Spatial Patterns and Temporal Trends in Shoreline Biota in Puget Sound: Analyses of Data collected through 2004

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OBJECTIVES

This project has continued to examine the spatial and temporal variability of shoreline biota in southern and central Puget Sound, using the Shoreline Classification and Landscape Extrapolation (SCALE) model. We now have a dataset including over 40 sites throughout the Sound, and extending over 6 years at some sites. These data provide an unusual opportunity to examine spatial and temporal variation. In particular, the estuarine gradient along the north-south axis of Puget Sound allows us to examine whether variability depends on background diversity (since the northern sites are much more diverse than the southern), and whether temporal variability is greater in more-estuarine or more-marine environments.

The following report summarizes analyses to address 5 questions of this type. Methods of data collection and analysis generally follow the same protocols used in previous reports. One exception in the analytical protocols is that most multivariate analyses were run using Primer 5 software, and were run on complete, untransformed datasets (i.e. not removing rare species, and not using square- or 4th-root transforms). Clarke and Gorley (2001) recommend against omitting rare species for standard among-sample analyses, as the presence of these species does constitute real data, and untransformed datasets will naturally show these as being of relatively minor importance anyway. Several of the following tests were run with different versions of the datasets, some with rare species removed and some with transformations; in each case, no substantial differences existed in the statistical strength or the visual clarity of the patterns found.

QUESTIONS AND ANALYSES

1. East/West Patterns

Previous analyses of the biota of East-versus-West Puget Sound pebble beaches suggested that there were no clear cross-sound differences (Dethier et al. 2003). Using a dataset that includes more than one year, does an East/West pattern become visible, or does there still seem to be no consistent pattern across this gradient? We now have a dataset that includes 8 sites in central Puget Sound (4 east and 4 similar-latitude west) sampled both in 2001 and 2002, at high resolution. These sites also encompass a considerable north-south gradient (Hansville and Possession to Maury and Redondo: Figure 1), allowing us to examine variation along that gradient.

Figure 2A shows a multidimensional scaling (MDS) plot for the 8 sites and 2 years, coded for whether they are on the east versus west side of central Puget Sound. No pattern is visible here; the east and west sites entirely intermix in ‘species-space’, showing that the biota are not consistently different based on this parameter. When the same data are examined with the sites coded for placement along the north-south axis, however, a pattern becomes visible (Fig. 2B); the more-southern sites (both years) are generally to the lower right, and the northern sites generally to the upper left of this
diagram. Note that there is a clear outlier: Hansville beach 2 from 2002. The main probable contributor to this anomaly is visible in Figure 3A, which shows the same data but with “bubbles” indicating the amount of sand (average percent cover among the 10 surface quadrats per beach). The striking pattern here is that the high-sand samples clearly group together at the right of the graph regardless of their location or year. Also note that Hansville 1 (2001), in the upper center, had much sand (large bubble) in that year, but the biota were still fairly typical for the area (i.e. that point grouped with the other Hansville 2001 points). By 2002 the sand wave had moved on from that beach (small bubble, far left side) but the biota were left atypically depauperate, making the biota of that beach an outlier relative to the other Hansville sites. In 2002, Hansville 2 had the largest amount of sand seen in any of the samples (far right side) and the biota were quite anomalous. These examples re-emphasize the important role of sand on these pebble beaches, as noted previously. To be certain that listing sand as a “species” in this database was not driving the biota pattern illustrated, I re-ran the MDS analysis omitting sand, but the patterns of site-years were virtually identical (including the two Hansville outliers).

The potential roles of various physical parameters besides sand in driving community structure were examined using a dataset of location (latitude and longitude), nearshore salinity and temperature (as measured on each June sampling date), and porewater salinity and temperature (likewise measured during June sampling) for each beach. Some strong correlations, not surprisingly, exist among these parameters. For example, nearshore salinity and temperature are strongly negatively correlated ($r = -0.786$), and there are fairly strong correlations (ca. 0.3) between longitude and nearshore salinity and temperature (with lower salinity and higher temperature on the east side, as discussed in Dethier et al. 2003). Perhaps more surprisingly, porewater salinity increased with latitude (higher salinity at the northern sites).

