Habitat related benthic macrofaunal assemblages of bays and estuaries of the western United States

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Abstract

Data from seven coast wide and regional benthic surveys were combined and used to assess the number and distribution of estuarine benthic macrofaunal assemblages of the western United States. Q-mode cluster analysis was applied to 714 samples, and site groupings were tested for differences in four habitat factors (latitude, salinity, sediment grain size and depth). Eight macrofaunal assemblages, structured primarily by latitude, salinity, and sediment grain size, were identified: Puget Sound fine sediment (A), Puget Sound coarse sediment (B), southern California marine bays (C), polyhaline central San Francisco Bay (D), shallow estuaries and wetlands (E), saline very coarse sediments (F), mesohaline San Francisco Bay (G), and limnetic and oligohaline (E). Assemblages A, B, C, D, and G were geographically distinct, while Assemblages E, F, and H were distributed widely along the entire coast. A second Q-mode cluster analysis was conducted after adding replicate samples that were available for some sites, and temporal replicates that were available for sites sampled in successive years. Variability due to small spatial scale habitat heterogeneity and temporal change were both low in Puget Sound, but temporal variability was high in the San Francisco estuary where large fluctuations in freshwater inputs and salinity among years leads to spatial relocation of the assemblages.

Introduction

Although individual species are typically distributed in complex ways along environmental gradients, the combined result is often a series of identifiable assemblages that partition available habitat along gradients of a few variables (Boesch 1973, Orloci 1975, Boesch 1977, Whittaker 1978, Smith *et al*. 1988, Thompson *et al*. 2000, Bergen *et al*. 2001, Llansó *et al*. 2002, Hyland *et al*. 2004). Identification of assemblages along habitat gradients has taken on an applied significance more recently, as biocriteria have become a central focus of ecological assessments in the United States (USEPA 1991, Jackson and Davis 1994, Gibson *et al*. 2000). Similar measures are being developed in Europe under the Water Framework Directive (European Commission 2000). Biocriteria require definitions of reference condition, which typically vary among habitats because species composition and abundances also differ naturally between habitats (Weisberg *et al*. 1997, Van Dolah *et al*. 1999). Therefore, determining the habitat variables that are most important in structuring biological assemblages and identifying the threshold values of these variables that result in natural breaks in biological assemblages are necessary components of defining reference conditions (Hughes *et al*. 1986, Bald *et al*. 2005). Information on the state of ecosystem condition contributes to the baseline needed for implementation of ecosystem based manage-

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ment (EBM), a rapidly evolving paradigm for managing coastal resources in the United States and elsewhere (UNESCO 2006, Murawski 2007).

Although benthic macrofauna have long been used as indicators of human impacts in marine environments, macrobenthic assemblages of the western United States bays and estuaries are poorly described, at least from a coast-wide perspective. There have been previous regional studies of benthic assemblages in Puget Sound (Llansó *et al*. 1998) and San Francisco Bay (Thompson *et al*. 2000), but there are substantial data gaps along the 12,654 km of western U.S. shoreline (National Oceanic and Atmospheric Administration 1975) that have prevented a coast-wide assessment. In addition, combining data from the regional studies has been difficult because of differences in the types of sampling gear and sieve mesh-sizes that were used.

The US Environmental Protection Agency (USEPA) Coastal 2000 initiative led to a west coast, coast wide benthic sampling effort with compatible sampling designs and collection methods. This study used those data, in combination with data from several regional programs that were collected using similar methods, to identify benthic assemblages that occur naturally in bays and estuaries of the western United States, and to identify habitat factors associated with assemblage differences. Additional data from programs that collected replicates in space and time were used to evaluate the effects of small spatial scale heterogeneity and interannual variability on assemblage similarity.

METHODS

This study used hierarchical cluster analysis of macrobenthic species abundance data to identify the benthic assemblages that occur naturally in bays and estuaries of the western United States and the habitat factors that structure them. These analyses were based on 1086 benthic samples from seven coast-wide and regional projects conducted between 1994 and 2003 (Table 1). All but one of the programs included probability-based sampling designs, so that all bay and estuary areas had chances of inclusion.

All samples were collected with a 0.1 m^2 Van Veen grab, except in San Francisco Bay, where a 0.05 m^2 Van Veen grab was used. Samples with a penetration depth of at least 5 cm and no evidence of post-sampling disturbance (i.e., washing or slumping) were sieved through 1-mm mesh screens. Sieve contents were placed in a relaxant for 30 minutes and then preserved in 10% sodium borate buffered formalin. Samples were rinsed and transferred from formalin to 70% ethanol after approximately one week. Specimens were then identified to the lowest practical taxon, most often species, and enumerated. Taxonomic inconsistencies among projects were eliminated by cross-correlating the species lists, identifying differences in nomenclature, and resolving discrepancies by consulting project taxonomists. Taxonomic nomenclature for provisional taxa (e.g., *Cossura sp*. A) followed Southern California Association of Marine Invertebrate Taxonomists (SCAMIT) Edition 4 (2001). Species abundances for all samples were normalized to an area of 0.1 m^2.

