The Shoreline Biota of Puget Sound: Extending Spatial and Temporal Comparisons

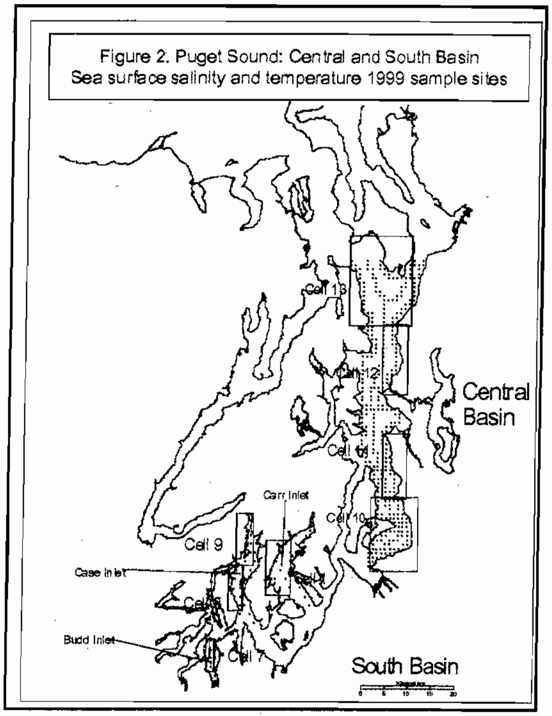
Figure 2. Puget Sound: Central and South Basin
Sea surface salinity and temperature 1999 sample sites

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EXECUTIVE SUMMARY

Many ‘user groups’ have a stake in the marine habitats and natural resources of Puget Sound, and could benefit from a comprehensive and detailed map of shoreline and shallow-water habitats. In addition, various state and local agencies are trying to find ways to determine the ‘health’ of Puget Sound and to quantify changes through time, both of which require baseline information or data from pristine areas. At present, there are no maps or databases of biota at a fine enough detail to study such patterns, and gathering this level of information for such a large area is daunting. As contractors for the Department of Natural Resources’ Nearshore Habitat Program, we have been refining and testing a method for gathering habitat information in a cost-effective yet detailed manner. This methodology is called SCALE (Shoreline Classification and Landscape Extrapolation). At its core is the fact that most marine organisms, including seaweeds, seagrass, invertebrates, and fishes are linked rather tightly to their physical environment, including such factors as salinity, wave or current regime, and substrate type (i.e. rock versus sand versus mud). Thus detailed mapping of the physical habitats in an area should provide us with information on the biota inhabiting (or potentially inhabiting) that area. In this way, by linking geophysical attributes of ecological importance to the associated biota, we can make inferences (extrapolate) about communities over large areas of shoreline. Labor-intensive biological sampling can be thus be limited to a random subset of each habitat type in each region.

Previous, related projects involved testing the SCALE methodology in Carr Inlet (South Puget Sound Basin), studying the shoreline biota at 3 intertidal levels and in 4 different substrate types; we classified the entire shoreline of this bay in 1997, and found a strong linkage between the geophysical features and the flora and fauna (Schoch and Dethier 1997). In 1998, we looked further at spatial and temporal variability in shoreline biota in South Sound (Schoch and Dethier 1999). We tested 1) temporal variability, by resampling a subset of the Carr Inlet beaches; 2) our ability to extrapolate our results within Carr Inlet by sampling new sets of beaches of the same habitat types; and 3) the applicability of our results at a larger spatial scale and in slightly different oceanographic regimes, by sampling beaches in Case and Budd Inlets.

The overall objective of the 1999 SCALE sampling of low-intertidal pebble beaches of Puget Sound was to extend our previous work testing patterns of spatial and temporal variability in shoreline biota. This was accomplished by returning to the South Sound beaches sampled in 1998 to test for temporal stability, and by extending sampling along the entire eastern side of Central Puget Sound. The latter work enabled us to test not only basin-level differences (South vs. Central Sound), but also within-basin differences along the extensive Central Sound shoreline. The waters of Central Sound vary in temperature, salinity, and wave energy along and across the axis of the basin. Our nested sampling design allowed us to test the role of these physical forcing functions in controlling the shoreline biota in this estuary. The result is a dataset unique in its geographic breadth, statistical rigor, and use of consistent methodology.

The nested sampling design for the 1999 sampling looked at biota at three spatial scales: replicate beaches within ca. 1 km areas (with relatively uniform substrate type and wave energy), replicate areas within 1-10 km oceanographic cells (with relatively uniform temperature and salinity), and replicate cells within broad basins (Central vs. South Puget Sound). The hypothesis was that benthic communities of algae and invertebrates would be decreasingly similar at these increasing spatial scales.

Overall, the SCALE methodology allows an unusually clear view (compared with other estuarine studies, where substrate and other variables are not held constant) of patterns of variation in species' distributions and richness along a wide range of spatial scales. As seen before in South Sound, variation in the composition of shoreline biota increases with increasing spatial scales. Species found in beach segments within an area are very similar, areas within an oceanographic cell are less similar, and areas in different cells are even less similar. And, as anticipated, there are substantial differences in biota between beaches in the South and Central Sound basins.

Correlations of differences in biota with differences in physical features among sites (e.g., in wave energy, salinity, temperature, percentages of different substrate grain sizes) provide clues about the key driving forces affecting the biota at different spatial scales. Within a beach (i.e., among quadrats and cores), small-scale variation in grain sizes and pore-water characteristics are probably important. At larger spatial scales, the analyses clearly indicate that wave energy (as quantified by wave fetch and beach slope) and salinity are important determinants of community structure. For example, the ordinations suggest that the key difference among basins (South Sound vs. Central Sound) is wave energy, and that within each region salinity and energy differences correlate the most highly with differences in biota. This agrees (but with much greater rigor) with previous estuarine studies emphasizing the role of salinity. The strength of these correlations means that for a pebble beach sampled in 1999 on the east side of Puget Sound, if salinity and energy are measured, we can predict with a 70% probability the taxa and their abundances that can be expected in those communities.

The data suggest that the 'basins' of Puget Sound represent parts of a continuum, not a real break; few biota show abrupt transitions in abundance between the South and Central basins. Both the quadrats (surface biota) and the cores (infauna) show striking patterns in species richness from the south to the north within Puget Sound; as one proceeds towards higher-salinity, and higher-energy environments, the number of species per beach increases.

A similar trend is seen in the abundance of juvenile clams, which were virtually absent in all the South Sound sites in 1999, but increasingly abundant to the north. Since all the sites were clearly appropriate for clams (as witnessed by the presence of adults), the pattern for juveniles may relate to differences either in larval transport/distribution, or survival of juveniles in the sediment (e.g., as related to salinity fluctuations, predation, desiccation, etc.).

As found in earlier reports and in other estuarine studies, inter-annual variation in biota is high. However, while temporal variation within the biota of a beach can be expected from one year to the next, the replicate beaches within an area tend to remain similar to each other. Thus quantifying anthropogenic change will require finding a pattern in the data where one beach (or area, or even cell for very large-scale changes) deviates from other replicates monitored at that same spatial scale.

Despite numerous methodological differences between studies, it is possible to qualitatively examine patterns of species' distributions and abundances between 'historical' surveys in the 1970s and 1980s and SCALE surveys. Overall, these surveys show a high degree of overlap in flora and fauna when beaches of similar location, tidal height, and substrate type are compared. Substantial similarity was seen both in epibiota and infauna at most sites. Species that did not appear to be similar can often be explained by differences in sampling methodology, e.g. the historic surveys often used smaller sieve sizes (thus capturing more tiny infauna such as spionid polychaetes) and involved sampling deeper into the substrate (thus finding more adult clams). In both SCALE and historic surveys, certain species tended to appear only in more northern beaches, or only at certain sites.

A major exception to trends in richness, and to similarity between historic and SCALE surveys, was in the beaches near Point Wells. These beaches had much lower richness and many fewer juvenile clams than those to the north and to the south. In addition, many taxa found commonly in the historic surveys from these sites (as well as found to the north and south in the 1999 surveys) are conspicuously missing. Possible causes of these absences include pollution from the refinery or from nearby stormwater outfalls, unusual or highly variable substrate conditions, or other anthropogenic influences (clam diggers, nearby park, etc.).

For DNR to establish 'reference sites' for monitoring the 'health' of Puget Sound, it is clear that the spatial scales of interest must be well defined. Since our data show substantial differences from South to Central Sound and from south to north within Central Sound, reference sites will need to be nested to incorporate these different scales of variation. However, we now know that the SCALE method provides a powerful tool for researchers and managers, enabling them to 'factor out' differences in organismal distributions that result from variation in physical features (such as salinity, depth, and sediment composition, all of which affect benthic assemblages) from those that might be caused by sediment contamination or other anthropogenic effects.

INTRODUCTION

The overall objective of the 1999 sampling of shoreline biota of Puget Sound was to extend our previous sampling, using SCALE methodology, in 3 major ways:

1. In time, by resampling beaches sampled in 1998 in South Sound (Carr, Case, and Budd Inlets), using the same methodology;
2. In space, by examining the similarity of communities in pebble beaches between South and Central Puget Sound, and also along a north-south gradient within Central Puget Sound; and
3. Over long time scales, by qualitatively comparing biota found by SCALE surveys in the 1990s with that found in the 1970s and 1980s at nearby sites.

