q-mode cluster analyses using flexible sorting of Bray–Curtis dissimilarity values with $\beta=-0.25$ (Bray and Curtis 1957; Lance and Williams 1967; Clifford and Stephenson 1975). The influence of dominant species was reduced by cube-root transformation of species abundances, and nodal analysis (two-way table) interpretation was facilitated by standardization of abundances by the species mean across all samples for abundance values higher than zero (Smith 1976; Smith et al. 1988). The step-across distance re-estimation procedure (Williamson 1978; Bradfield and Kenkel 1987) was applied to dissimilarity values higher than 0.80 to reduce the distortion of ecological distances caused by joint absences of a high proportion of species. Principal coordinates analysis (ordination, Gower 1967) was used to confirm the cluster analysis results and evaluate the relationships among the assemblages, and with selected abiotic variables. Ordination analysis was also based on Bray–Curtis dissimilarity values.

Three classification analysis runs were conducted (Table 2). Run 1 provided the primary basis for our assemblage designations and for the mean taxa abundances and abiotic variables reported. Run 1 was conducted using 501 samples and 504 taxa sampled during the dry season (July through October). Only one replicate sample per site/date was included. Run 2 included samples from additional seasons and years to assess the extent to which seasonal variability affected assemblage determination. This increased the number of samples by 80% but did not affect the number of taxa included (Table 2). Run 3 was conducted to evaluate the effect of using expanded taxonomy in the Delta samples, where taxon names were reported at the lowest practical level. Those samples were dominated by freshwater tubificids and chironomids. Those taxa were lumped into Tubificidae or Chironomidae in Run 1, as they were not identified to species by studies conducted in other portions of the Estuary.

Benthic macrofaunal assemblages were identified by sequentially considering the divisions in the site classification dendrogram (Fig. 3), and identifying a minimum ecological distance below which the divisions had similar dominant taxa and abiotic habitat variables to justify designation of an assemblage. Decisions about assemblage designation were based on: (1) consideration of the

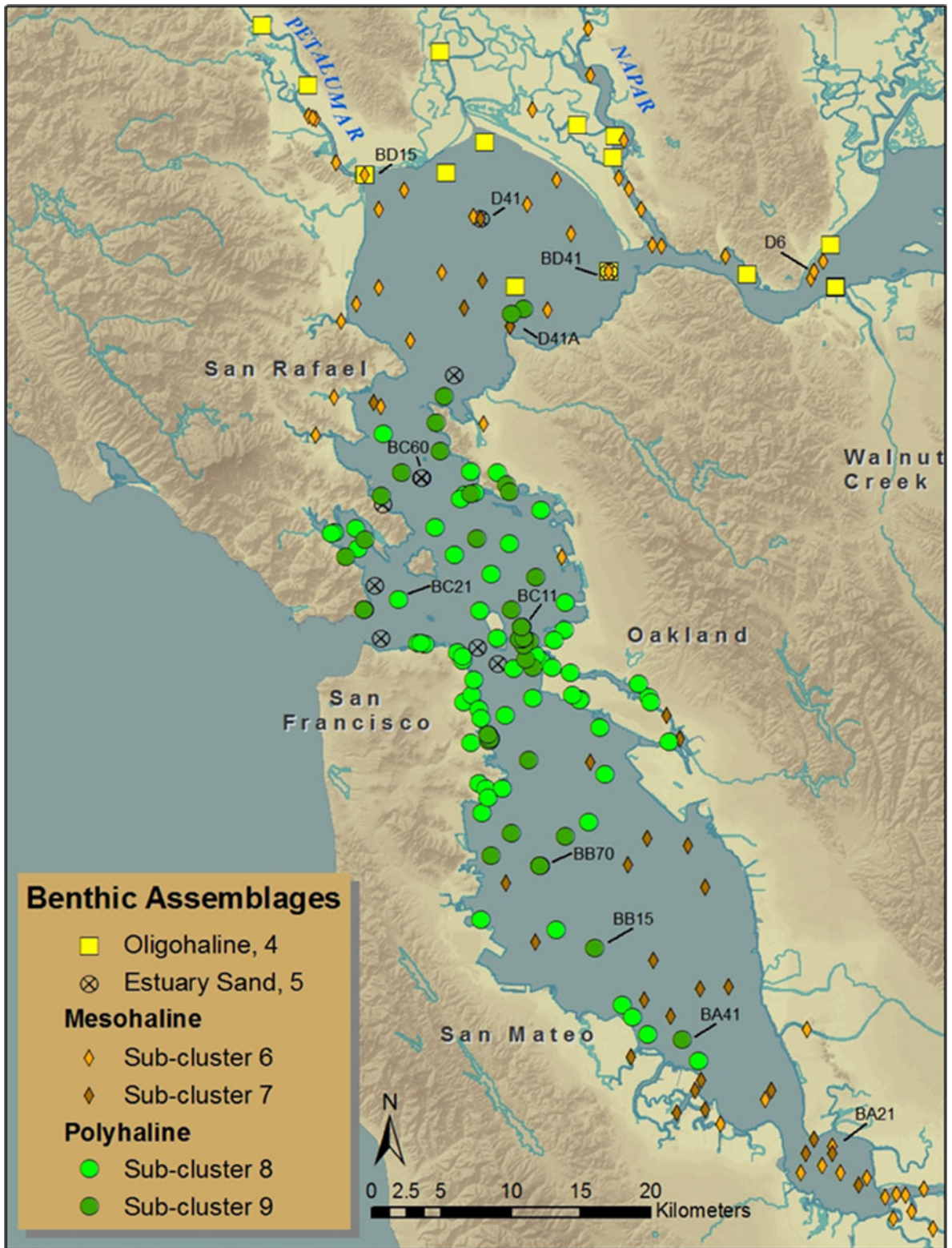


Fig. 1 San Francisco Estuary sampling locations and assemblage designations. The oligohaline assemblage was defined by sub-cluster 4 and the estuary sand assemblage by sub-cluster 5

