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Assessment of spatial patterns in benthic macrofauna of the U.S. west coast continental shelf.

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Abstract

Aim—We assessed whether currently described marine biogeographic boundaries apply to shelf macrofauna and which environmental drivers were most associated with species differences among regions.

Location—Pacific coast of North America from the Strait of Juan de Fuca in Washington to the California-Mexico border.

Methods—Van Veen grab samples were collected from soft sediment 28–138 m deep and sieved using 1 mm mesh. Spatial patterns of species richness, diversity, and abundance were examined in relation to latitude and environmental parameters (temperature, salinity, dissolved oxygen, sediment % fines, and total organic carbon). Analyses of latitudinal distribution patterns of individual species were combined with multivariate analyses of community composition to determine biogeographic and habitat boundaries for mid-depth continental shelf macrofauna.

Results—Species richness, diversity, and abundance significantly decreased with increasing latitude, primarily between 32 and 40° N. There were positive associations of richness, diversity (H'), and abundance with upwelling index, sediment % fines, and TOC (<2%). Temperature and DO also were significant for richness and H' but not abundance. Assessment of individual species ranges found major faunal transitions at latitudes 33–34°, 37°, 44°, and 46–47°. Major assemblage differences were found at 34.5°, and 42°. Within each latitudinal region, significantly different macrofauna communities were found in sediment with <5% fines.

Main Conclusions—The biogeographic boundaries proposed under the Marine Ecoregions of the World schema are more closely aligned with shelf fauna distributions than those developed using west coast rocky intertidal communities. However, the proposed province boundary at Cape Mendocino is not apparent in the shelf macrofauna, and a transition appears to occur closer to the Oregon-California border. Further, the shelf macrofauna indicate the Channel Islands should be a separate subregion from mainland southern California Bight. Multivariate community analyses minimizing the impact of rare species appeared more useful in determining macrofaunal

community biogeographic boundaries than analysis of individual species range endpoints, which are strongly influenced by uncommon species.

Keywords

benthic assemblage; benthic infauna; biogeographic province; latitudinal gradients; sedimentary habitat; species richness

Introduction

Definition of the patterns and causes of biogeographic scale variation in diversity of marine taxa along the west coast of North America has been a topic of study for nearly 60 years (e.g. Fischer, 1960; Hall, 1964; Valentine, 1966; Roy et al., 1996, 1998; Connolly & Roughgarden, 1998; Sagarin & Gaines, 2002; Schoch et al., 2006; Blanchette et al., 2008). Continental shelf macroinfauna in limited parts of this broad region have received extensive study, in particular for the Southern California Bight (e.g. Bergen et al. 2000, 2001; Bay et al., 2005; Ranasinghe et al., 2007), and for the Monterey Bay to San Francisco Bay area (Hodgson & Nybakken, 1973; Oliver et al. 1977, 2008, 2011; Hyland et al., 1991). However, the shelf macrofauna from mid-California to the Canadian border has received much less attention. Early continental shelf sampling studies along the coasts of Washington and Oregon were limited not only in spatial extent but also in providing only partial assessment of the benthic fauna (Lie & Kelly, 1970; Lie & Kisker, 1970; Bertrand, 1971; Nittrouer & Sternberg, 1981). More recent studies in the more northern region have generally been site-specific studies (e.g. SF PUC 2006; de Marignac et al., 2008; MRS, 2016; U.S. EPA, 2016; Henkel & Politano, 2017). Thus, in contrast to some other basins (e.g. Engle & Summers, 1999; Gray, 2000; Ellingsen, 2001, 2002; Ellingsen & Gray, 2002; Hale, 2010; Piepenburg et al., 2011), the ability to conduct quantitative assessment of distributional patterns on continental shelf macrofauna at broad geographic scale for the west coast of the US has been limited.

The present study represents the most spatially and taxonomically comprehensive benthic macrofaunal survey of the west coast mid-depth continental shelf environment of which we are aware, spanning three Marine Ecoregions of the World (MEOW) (Spalding et al., 2007). The study was a cooperative sampling effort of the U.S. Environmental Protection Agency (EPA), the National Oceanic and Atmospheric Administration (NOAA), and Southern California Water Resources Research Project (SCCWRP). Benthic grab samples were collected during summer 2003 as part of an effort to determine the condition of the soft-sediment benthic resources and overlying water quality of the continental shelf, in the depth range 30–120 m, from the Strait of Juan de Fuca in Washington to the Mexican border (Nelson et al., 2008). In addition to this original primary objective, this broad regional data set offers the opportunity to explore distribution patterns and to determine whether biogeographic boundaries as currently described apply to the shelf macrofauna. Accurate determination of macrofaunal community distributions will be increasingly important in the face of increased exploitation of nearshore resources for wave energy (Henkel et al., 2014) and other purposes, as well as the need for more effective models of cumulative ecological risk assessment under scenarios of climate change (Lee et al., 2015).

Much of the work to date on the US west coast to determine biogeographic patterns of marine taxa has either focused on major taxonomic groups, particularly molluscs (Fischer, 1960; Hall, 1964; Valentine, 1966; Roy et al., 1996, 1998), or has focused at the community level on rocky intertidal habitats (Connolly & Roughgarden, 1998; Sagarin & Gaines, 2002; Schoch et al., 2006; Blanchette et al., 2008). The soft sediment, continental shelf macrofauna of the west coast is dominated by polychaete worms and crustaceans, with only 4 of the top 50 species being molluscs (Nelson et al., 2008). Thus, existing biographic boundaries may not be appropriate for this ecological community. Among current proposals, Blanchette et al. (2008) assessed rocky intertidal community composition and found general support for the biogeographical boundaries derived from molluscan distributions by Hall (1964) and Valentine (1966). The MEOW biogeographical schema (Spalding et al., 2007) has been proposed based on a combination of “multiple divergent taxa or multiple oceanographic drivers in the derivation of boundaries” (p. 575) with a prime focus on “the benthos above 200 m and the overlying water column” (p. 579), and thus might be expected to better reflect distribution patterns of the shelf macrofauna than that based on intertidal organisms. We thus hypothesized that we would detect regional differences in soft sediment community composition that more closely corresponded to the MEOW ecoregions than to the biogeographic boundaries proposed by Blanchette et al. (2008), although the two frameworks have much overlap. We additionally assess the patterns of the range extent of individual taxa, and seek to determine which environmental drivers were the main contributors to differences observed among regions in the study area.

