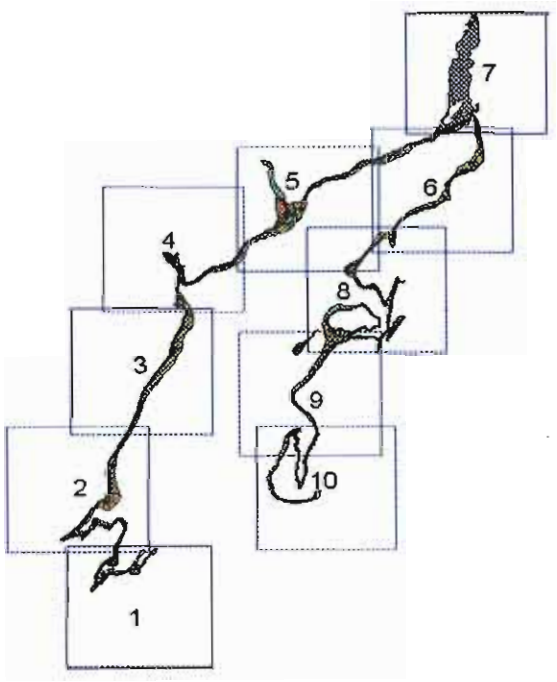
Analysis of shoreline classification and bio-physical data for Carr Inlet

(FY97-078, Task 1 and Task 2)



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EXECUTIVE SUMMARY

This report summarizes the results of a project (FY97-078) performed for the Dept. of Natural Resources that was designed to test the feasibility and power of a method of classifying the shorelines of Puget Sound, and linking geophysical features of the beaches to the biota therein. A major purpose of the model is to be able to predict differences among the flora and fauna found in the different beach types (mostly soft-sediment) present in the Sound. The project's goals were to: 1) provide a test-case for a new methodology to aid in DNR's current shoreline inventory efforts; 2) help define ways to choose "reference sites" for PSAMP monitoring efforts; 3) begin to quantify what and how many habitat types are present in Puget Sound shorelines; and 4) determine how similar are the biotic elements within and among habitat types.

The 'health' of Puget Sound can have many definitions, including physical, chemical, and biological characteristics. Because biotic features may respond rapidly and sensitively to changes in the other two types, these may provide a useful indicator of overall health. However, the extensive and complex nature of the shorelines of Puget Sound mean that it is unrealistic to monitor the biota in all regions. In addition, monitoring change in biota encounters two fundamental problems. The first is the large variation through time in abundances of organisms in natural ecosystems, which masks our ability to statistically separate an actual change caused by a perturbation (the signal) from natural cycles (the noise). Many monitoring and impact-detection programs have run afoul of the problem of confounding spatial and temporal variation, i.e. of assuming that change has occurred at an impacted site because it is different from a control site, when really the sites were not adequately matched to begin with. Second, if monitoring is done at selected reference sites, we cannot necessarily extrapolate or generalize the results to broad areas. Yet such extrapolation is critical as we try to make predictions about impacts of large-scale environmental phenomena.

One solution to both these problems in the marine realm is to systematically quantify and eliminate physical gradients among sample sites. Minimizing gradients in the physical environment can enhance our ability to detect change, because variation in the environment results in variation in the biota (Schoch & Dethier, 1996). If organisms in Puget Sound are ecologically linked with their physical habitats, then it should be possible to extrapolate results from a few biotic surveys to similar habitats elsewhere.

We describe here the application of a model (Shoreline Classification and Landscape Extrapolation: SCALE) that involves dividing a shoreline into segments of decreasing size and thus increasing geophysical homogeneity. The smallest unit is the alongshore beach segment, which encompasses three regions (polygons) representing different intertidal elevations. Physically similar polygons are grouped together by statistical clustering techniques, and from these groups a random selection is sampled for biota. We then test each sampled beach segment for community-level homogeneity, i.e. biotic similarity among the replicate samples. If within-segment biota is homogeneous, then physically similar segments are compared for within-group homogeneity. If segments within a group are biologically similar, then inferences can be made about the

biota in other segments sharing the physical features of that group. Likewise, if the biota at larger spatial scales (e.g., in one habitat type across several inlets) can be shown to be homogeneous, then extrapolation to similar (but unsampled) beaches is possible. In this way, by linking geophysical attributes of ecological importance to the associated biota, we can make inferences about communities over large areas of shoreline, whereas actual biological sampling will always be more labor intensive and therefore limited in spatial extent.

The site selected for this study was Carr Inlet (including Henderson Bay), the first major embayment south of the Tacoma Narrows (South Sound District). Carr Inlet was first divided into 100 - 1,000 m segments based on principal shoreline substrate characteristics, using low altitude color infrared (CIR) aerial photography. Geophysically homogeneous alongshore segments (10-100 meters in length) were then identified and delineated on orthophoto basemaps while walking the intertidal zone. This partitioning resulted in 310 alongshore segments that could be grouped into 4 spatial blocks corresponding to 4 quadrants of Carr Inlet (varying in wave energy, temperature, and salinity).

Epiflora and fauna (in quadrats), and infauna abundances (in cores) were sampled at 3 sand, 3 mud and 3 gravel beach segments in each of 3 intertidal zones in one spatial quadrant, and additional data were taken at 6 sand, 3 mud and 2 gravel segments in only the lower zone from the three remaining quadrants. The upper and middle zones for both the 'sand' and 'gravel' shoreline segments were characterized by cobbles and pebbles, usually with interstitial sand or with underlying hardpan. The lower zones tended to be characterized by less mixed substrates, e.g. sand or mud (although the 'gravel' shores were still a mix of cobbles, gravel, and sand or mud). A total of 840 quadrats and cores were sampled, with a total richness of 114 taxa (mostly identified to the species-level).

We used multivariate analyses to evaluate the relative homogeneity of communities within and among clusters of beach segments following two types of data transformations. "Indicator values" were calculated for each species, combining information on frequency and abundance in a particular group of samples. Matrices of indicator values for each tide level were analyzed to determine the organisms consistently driving the differences among segments and among groups.

The multivariate analyses clearly illustrate that for Carr Inlet, it is possible to divide and classify intertidal shorelines such that geophysical homogeneity is minimized within a given segment of the shore, and that with this geophysical homogeneity comes relative biological homogeneity. Reducing physical and chemical differences among sites reduces the environmental variation that inevitably results in biotic variation. At larger spatial scales (e.g., different sides of the inlet), biotic similarity within each habitat type (e.g., sand) decreases, as expected, because at these scales there are greater differences in geophysical features such as energy and salinity.

The organism-environment link we were testing is perhaps best seen in the cases where the infauna did not "match" the habitat type as we had classified it; in several

cases, errors in beach classification were 'pointed out to us' by the organisms. For example, based on the fauna in the other members of one group of mud segments, we predicted that mud segment 194 should not have sand dollars but it did, probably because of the relatively high proportion of subsurface sand there. Future mapping efforts will be careful to note such subsurface sediment and also seepage characteristics, which were not in the original model.

A variety of species (both infauna and epiflora and fauna) were found to have large indicator values, i.e. had either even abundances or high frequencies in a given set of samples. These species potentially can help to detect change and extrapolate biotic data because they are important to a given habitat type (e.g., mud vs. sand); they can be predictably found in a given substrate type or region, so that their absence would be indicative of unusual conditions. We also used nested ANOVAS to analyze the spatial scales at which each indicator species was most variable, and were able to pick out the taxa that would be best at detecting change at any given scale.

Sixteen older surveys from other Districts of Puget Sound were compared to the data from Carr Inlet. Some habitat types (e.g., the mixed-coarse 'gravel' habitats) had moderate biotic consistency among surveys, whereas others (especially the sand and the mud) were very different. By resampling some of these old sites, both geophysically and biotically, using our methodology, valuable information could be gained about how much of the variation between the old surveys elsewhere in Puget Sound and ours in Carr Inlet might be due to temporal changes, regional differences, or methodological differences.

CONCLUSIONS

•Our work in Carr Inlet constitutes the first significant test of a model and methodology that we believe can provide a relatively low-cost, low-tech, *high-resolution* way to quantify the state of Puget Sound shoreline habitats as they are today. Overall, we found a strong relationship between geophysical features and biota, and through extrapolation can predict with reasonable accuracy what organisms (and in what abundances) should be found in beaches in Carr Inlet that we did not sample.

•With some further testing, this methodology should be useful for comparing communities in clearly degraded areas versus relatively pristine ones, and for detecting change into the future.

•Data from old surveys and anecdotal information indicate that the model cannot yet be extrapolated to areas outside of Carr Inlet; extrapolation will be valid only to similar beaches within a given region. **However, the basic methodology we have described should be able to be applied at these larger scales.**

•Any attempt to scale up biotic data (whether from a beach to the inlet, or from the inlet to the Sound) will involve adding new sources of variation. At some point in this scaling process, the communities in 'similar' beaches are likely to become so different (e.g., as one moves into a different oceanic mixing regime or biogeographic province) that comparisons are not meaningful.

•Future decisions about monitoring programs need to be question-driven, with the questions specifying the scale of resolution needed (and thus the scale of variation that must be accepted). Regions, habitat types, and species of particular concern need to be identified by the potential users of monitoring programs.

•We recommend that an effort be made to obtain maps of the whole Sound generated by the Harper methodology, and that these be used as a basis for choosing regions and substrate types for further research.

•Reference sites need to be chosen on a finer spatial scale, and should be matched geophysically, either with each other or with degraded sites under study. Concentrating research in the low intertidal zone may provide the most information per unit cost in terms of the biota at this level being diverse, productive, and vulnerable to stressors from land and sea. Sampling methodologies need to be consistent among sites, and must include large enough sample sizes to deal with the high natural spatial variability within a site.