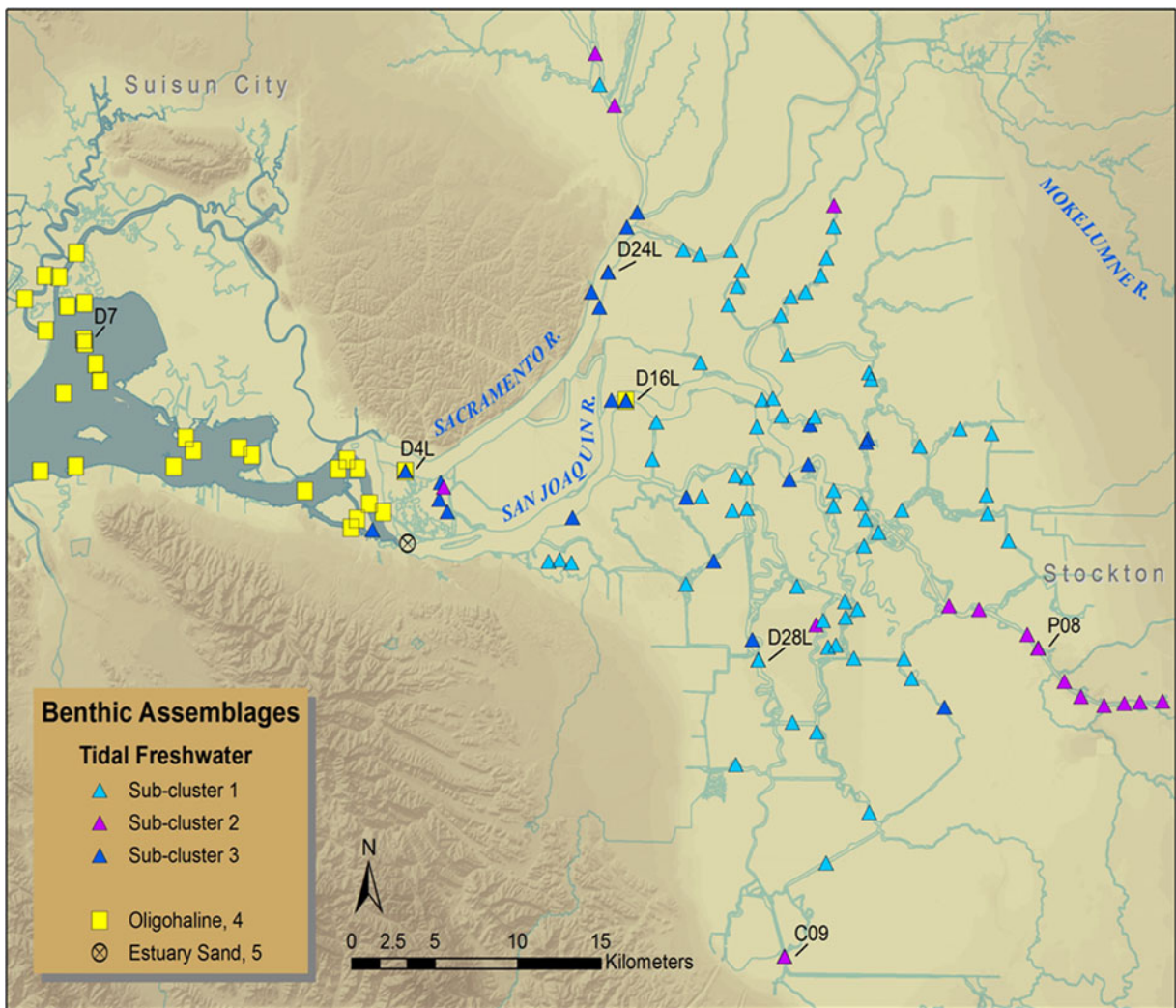


Fig. 2 Suisun Bay and the Sacramento–San Joaquin River Delta sampling locations and assemblage designations. The oligohaline assemblage was defined by sub-cluster 4 and the estuary sand assemblage by sub-cluster 5

similarity of dominant taxa between adjacent and subordinate clusters. Similarity was calculated as the percentage of dominant taxa shared among the ten most common (percent occurrence) and abundant taxa, with a similarity of 50% used as a guideline to distinguish assemblages. (2) Statistical differences in salinity, percent fines, and TOC between adjacent cluster groups, using the Mann–Whitney–Wilcoxon test to evaluate whether those habitat variables showed significant changes between cluster groups.

Since most of the assemblages are shown to be primarily controlled by salinity, the assemblage designations used in this paper generally follow the nomenclature of the Venice system of estuary classification (Carrier

1967; Boesch 1977). However, the term “limnetic,” referring to fresh water habitat, has been replaced with “tidal-freshwater” following Weisberg et al. (1997). The assemblage designations indicate the general salinity regime of each assemblage but do not correspond exactly with the Venice system salinity ranges.

Results and discussion

Identification of macrobenthic assemblages

Five benthic assemblages were identified in the San Francisco Estuary and Delta by Run 1 (Figs. 1 and 2).