2. Methods

2.1 Sampling Design

Sample collection was conducted under the U.S. EPA National Coastal Assessment (NCA) programme together with the companion assessment, Bight '03, that was conducted by SCCWRP during the same time-frame (summer 2003). Both studies utilized an integrated, stratified, random-sampling design (Generalized Random Tessellation Stratified (GRTS), Stevens & Olsen, 2003). Sampling design included both primary target stations and alternate stations if primary stations could not be sampled (see Nelson et al., 2008, for details of sampling design). NCA successfully sampled 146 stations from Cape Flattery, WA, to Pt. Conception, CA in the period June 1 – 26, 2003 (NOAA Cruise AR-03-01-NC), with data from one additional NCA station off Santa Catalina Island provided to the study by SCCWRP. Fifty stations each within Washington and Oregon and 47 stations from California were successfully sampled. An additional 110 stations, located within the Channel Islands National Marine Sanctuary (27) and throughout the Southern California Bight (83, Pt. Conception, CA to the Mexican border), were successfully sampled for some or all of the NCA parameters within the target depth range by participants in the Bight '03 survey (Ranasinghe et al. 2007). Benthic macrofaunal samples were obtained from these 257 stations, but two stations (OR03-0010, CA03-4339) failed quality assurance checks, and the final total included benthic samples from 255 stations. A complete list of stations with depth, sampling date, and coordinates is given in Nelson et al. (2008).

2.2. Sampling Methods

Sediment samples were obtained with a double Van Veen grab composed of two 0.1-m² samplers, joined together in a single frame weighing 204 kg, including 90.7 kg of supplemental weights to assist in bottom penetration. One grab per station was used for analysis of macrofaunal communities, with additional grabs used for sediment % silt-clay (fines), total organic-carbon (TOC) content, and contaminants (not considered here). A grab sample was deemed successful when the grab unit was > 75% full (Strobel & Heitmuller, 2001). The benthic samples were sieved on shipboard through nested 0.5-mm and 1.0-mm screens, and preserved in 10% buffered formalin. Fauna from Washington and Oregon in the 0.5–1.0 mm sieve fraction were archived but not processed, while those for California were processed as part of a supplemental study and are not considered here. In three cases, duplicate benthic faunal grab samples were collected, but for the sake of consistency of comparison, only the first sample was included in the present data set.

Upon return to the laboratory, samples were transferred to 70% EtOH as per the NCA Quality Assurance plan (Heitmuller & Summers, 2001), and then sorted and identified by laboratories experienced with west coast benthic macrofaunal samples. Washington and Oregon samples were processed by Washington Department of Ecology (Partridge, 2007), and California NCA samples by Moss Landing Marine Laboratories. Bight '03 samples were processed by the consortium of laboratories led by SCCWRP (Ranasinghe et al., 2007). Quality control for identification of infauna samples was provided by a network of secondary QA/QC taxonomic specialists (list provided in Partridge, 2007) to confirm identifications made by the primary taxonomists and to provide standardization among the state participants. Additional QA/QC measures for taxonomy included sending vouchers, voucher sheets, and a portion of the QA samples to the secondary QA taxonomists, and feedback to the primary taxonomists was used to correct work and standardize identifications between regional taxonomists. In spite of these measures, some differences were detected in the level of taxonomic resolution for echinoderms and nemertean between regions. Thus, the multivariate assemblage analyses were conducted using the polychaete, mollusc, and arthropod data only. Although some taxa could not be identified to species, the term “species richness” is used throughout to refer to the total number of separately identifiable taxa.

Details of methods and quality assurance procedures for conducting vertical water-column profiles and water column (water bottle) sampling, together with a complete list of parameters sampled, are provided in Nelson et al. (2008). For the current study, only near-bottom measurements of temperature, salinity, and dissolved oxygen (DO) were included in the statistical analyses. Physical water column data were available from a more limited number of stations than the benthic macrofaunal samples. During the cruise leg on the Oregon shelf, equipment malfunction limited water column profiling. Due to independent design aspects of the Bight '03 study, the water column parameters measured varied considerably and were more limited than for the NCA study. Total sample size for water column parameters ranged from 152–164.

In addition to the water column parameters measured *in situ*, an index of summer upwelling intensity was calculated. The NOAA Pacific Fisheries Environmental Laboratory (PFEL)

computes the upwelling index at 3° latitude intervals along the west coast of North America. Monthly upwelling index values were downloaded from PFEL: https://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/upwell_menu_NA.html. Monthly upwelling index values for summer months (May–September) were averaged over the period 2000–2003 to give a single index number for the 5 available latitudes between 33°–48°. The averaged upwelling index value was assigned to all stations falling within the range $\pm 1.5^\circ$ of each available index latitude across the study area, and the index was included as an independent variable in exploratory multiple regression analyses.

2.3 Statistical Analyses

Summary data are provided in Nelson et al. (2008). Raw data are currently available to download from an archived EPA web site, <https://archive.epa.gov/emap/archive-emap/web/html/index-78.html>

2.3.1 Latitudinal patterns of benthic diversity—Data from the NCA and Bight '03 studies were combined to form a composite data set of 255 stations by 1470 taxa. Bivariate relationships among species richness, H' diversity, infaunal abundance, latitude and environmental variables were examined with both linear and nonlinear curve fit routines in Sigmaplot 13®. A correlation matrix among latitude and physical variables (depth, sediment % fines (fraction less than 0.625 mm), sediment % TOC, bottom DO, bottom salinity, bottom temperature, upwelling index) was computed with SAS® 9.4 to help inform model selection for multivariate regression. For both richness (number of species) and diversity (Shannon-Wiener, H'), best fit, multivariate regression model selection was conducted with SAS® 9.4 PROC GLMSELECT. Stepwise selection of variables was selected with the stopping criteria that none of the variables omitted from the model was significant at the entry significance level (0.15) and every variable included in the model was significant at the stay significance level (0.15). AIC (Akaike's information criterion) was used as the best fit criterion. Multicollinearity of variables was explored by computation of the variance inflation factor using SAS® 9.4 PROC Reg, together with results from the correlation analysis. Since best fit multivariate regression model selection using stepwise selection has been criticized (Whittingham et al. 2006), results of the stepwise regression were compared to the best models selected by the procedure suggested by Beal (2005). Models with all possible subsets of variables were compared with SAS® 9.4 PROC Reg and the best model was selected based on the minimum AIC Beal (2005). For both species richness and H' diversity, the variables included in the best fit multivariate models were the same for both approaches, and the stepwise regression results are presented here.