In each case, tests of temporal and spatial similarity are possible because the SCALE methodology is applied in the same way at all sites, and uses sufficient replication at all spatial scales (within and among beaches) to allow statistical comparisons. Using a nested sampling design, and measuring a suite of physical parameters thought to affect shoreline and estuarine biota, we can begin to test the importance of different physical forcing functions (e.g., salinity, wave action, sediment grain size) on the organisms of Puget Sound. Since the beach type chosen for our 1998 and 1999 sampling (mixed-coarse, or cobble-pebble-sand beaches) is very common along Puget Sound's shorelines, our results have broad applicability to understanding intertidal habitats of the region.

Previous attempts to define critical physical forcing functions controlling the nature of the biota in estuaries have been slowed by three major factors, two of which are linked sampling artifacts. The majority of estuarine research programs examining benthic communities have consisted of extensive sampling regimes where bottom grabs or cores are taken at a variety of stations, often seasonally and sometimes over a number of years. The artifacts occur because 1) usually replication at the per-site level is very low, often only 2-3 samples (e.g., Service and Feller 1992, Flint and Kalke 1985), so that within-site variability cannot be statistically separated from among-site or among-time variability; and 2) there is usually no attempt to separate the physical variables or gradients that are so characteristic of estuaries, e.g. substrate type vs. salinity vs. temperature vs. turbidity. The third (unavoidable) factor making such research difficult is that these variables are often inextricably linked, for example sediment type covaries with wave action, and salinity often fluctuates with temperature. Our research program uses a unique sampling design tailored to avoid these artifacts as fully as possible.

Much estuarine literature focuses on the primary role of salinity in determining biotic communities, both benthic and pelagic. Tenore (1972) states that salinity is "… likely the single most important factor affecting the distribution of the benthos" in estuaries, and a review of the physiological literature by Carriker (1967) notes that "for the majority of benthic estuarine species the minimal survivable salinity imposes a restraint" on distribution. Reduced or more-variable salinity has a clear negative effect on species diversity, to the extent that one estuarine index of 'health' used as one of its variables the expected species diversity "adjusted to remove the effects of salinity" (Engle and Summers 1999). Many authors, however, note that salinity may be a proxy for other variables that directly affect organisms, e.g. substrate types or water column turbidity, or that in some cases it is not the mean salinity that is critical but the variation (e.g, through the year) in this parameter (e.g., Montague and Ley 1993). In addition, the physiological effects of salinity fluctuations are confounded (as are ecological effects) by other variables; for example, mortalities due to low salinities are often increased with higher temperatures (Carriker 1967), and salinity changes affect the toxicity of various pollutants such as heavy metals (Vernberg and Vernberg 1974). Lower salinity generally increases lethal and sublethal impacts of other stressors. The correlation of the distribution of many commercially important taxa (especially pelagic fishes and crustacea) with particular salinity regimes has led to the description of "salinity zones", which can be used as a basis for mapping these resources (e.g., Bulger et al. 1993, Christensen et al. 1997). Ontogenetic shifts in optimal salinity zones are often seen.

Attempts to separate the effects of salinity from those of other estuarine forcing functions have usually involved multivariate analyses of data collected from many sites. For example, Flint and Kalke (1985) sampled repeatedly from 4 sites along an estuarine gradient, and then used discriminant analysis to suggest that the key variables affecting the benthos were variance in the bottom water salinity, and secondarily differences in sediment structure. A more systematic design was used by Mannino and Montagna (1997), who sampled each of 3 sediment types in each of 4 salinity regions in a randomized, partially hierarchical design to try to separate these variables. They found both sets of variables to critically influence the benthos; for example, animal diversity, abundance, and biomass were all affected both by grain size and by salinity, with the greatest values in sand (rather than mud) and in higher salinity areas. Species responded individually to the parameters, however; e.g. the polychaete *Streblospio* was most abundant in low-salinity sediments. Similar broad effects of sediment type and salinity (with individual species showing different patterns) have been noted by many other authors (e.g. Chester et al. 1983; reviewed in Schoch and Dethier 1997, Estacio et al. 1998). Unfortunately, little specific information about 'indicator organisms' can be extrapolated from these studies (performed largely in the Chesapeake or in Gulf of Mexico estuaries, and largely subtidally) to the distantly related fauna of Puget Sound.

Holland et al. (1987) stratified their estuarine sampling by habitat type (e.g., nearshore sand vs. deepwater mud) and gathered 14 years of data from many sites in these strata, thus comprising an unusually thorough long term dataset. They found each of their habitat strata to have a 'corresponding' benthic assemblage in terms of the biota being grouped together each season and year in multivariate analyses, although the assemblages are clearly part of a continuum. However, *abundances* of organisms varied hugely from year to year, with major station-year interactions apparently driven by salinity shifts up and down the estuary. In addition, for every species evaluated, significant differences in abundance were seen among years even when season, sediment characteristics, and salinity distribution were accounted for; the cause appeared to be variation in recruitment pulses, confounded when salinity changes occurred following recruitment events because of the sensitivity of early life history stages.

The SCALE methodology, while not yet used long enough to see these sorts of long term patterns, does have the ability to better separate the roles of sediment type, salinity, wave action, and other factors in controlling benthic communities. In particular, the 1999 sampling effort was designed to allow a statistical examination of the effects of nearshore salinity and wave action on the shoreline biota of Puget Sound while controlling the other key variable, substrate type. We paid particular attention to the level of replication used at all scales in the sampling design, thus avoiding the very common difficulty of distinguishing patchiness at the local level (a core or a beach) from real variation at larger levels. Bell et al. (1997) note that most ecological studies are done at microscales (<1m) and most oceanographic studies at macroscales (km), making linkages between them almost impossible. Many physical processes (e.g., local wave action, topography) act at mesoscales (100's m). Thus "quantifying the linkages and interactions between physical factors and benthic community structure is difficult and continues to be debated" (Bell et al. 1997). Local biota integrate physical (e.g. hydrodynamic) and biotic (e.g. predation) events operating on a variety of temporal and spatial scales (Thrush et al. 1997). An entire workshop and journal issue were recently devoted to these difficult issues of scaling in soft-sediment ecology (J. Exp. Mar. Biol. Ecol. vol. 216, 1997). The summary from this workshop (Thrush et al.) notes that intense local replication (e.g., many cores per beach) can give us confidence in local results, but does not provide generality. Very broad sampling can give generality but if it comes at the expense of low local replication, the confidence or certainty is reduced. We attempt to overcome this dichotomy with our nested sampling design, which replicates adequately at the local (beach), regional, and basin scales:

Sample Unit	Labeling in Figures	Spatial Scale	Type of Homogeneity Sought
Beach	3 per area	10-100m	local geophysical (e.g. substrate)
Area	#1-15, Figure 1	1-10km	wave energy
Cell	#1-13, Figure 1	10-100km	oceanic temperature, salinity
Basin	South vs. Central	>100km	watershed, circulation

This enables us to distinguish local patchiness of organisms (within or among beaches) from larger-scale patterns such as salinity-driven variation among regions.

METHODS

General Approach

We used the SCALE sample site selection protocols to reduce the physical and chemical variability of physical habitats. In previous studies (Schoch and Dethier 1997, 1999), we have shown that sampled communities show significant fidelity to their physical habitat type, thus allowing extrapolation or scaling up of localized community structure to larger regions. Predictions of community structure are most likely to be valid among replicate segments within the spatial range of nearshore cells with similar water properties. Furthermore, as ocean properties change we can expect the biota to respond by gradually shifting towards species tolerant of the prevailing conditions. We chose a nested sampling design to test the hypothesis that benthic communities of macroalgae and invertebrates will be less similar at incrementally increasing spatial scales; e.g. more community similarity among three beaches within a (~) 1 km area than among areas, more similar within nearshore cells of oceanic homogeneity than among cells (10's of km), and more similar within a basin than among basins.

In the summer of 1999, we evaluated the spatial and temporal variation of nearshore biota from physically similar pebble beaches in South and Central Puget Sound. Our approach consisted of the following general steps:

1. identify nearshore cells based on regions of oceanic homogeneity, especially in salinity and sea surface temperature, at scales greater than 1 km (grid);
2. select and prioritize habitats of interest for high resolution SCALE modeling;
3. field map the shoreline (on the ground) to partition and quantify the habitats identified and selected in Step 1-2 into geophysically homogeneous segments (10-100 m linear), quantifying the geophysical attributes known to force biological community structure in the nearshore;
4. sample selected reference shore segments (from geophysically similar segment clusters) for benthic macroalgae and invertebrates;
5. statistically compare these community or population data among segments within geophysically similar clusters within an oceanic cell.

In South Puget Sound, we resampled the pebble beaches from the 1998 study to determine whether the community structure and population abundances had changed significantly over a one year period. In Central Puget Sound we identified and sampled a series of 36 similar pebble beaches in 4 nearshore cells from Browns Point (near Tacoma) to Double Bluff (on Whidbey Island), as shown on Figure 1.