Table 1 Data sources for Run 1

Study	N	Dates	Sampler	Sieve	Locations	Reference
Bay Area Dischargers Assoc. Local Effects Monitoring Program	30	1994–1997	0.05 m ² Ponar	0.5 mm	San Francisco Bay, Suisun Bay	Thompson et al. 1999
U.S. EPA Coastal Intensive Sites Network	4	2000	0.05 m ² Ponar	0.5 mm	San Pablo Bay, Napa-Sonoma Wetlands, Napa and Petaluma Rivers	Thompson and Lowe 2002
CA DWR Environmental Monitoring Program	189	2000, 2007, 2008	0.05 m ² Ponar	0.595 mm	San Pablo Bay, Suisun Bay, Delta	DWR 2006
NOAA SF Bay Study	145	2000–2001	0.044 m ² Young-modified Van Veen	0.5 mm	All SF Estuary, sub-tidal	Unpublished
SWRCB Bay Protection and Toxic Cleanup Program	3	1994	0.05 m ² Ponar	0.5 mm	Northern Central Bay, San Pablo Bay	Unpublished
SFEI Regional Monitoring Program	62	1994–2003	0.05 m ² Ponar	0.5 mm	All SF Estuary, not Delta	Thompson et al. 2000
SWRCB Sediment Quality Objective Delta Survey	18	2007	0.05 m ² Ponar	0.595 mm	Sediment Quality Objectives Phase II: Delta Survey	Unpublished
U.S. EPA Environmental Monitoring and Assessment Program	50	2000	0.044 m ² Young-modified Van Veen	0.5 mm	All SF Estuary except Delta	U.S. EPA 2004

DWR Department of Water Resources, SWRCB State Water Resources Control Board, RMP Regional Monitoring Program

The first major division in the classification analysis dendrogram (Fig. 3) occurred between the tidal freshwater sites in the Delta and the higher-salinity estuarine assemblages in the San Francisco Estuary at an ecological distance greater than 13.0. The estuarine arm of the dendrogram was secondarily divided at an ecological distance of 9.5, into two cluster groups: the polyhaline–mesohaline group and the estuary sand–oligohaline group. Those two groups were further divided at ecological distances of around 6.5 into the designated assemblage clusters. Evaluations of subordinate assemblage clusters showed that they were similar in species composition to the nominal assemblage.

Comparisons of the dominant taxa in adjacent assemblage clusters of the dendrogram showed that the dominant taxa of each cluster group were 50% or less

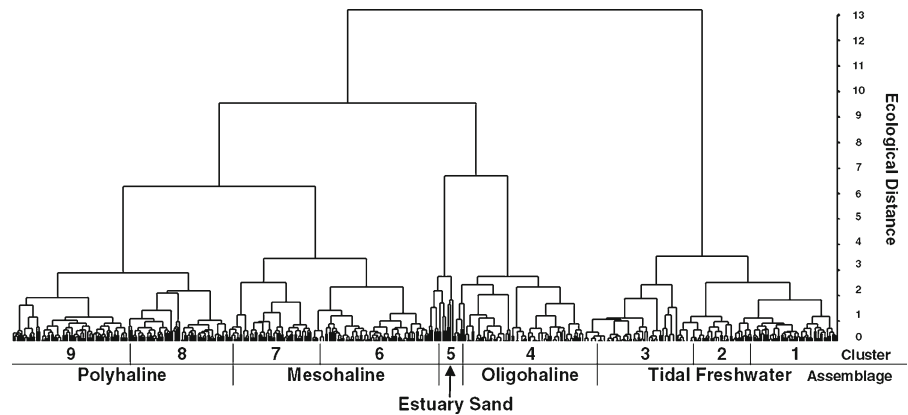
similar: The tidal freshwater assemblage was 30% similar to the oligohaline assemblage in Suisun Bay. The oligohaline assemblage was 20% similar to the estuary sand assemblage. Although not directly adjacent to each other on the dendrogram, the dominant taxa of the mesohaline and oligohaline assemblage were 50% similar. The mesohaline and polyhaline assemblages were 30% similar. Comparisons between sub-clusters within each assemblage cluster showed that the dominant taxa were 50% or more similar. Dominants in the three tidal freshwater sub-clusters were 60% similar; the two mesohaline sub-clusters were 50% similar, and the two polyhaline sub-clusters were 70% similar.

Principal coordinate axis 1 accounted for 30.6% of the variation in species composition and abundances

Table 2 Description of classification runs

Classification run	N samples	N taxa	Years	Seasons
All SF Estuary and Delta	501	297	1994–2000, 03, 07, 08	Jul–Oct
All SF Estuary and Delta	894	297	2000, 2001, 2007, 2008	All months
Delta only, enhanced taxonomy	154	131	2000, 2007, 2008	Jul–Oct

Fig. 3 Site classification dendrogram (Run 1) showing assigned assemblages and sub-clusters



among the samples. The axis 1 scores were most highly and significantly correlated with salinity (Table 3), demonstrating that the estuary salinity gradient is a key factor in the organization of the benthic assemblages. The plot of axis 1 scores versus salinity for all samples shows that the salinity ranges of adjacent assemblages (except tidal freshwater) overlapped considerably (Fig. 4). Axis 2 scores were not significantly correlated with any of the measured habitat factors. Axis 3 scores were most highly and significantly correlated with percent fine sediments. The plot of axis 3 scores versus percent fine sediments clearly separated the estuary sand assemblage samples from all others (not shown). Thus, the assemblages described below are based on species composition that primarily reflected differences in salinity and sediment conditions.