Data analyses for assessment of potential biogeographic transition zones were conducted in SAS®. The initial dataset was reduced by excluding taxa which were not resolved to the species level, yielding a dataset of 255 stations and 1356 species. The latitudinal range, and both minimum and maximum latitude recorded for each species were determined. Following the approach used by Roy et al. (1998), the number of species with end of range, both minimum and maximum, were separately tabulated for 1 degree of latitude bins over the latitudinal extent of the study. The number of species with end ranges was divided by the total number of species occurring within the same latitudinal bin, and expressed as per cent.

Based on Roy et al. (1998), latitudes with >20% species range endpoints were deemed to represent suggested regional transition zones in the benthic macrofaunal composition. Latitude bins at 32° and 48° were excluded from consideration because these latitude intervals were truncated in the sampling plan. These analyses were conducted for all collected taxa. Latitudinal patterns of range endpoints were also determined for polychaeta, mollusca and arthropoda separately. The patterns for the individual taxa groups were not different from all taxa and are presented in Supplementary Material.

2.3.2 Benthic community analyses—Because biogeographical patterns largely reflect shifts in relative abundance of taxa, rather than complete species turnover (Blanchette et al., 2008), we used a variety of multivariate analyses in PRIMER (Clarke & Gorley, 2006) to test hypothesized ecoregions and assess latitudinal and habitat breaks in faunal assemblages. Because of differences detected in taxonomic resolution for echinoderms and nemerteans between regions as described above, multivariate analyses were conducted for only arthropods, molluscs, and polychaetes both together and separately. Density data (no. individuals per grab) were 4th root transformed to reduce the influence of highly abundant species without giving as much weight to rare species as would the more severe log(x+1) transformation (Clarke & Warwick, 2001). Bray-Curtis similarity matrices were then created based on the 255 stations as the basis for most of the subsequent analyses.

To assess the appropriateness of the two previously defined ecoregional schemes to shelf macroinfauna (and our hypothesis that that MEOW scheme would be a better fit than Blanchette et al.), we coded each station with its ecoregion and tested for similarities within/between regions using a one-way ANOSIM (Analysis of Similarities). ANOSIM tests the null hypothesis of no differences among groups of samples based on a priori assignment of samples to groups (Clarke & Gorley, 2006). Groupings tested were based on two systems. The Marine MEOW scheme places biogeographical boundaries at 40 degrees and 34.4 degrees resulting in three regions along the coast: Oregon, Washington, Vancouver Coast and Shelf, (OWV), Northern California (NOC), Southern California Bight (SCB) (Spalding et al., 2007). Alternately, Blanchette et al. (2008) distinguished four coastal regions based on intertidal community assemblages that overlap with the current study area: Mendocinian (MEN), Montereyan (MON), Southern California (SCB; restricted to Santa Monica Bay), and Ensenadian (ENS). Nonmetric multidimensional scaling (nMDS) was used to plot stations on a two-dimensional ordination plane based on taxa composition similarities and dissimilarities, and stations were labeled with the various tested schemes.

The BEST routine in PRIMER can be useful in comparing the multidimensional patterns of species with the multidimensional patterns of abiotic variables. However, we only had the complete suite of abiotic variables for 144 stations (41 WA stations, 46 OR stations, 42 CA north of Point Conceptions stations, 14 SCB mainland, and a single Channel Islands station), and the routine cannot be run with missing values. Thus, we used two different approaches. First, we ran the BEST routine using only the physical variables for which we had nearly complete coverage: latitude, upwelling index, depth, per cent fines, and TOC. Second, we ran the BEST routine using a resemblance matrix that included only those stations for which we had all available abiotic variables.

Cluster analysis (CLUSTER) was run on all stations, along with the Similarity of Profile (SIMPROF) routine, to identify statistically significant groups of sample stations based on an assumption of no prior structure of similarities and dissimilarities of the taxa composition. We then “sliced” the dendrogram at 30% similarity to generate more generalized groups based on species assemblages. The station compositions of identified groups were then compared to the hypothesized ecoregions, and the average physical characteristics for each group were determined. Finally, we determined regional and habitat breaks specific to shelf macroinfauna based on the results of the cluster analysis. To assess which species group was driving the resemblance among the stations in the entire dataset, the RELATE procedure was used to determine the Spearman correlations among resemblance matrices for four taxonomic groups (arthropods, molluscs, and polychaetes, and the three combined). The major taxa (of polychaetes, molluscs, and arthropods only) characteristic of these habitat-regions were determined using the Similarity Percentages (SIMPER) routine.

3. Results

The depth range of samples collected was 28 – 138 m, with only 9 samples from outside the target depth range of 30 – 120 m (Nelson et al., 2008). Average depth of samples was 72.7 m. Upwelling index had a significant negative relationship with latitude ($r = -0.960$, $p < 0.0001$), as the upwelling index of each station was based on station latitude, and was the only linear correlation greater than 0.9 (Appendix S1, Supplementary Table 1.1). Although significant, there were low correlations between depth and per cent fines ($r = 0.178$) and per cent fines and per cent TOC ($r = 0.374$). Using quadratic relationships for the best fit, bottom temperature and DO also were negatively related to latitude: Temp: $r = 0.95$, $p < 0.0001$; DO: $r = 0.8$, $p < 0.001$. The benthic macrofaunal collections were dominated by polychaetes (43.5% of species, 58.7% of abundance), arthropods (26.1%, 17.7%), and molluscs (17.1%, 13.2%), making up a total of 86.7% of species and 89.6% of abundance.

3.1 Macrofaunal Community Parameters

Sample species richness (alpha diversity) in the 255 benthic grab samples ranged from 19–190 taxa per grab sample. Although variability was high, there was a significant negative linear relationship of species richness to increasing latitude (Table 1, Fig. 1). Much of the change in species richness with latitude occurred between 32° and 40°, and there was no significant relationship between the two variables between 40° and 48° (Table 1). A highly similar relationship was found for the linear regression of H' diversity versus latitude (Table 1), although H' had a significant relationship that explained only 10% of variation. Species richness had a significant positive relationship to abundance ($r^2 = 0.41$; $p < 0.0001$), and abundance was significantly positively related to latitude, but explained very little (4%) of total variance (Table 1). While this study included samples across the depth range of 28 – 138 m, there was no significant relationship of species richness or H' to depth (Table 1), although abundance showed a significant, but weak negative relationship. In relation to water column characteristics, there were significant positive linear relationships of species richness and H' to both bottom DO and bottom temperature, but not for abundance (Table 1). There was no significant relationship of any of the three community descriptors to

bottom salinity (Table 1). Species richness, H' and abundance all had significant, positive linear relationships to upwelling index (Table 1). R was improved (0.58 to 0.83) by a linear fit for mean data only ($n = 5$, $p = 0.042$).