•In contrast with other, lower-resolution shoreline mapping methods, potential applications of the SCALE methodology and resulting maps include: 1) selecting matched sites for field research or applied monitoring programs; 2) denoting sensitive habitats, e.g. to oil spills; 3) predicting resource-rich habitats, or those where key resource species could exist; 4) assessing biotic damage following unnatural events; 5) choosing areas for conservation efforts; and 6) improving change detection by choosing sites where much of the environmental variation has been factored out.

Chapter 1

Bio-physical Coupling in Carr Inlet

This chapter summarizes the technical methods and results of the test of the SCALE methodology for Carr Inlet: if a shoreline is classified into geophysically similar units, how similar are the biota among these units? At what spatial scales do these similarities break down? To what extent can we extrapolate to the biota found in other beaches in the same region?

1.1 Introduction

Biological data from ecological studies are plagued by two fundamental problems. The first is the large temporal variability of organism abundances in natural ecosystems which masks our ability to statistically separate an actual change caused by a perturbation (the signal) from natural cycles (the noise). Natural variation results from both biological interactions among populations (competition, predation, etc.), and physical gradients in space and time. Detecting change in biological communities is often the underlying objective for small spatial scale field experiments in basic ecology, and for large scale inventory and monitoring programs by resource agencies.

The second issue is a scaling problem. Ecologists and regulators are increasingly concerned with processes operating on scales of the landscape or region, but our conventional knowledge base is comparatively fine-scale. Scaling involves a trade-off between resolution (grain, or level of detail) and extent (the area or scope of the study), forcing an incompatibility across scales. Extrapolating or generalizing the results of localized studies to broad areas is fraught with problems. Large-scale studies typically are based on different conceptual models and different data than fine-scale studies. For example, anthropogenic climate change broaches issues of very large scale importance,

but our best empirical understanding of the mechanism of ecological response is at the level of the individual organism.

In the marine realm, virtually all nearshore benthic research has been done at only one or a few sites, with experimental areas often encompassing only a few square meters. As a consequence, we know little about how large-scale habitat heterogeneity affects small-scale ecological processes. Such understanding is especially critical as we try to make predictions about impacts of large-scale environmental phenomena, from oil spills (Paine et al., 1996) to shifts in weather patterns and wind driven processes (ENSO), to global climate change. Small-scale variation may be maintained by local processes such as competition and predation, but if we are interested in large-scale patterns or long-term change, we cannot necessarily extrapolate from the numerous studies done only locally (Underwood and Petraitis 1993). Sampling sites are often selected and replicated randomly, haphazardly, or based on logistical convenience, but these sites may have little relationship physically or biologically to surrounding habitats, making extrapolation difficult (Gilfillan et al. 1995). Replication along unquantified physical gradients risks introducing variability into the data. There is a need for well replicated, nested sampling designs that can quantify the contribution of variation at each scale (in space or time) to the total variation among samples (Morrissey et al.1992, Underwood and Petraitis 1993, Thrush et al. 1994, James and Fairweather 1996).

One solution to both these problems in the marine realm involves systematic quantification and elimination of physical gradients among sample sites. Minimizing gradients in the physical environment can enhance our ability to detect an actual change from natural variation, because at least in some systems, sampled communities show significant fidelity to their physical habitat types (Schoch & Dethier 1996). We describe here the application of a model that increases geophysical homogeneity and minimizes biological variability by partitioning a shoreline into physically similar units. By then aggregating similar but spatially separated units, we can scale up localized biological data to larger regions.

Background

Nearshore marine habitats (< 10 m depth) serve a number of ecological functions including nesting, breeding and refuge areas for wildlife, spawning and rearing for fishes, support of food web linkages, sediment trapping and nutrient cycling. These habitats are defined by interacting environmental variables such as substrate size, wave energy, water temperature, salinity, nutrient concentrations, and processes and patterns of coastal sediment transport. Information regarding the distribution and functions of nearshore habitats is critical for making sound management decisions. Regulatory and proprietary agencies require this information for long term planning as well as for responding to episodic or catastrophic perturbations. However, intertidal functions such as habitat use, primary productivity, biodiversity, etc., and habitat values such as esthetics and recreation are poorly understood due to inadequate baseline monitoring and inventories.

Many scientists and resource agencies have attempted to monitor localized intertidal and subtidal transects in hopes of finding a short term response to a "pulse" experiment or a long term indicator of ecosystem health. Long term monitoring presumably will provide a statistical baseline from which a change can be detected. However, the dynamic nature of the marine environment causes high spatial and temporal variation in organism abundances and community structure, and generally confounds our ability to detect non-catastrophic perturbations. The intertidal environment is dynamic across multiple scales of space and time. Atmospheric and oceanic examples in the eastern Pacific margin range from El Ninos at large scales (>5 years and >1000 km), to subtle changes in substrate size and moisture retention during a diurnal tide cycle (<12 hours and <10 m). Between these extremes lie many other sources of variation, e.g. in seasonal water temperature and nutrient availability, in salinity due to regional and local hydrographic regimes, and in daily or local wave height and energy. Detection of ecological change must involve an attempt to factor out these environmental variables in order to extract any signal from the seemingly vast sources of noise.

Marine soft-sediment habitats, while often rather uniform on the surface, vary highly in many geochemical parameters that are thought to affect benthic infaunal communities. Numerous studies in estuaries and on sandy and muddy shores have found

correlations between physical parameters such as grain size, organic content, O_2 content, or salinity and biotic parameters such as diversity, biomass, or abundance of particular species (e.g., Boesch 1973, Gray 1974, Flint and Kalke 1985, Holland et al. 1987, Service and Feller 1992, Chester et al. 1993, Mannino and Montagna 1997, reviewed in Snelgrove and Butman 1994). In most studies, the geochemical parameters are highly intercorrelated (e.g., Mannino and Montagna 1997). How each of these factors (e.g., low salinity) actually affects the infauna varies among studies. Although classification procedures have defined infaunal communities associated with particular physical conditions (e.g., muddy low-salinity assemblages), many studies conclude that these assemblages are not discrete but rather segments of a continuum; Thorson's (1957) concept of distinct "parallel-level bottom communities" has been replaced by a sense of the artificiality of such groupings (e.g., Boesch 1973).

Infaunal communities also vary widely spatially and temporally, in part because of the dynamic nature of their physical habitat. Since most benthic infauna are relatively immobile, their numbers tend to reflect current local environmental conditions. Seasonal shifts with salinity or level of hypoxia are common, as are recruitment pulses that cause major changes in community structure and biomass (Holland et al. 1987). Small-scale spatial variation, when examined, is often very high; Service and Feller (1992) and Morrisey et al. (1992) both found high variance in abundance of many taxa among replicate cores at each sampling date. This high small-scale variance made it impossible (even in a properly nested design) to detect significant patterns at larger spatial or temporal scales.

Many estuarine studies have been done on geochemically diverse habitats, but few have attempted to "control" habitat type in their analyses of temporal trends (but see Holland et al. 1987). Given the already-high variability within habitats, detection of change (or pollution impacts) will be impossible unless these habitat differences can be factored out (Weisberg et al. 1997). Underwood and Petraitis (1993) recommend either 1) randomizing physical habitat features such that sites selected for experiments or monitoring are "properly representative" of all the habitats in a region, or 2) stratifying habitats and then replicating studies only within the chosen strata. The disadvantage of

the first option is in the high variances that will exist among randomly chosen sites, while the second option will involve difficult choices about habitats to study vs. ignore.

Choosing habitats that are directly comparable needs to be done in a systematic and rigorous fashion. Our approach is to reduce variation among habitats by minimizing geophysical gradients within and among sites to be compared. In the intertidal zone, these gradients serve as indicators of prevailing hydrodynamic processes that directly and indirectly affect the abundance, distribution, and fecundity of nearshore organisms. If organisms are ecologically linked with their physical habitats, then a morphodynamically homogeneous shoreline, for example with uniform wave climate and substrate dynamics, should have minimal variation in community structure. Minimizing gradients in the geophysical environment should enhance our ability to distinguish change from natural variation in biological populations. We have shown that it is possible to partition a shoreline according to quantified geophysical attributes, and that variation among and within biological communities on one rocky shore was reduced when similar habitats were compared (Schoch and Dethier 1996). This model needs to be more broadly tested in other regions and other substrate types.

The objective of this study was to test the hypothesis that minimization of geophysical gradients among soft-sediment habitats in an estuary will reduce the biological variability seen. If this methodology for characterizing habitats is effective, then it should be broadly useful for both basic and applied research. If the biota in a region are linked relatively consistently to geophysical beach types, then mapping of large areas can be done using these quantifiable features, and extrapolations to areas inhabited by particular species can be made. Sites for basic research can be chosen from such maps, reducing the site-to-site variation that has plagued many studies (refs. above). Such a mapping scheme should also be useful for helping preserve biodiversity; a spectrum of the different, physically defined habitats in a region should be set aside in order to preserve the spectrum of local biota. Studies of pollution (e.g., oil spill) impacts in a mapped region can be done in sites that should have been biotically similar before a pollution event (e.g., Gilfillan et al. 1995); our inability to do this systematically in, for example, Prince William Sound has made quantifying the impacts of the Exxon Valdez

oil spill very difficult (e.g., McDonald et al. 1995, Paine et al. 1996). Finally, there is increasing need for large scale monitoring programs along all types of shorelines in order to detect anthropogenic change.