Salinity was significantly different ($p < 0.01$) between adjacent assemblage clusters and between the sub-clusters in each assemblage. The tidal freshwater clusters were not included in this analysis because salinity was estimated as < 0.05 psu for all samples. Percent fine sediments were significantly different between adjacent assemblages ($p < 0.05$), except tidal freshwater and oligohaline ($p = 0.373$). TOC levels were also significantly different between adjacent assemblages ($p = 0.02$), except mesohaline

and oligohaline ($p = 0.474$). There was no significant difference in percent fines or TOC between the sub-clusters of each assemblage ($p > 0.05$).

Polyhaline assemblage

The polyhaline assemblage included 131 samples from central San Francisco Bay, between southern San Pablo Bay to the north and Blair Island to the south (Fig. 1). The polyhaline assemblage extended farther south along the western side of the Bay than on the eastern side, apparently due to a complex set of factors including the proximity of salt and fresh water sources and currents (Conomos 1979, Gross et al. 1999). Salinity in the polyhaline assemblage averaged 30.4 psu (Table 4), the highest of all assemblages, owing to its proximity to marine waters through the Golden Gate. Sediments were mostly silt–clay (mean = 73% fine sediments), but the samples varied widely. This assemblage included samples from greater depths (maximum = 16 m) than the other assemblages.

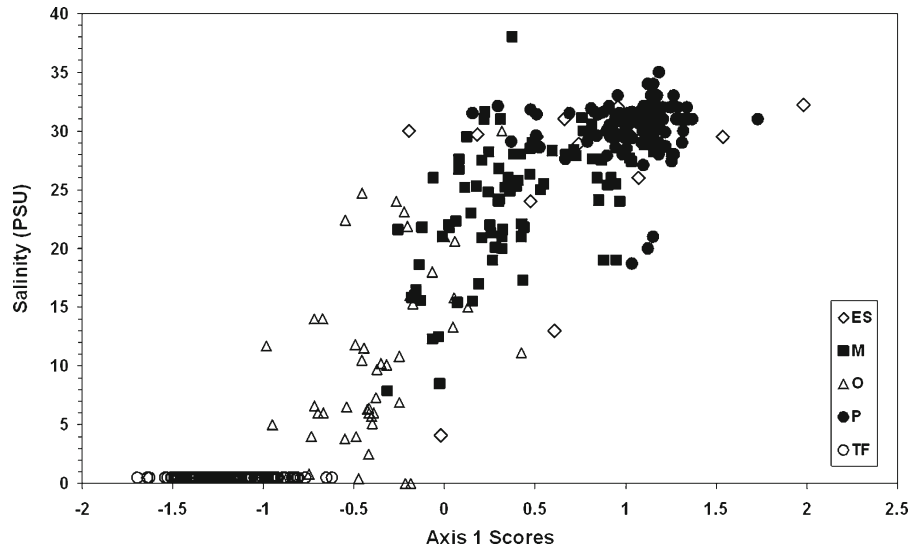
The polyhaline assemblage included two sub-clusters that represented slight changes in species dominance related to locations within the Central Bay. The amphipod *Ampelisca abdita* was the most abundant species in both sub-clusters. Sub-cluster 8 had higher occurrences and abundances of several tolerant taxa such as tubificids, *Mediomastus* spp. and *Dorvillea (Schistomeringos) annulata*. Sub-cluster 8 included a larger proportion of samples near the bay margin (70%) than sub-cluster 9 (21%) and was composed entirely of samples from the NOAA and WEMAP studies, suggesting possible subtle taxonomic differences. However, this was probably not the case because sub-cluster 9 included 22 NOAA-

Table 3 Spearman's correlations between principal coordinates axis scores and selected abiotic variables

Variable	n	Axis 1	Axis 2	Axis 3
Salinity (psu)	424	0.897*	-0.032	0.004
Fine sediment (%)	421	0.042	0.014	-0.276*
TOC (%)	413	-0.361*	0.074	-0.181*

*= $p < 0.01$

Fig. 4 Plot of principal coordinate axis 1 scores vs. salinity for Run 1 samples ($n=501$). Assemblages: TF=tidal freshwater, O=oligohaline, ES=estuary sand, M=mesohaline, P=polyhaline



WEMAP samples. Owing to the high degree of similarity in dominant taxa, these sub-clusters were considered to represent slight variations of the same assemblage.

The most common and abundant species in the polyhaline assemblage (clusters 8 and 9 combined) were several amphipods, dominated by *A. abdita* and *Monocorophium acherusicum* (Table 5). Another

amphipod, *Photis brevipes* was mostly restricted to this assemblage. The benthos in the polyhaline Central Bay had the highest average number of taxa and highest abundances in the San Francisco Estuary but with a wide range of values (Table 4). One notable phenomenon was the episodic appearance of large numbers *M. acherusicum* (up to 12,344 per sample) which accounted for the high maximum range. Four sites

Table 4 Mean and range for habitat and biological community variables (per sample) in each assemblage