Although variability was high, species richness, H' , and abundance showed significant, convex, curvilinear relationships (Appendix S1, Supplementary Table 1.2 in Supporting Information) to per cent fine sediments, with lower values at both low and high per cent fines, and highest values at intermediate levels (20–60 %). Scatter plots of per cent TOC versus per cent fines in sediments revealed a number of stations with higher than expected TOC for a given per cent fines, and all of these stations, which had TOC >2%, were from the Channel Islands. Excluding these stations, species richness, H' and abundance had significant convex, curvilinear relationships (Appendix S1, Supplementary Table 1.2) to per cent TOC (<2%), with lower species richness at both high and low values of TOC.

The correlation analysis (Appendix S1, Supplementary Table 1.1) indicated that the upwelling index was highly correlated with bottom temperature and so was excluded from the multivariate analysis. Latitude was significantly correlated with 5 of 7 of the other environmental variables and was also excluded. While bivariate analysis suggested non-linear relationships between biotic variables and %fines and %TOC, inclusion of squared terms as independent variables resulted in high levels of multicollinearity and thus were not included in the final model efforts. The multivariate model for species richness (Table 2) included terms for the intercept, infaunal abundance, bottom temperature, and depth, with an overall adjusted r^2 of 0.65. The model for H' diversity (Table 2) included the intercept, depth, bottom temperature, and bottom DO, with an overall adjusted r^2 of 0.4. While bottom DO was included, it contributed very little to overall r^2 for the best fit model for H' . The inclusion of infaunal abundance in the species richness model and not the H' model is consistent with the fact that H' is relatively insensitive to variations in abundance (Sanders, 1968) whereas species richness is not (Gotelli and Colwell, 2001).

3.2 Species distribution patterns

Of the 1470 taxa collected, 383 (26%) occurred in only one sample, and 185 (12.5%) occurred in two samples. There were 264 (17.9%) taxa with a total abundance of 1 individual, and 134 (9.1%) taxa with total abundance of 2. Reflecting the high number of rare taxa, the majority of taxa recorded had limited spatial distribution, whether measured as number of sites occupied by a taxon (999 taxa occurred at <10 stations), or as total latitudinal range (approximately 45% of all taxa recorded were found in a range of <1° latitude; Fig. 2). Numerical dominance was extremely low, with the two most abundant species (*Mediomastus* sp, *Axinopsida serricata*), representing only 3.5 and 3.3 % of total abundance, respectively.

The assessment of range endpoint transitions versus latitude found regions of elevated per cent transition at 33–34°, 37°, 44°, and 46–47° latitude (Fig. 3, Fig. 4, Supplementary Figures 1–3). The highest per centage was at 33° where over 90% of the species collected also had range endpoints there. The 33 and 34° latitude bins include the Channel Islands as well as Point Conception (at 34.5°) (Fig. 5), and the 37° latitude bin corresponds to the region between Año Nuevo and Point Reyes (including offshore San Francisco Bay; Fig. 5).

There was no indication of increased per cent endpoint transitions at 40°, corresponding to Point Mendocino (40.4°) in northern California; in fact, it had the lowest per centage of range endpoints (Fig. 3). More maximum latitudes were found in the 41°N bin and more minimums were found in the 42°N bin (Fig. 4), making the California-Oregon border (42°N) a more likely faunal break. The 44° latitude bin is where the Oregon shelf widens and sandy sediment is found much further offshore, while the 46° bin includes the mouth of the Columbia River (Fig. 5).

3.3 Biogeography of Species Assemblages

Plotting the resemblance among the stations (using only the consistently identified polychaetes, arthropods, and molluscs; 89.6% of all organisms) and coding with MEOW ecoregions on the MDS plane demonstrated a fairly good match between the distribution of the points and the hypothesized matching regions (Fig. 6) but with some overlap of the OWV and NOC stations at the top of the plot. ANOSIM of stations based on MEOW regions gave a significant Global R of 0.62, and all pairwise comparisons were significant as well. The lowest differences (Rs) were between NOC versus OWV (0.417) (Table 3).

In contrast, coding stations according to the biogeographic provinces provided in Blanchette et al. (2008) showed a poorer fit for the mid-shelf organisms, as hypothesized (Appendix S1 Supplementary Fig. 1.4). ANOSIM using these provinces gave a significant but low Global R of 0.386 (Appendix S1 Supplementary Table 1.3), and not all pairwise tests were significant. In terms of adjacent provinces, differences were small between the Mendocinian and Montereyan provinces (break at 37°N; R = 0.280) and between the Southern California and Ensenadian provinces (break at 34°N; R = 0.115). While the greatest difference between adjacent provinces was found between the Montereyan and Southern California provinces (break at 34.45°N; R = 0.428).

Cluster analysis with SIMPROF of the 255 stations resulted in 111 statistically distinct clusters, including singletons (Fig. 7), indicating a high degree of spatial heterogeneity. Slicing the dendrogram at 30% similarity (decision based on major visual clusters) resulted in 35 clusters: 9 multi-station, 7 doubletons, and 19 singletons. In most cases, this resulted in lumping of groups that were statistically distinct as determined by SIMPROF but at least 30% similar in their benthic assemblages. In a few cases, statistically similar groups that were less than 30% similar in benthic assemblages were split (see Appendix S1, Supplementary Table 1.4 for comparisons of the two sets of groupings).

At the 30% resemblance level, the southern California Bight contained 16 total clusters (6 multi-station and 10 singletons). Group Q spanned both the Channel Island and mainland SCB (average depth = 82.7 m, purple dots; Fig. 5) while the remaining Channel Island stations either clustered together into Group O (11 stations, average depth 82.5 m, olive dots) or were less than 30% similar to any other stations (singletons AG, AH, E, F, K, L). The majority of the remaining SCB stations (n = 53) clustered together into the shallower (52.2 m) Group R (green dots Fig. 5) or were doubletons (H, J, P) or singletons (G, I, M, N).

There was little variability along the central and northern California coast. Four of the northern California stations that had been considered part of the MEOW OWV region

clustered with most of the rest of northern California in Group B (39 total stations; blue dots Fig. 5), reinforcing the conclusion that the faunal break may actually be the Oregon-California border. The remaining northern California stations were singletons or the doubleton group U (orange dots, Fig. 5) with much lower per cent fines (Table 4).