Identification of nearshore cells

Field measurements of sea surface temperature and salinity (at 2 meters depth) in the south and central basin of Puget Sound were made over a six day period (6/5/99-6/10/99) with a temperature/conductivity meter (YSI Model 30), at stations spaced approximately 1 km apart in the central basin and 2 km apart in the southern basin (Figure 2).

Beach selection

In 1998, we selected groups of three replicate pebble beach segments for biological sampling in Carr, Case and Budd Inlets. To compare the physical attributes among segments in each group and among groups, we measured pore water salinity and temperature, slope angle, grain size, wave energy, wave energy dissipation, and aspect for each segment. Pore water was measured in a hole excavated in the beach and the temperature/conductivity probe recorded in situ salinity and temperature. Slope was measured in the field with a hand-held digital inclinometer. Grain sizes were determined based on 3 photo-quadrat samples (.25 m^2) spaced randomly along a 50 m horizontal transect at MLLW. The photos were scanned (e.g., Figure 3) and grain sizes were measured at each 5 cm grid intersection (16 intersections per quadrat). The grain samples were sorted by size and a histogram plotted. Wave energy was calculated for each beach segment based on mean maximum annual wind velocity and the maximum wave fetch according to Komar (1998). Based on the similarity of these attributes among beach segments, in 1998 we selected Carr Inlet pebble beach segments 27, 53, and 102 for biological sampling.

The geomorphology and beach structure of the Case Inlet shoreline differed slightly from Carr Inlet. Large pebbles and small cobbles (barnacle encrusted, where wave energy is low), and interstitial sand characterized this shore. There was a strong particle size gradient with grain size decreasing towards the head of the inlet. In 1998, pebble beaches were selected on the western shore of the inlet from Cell 9 (Segments 15-17). Based on the results of the biological comparisons in 1998, an additional 3 beaches were selected in 1999 from a nearshore cell further south in higher salinity water (Segments 18-20).

In Budd Inlet, coarse substrates dominated the northern shores and fines in the south. In the north, gravel beaches (mostly pebble and cobble with interstitial sand) were found on the west shore and sandy pebble beaches on the east. In 1998, 3 pebble beaches from the northwest shoreline were selected for biological sampling (Segments 4-6), and these were resampled in 1999.

In 1999, to extend our spatial comparisons, we also evaluated the similarity of pebble beach biota between the south and central basins of Puget Sound. To minimize costs we did not map the nearshore beaches in Central Puget Sound, opting instead to qualitatively select beaches similar to those pebble beaches sampled in South Sound. Similarity was primarily based on substrate size and slope angle. Pore water salinity and temperature were also measured, and wave energy was calculated. The Central Sound sampling used a spatially nested design (Fig. 1):

1) beach segments (3) within areas (100-1000 m apart);
2) areas (3) within nearshore cells (1-10 km apart);
3) nearshore cells (4) within a basin (10-100 km apart); and
4) among basins (2).

No other estuarine sampling design described in the literature has attempted this sort of detailed spatial analysis for intertidal communities while holding substratum type and slope angle constant, especially not with adequate replication at all scales.

Biological sampling

Spatial and temporal variation of macrofauna and macroflora on pebble beaches were examined during springtime low tides in May and June, 1999. We resampled the biota of 3 replicate pebble beaches in Carr, Case and Budd Inlets on 3 consecutive days to compare the community structure to 1998 samples. To improve tests of comparability among biota found in Carr Inlet to geophysically similar beaches in similar nearshore cells in a nearby inlet, we sampled 3 additional pebble beaches in Case Inlet and one more pebble beach in Carr Inlet (Figure 1). Two tide series were used to sample macroalgae and invertebrates over three nested alongshore scales in Central Sound in June 1999.

Samples were collected in the lower zone only (MLLW or 0 meters elevation). At this level the biota are diverse and productive and probably sensitive to changes in the marine environment, both because change is easier to detect in a diverse community, and because these taxa are not as broadly tolerant of physical extremes as are high-shore organisms. In addition, this low level is still subject to anthropogenic stressors from both land (when emersed) and sea (when immersed). We collected 10 random samples along a 50 m horizontal transect positioned near the center of the beach segment. Each sample consisted of quantifying surface macroflora and fauna abundance in a 0.25 m^2 quadrat, and infauna in a 10-cm diameter core dug to 15 cm depth. Percent cover was estimated for all sessile taxa in the quadrats, and all mobile epifauna were counted. Core samples were sieved through a 2 mm mesh and taxa were counted. All organisms not identifiable to the species level in the field were placed in formalin and identified in the lab. Taxonomic identifications for invertebrates were according to Kozloff (1987), and Gabrielson et al. (1989) for macroalgae. The identified taxa are listed in Appendix A.

Data Analysis

The multivariate analyses methods of Clarke (1993) and PC-Ord software (1999) were used to detect patterns in the distribution of communities of macrofauna and macroflora. A fourth root transformation was applied to the abundance values so that analyses considered both high and low indicators. A matrix of Bray-Curtis similarities was generated, and the technique of non-metric multidimensional scaling (NMS) was used on the matrix. Graphical plots of ordination results for the two axes explaining the greatest proportion of the variance were examined for obvious sample groupings. Analyses of similarity (MRPP) tested the significance of hypothesized differences among sample groups. Vector overlays of species with R^2 correlations >0.2 were plotted on the ordinations to show which species were most important in driving the community differences among sampled groups (e.g. years or nested spatial scales).

Our ability to detect change in marine communities depends largely on how reliable different species are as response organisms to environmental conditions. Therefore, we calculated the indicator value of Dufrene and Legendre (1997) for each taxon (based on ten replicates per beach segment). This metric combines information on the evenness of taxon abundances in a particular group of samples and the fidelity of occurrence (frequency) of a species in that group. We plotted these values on GIS maps for the taxa driving group differences identified in the multivariate analyses for qualitative comparisons among years and nested spatial scales.

Univariate analyses of between year comparisons were done with simple t-tests of each taxon sampled. Quantitative tests for spatial autocorrelation were also made for each of these taxa. Spatial autocorrelation shows how the abundances of a taxon among neighboring samples are related over different spatial scales.

Nested ANOVAs for each taxon were used to show how population abundance varied over different spatial scales, thus determining the species whose abundances could be extrapolated from segment-level spatial scales to larger areas with a minimum of increased variability (Sokal and Rohlf, 1995). The effect of scale was tested by the standard nested procedure of using the mean square of the next lowest factor as the error term for each analysis (e.g., the effect of the within-group scale was tested with the MS of within-segments). All abundances were square root transformed to improve assumptions of normality and homogeneity of variance. ANOVA assumptions of normality of residuals and equality of error terms were determined by visually examining plots of estimated values against residuals. Taxa that still violated the assumptions of normality were omitted from further analyses.

Comparisons with Historical Surveys

Data gathered in the 1970s and 1980s on abundance of epibiota and infauna of Puget Sound beaches were compared to biota found by SCALE in 1999. For a variety of reasons (see Results and Discussion), quantitative comparisons between these datasets were not possible; thus tables of biota were made to facilitate qualitative comparisons. In addition, data from historic studies from the Straits of Juan de Fuca and other more-northern sites were qualitatively compared with the more southern surveys to examine geographic trends. In each case, only historic surveys that had data from similar beach types (cobble-gravel-sand, or ‘mixed-coarse’) and similar tidal heights (ca. MLLW) were compared with the SCALE data.

RESULTS

Selection of Nearshore Cells

In South Puget Sound, the field data confirmed the salinity and water temperature patterns observed in previous years along and across the axes of Carr, Case and Budd Inlets. Following the winter period of high rainfall, a slightly stratified fresh water surface layer appears to flow along the coast. These flows are trapped along the shoreline by frictional shears and planetary vorticity. Thus, outbound less saline surface water flows north along the east side of the Central Basin, and the west side of Carr and Case Inlets, and the east side of Budd Inlet.

The SST distributions in Carr, Case and Budd Inlets are shown on Figures 4-6. The Carr Inlet mean SST was 13.8°C,compared to 12.1°C in 1998, and the mean salinity was 27.3 psu (practical salinity units), compared to 28.5 psu in 1998. As opposed to 1998, the water in Carr Inlet appeared to be well mixed during the time of our sampling (Fig. 4). There were negligible temperature or salinity gradients across the axis of the bay. This is likely due to the strong winds that prevailed before and during the survey. The along axis salinity gradient in Carr Inlet was about 1.0 psu, and the SST gradient was about 2°C.

The mean SST in Case Inlet was 13.2°C (compared to 11.7°C in 1998), and the mean salinity was 28.9 psu (compared to 28.3 psu in 1998). The temperature range was 3.8°C along axis and <1°C across axis, and the salinity range was 5.0 psu along the axis and about 1.0 psu across the axis as shown on Figure 5. This pattern is very similar to 1998. Relative to Carr Inlet, there were lower lows and higher highs for salinity in Case Inlet, also consistent with 1998 observations.

The SST and salinity patterns in Budd Inlet are consistent with those observed in Case and Carr Inlets. A strong salinity gradient existed along the axis of the inlet and across the axis (Fig. 6). The average salinity was 28.1 psu (compared to 26.0 psu in 1998). The average SST was 12.1°C (compared to 13.5°C in 1998). There was a strong across-axis gradient from west to east in the southern half of the inlet but in the north the across-axis gradient was minimal.