The separation of sites in terms of their physical parameters was examined with a Principal Components Analysis, illustrated in Figure 3B. All the variables measured appear as correlated with at least one PC axis, but the ones more important in driving the two axes illustrated are (for PC1) decreasing nearshore salinity, increasing nearshore temperature, and easterly longitude; for PC2, decreasing porewater salinity, increasing sand, and decreasing latitude. Together, these two axes account for 59% of the variation in physical parameters among sites. Several interesting anomalies again appear on this graph. For example, po1 (Possession 31), at the mouth of Possession Sound is separated from the other two Possession sites by having consistently warmer and lower-salinity nearshore water readings. Perhaps not surprisingly, the biota at these beaches (most readily visible in Figure 4A) is more similar to that of beaches further to the south (Jefferson and Carkeek) than to the other Possession beaches. Maury beaches 2 and 3 (2002 only) also appear isolated from other Maury readings in the PCA, but in this case only 2002 had warmer and lower-salinity water. The lack of chronic conditions like this may have kept the biota from being ‘pulled’ away from the other Maury biota points (Figure 2B).
The BIOENV routine in Primer seeks to further link biotic with environmental data by computing correlations between the biota matrix and a variety of environmental matrices. For these data, a BIOENV analysis suggested that the three most important physical variables (i.e. those with the strongest correlations) are abundance of sand, latitude, and longitude. Surprisingly, nearshore salinity did not show up as an important parameter even when 5 variables were considered at once. However, since salinity correlates with longitude, its importance could be statistically subsumed in that variable. Porewater salinity also appeared as moderately important (4th, after the previous 3 parameters).

ANOSIM tests compare the biotic data from different sites grouped by particular factors, illustrating the relative strength of each grouping variable in terms of explaining overall site-to-site variation. Table 1 lists the Global R and p values for each grouping variable for this dataset. Global R = 1 if all replicates (e.g. years and beaches) within sites are more similar to each other than any replicates from different sites; Global R = 0 if similarities within and between sites are the same, on average (thus generating a complete lack of spatial pattern in the graphed multivariate analyses). While all grouping variables tested are significant, the great variation in the R values shows that some are much more important than others; sites (looking across the 3 beaches and 2 years per site) are the strongest generator of pattern, illustrating that the biota of sites are fairly consistent among beaches and among years. When sites are grouped along the north-south gradient (into 4 categories, paired across the Sound), this gradient explains a moderate amount of the variance among sites (as discussed above). Pairwise comparisons showed all 4 North-South groups to be distinct from each other, although the R value for the 2 sets of central-sound sites (Blake, Brace, Carkeek, and Jefferson) was low. The East/West grouping has a very low R value, illustrating the relative lack of pattern generated by that categorization. The Years factor had an intermediate R value, showing that there is variation among years but not as much as among sites or latitudes. Pairwise combinations of all sites (pooled across years) showed that only 6 out of 28 combinations were not different; all of these involved comparisons with either Brace or Blake, which are very much “central” in this sense.

SIMPER analyses allow consideration of the species-level patterns contributing to these site groupings. Extensive study of these patterns was not possible at this time, but it appears that the “central” sites are a sort of average for the sound in terms of species. They have average or high abundances of all the common flora and fauna: ulvoids, Lottia, crusts, barnacles, Lacuna, gammarid and sphaeromid crustaceans, Notomastus, and sand. Sites to the south tend to have fewer species and fewer individuals of the common species; sites to the north tend to add more species or many more individuals of some species (like Lacuna).