The Pacific Northwest regions (Oregon and Washington) hosted 9 different multi-station clusters and two singletons with most of the multi-station groups spanning both states. Group D represents an offshore (average 99 m deep), muddier sediment assemblage (28.8% fines; the highest for the region) that spanned Oregon and Washington, containing approximately half the stations in this region (bright green dots; Fig. 5). Low silt assemblages AA (light blue) and W (light olive) spanned both states (Table 4, Fig. 5). Group AB was a more northern, low-silt assemblage (purple dots; Fig. 5) that spanned 23 Washington stations and 1 in Oregon. In Oregon there was much more species heterogeneity among the low-silt stations (V, X, Y, AC; Table 4), particularly starting at 44° where the shelf widens.

In the cluster analysis, the WA, OR, and northern California stations in the larger outgroup on the right of the dendrogram (Fig. 7) had an average of 5.1% fine sediment with 75% of stations (41/55) in the group having less than 5% fine sediment. In comparison, the rest of the WA, OR, and northern California stations averaged 37% fine sediment with no stations having less than 5% fines. Although these outgroup stations were, on average, shallower (59.0 m) than the other stations (90.6 m), the depth range was not distinct (station depths ranged 28 to 103 m in the <5% group and 40 to 126 m for WA, OR, and northern California stations with > 5% fines). Likewise, although the average values for TOC were lower at the less than 5% fines stations, there was overlap of the range of TOC values between the two per cent fines groups.

Based on high faunal transitions in the 33–34°N and 41–42°N latitudinal bins and the distinct assemblages found in sediments with less than 5% fines, we tested the fit of 7 groups we refer to as supervised habitat-regions (Figs. 7, 8). Major groups were the Channel Islands (CI), the mainland Southern California Bight (SoCal), Northern Californian (NorCal, bounded by Point Conception and the Oregon border) and the Pacific Northwest (PNW, OR and WA). Within those latitudinal boundaries, we considered habitat breaks at the 5% fines delineation (PNW<5, NorCal<5, SoCal<5) for all but the Channel Islands (which did not have any stations with <5 % fines). ANOSIM of this supervised region-habitat classification had the highest significant R-value of the groups tested (0.745). Compared to the MEOW classifications, the differences between northern California and the PNW increased to 0.65 and the greatest difference increased to 0.87 (between Channel Islands and PNW) (Table 5). Within region differences between stations that had more or less than 5% fines were similar in magnitude to differences between regions.

The structuring of the resemblance matrix (on which the cluster and the nMDS analyses are based) was largely driven by the abundances and distributions of polychaetes, with a Spearman correlation of 0.934 between the polychaete and combined macrofauna resemblance matrices. The correlations between both arthropods and molluscs and the

combined dataset were similar (~0.65); however, there was little correlation between molluscs and arthropods (0.352) (Table 6).

The average abundances in each habitat-region of the ten benthic taxa that contributed the most to within region similarities (based on SIMPER analysis) are given in Supplementary Table 1.5. The table also notes Presence (P)/Absence (–) in other regions, indicating general extent of species distributions. While the Channel Islands and the Southern California mainland stations (with >5% fines) had nearly complete overlap of species presence, they shared just four of the top ten characteristic species. SoCal and NorCal stations with greater than 5% fine sediment had similar species present and shared five characteristic species. Regional differences were greater between NorCal and PNW, which shared just three characteristic species, all of which were widespread. There were fewer shared characteristic species between habitats within region. The mainland southern California Bight with less than 5% fines shared only one characteristic species (*Prionospio jubata*) with the rest of the region. Within northern California, the two habitat designations shared only one characteristic species (*Pinnixa occidentalis*). In the Pacific Northwest (OR and WA), five taxa were characteristic of both habitats. Four of these species (*Spiophanes berkeleyorum*, *Axinopsida serricata*, *Ampelisca careyi*, and Euclymeninae sp A) are ubiquitous along the west coast (shared with northern and/or southern California), while *Galathowenia oculata* is the one distinctly PNW species characteristic of both habitats. Within habitats across regions, *Paraprionospio pinnata* was characteristic of silt-containing stations across all regions, while the *Spiophanes bombyx/norrissi* species complex was characteristic of low-silt habitats in both southern California and the Pacific Northwest.

Results of the BEST analysis using all stations and the abiotic variables of latitude, depth, per cent fines, TOC, and upwelling index gave a correlation of 0.610 using all but TOC. Including TOC dropped the correlation. When considering variables in isolation due to their correlation with each other, latitude alone had a higher correlation (0.592) than upwelling index alone (0.570), likely because of the higher resolution of the latitude data. The BEST routine that was run on only the stations for which we had data for all abiotic variables (which excludes most of southern California and the Channel Islands) gave a correlation of 0.591 including latitude, depth, TOC, temperature, and upwelling index. When considering variables in isolation, latitude alone had a higher correlation (0.484) than upwelling index alone (0.442); temperature alone was 0.362.

4. Discussion

4.1 Macrofaunal community patterns

In this study, we found a pattern of declining macrofaunal species richness with increasing latitude up to 40°N, while from 40°–50° latitude, faunal richness showed no trend on the continental shelf of the U.S. west coast. These results confirm the pattern reported by Roy et al. (1998) for gastropod molluscs. Similarly, Ellingsen and Gray (2002) reported no significant relation of species richness to latitude for macrofaunal samples at higher latitudes (56–71° N) along the Norwegian continental shelf, although their samples occurred over a considerably wider depth range (65–434 m) than the present study.

Depth was included in the multivariate regression models of species richness and H' . Similarly, Bergen et al. (2001) and Hyland et al. (1991) both found important relationships of macrofaunal community structure to depth for studies of the shelf fauna in Southern California, but in both cases the depth range of samples (Hyland – 90–565 m; Bergen 10–219 m) was much greater than that in the present study (28 – 138 m). Bergen et al. (2001) found 4 assemblages, one shallow (10–32 m), two deep differing in sediment grain size (115–219 m), and an intermediate depth assemblage (32–115) which would encompass the depth range of the present study. Within the 30–130 m depth range targeted in the current study, depth contributed but was not the largest influence on species richness and diversity at regional scale. This conclusion is also supported by the correlation results of Table 1 for depth, which included the entire set of stations, in contrast to the multiple regression analyses which were restricted to the subset of stations with complete data for all variables.

In our study, regression models suggested that bottom temperature contributed significantly to both species richness and diversity, while sediment parameters were not included. The highest correlations with multivariate assemblage data (BEST analysis), reflecting the overall composition of the benthic faunal communities, also included temperature and depth as well as upwelling, latitude, and sediment parameters. In the BEST analysis, removing latitude lowered the correlation with the assemblage data, indicating that there is latitudinal variability at a scale finer than the upwelling indices we utilized. However, the correlation with temperature was lower than both latitude or upwelling index, indicating temperature alone does not explain the latitudinal variability in community composition. Thus, for shelf macrofauna in the California Current, species richness and diversity patterns appear related to bottom temperature and depth, while community composition patterns appear to be most closely associated with upwelling (of which temperature is one component) and sediment conditions. Blanchette et al. (2008) found that rocky intertidal community composition was significantly correlated with sea surface temperature (SST) independent of latitude. Within the Pacific Northwest region, Henkel and Politano (2017) also found significantly different species assemblages associated with sediment conditions.