The apparent gradients in these estuaries observed in 1999 are associated with the turbulent mixing caused by tidal flow over the rapidly shallowing bathymetry at the head of each bay, the discharge of fresh water from rivers, and various degrees of protection from wave energy along the convoluted shoreline. The temperature distributions were relatively homogeneous along and across the axes of each inlet, indicating that wind-driven mixing before and during the field survey had removed the patterns observed the previous year. The only apparent gradients that persisted were the along axis gradients of salinity in Carr and Case Inlets and the across axis salinity gradient in Budd Inlet.

Figures 7-9 show the temperature and salinity data (respectively) collected from Central Puget Sound. The temperature field on the survey dates was relatively homogeneous, both along and across the basin axis. The salinity field, however, shows a strong across axis gradient and a stepped gradient along the western shoreline. The water along the western shore is 3-5 psu more saline than along the eastern shore, even though the temperatures are nearly the same. The lowest salinities measured in the Central Basin were at Commencement Bay and Possession Sound at the farthest southern and northern endpoints of the project area (Figure 9).

In Central Puget Sound, these temperature and salinity data show a strong gradient across the axis of the basin, particularly north of Alki Point, thus defining four nearshore cells along the eastern shore based on the constraints of an alongshore salinity gradient of no more than 2 psu and water temperature of 2°C. The exact spatial extent of each nearshore cell was determined quantitatively by these salinity and temperature distributions, and qualitatively by the configuration of the shoreline with respect to the prevailing winter wind direction, which influences nearshore sediment transport processes such as net shore drift.

Selection of Beaches

Figures 10 and 11 show the pore water salinity and temperature distributions for every sampled pebble beach in the south and central basins. Although variation among areas is evident, there are only slight differences among segments (within areas). These figures show that neither salinity nor temperature have significant spatial autocorrelation, i.e., the pore water salinity and temperature on neighboring beaches is independent. Figures 12 shows the measured slope distributions for the sampled pebble beaches. There was no significant spatial autocorrelation for beach slope which ranged between 2 and 7 degrees and is qualitatively more similar among beaches in each area than among areas. Wave energy is highly correlated to beach location as shown on Figure 13. The high wave energy beaches are to the north where exposures to longer fetches and to the Strait of Juan de Fuca result in larger waves.

Figures 14, 15, and 16 show the sand, pebble, and cobble distributions in the south and central basins for each pebble beach sampled. The figures allow qualitative comparisons within and among areas. There was no significant spatial autocorrelation for any of the grain sizes, and the within-area comparisons also showed no significant differences (sand: p=.061; pebble: p=.370; cobble: p=.145). However, within-cell comparisons showed that pebbles were significantly different (.037), while sand and cobbles were not (p=.104 and p=.397 respectively).

The calculated wave energy dissipation coefficient (Komar 1998) is the same for all the sampled beaches since substrate size (mostly pebbles) and slope angle (within 5 degrees) are roughly constant, therefore the net wave force also increases from south to north.

Biological Sampling

In May and June of 1999, the biota of pebble beaches in the south and central basins were sampled in 488 quadrats and an equal number of cores (360 in the central basin and 128 in the south basin). 232 taxa were identified in 1999, a total of 156 taxa in the central basin and 76 taxa in the south basin, many of these were the same in both basins. Combining the 1998 and 1999 data, 101 taxa were identified in the south basin from 180 samples taken over the two years. Appendix A gives the raw data for all 1999 samples, and Table 1 lists the taxa found.

The number of taxa identified in 1999 in both the south and central basins were tallied and the biodiversity or species richness was plotted on Figure 17. Note the very strong richness gradient along the axis of the Sound. This result prompted the question: what elements of the biota generate this pattern? Figure 18 shows the species richness for the epiflora and fauna and Figure 19 for the infauna. The same gradient persists in both groups of organisms, with high richness in the north and low in the south. Note that the plotted values are relative so that the heights of each bar vary in absolute value among the three plots. Case segment 18 has persistently low richness in cores and quadrats. Figures 14 and 16 show that this segment consisted mostly of cobbles and sand with few pebbles. The large amount of sand at this site may have an adverse effect on the number of taxa, since fewer organisms are tolerant of a sandy habitat. The other attributes of that beach are relatively consistent with the two replicate segments in that group. Figures 20-22 show the species richness broken down by trophic level. Figure 20 shows a plot of the primary producers, herbivores, and carnivores sampled in 1999. A qualitative comparison suggests that producers and carnivores dominate all the sample groups with incrementally increasing numbers from south to north. Figure 21 shows a plot for the numbers of deposit, deposit/suspension, and suspension feeders. There is considerably less pattern to the distributions with the exception of deposit/suspension feeders, which seem to be outnumbered by the other two trophic levels at almost every sampled area but especially towards the north. Figure 22 shows that scavengers outnumber commensals and omnivores almost five to one overall.

Patterns of Temporal Variability

We used the multivariate methods discussed above to first assess community shifts among the sampled years and then determine the species responsible for those shifts. Figure 23A shows the two-dimensional plot of samples in species space for the 1998 and 1999 samples collected in South Sound. Note the dark points (1998) towards the left side of the diagram and the lighter points (1999) towards the right. With the exception of one sample (Case #18), the sample groups by year are quite distinct. Figure 23B shows the same plot with a vector overlay of species with correlation coefficients greater than 0.2. These are the taxa driving the group differences. The taxa represented by longer vectors are more strongly correlated in the directions shown. For example, *Armandia brevis* was more abundant in 1998 than in 1999, but more clams, especially

Saxidomus giganteus were found in 1999. We tested the hypothesis that there was no difference between pebble beach community structure in 1998 and 1999. The MRPP analysis of group difference gave a p-value of <<0.001, suggesting that the community structures of 1998 and 1999 were significantly different. The MRPP analyses also showed that there was slightly more variability within 1999 than 1998 (the 1998 samples grouped closer together and were thus more similar than the 1999 samples). This could not apparently be explained by any physical factors since none correlated with the observed group differences, but it is likely that slight differences in recruitment among beaches within a year caused the observed differences among years. *Armandia* is known to recruit in highly variable pulses (C. Rice, pers. comm).

We also tested the hypothesis that there was no difference in population abundance for any taxon between 1998 and 1999. Univariate t-tests were run on each of the sampled taxa. These results are summarized in Table 2. Out of 97 taxa, 29 were significantly different between the two years (70% were the same). In terms of p-values the most significant taxa driving the differences were the amphipod *Allorchestes angusta* (more in 1999), the polychaete *Armandia brevis* (more in 1998), the slipper limpet *Crepidula dorsata* (more in 1998), the burrowing anemone *Edwardsia sipunculoides* (more in 1999), the amphipod *Eogammarus oclairi* (more in 1999), the crab *Hemigrapsus oregonensis* (more in 1998), clam siphon holes (more in 1999), the sea cucumber *Leptosynapta clarki* (more in 1998), the periwinkle *Littorina scutulata* (more in 1999), the crab *Lophopanopeus bellus bellus* (more in 1998), and ulvoids (more in 1998). Thus, there was no general trend towards organisms being more abundant in either year, but rather large and seemingly haphazard variation from year to year in 30% of the taxa.

Appendix B shows the GIS maps for each taxon identified as driving the community difference between 1998 and 1999. The relevant t-tests are summarized for these organisms on the figures. Appendix C lists all the taxa sampled and the complete results of the t-test analyses with t-values, degrees of freedom, p-values, and confidence limits at the 95% level.

Patterns of Spatial Variability

We analyzed the difference in community structure among pebble beaches in the south and central basins of Puget Sound using the 1999 sample data and multivariate methods. Figure 24A shows the two-dimensional plots of ordination results for south and central sound samples in species space. Note that Basin 1 (South Sound) samples are all towards the left of the diagram and Basin 2 (Central Sound) samples are to the right. Figure 24B shows the same ordination plot but this time with the species vector overlay. As previously described, this figure shows the species that drive ($R^2 > 0.2$) the community differences between pebble beaches in the south and central basins. Note that the snail *Alia gausapata*, *Crepidula fornicata*, *Leptosynapta clarki*, and the brown alga *Scytosiphon lomentaria* are more dominant in the south basin. Red crustose algae (e.g. *Hildenbrandia* spp.), the red blade *Mastocarpus papillatus*, juvenile *Macoma inquinata* clams, and *Mediomastus californiensis* polychaetes (and others) are the predominant taxa in the central basin. We tested the hypothesis that there was no difference between the south and central sound pebble beach communities. The very low p-value ($<<0.001$) suggests that the difference is highly significant and the hypothesis must be rejected.

Figure 24A also shows the overlay of vectors representing the physical attributes that drive the group differences (all physical attributes with $R^2 > 0.2$). The only physical attribute meeting this criterion was wave energy. The other vector shown represents species richness which is also highly correlated to the group difference. Thus wave energy and species richness are the most important factors differentiating the south and central basins. Figure 24B corroborates this observation by showing that three times as many taxa are associated with the central basin.