Habitat data collected with each sample included depth, bottom water salinity, and dissolved oxygen concentration measurements. Sediments from the top 2 cm of additional grab samples were analyzed for grain size distribution, contaminant concentrations (trace metals, dichloro-diphenyl-trichloroethane (DDT), polychlorinated biphenyls (PCBs), and polycyclic aromatic hydrocarbons (PAHs)), total organic carbon (TOC), and acute toxicity to amphipods using standard methods, details of which are provided in (Schiff 2000, Long *et al*. 2003, Schiff *et al*. 2006). All data were evaluated for methodological consistency and normalized for units of measure.

Because the objective was to define natural groupings of samples with similar species composition, potentially contaminated sites were eliminated prior to analysis. The criteria for eliminating a site as potentially contaminated followed from those of Bergen *et al*. (2001): 1) more than three chemicals exceeded Long *et al*. (1995) effects range low (ERL) values; 2) one or more chemicals exceeded Long *et al*. (1995) effects range median (ERM) values; 3) bottom dissolved oxygen was <2 ppm; 4) amphipod survival in 10-day acute toxicity tests was <50%; or 5) the site was located close to a known highly contaminated area or a storm water or municipal wastewater outfall. Ni and DDT were not included in the exclusion criteria because the ERM and ERL values for these chemicals are known to be poor predictors of biological responses (Long *et al*. 1995, Vidal and Bay 2005). After eliminating potentially contaminated sites, data from 714 samples remained for analysis (Table 1).

Groups of samples with similar species composition were identified by cluster analysis and the groups were tested for habitat differentiation using

Table 1. Sampling programs contributing data.

Project	Location	Period	Samples		Reference
			Minimally Contaminated	Total	
WEMAP-99	USA-Mexico border to USA-Canada border	July-Sept. 1999	176	191	US Environmental Protection Agency (2004)
Bight'98	Southern California	July-Sept. 1998	58	146	Ranasinghe *et al.* (2003)
Bight'03	Southern California	July-Oct. 2003	55	166	Ranasinghe *et al.* (2007)
SFEI	San Francisco Bay	Feb. 1994-Feb. 2001	137	173	Thompson *et al.* (2000)
WEMAP-00	San Francisco Bay, Columbia River, and Puget Sound	June-Oct. 2000	75	80	US Environmental Protection Agency (2004)
WEMAP-01	Oregon	July-Sept. 2001	31	32	US Environmental Protection Agency (2004)
Puget Sound Spatial	Puget Sound	June 1997-June 1999	182	298	Long *et al.* (2003)
Total			**714**	**1,086**	

non-parametric statistical methods. Q-mode cluster analyses were conducted using flexible sorting of Bray-Curtis dissimilarity values with $\beta = -0.25$ (Bray and Curtis 1957, Lance and Williams 1967, Clifford and Stephenson 1975). Prior to analysis, the influence of dominant species was reduced by cube-root transformation of species abundances and standardization by the species mean of 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; distortion occurs due to the non-monotonic truncated joint species distribution. Prior to cluster analysis, species occurring only at one site were eliminated.

Habitat related assemblages were identified by sequentially examining splits in the cluster analysis dendrogram, starting with the first split and proceeding along branches, to assess whether each split reflected habitat differentiation. Habitat differentiation was defined as: 1) a significant ($p < 0.05$) Mann-Whitney-Wilcoxon difference in median for any of four habitat variables (bottom salinity, bottom depth, percent fine (<63-μ grain size) sediments, and latitude) between the two sample groupings defined by the dendrogram split; and 2) accurate segregation of more than 90% of the samples in the split according to criteria based on significant habitat variables. Probabilities were not adjusted to account for multiple testing because the present study was only interested in controlling the comparison-wise error rate.

For each habitat related assemblage, abundant and characteristic taxa were identified as those with a mean assemblage abundance >10 per 0.1-m^2 sample and fidelity >50% or exclusivity >80%. Fidelity was calculated as the frequency of occurrence of a taxon in assemblage samples expressed as a percentage. Exclusivity was the abundance of a taxon in assemblage samples expressed as a percentage of its total abundance in all samples.

A second cluster analysis was used to evaluate the effects of small spatial scale heterogeneity and interannual variability on assemblage similarity. In this analysis, data used in the first analysis were supplemented by triplicate samples from ten uncontaminated sites in Puget Sound that were collected each year from 1997 to 2002 and temporal replicates that were sampled 10 to 13 times from 1994 to 2001 in the San Francisco Bay. The sampling and laboratory methods for benthic species abundance and habitat data, and the cluster analysis details, were the same as for the first analysis. The relative magnitude of small spatial scale assemblage variability and stability over time were evaluated by measuring replicate clustering or adjacency defined as the percentage of samples from a single site that occurred next to each other on the dendrogram.