1.2 Methods

Overview

Our overall objective is to increase environmental homogeneity of sampled areas as a means of decreasing biological variability. Our basic approach (Schoch, 1996) is illustrated in Figure 1, which shows the conceptual model for partitioning a shoreline into segments of incrementally decreasing spatial scale and increasing biogeochemical homogeneity. Each spatial partition consists of nested partitions of smaller spatial scales. The smallest partition is the alongshore segment, which has three nested polygons representing different intertidal elevations. The across-shore polygons are hypothesized to be geophysically homogeneous at the scale of ecological sampling. Similar polygons are grouped together by statistical clustering techniques and from these groups a random selection of polygons is sampled for biota. We then test each sampled polygon for biotic multivariate homogeneity. If each segment's biota within a spatial block (i.e., a larger region) is homogeneous, then the segments are compared for within-block homogeneity. If segment communities are not statistically different, then inferences can be made about the biota in other non-sampled segments nested within the same block. Comparisons can also be made among indicator species. Successive aggregation of the biota at each incremental scale can then lead to further spatial extrapolation. Thus, aggregation of nested geophysical partitions provides a means to scale up ecological data over larger areas. The geophysical quantification of ecologically significant attributes can be performed over large areas of shoreline using this partitioning technique, whereas actual biological sampling will always be more labor intensive and therefore limited in spatial extent.

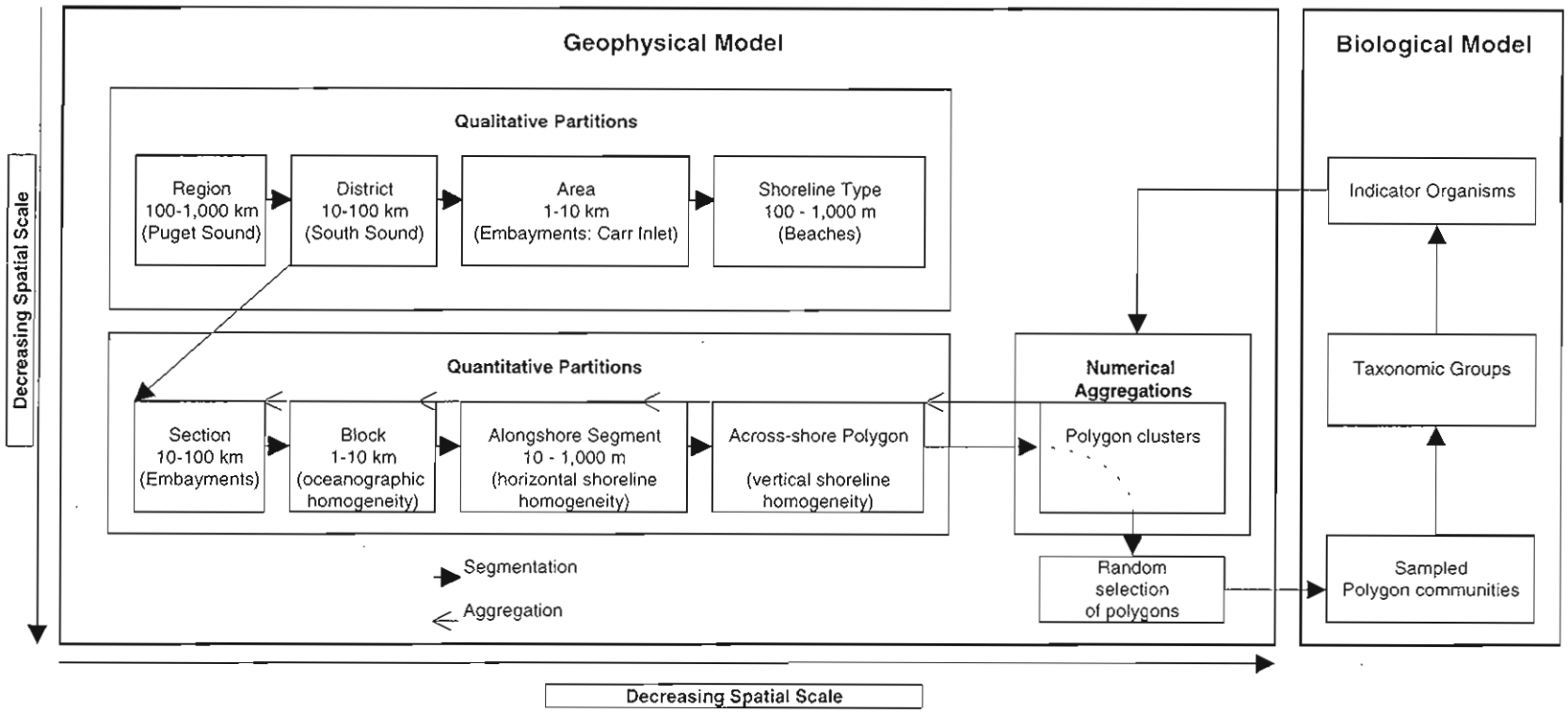


Figure 1. Conceptual model of the bio-geophysical linkage between shoreline habitats and intertidal communities.

Shoreline segmentation

The site selected for this study was Carr Inlet (including Henderson Bay), the first major embayment south of the Tacoma Narrows in the Puget Sound estuary. Puget Sound is divided into five regional water quality management districts (Figure 2, Puget Sound Water Quality Authority, 1986)), defined by flow characteristics, salinity, tide range and the distance from the Strait of Juan de Fuca (which affects timing of tidal ebb and flow). Our study site lies within the South Sound district. This district is further separated into eight major inlets, each characterized by distinct large scale geophysical differences such as orientation, salinity, turbidity, and timing of the ebb and flow, based primarily on the distance from the Tacoma Narrows sill.

At all spatial scales the primary environmental determinants of intertidal organism abundance and community structure are substrate size (e.g., gravel vs. sand) and elevation (height above low water) (Kozloff 1993; Ricketts et al. 1968). Substrate size determines the stability (movement potential) and dynamism (movement frequency), both factors in community disturbance. Solid surfaces generally preclude infauna, while dynamic mobile substrates preclude most sessile organisms. Many mobile but low dynamism substrates are extremely rich in biota, especially infauna. Sediment size also affects moisture retention, O_2 content, and organic content. The position or elevation within the intertidal zone leads to differences in immersion times which result in distinctive community zonation patterns. In regions of large tidal range such as the Pacific Northwest, the intertidal zone can become very wide (>100 m) when shore angles are low.

Another key physical feature is wave energy, which affects community structure both directly through episodic disturbance events (Denny et al. 1985) and indirectly by controlling substrate dynamics over short and long temporal periods. The magnitude of wave runup or swash can also affect community structure by elevating zonation levels, delivering nutrients and preventing desiccation. In relatively protected areas such as Carr Inlet, wave runup is practically non-existent and large waves are infrequent, such that wave energy does little to directly structure the intertidal community. However, indirect effects include current propagation and substrate movement over long temporal scales.

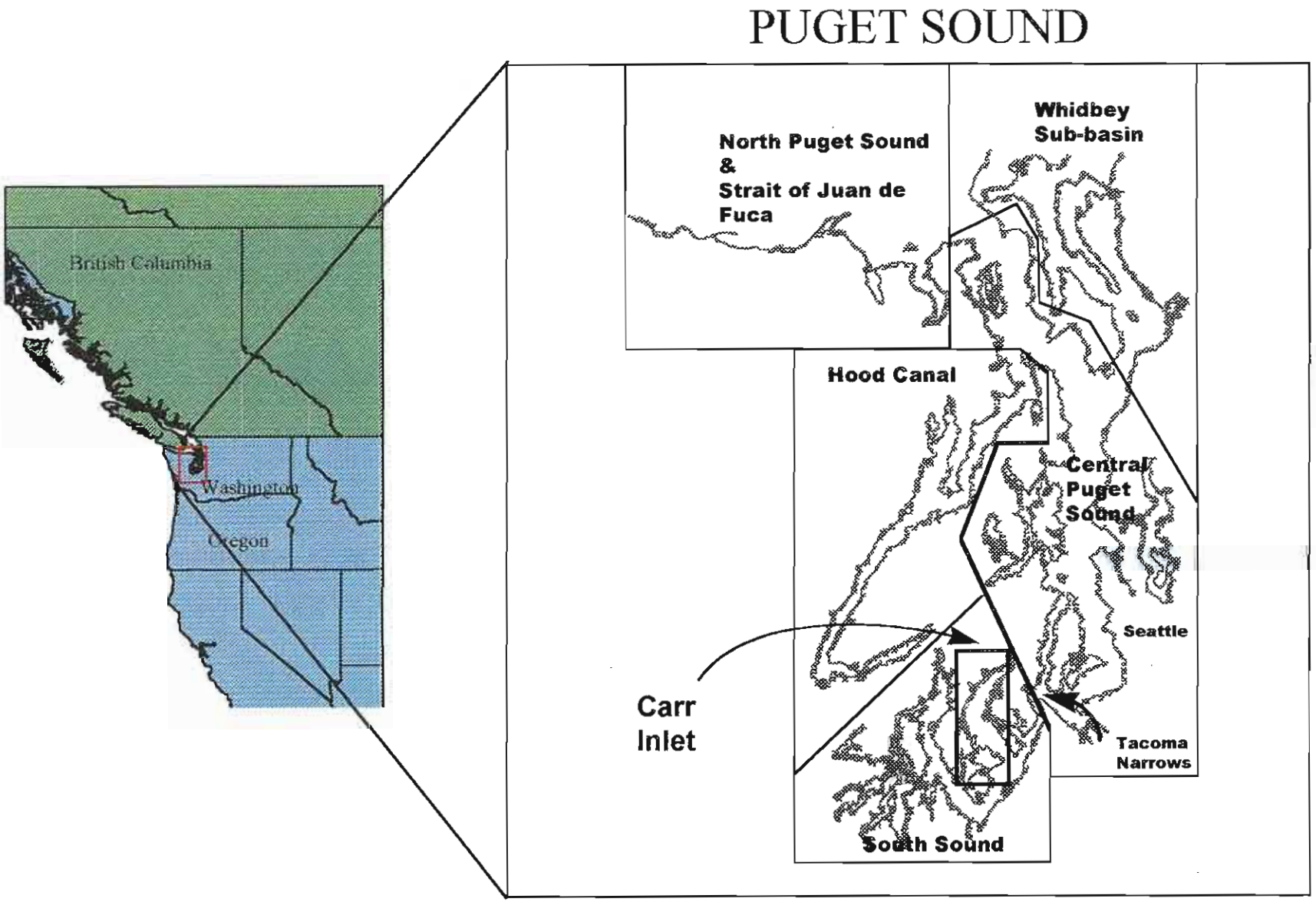


Figure 2. Map of project location. Puget Sound water quality districts and Carr Inlet embayment.