Variable	Tidal freshwater		Oligohaline		Estuary sand		Mesohaline		Polyhaline	
	Mean		Mean		Mean		Mean		Mean	
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
Depth (m)	nm		4.7		9.0		5.4		9.8	
Salinity (psu)	nm	nm	1.5	10.0	2.3	11.0	1.9	12.0	3.0	16.0
	<math>< 0.5^a</math>		10.9		26.3		24.5		30.4	
Fine Sed. (%)	nm	nm	<math>< 0.5</math>	30.0	4.1	32.2	7.9	38.0	18.7	35.0
	60.6		61.4		16.3		81.8		73.0	
TOC (%)	0.6	99.6	<math>< 0.5</math>	100.0	0.6	95.0	16.0	100.0	1.2	99.3
	4.50		2.80		0.52		1.75		1.14	
No. of taxa	0.06	55.40	0.08	37.80	0.08	2.70	0.15	5.90	0.10	3.77
	9		5		7		14		28	
Total abund.	1	29	1	13	1	17	3	40	5	59
	436		285		36		887		1694	
	3	2617	1	1446	1	112	49	5583	8	12760

Sample sizes were not uniform in all cells

nm=not measured

^aSalinity value for tidal freshwater is a mean value estimated from DWR (2006)

Table 5 Listing of the five most common (percent occurrence) and abundant (average abundance per sample) taxa in each assemblage

Species	Taxon	Tidal freshwater		Oligohaline		Estuary sand		Mesohaline		Polyhaline	
		Av. abund.	% Occ.	Av. abund.	% Occ.	Av. abund.	% Occ.	Av. abund.	% Occ.	Av. abund.	% Occ.
	<i>n</i>	154		79		15		122		131	
<i>M. speciosa</i>	P	71	41								
<i>A. spinicorne</i>	A	75	38	2	6			<1	2	<1	2
<i>Gammarus daiberi</i>	A	61	71	1	8						
<i>C. fluminea</i>	M	34	93	4	13						
<i>Laonome</i> spp.	P	3	30	6	13			1	2		
<i>Tubificidae</i>	O	120	94	20	57	<1	20	38	77	52	91
<i>Americorophium stimpsoni</i>	A	18	39	<1	1			1	3	1	2
<i>M. viridis</i>	P	<1	2	15	75			<1	5	<1	2
<i>C. amurensis</i>	B	<1	3	184	84	1	13	243	59	2	18
<i>S. benedicti</i>	P			1	6	<1	7	46	54	1	12
<i>N. hinumensis</i>	C	1	4	5	47	2	20	28	48	17	51
<i>Corophium alienense</i>	A			35	22			1	18	9	12
<i>Grandifoxus grandis</i>	A			<1	3	2	20				
<i>H. coineau</i>	P					2	7				
<i>H. heteromorpha</i>	P					13	60			<1	2
<i>Tellina nukuloides</i>	B					1	20				
<i>Exogone lourei</i>	P							2	9	51	71
<i>A. abdita</i>	A			1	24	2	27	289	86	603	89
<i>M. acherusicum</i>	A			<1	5	<1	27	47	63	453	82
<i>P. brevipes</i>	A							<1	1	38	38
<i>Mediomastus</i> spp.	P			<1	1	<1	13	<1	9	17	55
<i>C. heteroceratum</i>	A			1	1	2	27	2	20	99	73

The order of the assemblages and species are from the normal (station) and inverse (species) classification analyses, respectively
Taxon codes: A=amphipod, C=cumacean, O=oligochaete, B=bivalve, P=polychaete

sampled in August, 1995 near the Bay Bridge had densities over 8,000 per sample, while two other samples collected in July 1998 and 2000 also had abundances in the thousands.

Summer samples collected at three RMP polyhaline sites (BB70, BC11, BC21) between 1994 and 2000 were always classified as polyhaline (Table 6), demonstrating that the species composition in the polyhaline assemblage was stable over the years analyzed.

Mesohaline assemblage

The mesohaline assemblage was defined by 122 samples collected from San Pablo Bay and the South Bay (Fig. 1). These two areas are physically separated by the

higher salinity polyhaline assemblage and are nearly equidistant from the ocean entrance to the Estuary at the Golden Gate Bridge. The mesohaline assemblage extended further north along the western side of the Central Bay than on the eastern side, apparently due to a complex set of factors including the proximity of salt and fresh water sources and currents (Conomos 1979; Gross et al. 1999). The mean salinity of the mesohaline samples was 24.5 psu but ranged between 8 and 38 psu (Table 4). Sediments were mostly silt and clay, but percent fine values had a wide range; the mean percent fine sediments was the highest of all assemblages.

The mesohaline assemblage included two sub-clusters, each of which included samples from the South Bay and San Pablo Bay, with the main difference being

Table 6 Annual assemblage designations for fixed sites sampled repeatedly during dry months only (June–Oct), from Run 1

Site	n	1994	1995	1996	1997	1998	1999	2000	2003	2007	2008
Central Bay											
BB70	7	P	P	P	P	P		PP			
BC11	8	P	P	P	P	P	P	P	P		
BC21	6	P	P	P	P	P		P			
BC60	6	ES	ES	ES	ES	ES		ES			
South Bay, San Pablo Bay											
BA21	8	M	M	M	M	M	M	MM			
BA41	8	P	M	M	M	M	M	M	M	M	
BB15	6	P	M	M	M	M		M			
BD15	6		O	O	M	O	O	O			
BD41	6	M	O	O	ES	O		M			
D41A	11							M		M	M
D41	11							M		M,ES	M
Suisun Bay											
D7	11							O		O	O
D6	11							O		O	O,M
Delta											
D4L	11							TF,O		TF,O	TF,O
D16L	11							TF		TF,O	TF
D24L	11							TF	TF	TF	TF
D28L	11							TF	TF	TF	TF
C09	11							TF	TF	TF	TF
P08	11							TF	TF	TF	TF

P polyhaline, M mesohaline, ES estuary sand, O oligohaline, TF tidal freshwater

a shift in dominant species. The clam *Corbula amurensis* was the most abundant species in sub-cluster 6, but was not among the dominant taxa in sub-cluster 7. Tolerant taxa such as *Streblospio benedicti*, tubificids, *Mediomastus* sp., and *Grandidierella japonica* were more abundant in sub-cluster 6 than in sub-cluster 7.