2. Long-term temporal patterns

Previous data analyses have suggested that the biota of beaches changes to some degree from year to year, but that in general among-year differences are smaller than among-site differences. Does this pattern hold true for longer time series? Can we use
long time series to see unusual changes in biota at particular beaches? Two datasets allow us to address these questions: a dataset with two sites (Brace and Possession) examined over the identical five-year period, and one with 4 sites (Budd, Case, Carkeek, and Possession) examined over a different set of 5 years. The latter dataset also allows us to address Question 5, below.

Figure 4A illustrates the MDS plot comparing Brace and Possession over the years 1999 to 2003. As Brace is characteristic of the central sites in Puget Sound, as shown above, and Possession of the most northern of our regularly sampled sites, it is not surprising that these 2 sites separate readily in the ordinations. Within these broad site clusters, the years-among-beaches are quite intermixed; e.g. the Possession 33 (black points) data points from different years do not necessarily cluster together. However there is some tendency, especially for Possession, for the 3 beaches from each year to cluster together (especially the 1999 data: Fig. 4B); the Brace beaches tend to be further spread per year, probably because they were not as good ‘replicates’ of each other as were the Possession beaches. This suggests that in some cases the biota of all beaches at a site tend to ‘shift’ together among years (i.e. the biota change in similar ways at all three beaches), especially when the 3 replicate beaches are actually quite similar to each other, as they are at Possession.

The biotic communities of the Brace beaches were also examined in isolation, to examine year to year differences in more detail. This was of interest because one of the beaches (Brace 3 = North) was nourished with sediment by the Army Corps of Engineers prior to our 2003 sampling. While this nourishment largely consists of sediments dumped higher on the shore than our sampling area at MLLW, it is possible that some sediment would be washed downshore and affect the biota. Figure 5 illustrates the ordination of the three Brace beaches over 5 years. For this site (unlike Possession, above), the beaches clearly cluster better by location than by year; all 5 years for Brace 1 are on the left, for Brace 3 on the right, and for Brace 2 in the middle. A Multiple Response Permutation Procedure (see Glossary in Dethier and Schoch 2000) shows that the points group well by beach (p < 0.001) but not by year (p = 0.302). Looking at year to year changes in the biota at each beach (e.g. by connecting the points per beach in Figure 5) again shows some tendency for the biota to change in similar directions among years, at least during some time periods – e.g. from 2002 to 2003. Brace 3 (2003), the nourished beach, thus was not clearly different from the 2 replicate beaches at this site, in that datapoints for all three beaches are at the top of the ordination.

The dataset illustrated in Figure 6 encompasses beaches from 4 more broadly spaced areas (Budd, Case, Carkeek, and Possession) each sampled over 5 years (1999, 2000, 2001, 2002, and 2004). These plots generally show similar patterns of greater among-area differences than among-year differences. All the year-points except those for Case group fairly tightly within each site. However, the points for all 3 Case beaches, especially Case 18, are spread broadly across the plot, indicating high beach-to-beach and year-to-year variation. The data for Case 18 show large variation in the amount of sand along the transect (although this was not quantified prior to 2000); the outlier point Case 18 (2004), at the top of the graph, had the most sand of any of the points. When the MDS is rerun...
minus the Case sites (Fig. 6B), the patterns for the other 3 sites are more visible. They again show moderate variation within sites among years, but overall the biota remains more similar among years within a site than among sites.

3. Patterns visible with Low Resolution Data

Some of our previous analyses have shown that using low resolution biotic data (generally functional groups for algae, readily-recognizable taxa for invertebrates, and family-level groups for infauna) still allows the resolution of spatial patterns, e.g. the differences among northern versus southern pebble beach communities. How well do low-resolution data allow us to distinguish broad patterns as well as local spatial or temporal outliers? Figure 7 shows MDS plots for 5 sites sampled at low resolution over 3 years. The biota at the 3 more-southern sites (Seahurst, Blake, and Brace) show a high degree of similarity, while the northern Possession sites are relatively distinct. The Hansville sites varied greatly among years, as discussed above and shown in Figure 2; the outliers visible at high resolution-sampling in Figure 2 still appear as outliers at low resolution (e.g. 2002 samples at Hansville 1 and 2). Even when sand is removed from analysis of the ‘species’ list, these points remain outliers (Fig. 7B). ANOSIM tests (Table 2) show that all sites except Brace and Seahurst are distinguishable statistically, although all the R values for the more-southern comparisons are relatively low. More extensive analyses of spatial patterns vs. taxonomic resolution are discussed in Dethier and Schoch (in review).