Coarse grained or highly mobile substrates are generally indicative of relatively higher energy compared to fine and immobile substrates. Even moderate amounts of wave energy can keep fine particles in suspension while moving coarser sand and pebble grains along the beach face. Therefore, fine particles such as muds are generally confined to partially enclosed and sheltered embayments, while sand flats can be either stable in low energy or very mobile in high energy wave regimes. Pebble and cobble beaches are generally found only where wave energy is sufficient to prevent the settling of finer sands and silts. In Carr Inlet, the processes of sediment suspension and transport can be expected to occur primarily during the winter when strong southerly winds blow along the axis of the bay (Downing 1983).

Quantitative partitioning of 1 - 10 km long shoreline segments began with measurements of salinity and water temperature. Nighttime imagery from the Advanced Very High Resolution Radiometer (AVHRR) satellite sensor (band 4, 1 km resolution obtained from the National Environmental Satellite Data and Information Service) provided a large scale temporal data series of sea surface temperature (SST). These data showed a consistent (over a 2 year annual interval) temperature gradient from the cold deeper water in outer Carr Inlet to the warmer shallow water of inner Henderson Bay. Field measurements of conductivity and sea surface temperature near the shore were made over a two day period with a hand held instrument (YSI Model 30) at 14 sites, spaced approximately 5 km apart. Salinity was calculated and reported to 0.1 ppt.

LandSat 5 data from bands 1, 2, and 3 were used to locate sediment plumes, areas of urban, suburban, timber and agricultural development, and for measuring wave fetch at scales of 1-10 km. The only significant sediment plume identified emanates from Burley Lagoon and flows along the southeast shoreline. This provided justification for field measurements of salinity to define the spatial extent of fresh water influence. Based on subsequent ground observations, the sediment plume may persistently load the southeast nearshore substrate with fine particles from the mouth of Burley lagoon to approximately Allen Point, however, this can only be verified by a study of the suspended sediment volume and mineralogy which is beyond the scope of this project.

Carr Inlet was partitioned into 100 - 1,000 m segments based on photogrammetric analysis of principal shoreline substrate characteristics. The classification of shoreline type follows a system used for resource management in British Colombia (Howes et al. 1994; Harper et al. 1991). Low altitude color infrared (CIR) aerial photography (1:13,000 scale), flown at an extreme low tide, was used to delineate the intertidal zone from the uplands using the strong chlorophyll signature of terrestrial plants. The lower intertidal boundary was also shown clearly due to the dark body properties of water at infrared wavelengths. At horizontal scales of 10-100 m, the CIR were also useful for differentiating well drained or coarse substrates (high radiance) such as pebbles and cobbles from saturated or fine substrates with high moisture content (low radiance) such as silt and sand. The preliminary delineation generated 219 alongshore segments of magnitude 100-1000 m based on the photogrammetric interpretation of substrate roughness, moisture content, and shoreline aspect.

The shore delineations based on the CIR imagery were then augmented by ground surveys to further partitioned the shoreline in the alongshore and across-shore according to beach slope, and substrate sizes (primary, secondary, and interstitial). Geophysically homogeneous alongshore segments (10-100 meters in length) were identified and delineated on orthophoto basemaps while walking the intertidal zone during the spring low tides from April 8 -11, 1997. Each alongshore segment was vertically separated into four across-shore polygons centered at specific elevations that correspond to immersion times during the daily tidal cycle, based on the mean tidal statistics for Carr Inlet (Figure 3). The upper zone ranges from extreme high water (> 4.5 m) down to mean high water (3.8 m); we characterized its geophysical parameters at mean higher high water (4.0 m) where the substrate is immersed 10% of the time. For the majority of the project area this zone is characterized by man-made seawalls. The middle zone, from mean high water to mean low water (0.9 m), has previously been characterized at mean sea level (about 2.4 m) where the substrate is exposed 50% of the time. But in Carr Inlet, the middle zone spatially represents the majority of the exposed beach face at low tide and is generally vertically heterogeneous, so we separated it into an upper-middle zone, characterized at 3.0 m, and a lower-middle zone characterized at 1.5 m. These elevations generally

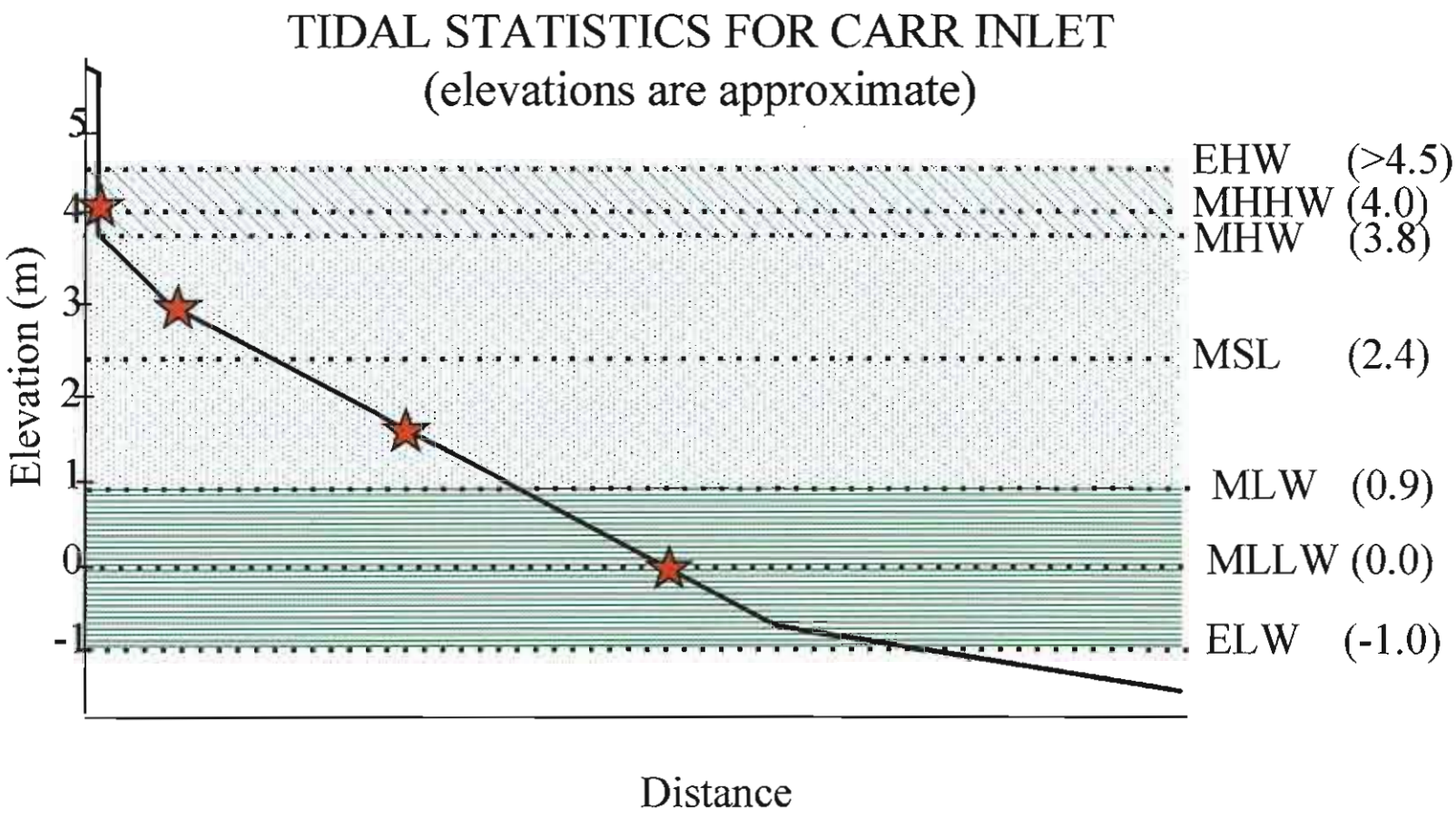


Figure 3. Tidal statistics for Carr Inlet based on the Wauna, Horsehead Cove, and Home secondary tidal stations. Stars indicate elevations used for habitat characterization.

avoided slope breaks and substrate transitions. The lower zone is from mean low water down to extreme low at -1.0 m, and we characterized it at 0.0 m where the substrate is immersed at least 90% of the time.