We tested each taxon for spatial autocorrelation among all samples collected in both basins in 1999. Appendix D lists these results for each organism, but the GIS maps in Appendix E summarize the spatial autocorrelation analyses with a graph and summary table for each of the relevant taxa shown to drive community differences from the multivariate analyses. Spatial autocorrelation is an important test for determining the predictability of each segment population based on neighboring segment populations. This analysis also reveals much about the larval or spore dispersal and distribution patterns. When spatial autocorrelation is significant then neighboring samples are not independent and assumptions of parametric statistics are violated. 73 out of 176 taxa (43%) were significantly autocorrelated, thus these taxa were predictable based on neighboring abundance values. The remaining 57% of the taxa were not spatially autocorrelated, indicating that to predict or model these distributions, a higher spatial frequency of monitoring sites will be required. Note, however, that these analyses included many sparse populations (e.g. rare taxa) that may not be found at every sample station or sampling interval.

We utilized a nested sampling design to assess the variability of species abundances at different scales of observation. We tested the partitioning of variation at different spatial scales by using a nested ANOVA. These results are summarized in Table 3 and shown in full for each taxon in Appendix F. Beach differences (within Area) had an effect on 24 out of 168 (14%) taxa, area differences (within Cell) had an effect on 39 out of 168 (23%) taxa, cell differences (within Basin) had an effect on 79 out of 168 (47%) taxa, and basins had an effect on 111 out of 168 (66%) taxa. Thus as we showed with the community level analyses and as expected, the population abundances showed increasing variation with increasing spatial scale. Note that this analysis considered all taxa sampled including the rare species, so the summary could be skewed by the high numbers of sparse and rare populations (e.g. amphipods, isopods, and some polychaetes). The GIS maps in Appendix E show and summarize the distributions of those taxa that tested as most important in driving the community differences among sampled groups.

Spatial Variation among communities in South-Sound Inlets

We separated and then ordinated the samples from the south basin to assess the variation among Carr, Case, and Budd Inlet pebble beach communities. Figure 25 shows the ordination results as a two-dimensional plot of samples in species space. Figure 25A shows Cell 1 (Carr Inlet), Cell 7 (Budd Inlet), Cell 8 (Upper Case Inlet) and Cell 9 (lower Case Inlet). Cell 7, Budd Inlet segments 4-6, are grouped along the right side of the plot, Cells 8 and 9, Case Inlet segments 15-17 and 18-20 respectively, are grouped at the lower left of the plot. Carr Inlet segments 53, 70, and 102 are grouped along the upper margin of the plot. Thus the samples are grouped most strongly by inlet (or cell). We overlaid the vectors representing the most highly correlated ($R^2 > 0.2$) physical factors and, as shown, substrate size appears to drive the difference between Budd (more sand) and Case Inlet (more cobble) pebble beach communities, while salinity, temperature and species richness differentiated the Carr Inlet samples. We tested the hypothesis that there was no difference among the four pebble beach communities using MRPP. The low p-value ($p<<0.01$) suggests that the differences among the groups are significant.

Figure 25B shows the same ordination plot but now with the vector overlays of taxa driving the group differences ($R^2 > 0.2$). Note the strong separation of taxa represented by the winged pattern of vectors. *Balanus glandula*, Nemerteans, and *Hemigrapsus oregonensis* (and others) appear to dominate in Case Inlet, while *Leptosynapta clarki,* the chiton *Mopalia lignosa*, ulvoids (and others) drive the separation of Budd Inlet. Polynoid polychaetes, the ghost shrimp *Neotrypaea californiensis,* and the brown alga *Punctaria expansa* (among others) appear to drive the difference between Carr Inlet and the other two. Since the Carr Inlet cell had oceanographic conditions that were less extreme (higher salinities and lower temperatures) than those of Budd (vectors in Figure 25A), the corresponding organismal vectors (Fig. 25B) suggest that these taxa may be less tolerant of physical extremes than those found in Budd Inlet.

Spatial Variation among Central-Sound Beach Segments, Areas, and Cells

We ordinated the central basin samples as shown on Figure 26A. Samples collected from Cells 10-13 are shown on the two-dimensional plot of samples in species space. The nine beach segments sampled from Cell 10 are shown in the lower left of the plot, and the nine segments sampled from Cell 13 are shown in the upper right of the plot. Samples from Cells 11 and 12 are in between, following a gradient of wave energy and species richness shown by the vector overlays. The strong correlation of the wave energy and richness vectors along the axis of central sound can explain most of the variation in community structure between Cells 10 and 13. The salinity vector explains the variation across the axis of the richness gradient. Thus these three factors explain almost all of the variation in community structure observed in the central basin. We tested the hypothesis that pebble beach communities are not different among the four cells using the MRPP program. The p-value ($p<<0.01$) suggested that a significant difference occurs and thus the hypothesis was rejected. Our nested ANOVAs showed that "cell" had a significant effect on 47% of the taxa.

Figure 26B shows the same ordination plot but with the sample points coded by area rather than cell as in Figure 26A. The sample points distinctly group by area suggesting that pebble beach communities are more similar within areas than among areas. We tested the hypothesis that there was no difference among area groups, but the p-value ($p<<0.001$) indicated a highly significant difference and the hypothesis was rejected. For population analyses, the nested ANOVAs corroborated this observation by showing that "area" had a significant effect on 23% of the sampled taxa.

Figure 26C shows the same ordination plot but this time with the vector overlays of highly correlated taxa ($R^2 > 0.2$). These taxa are shown on GIS maps in Appendix B. Note that the limpet *Lottia pelta*, the polychaete *Hemipodus borealis*, *Spiochaetopterus* tubes, and the isopod *Gnorimosphaeroma oregonense* are dominant in Cells 10 and 11 (Areas 4-6 and 7-9), while *Balanus glandula*, *Lacuna vincta*, *Lottia strigatella*, *Semibalanus cariosus*, and others were dominant in the northern Cells 12 and 13 (Areas 10-12 and 13-15).

Since species richness showed such a high correlation to the south-north axis of the central basin, we regressed richness first against wave energy ($R^2 = 0.54$), then the interaction terms of wave energy and salinity ($R^2 = .61$), and finally against the interaction term of wave energy, salinity, and sample location ($R^2 = 0.70$). We also regressed just the core richness ($R^2 = .70$), and just the quadrat richness ($R^2 = .44$). First, this suggests that wave energy and salinity account for much of the richness gradient but that some intangible attribute encompassed by the sample location accounts for some of the gradient as well. This intangible element could be the temporal variability of the physical environment, or some physical attribute not measured during our observations (e.g. nutrients, phytoplankton distributions, etc.). Second, this also suggests that core richness is more a function of wave energy, salinity, and location than is quadrat richness. The analyses show that we can predict (with 70% accuracy) the species richness of communities on any given pebble beach, when the physical attributes match the sampled beaches in the central and south basins.

Comparisons with Historical Surveys

Many of the sites sampled in the 1999 SCALE effort were sampled previously in 1971-6 (Armstrong 1977, Armstrong et al. 1976, Staude 1979) and 1982-4 (Thom et al. 1994), primarily as part of studies on the siting and effects of outfalls of sewage treatment plants. Many methodological differences exist both among these studies and between them and ours:

1) Armstrong et al. did not gather data on algal abundance, and sampled only the more north-central sites;
2) Thom et al. sampled only the more south-central sites, and list only common taxa, with no quantitative data;

3) Staude discusses only the West Point sites, although in considerable detail;
4) most previous studies had some samples where larger and deeper cores were dug, so that uncommon or deep-dwelling infauna (e.g., large clams) were more effectively sampled than by SCALE;
5) the historical surveys sampled at various times of year, so that some seasonal taxa were found that would be missed in our study;
6) mesh sizes of sieves varied;
7) relatively few replicates were taken per beach per date in the historical surveys (e.g., 3 versus our 10) so that quantitative comparisons, or even richness comparisons, are not possible; and
8) taxonomic uncertainties make comparisons of some groups difficult.

Nonetheless, it is possible to make qualitative comparisons with these surveys to look for changes through time, and also to combine information from these, ours, and those further to the north by Nyblade (1979a, b), Smith and Webber (1978), and Webber (1980) to look at possible geographic patterns. The discussion below relates to similarities and differences among studies that surveyed the same types of habitats sampled in 1999 by SCALE, i.e. mixed-coarse or cobble-gravel-sand beaches, and that contained data for tidal levels at or near MLLW.

Taxa that appear to be similar among studies are listed in Table 4, and dissimilar taxa in Table 5. Appendix G gives a complete listing of all the species found by SCALE, and qualitative comparison with the abundances recorded in Central Puget Sound by Thom et al., Armstrong et al., and Staude. Overall, we found a high degree of similarity among studies in terms of the presence/absence (and often relative abundance) of many taxa. Table 4 lists 17 taxa of worms or other small infauna, 22 taxa of epibiota, 3 species of clams, and 2 other (miscellaneous) taxa that are generally similar among studies. Some of these similarities are not surprising (e.g., the ubiquitous and environmentally tolerant barnacles and ulvoids appear throughout), but others are more striking, e.g. the appearance of nudibranch *Onchidoris* in only the more northern samples, or of the polychaete *Pholoe* only at certain sites (Appendix G). A major exception to this general similarity is seen at Point Wells, discussed below.