Analysis of the physical data for this set of beaches and years generated the PCA plot in Figure 8. Together, axes 1 and 2 of the PCA accounted for 56% of the physical variation among sites. PC1 correlated most strongly with decreasing nearshore salinity, increasing nearshore temperature, and increasing longitude; thus the western sites of Hansville and Blake are on the left, where the temperatures and salinities are more marine, and the low-salinity Possession 1 (as discussed for Fig. 3B) is far to the right. PC2 correlates primarily with decreasing latitude, so that all the more southern sites are to the top. As in the analyses for Question 1, the BIOENV procedure (which analyses the best physical predictors of the biota in the biotic data matrix) found little relationship between either nearshore temperature or salinity and the biota in this dataset; the best predictors were amount of sand, longitude, latitude, and the salinity of the porewater. The similarity of this result with that discussed in Question 1 probably stems from the high overlap of sites (4 out of 5 or 8) in the two datasets.

The other low-resolution dataset examined contained more sites (8) and spanned a larger region, including two South Sound sites. Most sites were actually sampled at high resolution in most years (1999, 2001, and 2004), but 3 of the 8 sites were only sampled at low resolution in 2001. Figures 9A and 9B compare the datasets from the high-resolution sampling (omitting the site-year combinations done only at low resolution), and the low-resolution sampling containing all 24 site-year combinations (with 3 beaches per site, in each case). The degree of separation of sites, as illustrated by the Stress value, is identical in the 2 analyses, and virtually identical spatial patterns are visible. As discussed above, the Case biota (“s18, 19, and 20”) are real outliers in both analyses, indicating very
different flora and fauna from other sites at all sampling dates. SIMPER analyses show that these differences derive from Case having fewer ulvoids, capitellids, isopods, amphipods, and other algae compared with all the other sites, and more Littorina, Pagurus, live barnacles, and Hemigrapsus. These patterns suggest that the Case sites are functionally higher on the shore than all the other sites, but it is not clear why this should be the case.

Figure 10 shows the same MDS analysis of the data but with the Case sites omitted, to make it easier to see the patterns among the other sites. Even though this is low-resolution data, it is easy to see separation of sites among the different portions of the sound (plotted as different colors). ANOSIM tests on the different groupings in the data show that the Global R values are highest for Sites, high for north-south groupings (illustrated in Figure 10A), and least high for years (Table 3). For sites, all pairwise comparisons are significantly different except for some of the adjacent sites in Central Sound. For years, 2001 and 2004 were not significantly different overall.

Figure 10B shows the same MDS plot as Figure 15 but with the abundance of sand plotted as bubbles. Note that sand was not quantified in 1999 (or in Budd in 2001). Again the importance of this one physical variable in separating sites and years is visible, with all of the high-sand beaches on the left side of the plot.

Finally, Figures 11A and 11B show a simple comparison of just the Carkeek beaches, over 3 years, at high and low resolution. The stress values and placement of points in the MDS plot are virtually identical, i.e. it is equally easy to see the spatial separation of the different years at both levels of resolution. Note that this pair of graphs also illustrates the commonly seen pattern of the biota of all 3 beaches ‘shifting’ in the same direction among years, so that the years-among-sites group together better than the sites-among-years.