Results

Sequential analysis of the spatial dendrogram yielded eight habitat related benthic macrofaunal assemblages in western US bays and estuaries (Figure 1). Statistically significant ($p < 0.05$) differences existed for bottom water salinity, bottom

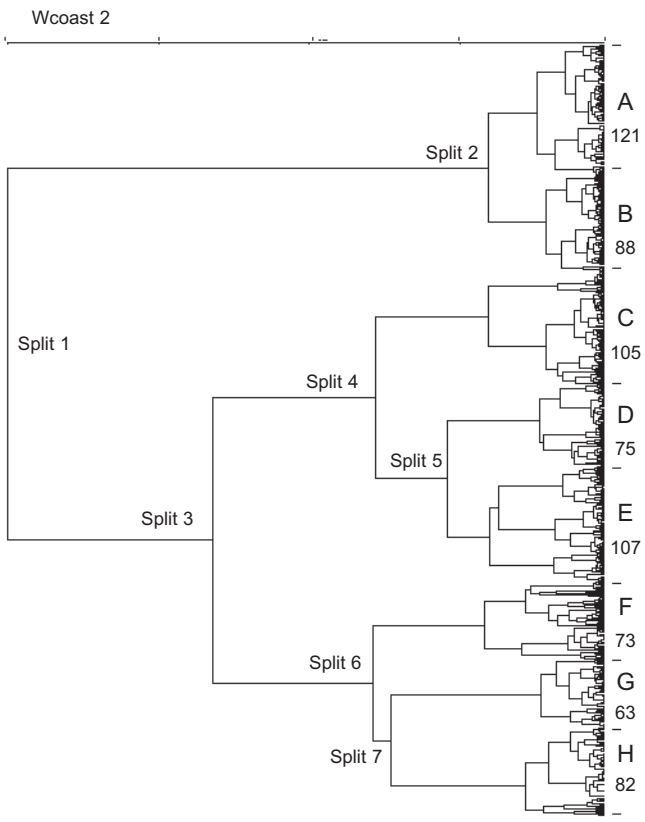

Figure 1. Dendrogram showing the habitat-related assemblages A - H identified by cluster analysis. A = Puget Sound fine sediment; B = Puget Sound coarse sediment; C = southern California marine bay; D = polyhaline San Francisco Bay; E = estuaries and wetlands; F = saline very coarse sediment; G = mesohaline San Francisco Bay; H = limnetic and oligohaline (tidal freshwater). The number of samples for each assemblage is presented under the assemblage letter. Splits 1 - 7 identify dendrogram branch points referred to in the text and tables.

depth, percent fines, or latitude across each of the seven dendrogram splits labeled in Figure 1 (Table 2). Split 1 and Split 7 were significantly different for all four habitat variables, while Splits 2, 3, 4 and 5 were significantly different for three. Split 6 was significant only for salinity and percent fines. Medians for latitude and percent fines were significantly different across six of the seven splits, while medians for salinity and depth were significant across five splits.

The habitat criteria classified samples across splits with greater than 90% accuracy for five of the seven splits in the species abundance dendrogram (Table 3). Classification accuracy was >98% for two splits. The splits with less than 90% accuracy separated heterogeneous branches with multiple assemblages that separated with higher accuracy in subsequent splits. The lowest accuracy of 76.8% was for Split 3, where each branch included three assemblages that separated with accuracy >94% in subsequent splits.

Although there were assemblage differences associated with all four habitat variables (Figure 2), habitat criteria separating samples across splits were associated primarily with differences in latitude, bottom water salinity, and sediment composition (Table 3). Latitude was included in the habitat criteria for separating assemblages across four of the seven splits, while bottom water salinity and sediment type were each included for two splits. Bottom depth was included only in one criterion, and even then only as a modifier of sediment type under limited circumstances.

The two assemblages including all the Puget Sound benthos were distinct from the other six western bay and estuarine benthic assemblages, separating from them at the first dendrogram branch (Split 1 in Figure 1; Table 3). The Puget Sound benthos then separated at Split 2 into two assemblages that were distinguished by a combination of sediment type and bottom depth. Although Assemblages A and B separated well at depths greater than 40 m, the two assemblages commingled at lesser depths (Figure 3).

The six benthic assemblages from outside Puget Sound split first on salinity criteria (Table 3), although differences in number of taxa were the most likely biological factor. Assemblages C, D, and E, with on average 43.3, 24.5, and 15.9 taxa per sample, respectively, separated from Assemblages F, G, and H, which had 8.9, 5.4 and 5.0 taxa per sample, respectively (Table 4). Assemblage F, which included benthos from mesohaline and higher salinity habitats with very coarse sediments, grouped with the other low diversity assemblages from limnetic, oligohaline, and mesohaline habitats rather than higher salinity Assemblages C, D, and E.

Subsequent dendrogram splits in the non-Puget Sound benthos were clearly related to geographic and habitat factors. The higher diversity branch split into Assemblages C, D, and E (Figure 1). The low diversity branch split into the saline habitats with very coarse sediments Assemblages F and G and the geographically widespread Assemblage H.