4.2 Range endpoints and biogeographic boundaries

The assessment of range endpoint transitions for the mid-depth benthic macrofauna of the continental shelf of the U.S. west coast found evidence for strong faunal transition zones at 33–34° degrees, in the vicinity of Point Conception and the Channel Islands in southern California, and at 46–47° off Washington state, as has been found for molluscs by many previous authors (reviewed in Valentine, 1966 and reported by Roy et al., 2000). Other strong faunal transition zones were found at 37° and 44°. In contrast to the findings of Blanchette et al. (2008) for intertidal fauna, the mainland shelf fauna showed no indication of biogeographic transition within the Southern California bight (Fig. 9), consistent with the results of Bergen et al. (2001).

Point Conception is a well-accepted marine biogeographic boundary for molluscs (Valentine, 1966), marine algae (Abbott & Hollenberg, 1976), and intertidal species assemblages (Blanchette et al., 2008), and as a result was proposed as a general biogeographic boundary for marine species by Spalding et al. (2007). The results presented

herein confirm this as a biogeographic boundary for shelf macrofauna as well (Fig. 9). In addition to the many range end points found here, there were no cluster groups containing stations from both sides of Point Conception.

Although most previous authors did not separate the Channel Islands, we found, as Carson and Hentschel (2006) did for polychaetes, a number of unique macrofaunal assemblages in the northern Channel Islands region (only a single sample was taken from Santa Catalina Island in the south), suggesting an additional biogeographic subregion for subtidal macrofauna which is not detectable using the latitudinal range endpoint approach (Fig. 9). While the most abundant and frequently occurring macrofauna from the Channel Islands were also abundant in the Southern California and present in Northern California regions (Supplementary Table 1.5), there were species that were characteristic of the Channel Islands that differed from the other regions. The distinctness of the island shelf macrofaunal community is consistent with patterns described for the intertidal fauna by Blanchette et al. (2006). The separation of the central and eastern portion of the Channel Islands from the mainland shelf by the deeper waters of the Santa Barbara basin may contribute to the formation of a distinguishable assemblage of shelf macrofauna in this region. Additionally, the Channel Islands represent a transition zone between dominance by different current systems with distinctive characteristics of temperature and DO (Blanchette et al., 2006; Gosnell et al., 2014), parameters which were correlated with species richness at the regional scale, and salinity, which was not. Aíramé et al. (2003) proposed that there are three biogeographic zones present in the Channel Islands, the Oregonian, the Californian, and a Transition zone. While we detected few assemblage differences among the northern Channel Islands at the 30% similarity level, the results of the full SIMPROF clustering are suggestive of the provinces proposed in Aíramé et al. (2003) (Appendix S1, Supplementary Fig. 1.5).

The elevated range endpoint percentage transition at 37° corresponds to the region between Año Nuevo and Point Reyes (including offshore San Francisco Bay). The sediment at stations sampled here and to the south had a lower proportion of fines (average 29.6%) than California stations to the north (average 63.5%). Valentine (1966) also detected a high number of species transitions in the 37° latitude region. Valentine (1966), citing Sverdrup et al. (1942), suggested that Monterey Bay may be an area that provides thermal refuge from the stronger upwelling on the more open coast, allowing thermophiles to extend their range to Monterey Bay, but not beyond, resulting in the high proportion of maximum latitudes detected there. This temperature distinction was seen in our data: temperatures at stations sampled from Point Conception to 37.9° averaged 9.1 °C while California stations from 38° to 41.97° averaged 8.2 °C. While all stations in the northern California region grouped together at the 30% similarity level, there were a number of statistically distinct cluster groups above and below 38°. Thus, the “Montereyan” could be considered a sub-province within northern California, with the boundary being 38° to include Monterey Bay, rather than at 37° as proposed by Hall (1964), Valentine (1966), and Blanchette et al. (2008).

Based on individual species ranges and the assemblage analyses, there was little evidence of a marked transition at 40° as hypothesized by Spalding et al. (2007), which corresponds to Point Mendocino (40.4°) as a coastal feature and the Gorda Escarpment and Mattole Canyon (40.3°) as submarine features. The similar analyses by Valentine (1966, for bivalves and

gastropods) and Roy et al. (1998, for gastropods), which included a comparable latitudinal range on the U.S. west coast, also found no increase in faunal transitions at 40°. Blanchette et al. (2008) also failed to find an intertidal faunal transition at this latitude. Thus, we recommend that the Northern California ecoregion described by Spalding et al. (2007) be expanded north to the California-Oregon border (42 °N) (Fig. 9).

Within the PNW region delineated in this study, the strong assemblage breakpoint at 42° was also detected in the range endpoint analyses, with the 41° and 42° bins having nearly as many range endpoints as 37°. Here again there was nearly a full degree drop in average bottom temperature, with stations from 42° to 48.3° averaging 7.3 °C.

The elevated frequency of faunal transitions at 44° falls in the region of Heceta Bank off the central coast of Oregon, where there is a considerable widening of the continental shelf and sediment with low per cent fines is found much further offshore. This latitude is the initial point where many stations to the north had less than 5% fines, and macrofaunal species assemblages shifted to reflect the sediment transition. In addition to coarser sediment, oceanographic processes associated with the wider shelf on the Heceta Bank result in increased water column productivity in this area (Hickey & Banas, 2003), both factors that are also similar to the environmental conditions in the area north of the Columbia River mouth.

The region at 46–47° includes the mouth of the Columbia River and the Columbia River plume, which flows north over the continental shelf in fall and winter and influences both water column and sedimentary processes (Hickey & Banas, 2003). This area is also just to the south of Cape Flattery (48.4°) at the entrance to the Strait of Juan de Fuca, which possesses a semi-permanent eddy offshore, which influences productivity in the area (Hickey & Banas, 2003). The 30% resemblance group AB was exclusive to the area north of the Columbia river, indicating a more northern sandy assemblage that may be limited from more southerly distribution by the Columbia River. Also potentially contributing to the separation of this group are the many species whose maximum latitudes are limited in their northern extent by either the Columbia River or the Strait of Juan de Fuca.