4. Overall patterns of site groupings

We now have data for many sites over many years. Overall, what sites are consistently similar to versus different from each other? Examination of the various datasets analyzed in this report shows that the south-central sites discussed in Question 1 consistently group together; this is especially true for Brace, Blake, and Redondo (e.g. see Figure 2), which are not significantly different in ANOSIM analyses from the 8 sites, 2 years analyses. Maury and Carkeek are also similar to these sites. Another site that tends to group with these is Seahurst, visible in the 5 sites, 3 years database (Table 2). A third dataset adds other sites to this central cluster: Brown (very similar to Normandy), and West Point (Table 3). Looking further north, Carkeek is very similar to Edmonds. Clearly these similarities run along a continuum from south to north in central sound; as described before, sites near each other are very similar (and these patterns hold through time), but comparing sites near the northern and southern ends of central sound shows significant differences (e.g. between Brown and Carkeek).
5. Patterns of temporal variability

De Biasi et al. (2003) noted a pattern of communities in the more-marine parts (i.e. near the mouth) of a Mediterranean estuary being less temporally variable (showing more ‘drift’ through time) than communities in more-estuarine parts. They did not discuss possible reasons for this pattern. Does such a pattern of greater temporal variation in more-marine areas exist for the Puget Sound data? Figure 12 shows the MDS plot comparing year to year variation (over 5 years) at Budd, Carkeek, and Possession, with points coded for individual beaches. If year to year variation was higher at the more marine sites, there should be greater spread among the 5 points of any one northern symbol (e.g., symbols 7, 8, and 9) than among the southern symbols (e.g. 1, 2, and 3), with the other beaches in between. No such consistent pattern is visible; individual beaches at each site show different amounts of variation (e.g. the Budd 4 beaches are more variable than the Budd 5), with no greater degree of spread in the northern than in the southern sites. Figure 13A illustrates a different dataset; for this, I pulled one beach (the southernmost one: using all 3 beaches makes the graph uninterpretable) from each of 7 sites (from the Low Resolution 8 sites x 3 years dataset, minus the anomalous Case data). This graph suggests that the spread among the points for the more-northern beaches (Carkeek, Edmonds, and Possession) may be somewhat lower than that among the more-southern ones (Budd, Brown, and Normandy). West Point, however, which is a central site in this series, had very low year to year variation. When these data are $4^{th}$-root transformed, thus down-weighting the importance of the very abundant species to overall similarity and increasing the relative importance of the rarer species, this pattern is even clearer (Fig. 13B). The northern sites are richer and tend to have more low-abundance species; these plots suggest that these species remain fairly consistent from year to year, ‘pulling’ the points closer together. The southern sites have fewer uncommon species, and the ones they have may be less temporally predictable, leading to the broader spread. These patterns deserve further analysis.

CONCLUSIONS

1. Despite the physical differences in temperature and salinity between the east and west sides of the Central Sound, no clear differences in biota exist when 2 years of high-resolution data are examined. North-South patterns remain and override any east-west trends, even when South Sound sites are not considered. The south-central sites are all quite similar to each other in a variety of analyses, with gradually increasing dissimilarity as one moves north along this geophysical continuum.

2. The abundance of sand per beach, either chronically (e.g. in Case sites) or as occasional ‘waves’ (e.g. in Hansville and Normandy south) is a major driver of biotic community structure on these pebble beaches.

3. Variation in biota from year to year within a site, while fairly high, remains lower than variation among sites, especially when sites farther apart are compared (e.g. north-central versus south-central sound). Replicate beaches within a site often “shift” together in biota from year to year. For some sites, beaches are more
similar to themselves from year to year than to their ‘replicate’ sites. Beaches that are clearly better replicates of each other (e.g. at Possession or Carkeek) cluster together better by year, whereas the less-well-replicated beaches (e.g. at Brace) cluster better by beach than by year.

4. Low resolution data (generally functional groups for algae, readily-recognizable taxa for invertebrates, and family-level groups for infauna) remain a valid way to distinguish most spatial and temporal patterns visible in the high-resolution dataset, including north-south patterns, and beach-year data points that are outliers in multivariate analyses.

5. Other physical variables (besides percent sand) that show up as important drivers of spatial patterns in the analyses are longitude and latitude (presumably because they correlate closely with nearshore salinity and temperature, and latitude probably with wave energy), and porewater salinity (i.e. that actually experienced by the infauna).