Assemblages A, B, C, D, and G included samples from narrow geographic distributions. The other three, including shallow estuaries and wetlands (Assemblage E), saline habitats with very coarse sediments (Assemblage F), and limnetic and oligoha-

Table 2. Ranges of values for salinity, depth, percent fines, and latitude for samples across splits in the spatial dendrogram (Figure 1). Bolded numbers indicate significant (p <0.05) differences in median across the dendrogram splits that were identified by Mann-Whitney-Wilcoxon tests.

	ssemblage	N	Salinity (psu)	Depth (m)	Fines (%)	Latitude (decimal degrees)
1	AB	209	**25.7 - 33.0**	**2.1 - 250**	**0.0 - 99.6**	**38.0023 - 48.9950**
	CDEFGH	505	**0.0 - 39.4**	**0.0 - 26.7**	**0.0 - 100.0**	**32.5568 - 48.3137**
2	A	121	28.5 - 33.0	**2.4 - 250.0**	**13.5 - 99.6**	**47.0575 - 48.9950**
	B	88	25.7 - 32.5	**2.1 - 213.0**	**0.0 - 93.7**	**38.0023 - 48.9842**
3	CDE	287	**3.8 - 39.4**	0.0 - 23.0	**1.2 - 100.0**	**32.6213 - 47.0053**
	FGH	218	**0.0 - 38.0**	0.4 - 26.7	**0.0 - 99.7**	**32.5568 - 48.3137**
4	C	105	**27.2 - 39.4**	**0.4 - 23.0**	2.8 - 100.0	**32.6213 - 34.1801**
	DE	182	**3.8 - 34.0**	**0.0 - 16.0**	1.2 - 99.5	**32.7585 - 47.0053**
5	D	75	9.7 - 34.0	**1.0 - 16.0**	**3.5 - 99.5**	**37.5591 - 46.9665**
	E	107	3.8 - 34.0	**0.0 - 13.8**	**1.2 - 99.4**	**32.7585 - 47.0053**
6	F	73	**0.1 - 33.2**	0.4 - 26.5	**0.0 - 63.0**	32.5568 - 48.3137
	GH	145	**0.0 - 38.0**	0.5 - 26.7	**0.0 - 99.7**	34.0326 - 46.3017
7	G	63	**0.0 - 38.0**	**0.7 - 12.0**	**0.0 - 99.7**	**37.4928 - 38.2089**
	H	82	**0.0 - 32.0**	**0.5 - 26.7**	**0.0 - 97.2**	**34.0326 - 46.3017**

Table 3. Habitat classification accuracy for samples across splits in the spatial dendrogram.

Split	Assemblage	Description	N	Habitat Criteria	Accuracy (%)
1	AB	Puget Sound	209	Latitude >47˚ N and Longitude <123.5˚ W	98.9
	CDEFGH	Not Puget Sound	505	Latitude ≤47˚ N and Longitude ≥123.5˚ W	
2	A	Puget Sound fine sediments	121	Fines >45% or Fines >45-Depth*0.75	91.9
	B	Puget Sound coarse sediments	88	Fines <15% or Fines <45–Depth*0.75	
3	CDE	High salinity	287	Salinity >25.0 psu	76.8
	FGH	Low salinity	218	Salinity ≤25.0 psu	
4	C	Southern California	105	Latitude <34.5˚ N	94.1
	DE	North of southern California	182	Latitude ≥34.5˚ N	
5	D	San Francisco Bay Polyhaline assemblage	75	Latitude >37.5˚ N and <38.0˚ N	94.5
	E	North or south of San Francisco Bay	107	Latitude ≤37.5˚ N or ≥38.0˚ N	
6	F	Very coarse sediments in mesohaline and higher salinity habitats	73	Salinity >5 psu and Fines ≤7.5%	87.6
	GH	Limnetic & oligohaline salinities, and mesohaline samples with fine sediments	145	Salinity ≤5 psu or Fines >7.5%	
7	G	San Francisco Bay mesohaline assemblages	63	Latitude 37.0˚ N to 38.5˚ N	98.6
	H	Limnetic and oligohaline assemblages elsewhere	82	Latitude <37.0˚ N or >38.5˚ N	