The most common and abundant taxa collected in the mesohaline assemblage (sub-clusters 6 and 7 combined) were the amphipod *A. abdita* and the clam *C. amurensis* (Table 5). The amphipod *M. acherusicum* was also common, and the clam *Gemma gemma* was mostly restricted to this assemblage. This assemblage also included several taxa known to be tolerant of disturbances, such as tubificids, and the polychaete *S. benedicti*. The mesohaline assemblage samples averaged about half the number of taxa and abundances as the polyhaline assemblage (Table 4).

Samples from all years included in Run 1 were classified into this assemblage. Annual samples from five fixed monitoring sites were consistently classified as mesohaline, suggesting that the species composition

within the assemblage was consistent through the years sampled (Table 6). However, samples from two sites adjacent to the polyhaline assemblage, RMP stations BA41, and BB15 in the southern Central Bay were classified as polyhaline in Feb 1994 (a dry year), but as mesohaline in subsequent summers. In San Pablo Bay, station BD41 was classified as mesohaline in summer 1994 and 2000, as estuary sand in 1997, and as oligohaline at other times. Site D41 was usually classified as mesohaline, but was classified as estuary sand during the summer of 2007.

Oligohaline assemblage

The oligohaline assemblage included 79 samples, mostly in Suisun Bay, the lower reaches of the Napa River and Petaluma Rivers, and occasionally in San Pablo Bay (Figs. 1 and 2). One sample in the Delta (DWR D16 L, Oct 2007) was also classified as oligohaline. Suisun Bay and the lower river reaches are the primary areas of estuary mixing of fresh and salt water

in the region (Jassby et al. 1995). The mean salinity of the oligohaline samples was 10.9 psu, but ranged between <0.5 and 30 psu (Table 4). Sediments tended to have more sand (lower percent fines) than in the higher salinity assemblages, averaging 61.4% fines, but included a wide range of values. Similarly, TOC values had a wide range, mainly due to two samples from D4 L in fall, 2007, with values greater than 30% TOC.

The most common and abundant species in this assemblage was *C. amurensis*, occurring in 86% of the samples with an average density of 180 per sample (Table 5). This clam has been the focus of considerable research over the past decades. Since its appearance in 1986, it has become numerically dominant, and its feeding activities have changed the ecology in the oligohaline habitat (Nichols et al. 1990; Jassby et al. 2002). The oligohaline assemblage includes many taxa that are commonly found in the mesohaline (*C. amurensis*, *Nippoleucon hinumensis*), and tidal freshwater (*Corbicula fluminea*, *Americorophium spinicorne*) assemblages. The polychaete *Marenzelleria viridis* was mainly restricted to the oligohaline assemblage. The oligohaline assemblage has the lowest taxa richness, with an average of only 5 and maximum of 13 taxa per sample (Table 4). Average abundances per sample were also reduced compared with the other assemblages.

The species composition of the oligohaline samples was relatively stable over the years sampled. Samples from most of the years analyzed (except 1994, 1997) were classified as oligohaline, and samples from DWR station D7 in Suisun Bay were always classified as oligohaline (Table 6). However, some sites that were usually classified as oligohaline switched assemblages. Station D6 near the entrance to Carquinez straight switched to mesohaline during the summer of 2008, and station D4 L at the confluence of the Sacramento and San Joaquin Rivers often switched assemblage-type. While 46% of the samples from D4 L included in Run 1 were classified as oligohaline, they were more often classified as part of the tidal freshwater assemblage. Station BD41 in eastern San Pablo Bay at the entrance to the Carquinez Strait was classified as mesohaline in 1994, a critical-dry water year and with estuary sand assemblage following flood flows in 1997.

Estuary sand assemblage

The estuary sand assemblage was identified from 15 samples from Central Bay, San Pablo Bay, and the

mouth of the San Joaquin River, where sediments were predominantly sand. Most of the sites were from the main channels of the Estuary (Figs. 1 and 2) where currents may be highest. The sediments at these sites averaged 16.3% fine sediments (=83.7% sand), the highest sand content of all assemblages. However, one sample from station SF01 in San Pablo Bay had very fine sediments (95%, Table 4); the 14 other samples all had less than 48% fine sediments (more than 52% sand).

The taxa that inhabited the sandy sites were dominated by two polychaetes, *Heteropodarke heteromorpha* and *Hessionura coineau* (Table 5). Apparently, few taxa are adapted to such sandy conditions, as the estuary sand assemblage samples averaged only 7 taxa and 36 organisms per sample (Table 4). This low diversity is presumably due to the elevated levels of disturbance from currents that eliminate fine sediments, leaving mostly sand and shell debris.

Some of the sandy sites switched assemblages in different years (Table 6). Assemblage changes at station BD41 were described above. Station D41C shifted to a sandy site once during the summer of 2007. RMP station BC60 near Red Rock was always classified as sandy.