6. Further analyses need to be done on the question of whether more-marine communities (i.e. those closer to the mouth of the Sound) tend to be more or less temporally variable than more-estuarine ones. Our data suggest that the marine communities are less variable (in contrast with some other literature), especially when the importance of the very common (and abundant) species is down-weighed analytically. The less-common species found only in the north may be quite consistent from year to year, driving community similarity over time.

REFERENCES


Table 1. Results of ANOSIM tests for the Question 1 dataset (8 sites over 2 years), illustrating the relative importance of different grouping variables. Larger Global R values indicate a greater importance for that factor in generating the pattern visible in the biotic multivariate analysis.

<table>
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<tr>
<th>Grouping Variable</th>
<th>Global R</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site (lumping years)</td>
<td>0.388</td>
<td>0.001</td>
</tr>
<tr>
<td>North to South</td>
<td>0.258</td>
<td>0.001</td>
</tr>
<tr>
<td>S vs S-Central</td>
<td>0.163</td>
<td>0.007</td>
</tr>
<tr>
<td>S vs N-Central</td>
<td>0.355</td>
<td>0.002</td>
</tr>
<tr>
<td>S vs N</td>
<td>0.431</td>
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<tr>
<td>S-Central vs N-Central</td>
<td>0.158</td>
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<tr>
<td>S-Central vs N</td>
<td>0.213</td>
<td>0.001</td>
</tr>
<tr>
<td>N-Central vs N</td>
<td>0.222</td>
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<tr>
<td>Year (lumping sites)</td>
<td>0.104</td>
<td>0.004</td>
</tr>
<tr>
<td>East vs. West</td>
<td>0.055</td>
<td>0.045</td>
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</table>
Table 2. Results of ANOSIM tests for the Low resolution dataset covering 5 sites over 3 years (Figure 1), illustrating the relative variation in biota among pairs of sites. Larger Global R values indicate a greater importance for that factor in generating the pattern visible in the biotic multivariate analysis.

<table>
<thead>
<tr>
<th>Groups</th>
<th>R</th>
<th>Significance</th>
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<tbody>
<tr>
<td>Blake, Brace</td>
<td>0.159</td>
<td>0.039</td>
</tr>
<tr>
<td>Blake, Hansville</td>
<td>0.358</td>
<td>0.001</td>
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<tr>
<td>Blake, Possession</td>
<td>0.452</td>
<td>0.001</td>
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<tr>
<td>Blake, Seahurst</td>
<td>0.352</td>
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<tr>
<td>Brace, Hansville</td>
<td>0.299</td>
<td>0.004</td>
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<td>Brace, Possession</td>
<td>0.38</td>
<td>0.001</td>
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<tr>
<td>Brace, Seahurst</td>
<td>0.053</td>
<td>0.17</td>
</tr>
<tr>
<td>Hansville, Possession</td>
<td>0.484</td>
<td>0.001</td>
</tr>
<tr>
<td>Hansville, Seahurst</td>
<td>0.33</td>
<td>0.002</td>
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<tr>
<td>Possession, Seahurst</td>
<td>0.448</td>
<td>0.003</td>
</tr>
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</table>
Table 3. Results for Analysis of Similarity tests for the 7 sites, 3 years Low Resolution dataset (plotted in Figure 15).

<table>
<thead>
<tr>
<th>Factor</th>
<th>Global R</th>
<th>p value</th>
<th>Pairwise tests</th>
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</thead>
<tbody>
<tr>
<td>Sites</td>
<td>0.468</td>
<td>0.001</td>
<td>All significant except Brown = Normandy, Carkeek = Edmonds, and Brown similar to West</td>
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<tr>
<td>North-South Groups</td>
<td>0.440</td>
<td>0.001</td>
<td>All significant</td>
</tr>
<tr>
<td>Years</td>
<td>0.180</td>
<td>0.001</td>
<td>Significant except 2001 = 2004</td>
</tr>
</tbody>
</table>
Figure Captions

Figure 1. Map of the study sites discussed in this report.