Substrate size was measured according to the Wentworth particle size classification for the following percent cover categories: primary (for particles comprising more than 60% of the substrate), secondary (for particles less than 40% of the substrate), and interstitial. Beach slope was measured with a hand held digital inclinometer. Substrate permeability and ground water salinity were measured in the lower intertidal zone by digging a hole to 0.3 m and inserting a perforated bucket. Permeability was quantified by the time required to fill the bucket with ground water, and salinity was measured *in situ*. Substrate roughness was qualitatively categorized based on the degree of particle rounding. Ground water seepage was estimated as a percentage of the polygon length exhibiting seepage from the beach prism based on photogrammetric interpretation of CIR aerial photos. Dynamism is the relative bed stability calculated using:

$$D = \frac{\text{critical rolling velocity}}{\text{predicted velocity}} = \frac{V_c}{V_p} \quad (1)$$

from Gordon et al. (1992). The velocities are calculated from:

$$V_c = 0.155 \sqrt{d} \quad (2)$$

where d is the grain diameter perpendicular to the rolling force, and

$$V_p \approx .3[g(H+h)]^{1/2} \quad (3)$$

where g is the gravitational acceleration (9.8 m/sec^2), H is the wave height, h is the local water depth, (Denny, 1995). Calculation of the surf similarity parameter is described below. Table 1 lists the attributes and spatial scales used for shoreline segmentation.

Table 1. Geophysical attributes for shoreline partitioning

Shoreline Type (100-1,000 m)	Block (1-10 km)	Segment (10-100 m)	Polygon intertidal zone	
(all qualitative)	(all quantitative)	(all quantitative)	(all quantitative except where noted)	
substrate size	salinity	aspect	surf parameter	(calculated)
slope angle	surface temperature	drift exposure	slope	
geomorphological form	average fetch	wave energy	dynamism	(calculated)
			roughness	(qualitative)
			substrate size:	
				primary grains
				secondary grains
				interstitial grains
			permeability	
			seepage	(qualitative)

Wave energy for each alongshore segment was quantified by the measured maximum wind fetch. The deep water energy flux or wave power is calculated by:

$$P = ECn \tag{4}$$

where P is the energy flux (watts/m),

$$E = 1/8\rho g H_s^2 \tag{5}$$

ρ is water density (1020 kg/m^3), H is the significant deep water wave height, C is the wave celerity corresponding to T, the wave period in seconds:

$$C = gT/2\pi \tag{6}$$

and n equals ½ in deep water (Komar, 1997).

The effect of waves on beaches in best represented by surf characteristics. Battjes (1974) developed a surf similarity parameter defined by the Iribarren number. The Iribarren number was calculated for each across-shore polygon based on values for beach slope, wave heights and wave lengths:

$$\xi_b = \frac{S}{(H_s/L_\infty)^{1/2}} \quad (7)$$

where S is the beach slope (e.g. tan α), and L_∞, the deep water wave length in meters is:

$$L_\infty = gT^2/2\pi \quad (8)$$

There are no published wave statistics for this area, so for each segment we derived the required parameters from measurements of maximum fetch, or the longest overwater distance unimpeded by a landmass (obtained from a GIS coverage of the South Sound district). We classified each distance measurement and estimated the wave statistics for each fetch class from graphs published in the Shore Protection Manual (CERC 1984) and listed on Table 2. Dissipative or low angle shorelines (e.g. slope = 0.03) correspond to very low Iribarren values (e.g. $\xi < 0.2$ to 0.3), and reflective or high angle shorelines yield $\xi > 2$. Values in between generally represent highly dynamic shorelines if the substrate is unconsolidated. Calculations were made for each across-shore zone since for any segment an upper intertidal seawall is generally highly reflective and a lower intertidal sand flat is highly dissipative.

Table 2. Wave parameters derived for calculating the surf similarity index.

Energy Category (SCALE)	Exposure Classification (Harper or Dethier)	Fetch Distance (km) (CERC)	Sustained Wind Speed (kts) (CERC)	Significant Wave Height (m) (CERC)	Wave Period (s) (CERC)	Wave Length (m)
1	very protected	<.1	5	0.1	1	1
2		.1-.5	10	0.2	1.5	2
3		.5-1	10	0.3	2	6
4	protected	1-5	20	0.4	2.5	10
5		5-10	20	0.5	3	14
6	semi-protected	10-50	30	1	4	25
7	semi-exposed	50-100	30	2	5	40
8		100-500	40	3	6	60
9	exposed	500-1000	40	4	8	100
10		>1000	50	5	10	150

Statistical analyses of segment data

Segment polygons at each intertidal level were aggregated separately using a combination of multivariate hierarchical agglomerative clustering and sorting to achieve a relatively high degree of similarity within groups while retaining a geophysical distinction among groups. The large number of segments (310 in about 56 km of shoreline) in the project area was an indicator of local shoreline heterogeneity. Most of this heterogeneity was explained by differences in wave energy and substrate particle size. These primary variables, in addition to an interaction variable for substrate stability (dynamism), were assumed the most important determinants of community structure. The secondary variables permeability and roughness, which covary with particle size, and groundwater seepage are known to be important to some organisms, thus possibly affecting abundances. The primary variables were given more weight by separately clustering the secondary variables and then adding the resulting grouping variable to the smaller matrix of primary variables. Each matrix was relativized by column maximum values to equalize the various measurement scales, then clustered using Sorenson's city block distance and the centroid linkage method. The centroid method was selected for providing the best separation of clusters, but since it is space-contracting, there is a chance that polygons may become part of a growing cluster when they should have formed the nucleus of a new cluster. An alternative would be to use a space-conserving method such as the group mean linkage, but results from preliminary trials produced a large number of small clusters with few natural groupings. Using the centroid linkage method, the dendrograms for the secondary variable clustering showed that most of the segments were clustered before 25% of the information was lost according to Wishart's (1969) objective function. Twenty groups were selected for the secondary group cutoff and twelve for the primary grouping based on the objective function criterion.

The cluster membership variable, and the spatial block variable (block extent was visually determined from maps of wave energy, salinity, and SST data, see Results section) were added to the polygon database. The database was sorted on the cluster variable and then the spatial block variable, resulting in groups of polygons nested within each spatial block. The biological sampling design was centered around these analysis

groups. The subset of cluster segment members within a spatial block were designated as 'segment groups' or 'groups'(see Table 3 in Results section).

Biotic sampling design

Epiflora and fauna, and infauna abundances were sampled during the spring low tides of May 6 - 10 and May 21 - 25, 1997. Data were taken at 3 sand, 3 mud and 3 gravel beach segments in each of the 3 zones, and additional data were taken at 6 sand, 3 mud and 2 gravel segments in the lower zone only. Sampled segments were selected randomly from within spatial blocks of statistically generated clusters. We sampled at the same elevations used to characterize the beach during the physical attribute mapping. The upper zone (at 4.0 m) was not sampled since it generally comprises seawalls or other shoreline protection structures that are ubiquitous in this area and largely depauperate of marine biota. Surveying equipment was used to locate the transect levels at 0 m, 1.5 m, and 3 m elevations, corresponding to the lower, lower-middle, and upper-middle intertidal zones respectively. At each sampled level, a 50 m horizontal transect was positioned near the center of the segment to eliminate edge effects.

Ten samples were collected along each transect, with 2 random samples in each of 5 blocks along the 10-m transect. There is no 'standard' methodology for this kind of soft- or mixed-sediment sampling, even for sieve sizes (see below). Many of the old surveys done in Puget Sound (see Chapter 2) used only 2-5 replicates per level. We chose our design based on the maximum number of replicates per transect that could be sampled within the workable exposure time at the lowest level (0 m). Each sample consisted of quantifying epiflora and fauna in a 0.25 m^2 quadrat, and infauna in a 10-cm diameter core dug to 15 cm depth. In the quadrats, we estimated the percent cover of algae and sessile animals in cover class categories (to approximate an arcsine square root transformation, Muir & McCune 1988), and counted mobile animals. Estimating cover classes is much more rapid than doing either percent cover estimates or random point contacts, and analyses of cover class data encounter many fewer problems with issues of variance and normality. would be adequate to sample the diversity and variance in these communities. The core size was a compromise between being small enough to make counting small

infauna feasible (many studies use much smaller cores) but large enough to capture some of the patchy, large infauna such as clams. Many of the old Puget Sound surveys (see Chapter 2) used a very small core (4 cm diam.) sieved to 1 mm, plus a larger box core (e.g., 0.25 m2) sieved coarsely (6 mm) for clams. If clams were a specific study target, the larger core size would be preferable (and a different sampling design should be used, e.g. that of the Washington Dept. of Fish and Wildlife).

Sediment samples from the cores were bagged, transported to a central location and sieved through a 4 mm and 2 mm mesh. Several samples from each substrate type were also sieved to 1 mm, but few additional organisms were retained. We chose to use 2 mm because: 1) for this general survey, the recruits, juveniles, and tiny infauna (e.g., oligochaetes, nematodes) were of less interest than the other infauna; and 2) given the coarseness of many of the substrates, clogging of finer sieves would have been a significant problem. A study focusing only on mud or only on small infauna should use a smaller mesh size. There is a suggestion in the literature (Pearson and Rosenberg 1978) that smaller infauna tend to dominate in polluted areas, so a pollution-oriented study should also use smaller mesh (see Chapter 3 for further discussion of mesh sizes). All organisms not identifiable in the field were placed in formalin and later identified in the lab, when possible to the species level.

The sampling design thus had four nested spatial scales for each level and shore type; samples (quadrats and cores) within each transect block (meters apart), transect blocks within each segment polygon (10's of meters apart), segment polygons within a group of polygons (kilometers apart), and groups of polygons within the project (among spatial blocks: 10's of kilometers apart). The design was balanced so that the number of samples were the same for each of the transect blocks, the same number of transect blocks for each of the polygons, and the same number of polygons for each of the groups. If the biota in these habitats are tightly tied to the quantified geophysical features, we hypothesized that (within a level and shore type) communities should be relatively uniform within transects, somewhat less so among segments within a spatial block, and should be most different among spatial blocks.