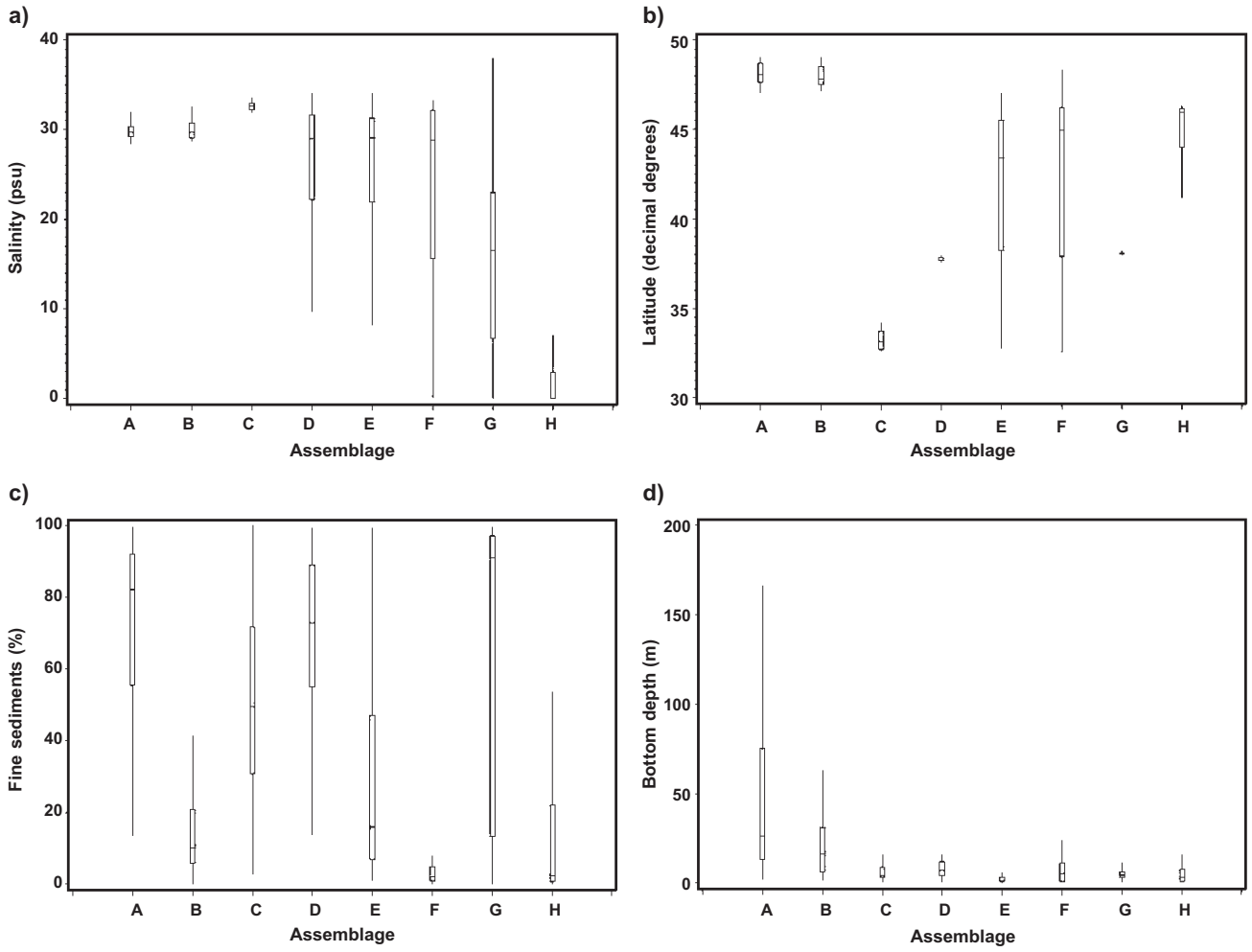

Figure 2. Box and whisker plots of habitat variables (Salinity (a), Latitude (b), Sediment grain size (c), and Depth (d)) for assemblages A - H identified by cluster analysis. A = Puget Sound fine sediment; B = Puget Sound coarse sediment; C = southern California marine bay; D = polyhaline San Francisco Bay; E = estuaries and wetlands; F = saline very coarse sediment; G = mesohaline San Francisco Bay; H = limnetic and oligohaline (tidal freshwater). Boxes indicate quartiles and medians. Whiskers join the box to the most extreme point within 1.5 interquartile ranges.

line (Assemblage H), had broad geographic distribution. Figure 2 presents salinity, geography, sediment grain size, and depth distribution for each assemblage.

Different macrobenthic taxa were characteristic of the eight assemblages and were distributed across many phyla and classes (Table 5). Of 69 abundant and characteristic taxa, 65 were abundant in and characteristic of only one assemblage. More than half the abundant and characteristic taxa in each assemblage had exclusivity values >80%. In other words, 80% or more of the abundance of those taxa occurred in that assemblage alone.

Only 4 of 69 abundant and characteristic taxa were characteristic of more than one assemblage. The capitellid polychaete *Mediomastus spp*. and annelids of the Class Oligochaeta were most widely distributed. Each was abundant and characteristic in three assemblages. *Mediomastus spp*. occurred in 45% or more of the samples in five of the six higher salinity assemblages (Assemblages A - E) and 22% of the samples of the sixth (Assemblage F). The taxon includes two species, *M. californiensis* and *M. ambiseta*, which have similar habitat distributions and are distinguishable only by setae on posterior segments that often break off as fragments during sample processing. The apparent broad distribution is likely true for both species, rather than an artifact due to uncertainty of species identity. Oligochaetes occurred in >30% of the samples in seven of the eight habitats and in 18% of the samples in the other (Assemblage F), and were not identified further. The broad oligochaete distribution likely reflects a com-