Figure 2. Multidimensional scaling (MDS) plot of community similarity (Bray-Curtis, untransformed) for 8 sites in central Puget Sound in both 2001 and 2003, four on the east side and 4 on the west. From south to north, the sites are: ma = Maury (W), re = Redondo (E), br = Brace (E), bl = Blake (W), ca = Carkeek (E), je = Jefferson (W), po = Possession (E), and ha = Hansville (W).

Figure 3. A) Same MDS plot as in Figure 2 but with site points sized by the amount (percent cover) of sand in surface quadrats. B) Plot of the first 2 axes of the Principal Components Analysis (PCA) using a dataset of measured physical parameters at each site. PC1 correlates primarily with decreasing nearshore salinity, increasing nearshore temperature, and easterly longitude; PC2 correlates with decreasing porewater salinity, increasing sand, and decreasing latitude.

Figure 4. A) MDS plot of the biota of 3 beaches at Brace and 3 beaches at Possession, over the same 5 years (1999-2003), with points coded by individual beaches. B) Same MDS, with points coded by years.

Figure 5. MDS of the biota of just the 3 Brace beaches over 5 years, to compare among-beach versus among-year variation.

Figure 6. MDS plot of community similarity of A) 4 sites over 5 years, and B) the same 5 years but with Case beaches omitted to clarify the patterns among the remaining sites.

Figure 7. A) MDS of low-resolution biotic data from 5 sites over 3 years. B) The same dataset, but with sand omitted as a ‘species’.

Figure 8. Plot of the first 2 axes of the Principal Components Analysis (PCA) using a dataset of measured physical parameters at each site. PC1 correlates primarily with decreasing nearshore salinity, increasing nearshore temperature, and easterly longitude; PC2 correlates primarily with decreasing latitude.

Figure 9. MDS plots comparing similarity of biota from 8 sites using high-resolution versus low-resolution level of identification. The plot in A) omits the 3 (of 24) site-year combinations where high resolution sampling was not done.

Figure 10. MDS plot of the same analysis as in Figure 9 but with Case omitted. A) Coded for north-south location; B) coded for amount of sand (sand data were not collected at any sites in 1999, or at Budd in 2001).

Figure 11. MDS plot of just the 3 Carkeek beach segments, over 3 years, comparing high-resolution and low-resolution analyses.
Figure 12. MDS plot of the biota at Budd, Carkeek, and Possession over 5 years, with points coded as individual beaches (i.e. the 5 green points labeled “1” in the key are the 5 years at Budd 4).

Figure 13. MDS plot of the biota of southern beach segment of each of 7 sites (e.g. Budd 5, Brown S, etc.) over 3 years. A) Untransformed data. B) 4\textsuperscript{th}-root transformed data, down-weighting the importance of abundant species.
Figure 1.
A. 8sites EW 2years

B. 8sites EW 2years

Figure 2.
**A. 8 sites EW 2years Sand Bubbles**

Figure 3.
A. Brace & Possession, 5 yrs

B. Brace & Possession, 5 yrs

Figure 4.
Figure 5.

Brace 5 yrs (Sqrt Transform)

Stress: 0.11

Brace 1
Brace 2
Brace 3
Figure 6.
A. Low Resolution 3 yrs 5 sites

B. Low Resolution 3 yrs 5 sites, Sand Excluded

Figure 7.
Figure 8.
A. High Res 8 sites 2-3 yrs

Stress: 0.18

South

S-Central

N-Central

North

B. Low Res 8sites 3yrs

Stress: 0.18

South

S-Central

N-Central

North

Figure 9.
Figure 10.
A. Carkeek High Res 3 yrs

B. Carkeek Low Res 3 yrs

Figure 11.
Figure 12.
A. Low Res, 1 beach/site, 3 years

B. Low Res, 1 beach/site, 4th root transform

Figure 13.