Statistical analyses of biotic data

Multivariate techniques were used to detect patterns in the communities across spatial scales. Data matrices of abundances of each species were transformed to reduce the beta diversity, skewness, and coefficients of variation for column (species) and row (sample unit) sums. High values for these statistics often indicate violations of the assumptions of normality, linearity, and homogeneity of variance that could affect the performance of multivariate distance measures (Tabachnik & Fidell 1989). Beta diversity is a measure of compositional heterogeneity in the data, calculated here as the ratio of the total number of species to the average number of species (alpha over gamma), where alpha is the total richness across samples and gamma is the average species richness per sample. Species with a frequency of occurrence of < 5 % (within the matrix under analysis) were deleted. Sample outliers were evaluated and deleted when greater than 2 standard deviations from the mean (Tabachnik & Fidell 1989). Two transformations were then applied independently, one that retained abundance information and the other derived from presence/absence data. The first was a double relativization, first by species maximum and then by sample unit totals. This equalized the data, reducing the effect of rare and abundant species, and allowed both percent cover of sessile species and counts of mobile species to be considered together. The second transformation applied the Beals smoothing function to reduce the effects of correlations among zero-rich data (Beals 1984). The effects of these transformations were evaluated by calculating descriptive statistics for each matrix before and after transformation.

The transformed data sets were ordinated using non-metric multidimensional scaling (NMS) to evaluate how each performed in describing the differences in community structure among the groups of sample units. Starting configurations were calculated by first generating a Bray-Curtis similarity matrix, with Sorenson's city-block distance measure (Bray & Curtis 1957). NMS was then run with 100 iterations on the 3 dimensions supplied by the Bray-Curtis results. The performance of the ordination on each transformation was assessed by evaluating the slope of the curve of final stress vs. the number of dimensions. Graphical plots of ordination results for the two axes explaining the greatest proportion of the variance were examined together with overlays

of the various grouping variables. Correlations between the axes and the species were tabulated and assessed for descriptions of community structure. Formal significance tests for differences among groups, either in species abundances or species presence/absence, were computed using a non-parametric multi-response permutation procedure (MRPP; Zimmerman et al. 1985). This was used to test the null hypothesis that two or more groups occupy the same region in species ordination space. MRPP has the advantage of not requiring assumptions such as multivariate normality and homogeneity of variances. Transformations, Bray-Curtis, NMS, and MRPP were computed by PC-ORD (McCune and Mefford, 1997).

The original raw data matrix was modified after inspection of the transformed ordination plots to achieve greater ecological resolution by evaluating within group homogeneity and separation among each group of samples. For example, biological community zonation resulting from different immersion times in the intertidal zone is a strong determinate of species composition (Kozloff 1993). First the habitat matrix was split into three matrices, one for each sampled elevation (3.0, 1.5, and 0 m). Then each of these was split again into a separate matrix corresponding to major shore habitat types (mud, sand, and gravel). After we examined the ordination results from each of the samples, ordination plots of each sub-matrix for the quadrat and core organisms were also evaluated to help determine the sources of differences among samples.

We evaluated the relative homogeneity of communities within and among clusters of beach segments by calculating the departure from perfect within-group homogeneity. This parameter can be used as a guideline for determining the amount of sample heterogeneity acceptable to a specific investigation. This measure of departure, the value R, defined as the chance corrected within group agreement, is calculated as:

$$R = 1\text{-}(\text{observed } \delta/\text{expected } \delta) \qquad (10)$$

where δ is the weighted mean within-group distance (Berry et al. 1983):

$$\delta = \sum_{i=1}^{g} C_i x_i \qquad (11)$$

C is the weight based on the number of members in a group, and x is the average distance in each group. A value for R of 1 indicates perfect within-group agreement and a value of 0 indicates within-group heterogeneity expected by chance. Negative R values occur when there is greater heterogeneity than expected by chance.

Nested ANOVA

Multivariate analyses were used to evaluate the variation in abundance at different spatial scales (transect blocks within segments, and segments within and among groups) for each organism at each elevation or zone. The sampling design was spatially nested and the samples were considered random, therefore the abundance data for individual taxa were analyzed with nested ANOVA (Sokal and Rohlf, 1995). ANOVA assumptions of normality of residuals and equality of error terms were determined by visually examining plots of estimated values against residuals.

Indicator organisms

Our ability to detect change in marine communities depends to a great extent on how reliable different species are as response organisms to environmental conditions. If environmental change can be represented by different groups of sample units, then Dufrene and Legendre (1997) provide a method for calculating the 'reliability' of each species. Their "indicator value" for each species combines information on the evenness of species abundances in a particular group of samples and the fidelity or faithfulness of occurrence (frequency) of a species in that group. Matrices of species indicator values for each tide level were analyzed with NMS to determine the indicator organisms driving the differences among segments and among groups.

1.3 Results

Shoreline segmentation

Based on the results of the AVHRR data analysis, and the field measurements of SST, salinity, and wind fetch, Carr Inlet was subdivided into 4 spatial blocks (quadrants) to reduce the effects of these gradients (Figure 4). While these gradients undoubtedly vary seasonally, the AVHRR imagery showed spring and summer trends for SST that were sufficiently consistent from year to year (1995-1997) to justify spatial blocking.

Photogrammetric segmentation by habitat type generated 23 partitions, with three principal substrate types represented (mud, sand, and gravel) (Figure 5). The mud type was typically low angle and sheltered, with a low radiance signature indicating relative impermeability. The sand beaches had a higher radiance with a smooth texture and often showed well developed bars and troughs over the low tide terraces. The "gravel" substrate is a complex mix of small boulders and cobbles overlying gravel, sand, and mud, with occasional areas of hardpan (consolidated clays). These show as high radiance textured features on the CIR imagery. Generally the beaches in the project area are vertically complex with the upper zone substrate being different from the middle and lower zones. Characterization at this spatial scale was based on the substrate type with the largest surface area for a given segment.

The low tide ground surveys delineated 310 alongshore segments, composed of 1232 across-shore polygons (309 upper, 306 upper-middle, 305 lower-middle, 289 lower: 'missing' polygons occurred, for example, in the shallow inlets where there was no low zone). See Appendix A for a complete listing of the physical attributes. Habitat clustering produced twelve groups for each zone shown in Table 3. Sorting the polygons by cluster and spatial block allowed each cluster to attain greater homogeneity in terms of SST and salinity. The across-shore polygon attribute matrices were then recombined and sorted to produce groups of matching alongshore segments. Random selections were made from these segment groups for organism sampling (Table 3, Figure 6).

Table 4 lists the attributes for the selected segments and polygons. For characterization purposes, we will use terminology referring to the principal habitat types (i.e. mud, sand, and gravel) to describe the sampled segment groups, even though in some

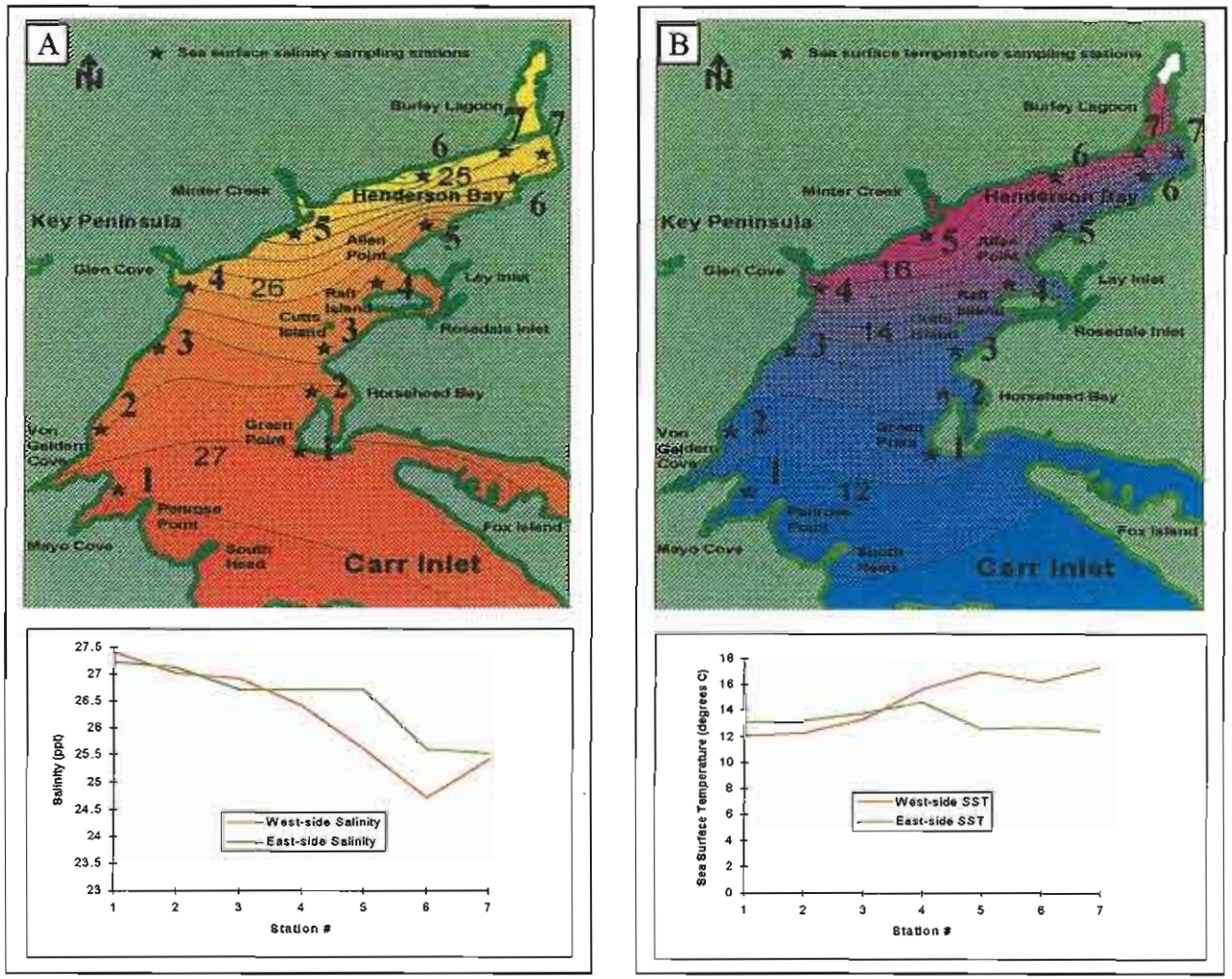


Figure 4. Figure 4A shows the sea surface salinity distribution and Figure 4B shows the sea surface temperature distribution for late April, 1997. The stars show the sample station locations.