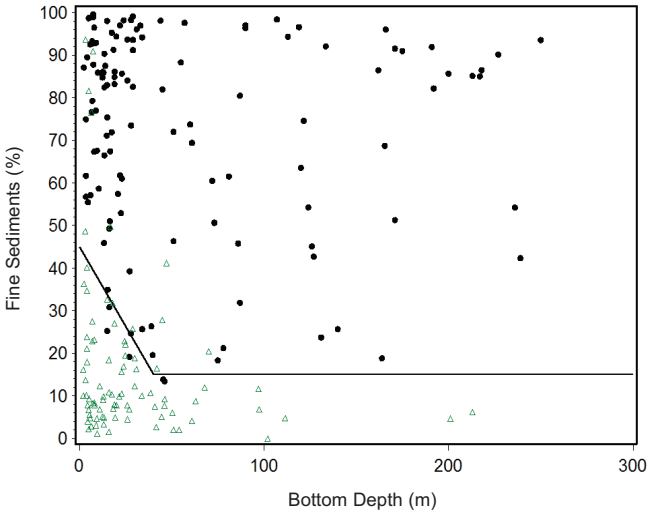

Figure 3. Distribution of assemblages A and B across dendrogram Split 2 (see Figure 1) relative to depth and sediment type. Closed black circles represent samples from Assemblage A; open green triangles represent samples from Assemblage B.

bination of *Tubificoides spp*. at mesohaline and higher salinities with a broad diversity of oligochaetes in limnetic and oligohaline salinities. The tolerant ostracod *Euphilomedes carcharodonta* and the syllid polychaete *Exogone lourei* were each characteristic of two assemblages and were abundant and occurred frequently in a third. *E. carcharodonta* was characteristic of Assemblages B and C and also occurred at abundance in 31% of the Assemblage A samples. *E. lourei* was characteristic of Assemblages C and D and occurred at abundance in 36% of the Assemblage B samples.

In the second cluster analysis, samples from stations in the supplementary Puget Sound data clustered together on the dendrogram, forming a single group together with the Puget Sound stations that were separated from all the other samples by the first split in the dendrogram. For nine of the ten supplementary stations, all samples clustered together (Table 6). For the tenth station, 17 of 18 samples clustered together, with the eighteenth sample separated by 26 stations in the dendrogram. In contrast, only about 50% of the San Francisco Bay samples clustered adjacent to their temporal replicates. All the temporal replicates clustered together at Station BC21 in Horseshoe Bay, which is located near the mouth of San Francisco Bay and presumably under the stabilizing influence of the Pacific Ocean. In contrast, only 40 - 50% of the temporal replicates clustered together at the other four stations, which are located away from the bay mouth and more strongly influenced by freshwater flows (Thompson *et al*. 2000).

Discussion

The results are consistent with those of other macrobenthic assemblage analyses, indicating that latitude, salinity, and sediment grain-size are among the primary determinants structuring assemblages over broad geographic areas with large latitudinal gradients (Van Dolah *et al*. 1999, Bergen *et al*. 2001, Llansó *et al*. 2002, Hyland *et al*. 2004). The polyhaline and mesohaline San Francisco Bay assemblages observed in the present study are essentially the same as the marine and estuarine assemblages of Thompson *et al*. (2000), and the Puget Sound assemblages are similar to those of Llansó *et al*. (1998). We also observed the same faunal break at Point Conception that Briggs (1974, 1995) and Cross and Allen (1993) observed for gastropod and marine fish

Table 4. Species richness and abundance (mean ± standard error) for each of the assemblages.

Assemblage	Habitat Related Assemblage Description	Samples	No. of Taxa ($0.1m^{-2}$)	Total Abundance ($0.1m^{-2}$)
A	Puget Sound fine sediments	121	42.2 ± 1.5	601.3 ± 57.3
B	Puget Sound coarse sediments	88	69.2 ± 2.4	865.1 ± 112.8
C	Southern California marine bays	105	43.3 ± 1.7	835.0 ± 80.1
D	Polyhaline central San Francisco Bay	75	24.5 ± 1.3	1,768.0 ± 324.9
E	Estuaries and wetlands	107	15.9 ± 0.8	2,260.9 ± 534.0
F	Salinity very coarse sediments	73	8.9 ± 0.8	84.7 ± 12.7
G	Mesohaline San Francisco Bay	63	5.4 ± 0.4	791.0 ± 204.1
H	Limnetic and oligohaline	82	5.0 ± 0.4	404.7 ± 66.7

Table 5. Exclusivity values for abundant (mean abundance >100 m^{-2}) taxa with fidelity >50% or exclusivity >80% in each assemblage. Taxonomic nomenclature for provisional taxa (e.g., *Cossura sp*. A) follows SCAMIT Edition 4 (SCAMIT 2001).