Tidal freshwater assemblage

The tidal freshwater assemblage included 154 samples from the Delta (Fig. 2). The western-most samples were from DWR station D4 L near the confluence of the Sacramento and San Joaquin Rivers, adjacent to Suisun Bay. The water in the Delta is fresh-brackish (<0.5 psu) and under tidal influence (DWR 2006). Sediment grain-size ranged widely in the Delta, with a mean of 60.6% fines (Table 4). Many areas of the Delta have large amounts of particulate organic material (peat) in the sediments, evidenced by TOC levels up to 55%.

The tidal freshwater assemblage included three sub-clusters that exhibited some geographic and habitat differences. Sub-cluster 1 samples were mostly from the central Delta channels, cross-channels, and open water tracts. Some of these samples had taxa that may be characteristic of submerged aquatic vegetation (SAV), including numerous chironomid taxa and the tubificid *Aulodrilus pigueti* (W. Fields, pers. comm.). The presence of SAV possibly provided an additional habitat layer, which enhanced the sample

Table 7 Percent of samples (*n*) classified in the same assemblage in different months or seasons, Run 2

Site	<i>n</i>	Frequency	Years	Percent	Assemblage	
Central Bay						
BA41	8	Wet/dry	1994–1997	88	P	
BB15	8	Wet/dry	1994–1997	88	P	
BB70	8	Wet/dry	1994–1997	100	P	
BC21	8	Wet/dry	1994–1997	100	P	
BC11	8	Wet/dry	1994–1997	100	P	
BC60	8	Wet/dry	1994–1997	100	ES	
South Bay, San Pablo Bay						
BA21	2	Monthly	2000	50	O M	
BD15	3	Wet/dry	2000, 2001	100	O	
BD41	3	Wet/dry	2000, 2001	67	O	
D41A	45	Monthly	2000, 2001, 2007, 2008	98	M	
D41	45	Monthly	2000, 2001, 2007, 2008	98	M	
PET	3	Wet/dry	2000, 2001	100	O	
SOCR	3	Wet/dry	2000, 2001	67	O	
CAN	3	Wet/dry	2000, 2001	100	M	
M14	3	Wet/dry	2000, 2001	100	M	
Suisun Bay						
D7	45	Monthly	2000, 2001, 2007, 2008	100	O	
D6	45	Monthly	2000, 2001, 2007, 2008	96	O	
Delta						
78 random	2,3	Wet/dry	2007, 2008	100	TF	
D4L	45	Monthly	2000, 2001, 2007, 2008	100	TF	
D16L	45	Monthly	2000, 2001, 2007, 2008	98	TF	
D24L	45	Monthly	2000, 2001, 2007, 2008	100	TF	
D28L	45	Monthly	2000, 2001, 2007, 2008	100	TF	
Central Bay data after Thompson et al. (2000)						
<i>P</i> polyhaline, <i>M</i> mesohaline, <i>ES</i> estuary sand, <i>O</i> oligohaline, <i>TF</i> tidal freshwater	C09	45	Monthly	2000, 2001, 2007, 2008	100	TF
	P08	45	Monthly	2000, 2001, 2007, 2008	100	TF

diversity. Sub-cluster 1 samples averaged 14 taxa and 624 organisms that were dominated by tubificids and the polychaete *Manayunkia speciosa*. Sub-cluster 2 samples were mostly from upstream or peripheral locations, including the Stockton Ship Channel and Clifton Court, and were dominated by tubificids and the clam *C. fluminea*. Sub-cluster 3 samples were mostly from the Sacramento and San Joaquin Rivers main channels, and some sites in the central Delta with more sandy sediments. These samples were dominated by amphipods. The similarity of taxa among the sub-clusters (60%) suggested that they were all part of a single tidal freshwater assemblage.

The macrobenthos in the tidal freshwater assemblage (sub-clusters combined) were predominantly

fresh-brackish species. The most common and abundant taxa in this assemblages were tubificids and the clam *C. fluminea* (Table 5). The tidal freshwater samples averaged only nine taxa, but 436 organisms, per sample (Table 4).

Nearly all Delta samples were classified as tidal freshwater assemblage. Only DWR site D4L at the confluence of the Sacramento and San Joaquin Rivers alternated between tidal freshwater and oligohaline classification, even within the same summer's samples (Table 6). Most of the other DWR permanent sites in the Delta were classified as tidal freshwater, except for one sample at D16-L in summer 2007 that was classified as oligohaline.

The use of enhanced taxonomy (Run 3) revealed similar cluster groups as Run 1, with only 3% of the

samples changing sub-clusters. Enhanced taxonomy provided species-level names mainly for the tubificid oligochaetes and chironomid insects and helped identify taxa possibly associated with SAV. The most common and abundant tubificid species in the tidal freshwater assemblage were: *Limnodrilus hoffmeisteri* (mean abundance=39 per sample, 72% occurrence); *Varichaetadrilus angustipenis* (35, 71%); *Quistadrilus multisetosus* (7, 25%); *Bothrionurum vej dovskyanum* (6, 46%); the most abundant chironomid was *Procladius* sp. A (2, 26%).

Seasonal variation of assemblages

Run 2 included samples collected from 95 sites in all months or consecutive wet-dry seasons and was conducted to determine whether there were meaningful seasonal differences in species composition or distribution of the assemblages. Run 2 generally produced the same five major assemblages as Run 1, but the site groupings were not as clear because some sites switched assemblage designations in the wet season. Some of the Run 1 oligohaline samples were included with the Run 2 tidal freshwater samples; some Run 1 mesohaline samples were included with Run 2 oligohaline samples; and the estuary sand samples were mixed with both oligohaline and mesohaline samples. At least 67%, and usually more than 96%, of the seasonal or monthly samples from the 17 repeated sites in Run 2 were classified in the same assemblage as Run 1 (Table 7). All of the 78 DWR samples in the Delta from consecutive wet-dry-wet seasons of 2007–2008 were classified as tidal freshwater samples across seasons. Run 2 did not include seasonal samples from the polyhaline assemblage, but previous analysis showed that the RMP sites in the Central Bay were almost always classified as polyhaline in both wet and dry seasons (Table 7). Samples from the two sites nearest to the southern limit of the polyhaline assemblage (BB15, BA41) changed to mesohaline in the wet seasons of 1995 and 1997, respectively.