Table 5 lists taxa that appear to be dissimilar among surveys. Almost half of these dissimilarities are probably caused by the sampling differences enumerated above; the historic surveys sampled other habitats (e.g. boulders), deeper, and with a smaller mesh size, and each of these differences probably contributed to differences in the communities found. For other taxa we cannot explain the apparent differences among decades; most different taxa were found in the historic surveys but not in 1999, but for a few species this pattern is reversed. Many differences may be taxonomic artifacts (e.g., the lumping of difficult taxa in one decade but not the other), and others may be further sampling artifacts. Some, of course, may represent genuine losses (or in a few cases gains) of species through time in this habitat type; these taxa deserve further study. Overall, we found no patterns in the types of taxa (e.g., particular feeding modes) in terms of what taxa were similar versus different through time; had there been some pattern such as a general increase in deposit feeders, this would have indicated cause for concern. In addition, although precise comparisons again are not possible, there were no obvious differences in diversity of taxa found at beaches sampled during both time periods.

The only clear discontinuity between the historic and SCALE data is the community found at the Point Wells/ Richmond sites. A scan of the data column in Appendix G for Area 12 shows a striking reduction in abundance or even absence of numerous taxa in 1999 relative to the Armstrong et al. surveys in the 1970s. Table 6 summarizes these data into two categories; 1) taxa that were absent or rare in 1999 at Wells but that we strongly expected to find, based both on their abundance in the historic surveys and on 1999 data from similar beaches to the north and the south, and 2) taxa expected to be more abundant in 1999 than what we actually found. Each list contains a diversity of taxa, both in terms of overall lifestyle (infauna vs. epibiota) and trophic category (deposit feeders to carnivores). In addition, species richness was strikingly dissimilar in the 1999 samples from physically similar beaches both to the north and the south (an average of 16 to 22 taxa per beach versus 25-31 to the south and 23-29 to the north). Juvenile clams (especially of the horseclam *Tresus*) were also much more abundant both to the south and the north (an average of 4.6-5.2 and 2.2-5.4 per sample, respectively, versus 0.2-4.2 in the Point Wells area). In contrast, the thorough sampling of Armstrong et al. showed no such discontinuity at Point Wells relative to their more southern sites (they did not sample further north).

DISCUSSION

Scales of variation in biota are often not discussed explicitly in estuarine literature. Many studies provide no indication of among-sample (core) variability (e.g., Flint and Kalke 1985) or they deliberately pool biotic data from replicate cores (e.g. Boesch 1973), eliminating the chance to examine spatial variability at this smallest scale. Other studies have noted that core-level variability is very high (e.g., Ferraro et al. 1989), statistically significant (Morrisey et al. 1992, James and Fairweather 1996), or even the greatest source of variation among all samples (Service and Feller 1992). But since variation at this scale is seldom of primary interest (e.g., as compared to variation among sites or along an estuary), discounting it or pooling across cores within a beach is ecologically reasonable. However, knowing the replication at this level is critical because taking only a few cores in a variable beach (in our case, even when the beach was chosen for its homogeneity) runs a high risk of obtaining misleading data about organismal richness and abundances; if the data at the within-beach level are flawed in this way, all higher-scale comparisons are meaningless.

Our well-replicated, nested SCALE sampling design enabled us to test variation across a wide range of spatial scales, from the within-beach to the among-basin scales (South vs. Central Puget Sound), and also to examine within-basin differences along the extensive Central Sound shoreline. The waters of Central Sound vary in temperature, salinity, and wave energy along and across the axis of the basin. Our design allowed us to test the role of these physical forcing functions in controlling the shoreline biota in this estuary, using a dataset unique in its geographic breadth, statistical rigor, and consistent methodology.

As seen before in South Sound, there is a clear pattern of increasing variation in biota with increasing spatial scales. The organisms in beach segments within an area are very similar, areas within an oceanographic cell are more different, and variation among cells is still greater. And, as anticipated, there are substantial differences in biota between beaches in the South and Central Sound regions. Correlations of differences in biota with differences in physical features among sites (e.g., in wave energy, salinity, temperature, percentages of different substrate grain sizes) provide clues about the key driving forces affecting the biota at different spatial scales. Within a beach (i.e., among quadrats and cores), small-scale variation in grain sizes and pore-water characteristics are probably important. At larger spatial scales, the analyses clearly indicate that wave energy (as quantified by wave fetch and beach slope) and nearshore salinity are key forcing functions. For example, the ordinations suggest that the key difference among basins (South Sound vs. Central Sound) is wave energy, and that within each region salinity and energy differences correlate the most highly with differences in biota. This agrees (but with much greater rigor) with previous estuarine studies emphasizing the role of salinity.

The differences in species richness between similar beaches in South versus Central Puget Sound are striking; there is a clear, almost unidirectional trend from South to North-Central Sound in the numbers of species found per beach. The one obvious anomaly is the low richness in the Wells samples, discussed below. The trend is visible both in the epibiota and in the infauna, although more strikingly in the latter. When the taxa are broken down by trophic mode, the south-north trend is still visible in virtually all the groups.

To further examine these south-north trends, Table 7 lists taxa that tended to be found either throughout the Sound (i.e. both South and Central Basins), or to be especially concentrated in one or the other basin. There is a long list (41 taxa) that were found in our MLLW samples either commonly or occasionally throughout the Sound; these include algae, herbivores, suspension and deposit feeders, and carnivores. All are presumably tolerant of the lowered salinities and other physical conditions characteristic of the southern sites, but are generalists in terms of their physical requirements. Some were abundant everywhere (barnacles, grapsid crabs, ulvoids,: Appendices E4, E13, E55), others were never common but appeared at many sites (e.g., the crab *Lophopanopeus*). In some cases, this apparent generality may be the result of lumping of taxa; for example, the species of "encrusting red algae"(App. E48) or "*Pagurus* spp."(App. E41) might change from south to north, but our sampling cannot differentiate these trends.

A few taxa (11) appeared exclusively or more frequently in our South Sound samples. Some of these (e.g. *Crepidula fornicata*)(App. E8) are associated with taxa cultured largely in this region (oysters) and not to the north. Interestingly, we found no *C. fornicata* at more northern sites despite its having a pelagic larval stage lasting at least 30 days (Pechenik 1984). Some taxa (e.g., *Edwardsia* spp.) appear to prefer reduced salinities. Still others (e.g., *Littorina scutulata*: App. E19) are taxa that can be found abundantly in central and northern sites, but which are found there at levels above our MLLW samples; this probably reflects the reduced wave action in the more southerly sites, which tends to result in many species living lower on the shore.

Twenty taxa are listed as 'patchy' throughout our samples, i.e. found in abundance in only some areas, and with no apparent geographic trend. Some of these are fairly narrow in their substrate requirements and it is likely that the 'right' kinds of beaches were sampled only occasionally; examples include *Dendraster* and the mud shrimps *Neotrypaea* and *Upogebia*. *Dendraster* also settles in an aggregative manner, increasing its tendency to be patchy. Other taxa on this list are predators, which are often large, mobile, and found patchily depending on their prey base; examples include *Cancer* crabs and moon snails. Still others are poor dispersers (no pelagic propagules) such as the small seastar *Leptasterias*.

Driving the south-north trend in diversity are the 58 taxa that tended to be more common in the Central or North-Central sites. This list again includes the diversity of benthic lifestyles in terms of location (epibiota vs. infauna) and trophic mode (algae to carnivores). The relative length of this list, and the corresponding richness data seen from our northern samples (Fig. 17), parallel many other estuarine studies that find the greatest benthic diversity in areas near the mouth of estuaries, where salinities and temperatures tend to be the least variable (and most marine), wave action highest, turbidity and sedimentation lowest, and pollution the least. Any or all of these factors may be affecting the trends seen in our Puget Sound samples. Many of the taxa on this list become steadily more abundant as one moves into more wave-exposed (coastal) areas in Washington, such as *Anthopleura elegantissima*, *Lacuna vincta* (App. E17), *Nucella lamellosa* (App. E38), and *Lottia strigatella* (App. E21); these trends may relate directly to waves (although the mechanism is unknown). Other organisms displayed the opposite trend with increasing abundances towards the lower salinity and energy environments of the south basin (e.g. *Alia gausapata* and *Notomastus tenuis*). Low-salinity stress may exclude many species from the South Sound, although we could find no literature on experimental salinity studies for the local flora and fauna. Some taxa may be excluded by higher sedimentation of fines in the South, for instance the suspension feeding phoronids, and these tube-builders in turn provide habitat for a variety of associated infauna (Rader 1980). Kozloff (1983) also notes that local phoronids are 'not likely' to be found in areas of reduced salinity. Studies on the west side of central Puget sound, where the nearshore salinities and temperatures are more marine, would make an interesting test of the relative importance of these factors.

Our data suggest that the 'Basins' of Puget Sound are largely artificial divisions; both the physical factors and the biota suggest more of a continuum. In general, patterns of abundance and diversity showed a gradual, rather than abrupt, change from South to Central Puget Sound. An exception in the 1999 SCALE data was in the abundance of juvenile clams. Appendix E16 illustrates the abundance of all juvenile clams (<2 cm) pooled, and Appendices E22, E23, and E28 show numbers of the most common species. In each case, the 1999 data show a sharp discontinuity, with no juvenile clams found in the MLLW samples in South Sound (i.e., south of the Tacoma Narrows), but some at virtually all beaches north of there. Within Central Sound there was no pattern along the south-north gradient; scattered beaches showed large numbers of different species. The Carkeek and West regions had large numbers of both *Macoma inquinata* and *Saxidomus* juveniles, but otherwise few patterns are visible.