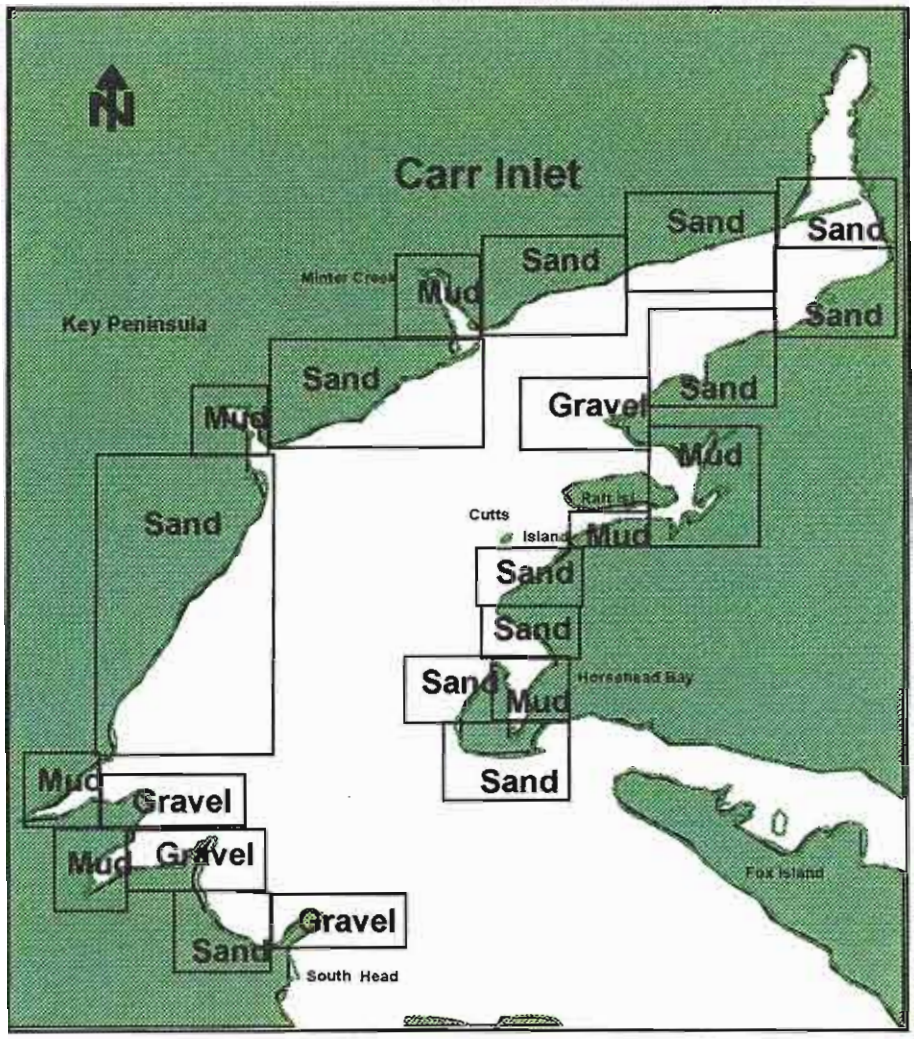


Figure 5. General shoreline type distribution for Carr Inlet.

Table 3. Spatially nested sample design for intertidal communities in Carr Inlet. The design is balanced at each level for sample plot.

Segment Clusters			Segment Frequency in Blocks				Selected	Across-shore	Cluster	Analysis	Shoreline
Zone	Cluster #	Cluster Characteristic	1	2	3	4	Segment	Polygon (zone)	Member	Group	Type
							Block 4 194	upper-middle	12		
								lower-middle	12		
upper-middle	8	silt/mud sheltered	7			17		lower	8		
	12	sand/mud sheltered	2			5	Block 4 233	upper-middle	3	Group 4	
								lower-middle	4		
								lower	8		
lower-middle	8	sand/mud sheltered	7		2	7	Block 4 251	upper-middle	4		
	9	silt/mud sheltered	7			12		lower-middle	5		
	12	sand/silt/mud sheltered	2			5		lower	8		MUD
							Block 1 59	upper-middle			
								lower-middle		Group 5	
							59	lower	8		
lower	4	sand/silt protected	15	11		10	Block 1 82	upper-middle			
	8	silt/sand protected	26			22		lower-middle			
	10	silt/mud protected	11			6		lower	8		
	12	silt/silt/mud	6	4	3	6	Block 1 93	upper-middle			
								lower-middle			
								lower	8		
							Block 4 164	upper-middle	2		
								lower-middle	3		
upper-middle	2	pebbles/sand protected	23	1	6	35		lower	3		
	3	sand/sand sheltered	5		1	6	Block 4 173	upper-middle	2		
	6	sand/pebble sheltered	5		4	8		lower-middle	3		
	7	sand/pebbles semi-protected	7		2	7		lower	3	Group 1	
	9	sand/sand sheltered	11	1		2	Block 4 216	upper-middle	1		
	10	sand/pebbles sheltered	1	1		5		lower-middle	1		
	11	sand/pebbles protected	1					lower	3		
							Block 2 108	upper-middle			
								lower-middle			
lower-middle	4	sand/pebbles sheltered	5		1	6		lower	3		
	7	pebbles/sand protected	8	1	4	10	Block 2 116	upper-middle			
	10	sand/sand protected	1	1		9		lower-middle			
	11	pebbles/sand protected	1					lower	3	Group 2	
							Block 2 122	upper-middle			
								lower-middle			
								lower	3		SAND
							Block 3 128	upper-middle			
lower	1	pebbles/sand protected	5	1	2	10		lower-middle			
	2	sand/sand protected	17	3		3		lower	3		
	3	sand/sand semi-protected	19		14	22	Block 3 133	upper-middle			
	5	sand/pebbles/mud protected	25			1		lower-middle			
	6	sand/pebbles/sand protected	8	1	5	6		lower	3	Group 3	
	7	pebble/sand protected	3	2	1	1	Block 3 146	upper-middle			
								lower-middle			
								lower	3		
upper-middle	1	pebble/pebbles exposed	62	19	10	12	Block 4 239	upper-middle	4		
	4	pebble/cobbles protected	11	2	6	8		lower-middle	5		
	5	cobbles/pebbles semi-protected	6	1	2	2		lower	11		
							Block 4 263	upper-middle	4		
lower-middle	1	pebbles/cobbles/sand protected	20	15	1	10		lower-middle	5		
	2	pebbles/cobbles/pebbles protected	42	4	9	2		lower	11	Group 6	
	3	pebbles/pebbles protected	31	1	6	34	Block 4 299	upper-middle	4		
	5	cobbles/pebbles protected	16	3	6	14		lower-middle	5		
	6	cobbles/pebbles/silt sheltered	5	1	2	2		lower	11		
							Block 1 103	upper-middle	1		
								lower-middle	1		
lower	9	pebbles/cobbles protected	3	1	5	7		lower	11	Group 7	
	11	cobbles/pebbles protected	6	2	2	6	Block 1 303	upper-middle	1		
								lower-middle	2		
								lower	11		GRAVEL
Total			430	76	94	318					