Taxon	Higher Taxon	Assemblage							
		A	B	C	D	E	F	G	H
Euphilomedes producta	Arthropoda : Ostracoda	92							
Eudorella pacifica	Arthropoda : Cumacea	91							
Axinopsida serricata	Mollusca : Bivalvia	89							
Protomedeia articulata Complex	Arthropoda : Amphipoda	89							
Protomedeia grandimana	Arthropoda : Amphipoda	82							
Amphiodia spp .	Echinodermata : Ophiuroidea	73							
Prionospio (Minuspio) lighti	Annelida : Polychaeta	68							
Levinsenia gracilis	Annelida : Polychaeta	47							
Ericthonius rubricornis	Arthropoda : Amphipoda		100						
Phyllochaetopterus prolifica	Annelida : Polychaeta		100						
Ampelisca agassizi	Arthropoda : Amphipoda		100						
Alvania compacta	Mollusca : Gastropoda		94						
Tellina modesta	Mollusca : Bivalvia		89						
Rochefortia tumida	Mollusca : Bivalvia		84						
Aphelochaeta glandaria Complex	Annelida : Polychaeta		81						
Prionospio (Prionospio) dubia	Annelida : Polychaeta		71						
Nutricola lordi	Mollusca : Bivalvia		63						
Parvilucina tenuisculpta	Mollusca : Bivalvia		55						
Euphilomedes carcharodonta	Arthropoda : Ostracoda		49	15					
Mediomastus spp .	Annelida : Polychaeta		9	42	16				
Amphideutopus oculatus	Arthropoda : Amphipoda			100					
Caecum californicum	Mollusca : Gastropoda			100					
Cossura sp . A	Annelida : Polychaeta			100					
Barleeia spp .	Mollusca : Gastropoda			100					
Synaptotanais notabilis	Arthropoda : Tanaidacea			100					
Scoletoma sp . C	Annelida : Polychaeta			100					
Paracerceis sculpta	Arthropoda : Isopoda			99					
Prionospio (Prionospio) heterobranchia	Annelida : Polychaeta			99					
Fabricinuda limnicola	Annelida : Polychaeta			99					
Tagelus subteres	Mollusca : Bivalvia			96					
Pseudopolydora paucibranchiata	Annelida : Polychaeta			89					
Musculista senhousia	Mollusca : Bivalvia			87					
Theora lubrica	Mollusca : Bivalvia			72					
Pista percyi	Annelida : Polychaeta			65					
Leitoscoloplos pugettensis	Annelida : Polychaeta			63					
Euchone limnicola	Annelida : Polychaeta			45					
Exogone lourei	Annelida : Polychaeta			28	56				
Sabaco elongatus	Annelida : Polychaeta				99				
Ampelisca abdita	Arthropoda : Amphipoda				94				
Caprella spp .	Arthropoda : Amphipoda				94				
Sinocorophium heteroceratum	Arthropoda : Amphipoda				94				
Molgula spp .	Chordata : Ascidiacea				92				
Photis brevipes	Arthropoda : Amphipoda				90				
Sphaerosyllis californiensis	Annelida : Polychaeta				87				
Monocorophium acherusicum	Arthropoda : Amphipoda				84				
Leptochelia dubia	Arthropoda : Tanaidacea				72				
Oligochaeta	Annelida : Oligochaeta				8	60			19
Americorophium stimpsoni	Arthropoda : Amphipoda					100			
Pygospio elegans	Annelida : Polychaeta					99			
Eogammarus confervicolus Complex	Arthropoda : Amphipoda					99			
Americorophium spinicorne	Arthropoda : Amphipoda					98			
Hobsonia florida	Annelida : Polychaeta					97			
Gnorimosphaeroma insulare	Arthropoda : Isopoda					97			
Potamopyrgus antipodarum	Mollusca : Gastropoda					93			
Cryptomya californica	Mollusca : Bivalvia					91			
Pseudopolydora kempi	Annelida : Polychaeta					91			
Neanthes limnicola	Annelida : Polychaeta					87			
Gnorimosphaeroma oregonense	Arthropoda : Isopoda					83			
Macoma balthica	Mollusca : Bivalvia					82			
Capitella capitata Complex	Annelida : Polychaeta					82			
Eohaustorius estuarius	Arthropoda : Amphipoda						90		
Corbula amurensis	Mollusca : Bivalvia							99	
Marenzelleria viridis	Annelida : Polychaeta							98	
Insecta	Arthropoda : Insecta								99
Boccardiella ligerica	Annelida : Polychaeta								93
Corbicula fluminea	Mollusca : Bivalvia								92
Chironomidae	Arthropoda : Chironomidae								86
Americorophium salmonis	Arthropoda : Amphipoda								29

Table 6. Percentage of temporal replicates from single sites that clustered adjacent to each other on the dendrogram.

Station Location	Station	Samples	Adjacent Samples (%)
Puget Sound, Washington	PST-03	18	100
	PST-04	18	100
	PST-13R	18	100
	PST-21	18	100
	PST-29	18	100
	PST-34	18	94
	PST-38	18	89
	PST-40	17	100
	PST-44	17	100
	PST-49	18	94
San Francisco Bay, California	SFE-BB15	10	40
	SFE-BC21	10	100
	SFE-BC60	10	50
	SFE-BD15	11	55
	SFE-BD41	13	46

species. However, we did not observe the Cape Mendocino faunal break described for gastropods by Briggs (1974, 1995). Gastropods are mostly broadcast spawners with pelagic larvae that are strongly influenced by ocean currents, whereas many benthic infaunal taxonomic groups brood their young and are less influenced by currents.