Some previous years' sampling in South Sound, as well as the existence of healthy populations of adults, indicate that juvenile clams can be found in this region, although we have never found many in Low-zone pebble-beach samples. Pebble beaches were not sampled in 1997, but Low and Mid-zone mud samples in Carr Inlet contained numerous "juvenile Macoma sp." (probably *Macoma nasuta*). In 1998, pebble beaches in Carr and Case Inlets had a few juvenile clams (mostly *Protothaca*) in the Low zone (a total of 26 in 6 beaches), but none were found in Budd. This suggests that our South Sound samples have not been biased in some way against juvenile clams, so the absence of juvenile clams in the 1999 samples probably represents a genuine failure in recruitment that year. All of the common intertidal clam species have larvae that spend substantial amounts of time (2-4 weeks) in the plankton; this means that larvae produced in South Sound may well be exported, but that larvae produced elsewhere should be able to be advected into the basin. Juvenile clams are subjected to many sources of mortality; small (<2 cm) individuals live in the top 2 cm of sediment and thus suffer variation in salinity and temperature not experienced by deeper-dwelling, older individuals, and predation in these shallow sediments is also likely to be higher. *Protothaca staminea* is known to suffer its highest mortality during the first year of life (up to 1 cm length), especially in the winter (Chew and Ma 1987), and this pattern likely holds for the other intertidal taxa as well. Annual variation in recruitment for *Protothaca* is very high. It is thus possible that either there was a problem with larval clam supply into South Sound pebble beaches in the summer of 1998 (many of these taxa spawn in the spring or early summer), or that high juvenile mortality occurred before our sampling in June 1999. The same set of circumstances did not affect, or less strongly affected, the Central Sound beaches where juvenile clams were often extremely numerous.

High annual variability has been found in many other estuarine studies (refs. in Introduction), including a subtidal benthic sampling program in Puget Sound (Llanso et al. 1998). They found that for some species, the temporal variation exceeded the spatial variation (but the opposite was true for other studies). They also found, as have we (Schoch and Dethier 1999), that species in related samples (e.g., within an inlet or a basin) often undergo parallel increases or decreases from year to year. For the purposes of this study, we emphasize that even though some population abundances vary from year to year and from place to place (as seen from the nested ANOVA results), the community structure *within* groups of samples is stable relative to differences *among* sample groups whether they be areas, cells or basins. For example, community patterns were consistent among replicate beach segments within an area within a year, but shifted among years or if compared to a different area (see also Schoch and Dethier 1999). The implication for the design of a monitoring program is that it is critical to monitor replicates within areas from year to year; temporal variation within each replicate can be expected, and the best signal of local change will be if one replicate begins to deviate from the others. Quantifying a signal of larger-scale anthropogenic change, e.g. within a whole area (Fig. 1) will require interannual data from other areas within the cell to provide an appropriate contrast.

Despite numerous methodological differences between studies, it is possible to qualitatively examine patterns of species' distributions and abundances between 'historical' surveys in the 1970s and 1980s and SCALE surveys. Overall, these surveys show a high degree of overlap in flora and fauna when beaches of similar location, tidal height, and substrate type are compared. Substantial similarity was seen both in epibiota and infauna at most sites. Species that did not appear to be similar can often be explained by differences in sampling methodology, e.g. the historic surveys often used smaller sieve sizes (thus capturing more tiny infauna such as spionid polychaetes) and involved sampling deeper into the substrate (thus finding more adult clams). In both SCALE and historic surveys, certain species tended to appear only in more northern beaches, or only at certain sites.

A major exception to trends in richness, and to similarity between historic and SCALE surveys, was in the beaches near Point Wells. These beaches had much lower richness and many fewer juvenile clams than those to the north and to the south. In addition, many taxa found commonly in the historic surveys from these sites (as well as found to the north and south in the 1999 surveys) are conspicuously missing. A variety of processes could have contributed to this apparent decline in biota, but the importance of these (or others) is unknown. First, the refinery at Point Wells (now operating at a reduced level as an asphalt plant, Kevin Li pers. comm.) could have influenced the nearby beaches through chronic discharges or spills of hydrocarbons. Secondly, stormwater discharges and sewage outfalls in the region may be having an effect. Third, local human activity in the form of clam digging, school groups, and a nearby park may be impacting the biota. Lastly, changes in sediment supply or wave action from increased boat wakes may have impacted the physical conditions and thus the biota at these sites. The most strikingly depauperate beach of the 3 sampled in this area, beach 26, was not the one closest to the refinery but was one where a school group was visiting on the day we sampled; this site had the fewest epibiota and clams of the 3, but the most capitellids and other deposit feeders, suggesting that both surface disturbance and organic input may be occurring.

Extensive surveys (Nyblade 1979a, b, Smith and Webber 1978, Webber 1980) of sites further north than the 1999 SCALE samples and the 1970s Central Sound studies discussed above allow us to qualitatively compare the biota found in beaches in the broader Puget Trough area. Overall, the taxa found by these northern studies are very similar to those found in the more northern of our Central Puget Sound samples. Again, methodologies vary sufficiently that quantitative comparisons are not possible, but it is often possible to see that dominant species in those studies are similar to ours, both in terms of epibiota and infauna. Most of the species found in 'mixed-coarse habitats' by Nyblade and colleagues at sites in the Straits of Juan de Fuca, the Whidbey Island area, and the San Juan Islands are the same as those listed in Table 7 under "taxa more common in central and northern Puget Sound" (and those listed as "throughout" the Sound). Unfortunately, the very low within-beach replication of these older studies has made either temporal or spatial analyses of trends impossible (see discussion of replication, above), and we see little feasibility or utility in combining those datasets with the SCALE datasets. As with the Central Sound comparisons, however, the apparent overall similarity between sets of studies suggests a lack of major long-term changes in these habitats.

We are beginning to achieve our goal of defining habitat-specific reference conditions, which we need if we are to define *expected* conditions. To detect change, we must have a clear method for describing what is at a site versus what was expected at a site; the power of this method can already be seen for the Point Wells samples, in terms of detecting how unusual they are compared to physically similar neighboring beaches. Our analyses show that the biotic communities at two of the Pt. Wells (Area 12) beaches are considerably different from those in Areas 11 and 13 (Figure 26B). Thus, the community analyses are useful to identify deviations in community structure relative to those on surrounding beaches. For individual species, the spatial autocorrelation analyses show that most of the populations we sampled exhibit strong relationships among beaches, (i.e., the populations are not independent). When this is not the case (e.g., for the polychaete *Mediomastus*, Fig. E25), we can identify beaches with "unhealthy" populations relative to those on nearby beaches.

Rakocinski et al. (1997) note that "natural gradients in salinity, depth, and sediment composition obscure[d] the detection of macrobenthic responses to sediment contamination"; this complaint is seen repeatedly in the literature exploring the 'health' of estuaries. Because the SCALE site-selection methodology 'factors out' most of these natural geophysical gradients, it allows managers to begin to actually distinguish natural vs. anthropogenic factors. Washington State's own subtidal benthic sampling program (e.g., Llanso et al., 1998) notes the problems in data interpretation that arise when sampling is of limited spatial coverage, is not random, or does not "integrate a variety of oceanographic conditions". The SCALE methodology should allow decoupling of natural vs. unnatural variability. A logical next step in investigating the decoupling power of this tool would be to sample areas that were matched geophysically but thought a priori to be pristine versus degraded.

In terms of the number of reference sites and potential locations, our data underscore the importance of explicitly defining the spatial and temporal scales for monitoring the biota of Puget Sound. We have seen that community similarity is a function of distance between sampled beaches. Near beaches are more similar than beaches far away even when we carefully control for the variability of the physical environment. The observed differences in community structure seem to be a function of wave energy and salinity, as suggested by strong correlations to these physical variables along the axis of the Central Basin. Many taxa also show strong spatial autocorrelation along the axis of the Central Basin, possibly explained by local patterns of larval or spore dispersal and recruitment (e.g. higher recruitment to neighboring beaches than to beaches farther away). This suggests that to capture change in community structure at high ecological resolution, for example at the observed scales of water quality gradients in the Central and South Basins of Puget Sound, monitoring sites will have to be numerous and spatially nested (e.g. on the order of the number of transects used for this study). An alternative strategy is that fewer transects can be used to detect ecological change at a lower resolution (e.g., among cells and among basins rather than among smaller water-quality gradients). But it is clear that a sampling frequency designed to detect (large) changes among cells cannot be used to detect (smaller) changes among areas within a cell. Unfortunately for resource managers, this has huge implications to the amount of money and staff time dedicated towards change detection in the marine environment. Small spatial scale, high ecological resolution sampling designs will be required to detect changes at small temporal scales (e.g. monthly), while large scale, lower ecological resolution sampling designs will only be useful for change detection over longer temporal intervals. The high degree of spatial autocorrelation through the south and central basins of Puget Sound will, however, be very useful for generalizing the results of lower order sampling designs since the biota among neighboring transects are now known to be highly correlated.