4.3 Comparison of approaches

The range endpoint approach frequently utilized for biogeographic province assessment (Hall, 1964; Valentine, 1966; Roy et al., 1996, 1998; Engle & Summers, 1999) relies on presence/absence, and uncommon species are given equal weight to abundant species. In contrast, assemblage-based assessments (used here and by Blanchette et al. 2008) minimize the role of uncommon species through data transformation, such that more common and frequently occurring species will more strongly influence outcomes. The degree to which rare species should be considered in determining biogeographic or regional boundaries depends on the objectives of the work. Conservationists might favor equal rating or perhaps even focusing on rare species while investigations focused on ecological functioning may favor approaches that elevate the influence of more abundant taxa.

Examination of the spatial abundance and occurrence patterns for the most characteristic species within the subregions of the west coast shelf (Supplementary Table 1.5) helps to

explain the differences in results from the analysis of range endpoints versus the multivariate community composition. Virtually all of the most characteristic species in each subregion occurred throughout most of the latitudinal range of the study but varied in the pattern of distribution of abundance. Sagarin and Gaines (2002) define four patterns of abundance over a latitudinal range, ramped south, ramped north, abundant edge, and normal. Ramped distribution species have highest abundances toward either the north or south ends of distribution, abundant edge species have highest abundances at both ends of the range, and normal distribution have a peak at some point in the middle of the range. An endemic species with narrow distribution might appear as an extreme case of the normal pattern if plotted over a wide latitudinal range, and a different pattern if examined within 1–2° of latitude. Species in Supplementary Table 1.5 with distributions that appear to be ramped north or south may be found to have normal distributions with wider latitudinal sampling.

Despite these substantial differences in approaches, the range endpoints generally were reflected in assemblage differences. However, a range endpoint analysis using only latitudinal endpoints will not identify important biogeographic breaks that do not correlate with latitude, such as offshore islands. In our analysis, the Channel Islands (which fell within the Southern California Bight region of Blanchette et al. 2008) were more different from the mainland Bight samples than the Bight was to the Ensenadian region to the south, as demonstrated by group O, which was unique to the Channel Islands, and group R, which was absent from the Channel Islands but spanned both the Southern California and Ensenadian provinces of Blanchette et al. (2008) on the mainland coast. It has long been assumed, and in some cases quantified, that oceanic islands and archipelagos are characterized by high rates of endemism (see Kier et al. 2009 for vascular plants) and that terrestrial fauna on islands are unique relative to mainland assemblages (Yoel et al. 2012). Our study suggests that even benthic marine assemblages of offshore islands are unique relative to mainland assemblages within the same latitudinal range.

Understanding current biogeographical boundaries and the processes that drive them are necessary for assessing and forecasting effects of climate/regime change. In our study, upwelling index was the most highly correlated abiotic variable (after latitude) with both the species indices and multivariate approaches. It is predicted (Bakun et al. 2015), and has already in some cases been observed (Sydeman et al. 2014), that atmospheric changes associated with climate change will result in increased intensity of upwelling-favorable wind. Changes in the magnitude and/or timing of upwelling have the potential to either further partition or homogenize existing biogeographic regions.

In the development of biogeographic regions, both Spalding et al. (2007) and Blanchette et al. (2008) considered the organisms and features of the overlying water column but not substrata explicitly. Sediment characteristics have often been found to affect benthic infaunal community patterns (e.g. Rees et al. 1999, Callaway et al. 2002, van Hoey et al. 2004, Schratzberger et al. 2006). It has sometimes been assumed that on a smaller spatial scale, the distributions of benthic species are more closely linked to sediment characteristics and small-scale bottom topography, whereas on larger scales, hydrologic and climatic variables might be more important (e.g. Reiss et al. 2010), although some studies describe both local and large-scale influences of sediment characteristics on macroinvertebrate distributions

(Rodil et al. 2012). In our study, per cent fines was just as highly correlated with species richness and diversity as temperature (Table 1), and some latitudinal assemblage breaks and range endpoints seemed to coincide with transitions in the distributions of sediment type on the shelf. Thus, the sediment characteristics might have both local and large-scale effects, and sediment characteristics should be considered along with features of the overlying water column when defining biogeographic boundaries.

In addition to the strong faunal breaks identified between the ecoregions and major sediment classes, the final habitat-regions determined in this combined approach had low within-group similarities, indicating quite a bit of heterogeneity in species distributions or microhabitats within regions as well. This has important implications for conservation efforts, particularly in place-based approaches such as marine reserves. The 111 statistically distinct clusters from 255 stations indicate that one site within a region is not necessarily representative of other sites in that region. Even within the PNW region, we detected six different multi-station clusters within the <5% fines “habitat” (at the 30% similarity level). This underscores the need for additional studies to determine if those different assemblage groups are functionally different. Such information will be needed in combination with new risk assessment approaches (e.g. Lee et al., 2017) in order to estimate the likely impacts to important system functions as benthic assemblages shift in response to species range adjustments resulting from climate change.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Biosketches

Dr. Sarah Henkel is a benthic ecologist addressing potential effects of human activities (e.g. marine renewable energy installations, marine reserve designations, coastal development, invasive species, climate change) on benthic habitats and organisms. In particular, she is focused on distributions and habitat associations of macro- and mega- invertebrates on the continental shelf and slope.

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Figure 1. Linear regression of sample species richness (number of taxa grab⁻¹) versus latitude for all taxa.

Figure 2. Distribution of taxa range sizes as degrees of latitude where a taxon was recorded for bin intervals of 1 degree of latitude, using n=1470 taxa. Numbers above bars are total number of taxa within a bin.

Figure 3. Percentage of range endpoints (both minimum and maximum latitude) for benthic taxa on the continental shelf of the U.S. west coast occurring within each degree of latitude. Data for bins 32° and 48° latitude are omitted because of limited sampling effort and artificial appearance of endpoints due to being the end latitudes for sampling.

Figure 4. Latitudinal pattern of the range endpoints (minimum and maximum) for taxa identified at least tentatively to species level, binned for each degree of latitude. Rare species may have maximum and minimum within the same bin. Data are restricted to the study samples, and true ranges may extend beyond the latitudinal limits shown.

Figure 5. Stations sampled in 2003 color coded to groups derived from cluster analysis at 30% similarity in species assemblages (Table 4). Substrata (north of 39°) are derived from the Primary Lithology Version 4 base map (Goldfinger et al. 2014).

Figure 6. Results of nMDS analysis of west coast shelf stations coded by MEOw ecoregions. Oregon, Washington, Vancouver Coast and Shelf (OWV), Northern California (NOC), Southern California Bight (SCB).

Figure 7.