Latitude was the dominant physical factor differentiating habitats across four of the seven dendrogram splits (Table 3), but the effect of salinity is probably understated because of confounding between latitude and salinity. For example, the mesohaline San Francisco Bay assemblage was geographically restricted, but the San Pablo and Suisun Bays in the San Francisco Bay estuary are the only extensive mesohaline salinity habitats on the west coast. Similarly, the paucity of rainfall in southern California creates a high salinity environment that predominates in that area. Further evidence for the importance of salinity as a structuring factor is the difference in assemblage stability between the temporal replicates in Puget Sound and those in San Francisco Bay. Puget Sound has a relatively stable salinity regime that is reflective of the consistently high rainfall of the region. In contrast, rainfall in the San Francisco estuary watershed is episodic and large intrabasin transfers for agriculture and drinking water exacerbate salinity fluctuations. The assemblages apparently are responding to salinity conditions at sites, rather than the geographic position of sites within the estuary; limnetic and oligohaline assemblages move downstream in response to seasonal freshwater outflows and move upstream during dry weather.

Substrate was of lesser importance for differentiating assemblages in lower salinities than it was in higher salinities, consistent with the findings of Weisberg *et al*. (1997). Sediment grain-size differences, on the other hand, were most important in differentiating the saline very coarse sediment assemblage fauna from the fauna of other habitats, and separating the Puget Sound fine and coarse sediment assemblages. Sediment differences may also play a role, together with salinity and bottom depth, in differentiating the estuarine and wetland assemblages which live at shallower depths (Figure 2d) than other assemblages. Bottom depth was important only as a modifier of sediment grain-size differences in shallow areas of Puget Sound (Figure 3). The lack of a strong depth influence on assemblage separation is most likely due to the relatively narrow depth range of stations outside Puget Sound; 95% of the samples for Assemblages C - H occurred at depths <15 m.

One of the concerns regarding assemblage identification is the dependence of cluster analysis results on methodological choices. Recent benthic macrofauna clustering algorithms usually include the Bray-Curtiss similarity index and flexible sorting with $\beta = -0.25$ (Bergen *et al*. 2001, Clarke and Warwick 2001, Hyland *et al*. 2004), but the results may be affected by algorithms chosen for data transformation, data standardization, and step-across distance reestimation. These choices are a necessary and integral part of the cluster analysis process. To evaluate the effect of these choices, we compared assemblage classification consistency and dendrogram sequence order of samples for six variations of our chosen cluster analysis protocol, altering one choice for each variation. The variations eliminated step across distance reestimation or data standardization, or transformed abundance values by presence-absence, fourth root, square root, or log transformations instead of a cube root transformation. Sample classifications and dendrogram sequences were consistent among the analyses. The variations classified an average of 84.6% of the samples within the contiguous groups identified as assemblages in the main analysis, with a minimum of 82.2% and a maximum of 89.1%. For the eight assemblages, average com-

position consistency ranged from 72.7% to 97.4% with a mean of 84.6%. Assemblages separating along steep biological gradients rich in species and organisms (e.g., Assemblage B: Puget Sound coarse sediment assemblage) and depauperate assemblages (e.g., Assemblage F: Saline very coarse sediments; Table 4) were most affected by algorithm choices. In the species rich gradients, the method variations slid the assemblage separation points along the sample sequences in the absence of sharp biological discontinuities. Depauperate assemblage separation was more haphazard, reflecting a paucity of consistent information. Rank correlation coefficients for the sample dendrogram sequence order between the original analysis and variations ranged from 0.86 to 0.94, averaging 0.91. These results suggest that the physical habitat variables driving species composition result in consistent broad scale assemblage clusters regardless of the statistical method employed, although outliers in susceptible assemblages may migrate between adjacent clusters.

Large differences in species richness were observed among the eight assemblages that were identified. The two lower salinity assemblages averaged only about 5 species per sample, whereas the higher salinity assemblages averaged as many as 69 species per sample. The low salinity assemblages also had few characteristic species, with the bivalve *Corbula amurensis* and the polychaete *Marenzelleria viridis* the only taxa characteristic of the mesohaline San Francisco Bay assemblage. *M. viridis* is also common in east coast mesohaline habitats in the Chesapeake Bay (Weisberg *et al*. 1997) and North Carolina (Hyland *et al*. 2004). Some of the lower species richness may have been due to the smaller size sampling gear used in the San Francisco estuary and because the freshwater Oligochaeta, Chironomidae, and Insecta were not identified to the genus or species level because of the time it takes to permanently mount individual organisms on microscope slides for identification, and because of the essentially marine backgrounds of the organizations conducting the sampling programs. However, lower species richness in low salinity environments is characteristic of the estuarine benthos (e.g., Boesch 1977) and is typically associated with the osmotic stress of that environment.

While there was a high degree of similarity within the eight assemblages identified, it is not clear that these are the only assemblages occurring on the west coast. The sampling programs on which the present study's analyses were based were extensive, but they all had probability based sampling designs. As such, spatially limited habitats, such as the shallow margins of estuaries, were not well represented. In addition, the cluster analysis was conducted on a coast wide data set, potentially masking microhabitat assemblages that might be more apparent in large data sets within a single estuary. However, the present study's large, coast wide data set allows identification of the major assemblages of the west coast and the principal factors that structure them.

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