We remain skeptical about the possibility of finding a simple indicator organism or index that will provide sufficient information about the condition of shoreline habitats and communities. While there are clearly ‘key species’ in some habitats, i.e. those that have a major impact on the rest of the community and are sometimes called ‘bioengineers’, these do not exist for all habitats (e.g., there is no obvious key species for the low-shore pebble beaches studied here). Even for habitats with such species (e.g., ghost shrimp in mud, sand dollars in sand, eelgrass in subtidal sand or mud), their local absence may often be a result of natural patchiness, not human disturbance. Although identifying and quantifying all the macroscopic species in a sample takes time and some expertise, it is necessary for the community-level multivariate analyses that have been shown by us and others to give an effective view of variation (or lack thereof) among samples in space and time. In addition, some of the few broadly agreed-upon indices of use in seeking patterns of stress or disturbance (natural or otherwise) are species richness and diversity, which require thorough community-level sampling. Use of these indices by themselves, however, i.e. without looking at species composition, could cause managers to miss changes in species distribution that could be indicative of pollution effects (e.g., Llanso et al. 1998). Trophic-level analyses also require detailed information, and may suggest changes of concern, e.g. a shift from a trophically diverse community to one dominated by deposit feeders (e.g., Weston 1990). Posey et al. (1998) found that proportional representation of different “functional guilds” showed less year to year variation than species-level patterns, and noted that guilds may thus be useful for detecting environmental changes. Brown et al. (2000) found that trophic structure (especially the number of surface deposit feeders) related to sediment contamination in a Gulf of Mexico study. Since the stressors of greatest impact on the nearshore habitats of

Puget Sound remain unknown, we cannot yet restrict our sampling to a few taxa or groups that might be effective indicators (if known); and if we did, we would run the risk of missing an important change caused by another stressor. Engle and Summers (1999) note: “For an indicator to be appropriate for the assessment of estuarine health, it should incorporate geographic variation and should recognize the inherent multivariate nature of estuarine systems”. The SCALE methodology is beginning to pinpoint key sources of geographic variation for this kind of analysis.

GLOSSARY

ANOVA

Analysis of Variance (ANOVA) is a statistical procedure that compares between the means of two or more samples. ANOVA requires that all of the groups of the interval variable are close to equal in variance within the group. Observations must be from a normal distribution and must be independent.

Forcing function

Any physical, chemical, biological, or geological force applied to the system with no good mechanism for determining the affect of the applied force. The force description is therefore critical to the actual prediction of the response of the system. For example, natural or anthropogenic factors that affects the system being studied, such as wind velocity and direction on the survival and recruitment of larvae from the water column to the shoreline. The wind velocity and direction, in this case, is the forcing function that determines the survival and recruitment of larvae.

Indicator value

A very common goal in community analysis is to detect and describe the value of different species for indicating environmental conditions. If environmental differences are conceptualized as groups of sample units, then Dufrene and Legendre's (1997) method of calculating species indicator values provides a simple, intuitive solution. The method combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species in a particular group. It produces indicator values for each species in each group. These are tested for statistical significance using a Monte Carlo technique. Groups are commonly defined by categorical environmental variables, levels of disturbance, experimental treatments, presence/absence of a target species, or habitat types.

MRPP

Multiple Response Permutation Procedure (MRPP, is a non-parametric test for the hypothesis of no difference between two or more groups of entities. The groups must be defined *a priori*. For example, one could compare species composition between disturbed and undisturbed transects to test the hypothesis of no effect. Discriminant analysis is a parametric procedure that can be used on the same general class of questions. However, MRPP has the advantage of not requiring assumptions (such as multivariate normality and homogeneity of variances) that are seldom met with ecological community data. A good introduction to the method is to read the appendix in Biondini et al. (1985). More details can be found in Mielke (1984) and Berry et al. (1983). See Zimmerman et al. (1985) for an ecological application similar to the example in the preceding paragraph.

ANOSIM (Analysis of Similarity; Clarke & Green 1988 ; Clarke 1993) is similar to MRPP in concept but uses a different test statistic. The R statistic of ANOSIM is qualitatively similar in interpretation to the A statistic of MRPP.

Non-metric multidimensional scaling (NMS)

Non-metric Multidimensional Scaling (NMS, MDS, NMDS, or NMMDS) is an ordination method that is well suited to data that are nonnormal or are on arbitrary, discontinuous, or otherwise questionable scales.

For this reason, NMS should probably be used in ecology more often than it is. This method can be used both as an ordination technique and as a method for assessing the dimensionality of a data set (plot minimum stress against k, the number of dimensions in the ordination space). NMS differs fundamentally in design and interpretation from other ordination techniques (Kruskal and Wish 1978; Clarke 1993). See Clarke (1993) for an excellent summary of the advantages and uses of NMS.

NMS is an iterative search for a ranking and placement of n entities on k dimensions (axes) that minimizes the stress of the k-dimensional configuration. The calculations are based on an n x n distance matrix calculated from the n x p-dimensional main matrix, where n is the number of rows and p is the number of columns in the main matrix. "Stress" is a measure of departure from monotonicity in the relationship between the dissimilarity (distance) in the original p-dimensional space and distance in the reduced k-dimensional ordination space.

Program NMS in PC-ORD is largely based on Mather's program NMMDS (Mather 1976; includes listing of source code). The central computational algorithm (steepest descent minimization to find minimum stress) in NMMDS is based on Kruskal (1964b).

The output plots graphically depict relatedness, or correlations between data, (i.e. sites, species etc). The points close together are more similar than points far apart. Vector joint plots are used with ordination plots to show the magnitude and direction of correlated variables. (i.e. showing forcing functions that explain variation in groups of samples) The length of the vector represents the strength of the correlation. The direction of the vector, relative to the observed pattern of points, represents how well the variable explains the pattern. Only correlations with $R^2 > 0.2$ are considered in this analysis.

Practical Salinity Units (psu)

The Practical Salinity Scale for measuring and reporting salinity of water and the International Equation of State of Seawater were published by UNESCO in 1981, after many years of work by the Joint Panel on Oceanographic Tables and Standards. For salinity measured from the conductance property of water, parts per thousand is an inappropriate unit. In the Practical Salinity Scale, salinity is defined as a pure ratio, and has no dimensions or units. By decision of the Joint Panel of Oceanographic Tables and Standards it does not have any numerical symbol to indicate parts per thousand. Salinity should be reported as a number with no symbol or indicator of proportion after it.

p-Value

The measured probability of occurrence for an observation, i.e. rejecting the null hypothesis, by chance alone given that the null hypothesis is actually true. By convention, a p value < 0.05 is often considered significant (i.e. there is less than a 5% probability that the finding [null hypothesis rejected] was due to chance alone).

Spatial autocorrelation

A potential problem with data obtained for many field studies is that they may have a spatial component. This can result in spatial autocorrelation which causes problems for statistical methods that make assumptions about the independence of residuals *(a residual is the difference between an observed and a predicted value)*. Cliff and Ord (1973) define spatial autocorrelation as *'If the presence of some quantity in a sampling unit makes its presence in neighbouring sampling units more or less likely, we say that the phenomenon exhibits spatial autocorrelation'*. If there is spatial autocorrelation in the data this will lead to a spatial correlation of residuals, for example positive residuals will tend to occur together. If spatial autocorrelation is present it will violate the assumption about the independence of residuals and call into question the validity of hypothesis testing. The main effect of such violations is that the Error SS is underestimated (Davis, 1986) thus inflating the value of test statistic. An inflated test statistic increases the chance of a Type I error (incorrect rejection of a Null Hypothesis). Most GIS provide tools to measure the level of spatial autocorrelation (e.g. Moran's I).

Species diversity

Species diversity is a combination of richness and evenness. Therefore, it is more than a measurement of the number of different species, it is species richness weighted by species evenness.

Species evenness

Value that measures the degree of evenness in population numbers between a number of different species in a community or given habitat. Evenness is maximum when all species have the same number of individuals.

Species richness

The number of species within a region.

Vector overlay

An increasingly popular method of showing the relationship between a set of variables (usually environmental variables) and ordination scores is a diagram of radiating lines, often called a "joint plot." The angle and length of the line tell the direction and strength of the relationship.

The lines radiate from the centroid of the ordination scores. For a given variable, the line forms the hypotenuse (h) of a right triangle with the two other sides being r values between the variable and the two axes. The angle of the line is arccos(rx*|rx|/h), where rx is the correlation of the variable with the horizontal axis and h is proportional to sqrt((rx^2)^2 + (ry^2)^2).

Wave energy dissipation coefficient

An empirical relationship used to calculate wave runup is:

$$\frac{R_{2\%}}{H_s} = C\xi_b$$

(Battjes, 1974; Holman, 1986; Meer and Stam, 1992; Shih et al., 1994; Tillotson, 1995) where $R_{2\%}$ is the runup exceeded only 2% of the time in a 20-30 minute interval, and C is a constant. Holman (1986) found that for combinations of runup and the rise in sea level caused by radiation stress (the build-up of water along the coast from incoming waves), the C coefficient equals 0.90. This relationship was successfully used by Shih et al. (1994) to calculate extreme wave runup for cliff erosion studies on the Oregon coast. Van der Meer and Stam (1992) used empirical data to refine the basic formula by considering new values for C when substrate roughness and permeability vary along with slope.

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