Cluster analysis with a horizontal slice (dotted black line) at 30% similarity. Solid lines designate significantly different clusters. Vertical dotted lines connect statistically similar stations. Stations are coded with the supervised biogeographic region-habitat designations. Pacific Northwest (blue filled squares), Pacific Northwest <5% fines (blue open squares), Northern California (aqua filled diamonds), Northern California <5% fines (aqua open diamonds), Southern California (red filled triangles), Southern California <5% fines (red open triangles), Channel Islands (orange triangles).

Figure 8.

Results of nMDS analysis of all stations coded with the seven, supervised region-habitat classifications. Letters indicate the 30% resemblance groups detailed in Table 4. Pacific Northwest (PNW), Pacific Northwest <5% fines (PNW <5), Northern California (NorCal), Northern California <5% fines (NorCal <5), Southern California (SoCal), Southern California <5% fines (SoCal <5), Channel Islands (CI).

Figure 9.
Comparison of biogeographic regions defined by this study (solid coastline), MEOW (hatched boxes) study, and Blanchette et al. 2008 (open boxes).

Table 1.

Matrix of correlation coefficients (r) of community parameters versus geographical or physical parameters. Significance levels: * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$, **** - $p < 0.0001$. Correlation coefficients with sediment characteristics are based on second order polynomial regressions, all others on linear regressions.

	Species Richness	H' Diversity	Abundance	Sample Sizes
Latitude	-0.61****	-0.61****	-0.21**	255
Latitude >40	-0.12	-0.32***	0.12	106
Depth	-0.05	0.09	-0.16*	255
Bottom DO	0.34****	0.30***	-0.02	152
Bottom Temp	0.55****	0.48***	0.15 ^{ns}	164
Bottom Salinity	0.03	0.05	0.12	163
Upwelling Index	0.58***	0.59****	0.24***	255
Per cent Fines	0.55****	0.50****	0.20**	255
TOC (<2%)	0.42****	0.39****	0.25***	234

Table 2.

Best fit, general linear regression models for species richness or H' diversity. Included in both model evaluations were depth, bottom DO, bottom temperature, infaunal abundance, % fines and % TOC in the sediment. AIC (Akaike's information criterion)

Species Richness			H' Diversity		
Model term	Model r^2	AIC	Model term	Model r^2	AIC
Intercept	0.00	1093.22	Intercept	0.00	54.15
Abundance	0.33	1037.35	Temperature	0.25	14.65
Temperature	0.56	981.24	Depth	0.39	-13.07
Depth	0.65	947.97	Bottom DO	0.40	-13.26

Table 3.

Results of ANOSIM analysis based on groupings derived from the MEOW (Spalding et al., 2007) biogeographic regions. Sample statistic (Global R): 0.62; $p < 0.1$. Oregon, Washington, Vancouver Coast and Shelf (OWV), Northern California (NOC), Southern California Bight (SCB).

<i>Pairwise Tests</i>	R Statistic	p	Actual Permutations	Number $\geq$ Observed
OWV, NOC	0.417	0.1	999	0
NOC, SCB	0.551	0.1	999	0
OWV, SCB	0.723	0.1	999	0

Table 4.

Cluster groups (designated by single letters in the first column) with 30% resemblance (and at least 2 stations) based on all macrofauna data and average benthic conditions in the groups. Stations within groups are identified based on the MEOW ecoregions (abbreviations as in Table 3). OWV stations identified as to state location, WA – Washington, OR – Oregon, NorCal – northern California. n.d. – no CTD data

Group	Stations	Depth (m)	% Fines	% TOC	Bottom Temp (°C)	Bottom DO (mg l ⁻¹)
O	11 CI	82.5	30.9	1.53	n.d.	n.d.
Q	19 SCB & 10 CI	82.7	47.3	1.42	n.d.	n.d.
H	2 SCB	71.5	95.6	1.46	n.d.	n.d.
J	2 SCB	33.5	7.55	0.22	n.d.	n.d.
P	2 SCB	47.0	70.3	0.98	n.d.	n.d.
R	53 SCB	52.2	38.8	0.60	12.40	6.30
B	35 NOC & 4 OWV (NorCal)	81.5	48.5	0.69	9.03	3.13
U	2 NOC	67.0	3.3	0.26	8.45	5.66
V	2 OWV (OR)	67.0	2.4	0.10	7.55	3.25
W	3 OWV (1 WA, 2 OR)	56.3	1.6	0.04	7.27	3.30
X	6 OWV (OR)	90.0	2.7	0.15	7.12	2.41
Y	2 OWV (OR)	70.0	1.3	0.08	7.18	2.72
AA	8 OWV (2 WA and 6 OR)	57.3	1.3	0.07	7.41	3.05
AB	24 OWV (23 WA, 1 OR)	49.0	7.2	0.18	7.69	4.40
AC	2 OWV (OR)	51.0	4.0	0.15	7.86	3.78
AD	2 OWV (OR)	60.0	13.2	0.34	8.03	4.07
D	48 OWV (23 WA, 25 OR)	99.0	28.7	0.69	7.07	3.26

Table 5.

ANOSIM results of pairwise comparisons of the seven, supervised region-habitat classifications. Bold rows indicate within-latitude sediment composition comparisons. Between habitat comparisons across regions (e.g. NorCal vs. SoCal <5) are not included. Sample statistic (Global R): 0.745; $p < 0.1$. Pacific Northwest (PNW), Pacific Northwest <5% fines (PNW <5), Northern California (NorCal), Northern California <5% fines (NorCal <5), Southern California (SoCal), Southern California <5% fines (SoCal <5), Channel Islands (CI).

<i>Pairwise Tests</i>	R Statistic	p	Actual Permutations	Number >= Observed
CI, SoCal	0.41	0.1	999	0
CI, NorCal	0.76	0.1	999	0
CI, PNW	0.87	0.1	999	0
SoCal, NorCal	0.65	0.1	999	0
SoCal, PNW	0.84	0.1	999	0
NorCal, PNW	0.65	0.1	999	0
SoCal, SoCal <5	0.64	0.3	999	2
NorCal, NorCal <5	0.84	0.1	999	0
PNW, PNW <5	0.58	0.1	999	0
NorCal <5, PNW <5	0.77	0.1	999	0
SoCal <5, NorCal <5	0.68	6.7	15	1
SoCal <5, PNW <5	0.82	0.1	741	1

Table 6.

Correlation coefficients among major taxonomic groupings for the resemblance matrices.

	Arthropods	Molluscs	Polychaetes
All	0.648	0.655	0.934
Arthropods		0.352	0.495
Molluscs			0.484