Conclusions

Benthic assemblages in the San Francisco Estuary were distributed primarily along the salinity gradient, consistent with that of benthic assemblages in

other US estuaries (Boesch 1977; Dauer et al. 1987; Weisberg et al. 1997; Llansó et al. 1998; Hyland et al. 2004). However, the estuary sand assemblage occurred at sandy locations in all but the tidal freshwater habitat. The benthic assemblages of the Bay and Delta were designated using Venice system nomenclature because distribution of the assemblages was most highly related to salinity and reflected Venice system salinity regime divisions. The lowest salinities in each assemblage were very similar to those of the Venice system. The lowest salinity in the polyhaline assemblage in our study was 19 psu, compared with the 18 psu limit of the Venice system; for the mesohaline, it was 8 psu compared with the 5 psu Venice system limit; for the oligohaline, it was 0.4 psu compared with 0.5 psu Venice system limit. However, maximum salinities in all but the tidal freshwater assemblage were higher than the Venice system upper limits, especially in the oligohaline assemblage (max=30 psu compared with 5 psu Venice system maximum). Thus, correspondence with the Venice system nomenclature was not exact. The benthic species that compose each assemblage respond, with appropriate time delays, to the seasonal and annual fluctuations in salinity, and to sediment conditions at specific geographic locations (e.g., Thompson et al. 2000; Petersen and Vayssièrè 2010).

While the identification of coherent benthic assemblages is a useful concept (see last paragraph), and allows comparisons with other estuaries, it is also important to acknowledge that the changes in species composition along the estuary gradient are gradual. Adjacent mesohaline, oligohaline, and tidal freshwater sub-clusters shared about half of their dominant taxa and did not exhibit well-defined, abrupt changes (Fig. 4). However, each assemblage also had some taxa that were restricted to, and thus characteristic of that assemblage. Among the estuarine assemblages, this gradual change properly reflects the estuary salinity gradient, but salinities within the tidal freshwater assemblage are constantly <0.5 psu, and the differences in species among the sub-clusters may represent responses to other factors.

Species composition of the assemblages was stable over the years and between seasons. Most of the sites that were sampled repeatedly were consistently classified into the same assemblage, even when comparing wet (1995–2000) and dry water years (1994, 2001,

2007, 2008). Some sites switched assemblages in the wet season when increased freshwater inflows changed the salinity gradient, consistent with findings of seasonal changes by Nichols and J. Thompson (1985) and Peterson and Vayssiere (2010). However, when the assemblage at a site changed, it was usually because salinity changed at that location. Thus, it is the species composition at a site that defines its assemblage designation, not necessarily its geographic location.

The assemblages described in this paper are similar to those described by Thompson et al. (2000), largely because some of their data were also used in this study. The assemblages are also consistent with Ranasinghe et al. (2012), who described assemblages based on a 1.0 mm sieve, in contrast to the 0.5 mm sieve used here. The polyhaline assemblage in both studies occupied central San Francisco Bay and was dominated by the amphipods *A. abdita*, *Monocorophium ascherusicum*, *Corophium heteroceratum*, and *P. brevipes*. *C. amurensis* was identified as a characteristic species of the mesohaline assemblage in both studies, though Ranasinghe et al. included *Marenzelleria viridis* as characteristic of the mesohaline, whereas it was a dominant of the oligohaline assemblage in this study. There was less concurrence in lower salinity areas, likely due to the more extensive sampling in this study which resulted in recognition of a separate oligohaline assemblage in Suisun Bay (classified as mesohaline by Ranasinghe et al.), and a tidal freshwater assemblage in the Delta, where Ranasinghe et al. had no samples. Their use of a 1.0 mm sieve-size resulted in lower taxa richness but had minimal effect on dominant taxa. This is similar to the findings of Hammerstrom et al. (2012), that 0.5–1.0 mm sieve size differences had a substantial effect on species richness and abundance, but little effect on sample distributions in ordination space.

The use of enhanced taxonomy in the tidal freshwater samples provided greater detail about the species composition of that assemblage. Such detail offers potential advantages for addressing trends or biological condition assessments, but we did not observe new assemblages when we used enhanced taxonomy in Run 3. Tubificids and chironomids were the primary groups identified to species in the enhanced taxonomy analysis and apparently there was not enough spatial separation of species within those groups to produce assemblage differentiation.

The species composition of the assemblages presented in this paper provides benchmarks for comparisons to future benthic samples that may be used to assess changes caused by biological invasions, water diversions, or chemical contamination. This study was conducted as part of a project to develop benthic assessment methods for California estuaries. Benthic assessments typically require definitions of reference conditions at the assemblage (habitat) level. The first step is defining the assemblages, their variation in space and time, and their relationships with abiotic factors. Such understanding may lead to the ability to identify threshold reference, or degraded conditions for an assemblage as part of integrated sediment quality assessments (Hughes et al. 1986; Bald et al. 2005).

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