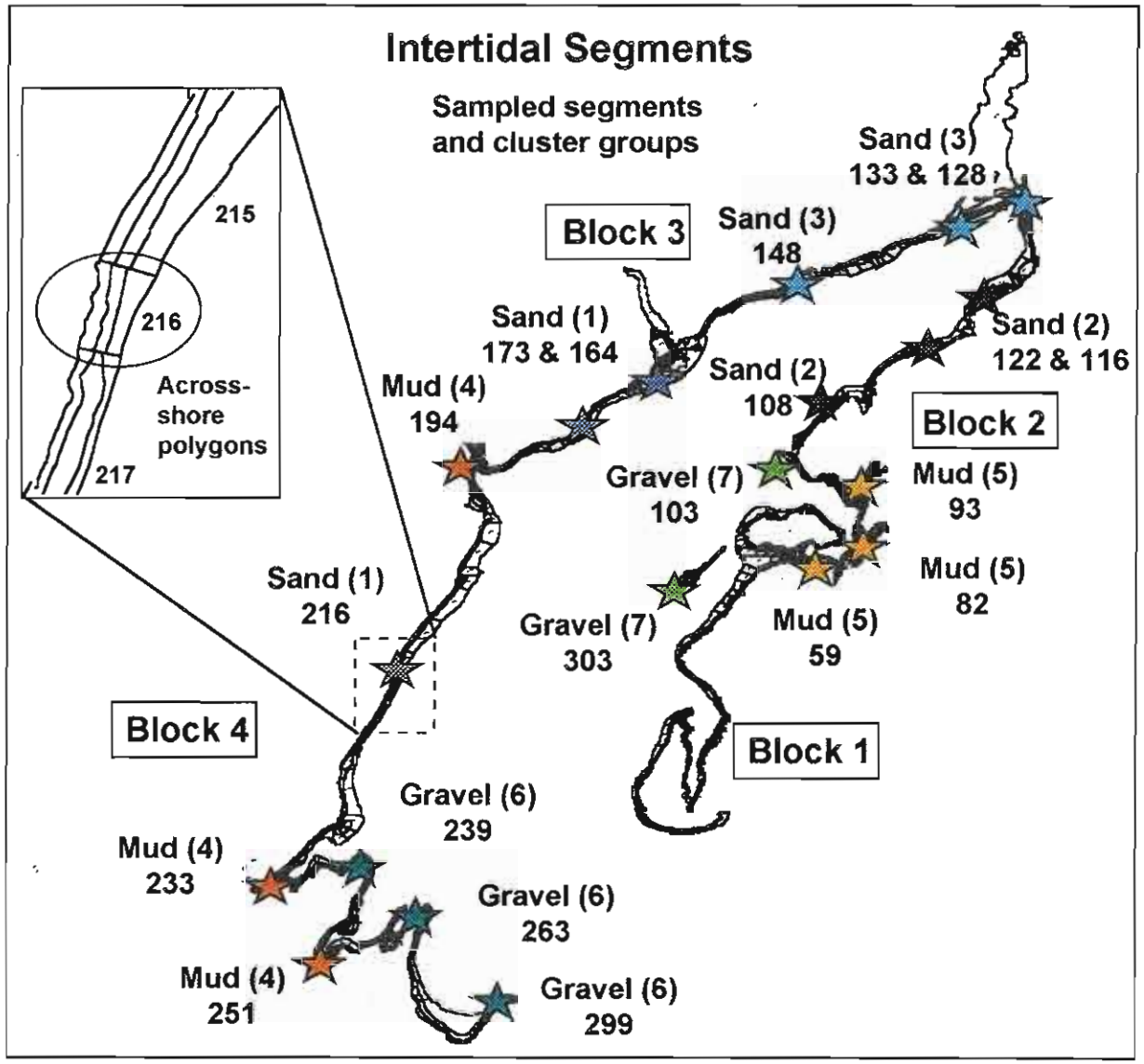


Figure 6. Map of Carr Inlet shoreline segments. The starred segments were randomly chosen for sampling the biota. Also shown are the spatial blocks, across-shore zones (inset), and segment group memberships in parentheses.

cases the segment substrate is considerably more complex. For example, the upper-middle and lower-middle zones for both the 'sand' and 'gravel' shoreline segments were characterized by cobbles and pebbles, usually with interstitial sand or with underlying hardpan (in the lower gravel areas: Table 4). Because exact physical matches for all zones among segments were unlikely, priority was given to matching the lower zones (there is some variation within groups in substrate type and seepage, especially for the middle zones for the mud and sand groups). For example, mud Group 4 is matched in the lower zone but diverges in substrate type and seepage in the lower-middle and upper-middle zones. The gravel segments were well matched in all zones.

Analyses of Biotic Data

Few algae were present in the higher zones and the dominant epifauna were barnacles (on the larger rocks). Mobile animals such as littorinid snails, gammarid amphipods, and shore crabs hid under the cobbles. Lower areas had some small mussels and limpets. Infauna included amphipods and some hardshell (in pebbles) or burrowing (in hardpan) clams. In the mud segments, the upper shore varied from pebbly to silty, with few surface-dwelling organisms (ephemeral green algae and shore crabs) and occasional ghost shrimp in the sediment. The lower-middle zones tended to be silty, sometimes with surface pebbles with a few barnacles or Fucus thalli, and with ghost shrimp. A complete list of sampled organisms is included in Appendix B.

The clearest separation of substrate types and organisms was seen in the lower zones. Low zone sand segments were either dominated by the sand dollar Dendraster (reaching densities of $>1000/m^2$) and had few other infauna, or had no Dendraster and a diverse infauna of burrowing sea cucumbers, anemones, and tube-building and mobile polychaetes. Low gravel segments were characterized by barnacles and ephemeral green algae on the surface, and extremely numerous capitellid polychaetes in the sediment, often with a variety of predatory worms such as nemerteans, glycerids, goniadids, and hesionids. Low mud segments were dominated by ghost shrimp and associated commensal fauna such as small clams and crabs that inhabit shrimp burrows, and by

Table 4. Summary of across-shore zone attributes for the sampled polygons.

MUD									
Group			4			5			
Segment			194	233	251	59	82	93	
Length			75	132	184	109	153	631	
Width			60	104	93	45	60	44	
Upper Middle Zone	Wave energy		very low	low	low				
	Substrate:	primary	sand	sand	pebbles				
		secondary	sand	pebbles	sand				
		interstitial	mud	mud	mud				
	Dynamism		moderate	moderate	moderate				
	Seepage		0%	0%	0%				
	Average richness:	quadrats	5	4	8				
		core	1	0	0				
Lower Middle Zone	Wave energy		very low	low	low				
	Substrate:	primary	mud	mud	mud				
		secondary	sand	sand	pebbles				
		interstitial	sand	mud	mud				
	Dynamism		low	low	low				
	Seepage		75%	0%	50%				
	Average richness:	quadrats	6	6	8				
		core	14	7	13				
Lower Zone	Wave energy		very low	low	low	very low	very low	very low	
	Substrate:	primary	mud	mud	mud	mud	mud	mud	
		secondary	sand	sand	sand	sand	mud	sand	
		interstitial	sand	mud	mud	mud	mud	mud	
	Dynamism		low	low	low	low	low	low	
	Seepage		0%	0%	0%	0%	0%	0%	
	Average richness:	quadrats	4	6	6	2	1	1	
		core	7	12	11	13	10	12	

SAND											
Group			1			2			3		
Segment			164	173	216	108	116	122	128	133	146
Length (m)			374	442	305	331	759	465	103	724	115
Width (m)			275	107	136	139	124	208	105	138	163
Upper Middle Zone	Wave energy		moderate	moderate	moderate						
	Substrate:	primary	pebbles	pebbles	pebbles						
		secondary	sand	sand	pebbles						
		interstitial	sand	sand	pebbles						
	Dynamism		moderate	moderate	moderate						
	Seepage		0%	0%	0%						
	Average richness:	quadrats	2	1	7						
		core	0	1	0						
Lower Middle Zone	Wave energy		moderate	moderate	moderate						
	Substrate:	primary	sand	sand	pebbles						
		secondary	pebbles	pebbles	sand						
		interstitial	sand	sand	sand						
	Dynamism		moderate	moderate	moderate						
	Seepage		75%	25%	50%						
	Average richness:	quadrats	7	9	12						
		core	0	6	11						
Lower Zone	Wave energy		moderate	moderate	moderate	low	low	low	low	low	low
	Substrate:	primary	sand	sand	sand	sand	sand	sand	sand	sand	sand
		secondary	sand	pebbles	sand	sand	mud	sand	sand	sand	sand
		interstitial	sand	sand	sand	mud	mud	mud	sand	sand	sand
	Dynamism		low	low	low	low	low	low	low	low	low
	Seepage		0%	75%	0%	0%	0%	0%	0%	0%	0%
	Average richness:	quadrats	4	3	4	2	7	2	9	7	4
		core	3	5	3	4	13	2	11	13	3

GRAVEL							
Group			6			7	
Segment			239	263	299	103	303
Length			401	192	234	188	272
Width			86	74	76	97	116
Upper Middle Zone	Wave energy		moderate	moderate	moderate	moderate	moderate
	Substrate:	primary	cobbles	cobbles	cobbles	cobbles	cobbles
		secondary	pebbles	pebbles	hardpan	pebbles	pebbles
		interstitial	pebbles	pebbles	pebbles	pebbles	pebbles
	Dynamism		moderate	moderate	moderate	moderate	moderate
	Seepage		0%	0%	0%	0%	0%
	Average richness:	quadrats	5	2	5	4	4
		core	0	0	3	1	3
Lower Middle Zone	Wave energy		moderate	moderate	moderate	moderate	moderate
	Substrate:	primary	cobbles	cobbles	cobbles	cobbles	cobbles
		secondary	hardpan	hardpan	hardpan	hardpan	hardpan
		interstitial	pebbles	pebbles	pebbles	pebbles	pebbles
	Dynamism		low	moderate	moderate	low	low
	Seepage		25%	50%	50%	0%	0%
	Average richness:	quadrats	9	10	12	12	9
		core	5	8	10	4	7
Lower Zone	Wave energy		moderate	moderate	moderate	low	low
	Substrate:	primary	cobbles	cobbles	cobbles	cobbles	cobbles
		secondary	pebbles	pebbles	pebbles	pebbles	pebbles
		interstitial	sand	sand	sand	sand	sand
	Dynamism		low	low	low	low	moderate
	Seepage		0%	0%	0%	0%	0%
	Average richness:	quadrats	7	7	10	8	8
		core	8	10	9	12	16

capitellid and predatory polychaetes. Ephemeral green algae, opisthobranch molluscs, and shore crabs were found on the surface in many segments.

A total of 840 quadrats and cores were collected for a combined total of 420 sample units with a total richness of 114 taxa (mostly species-level). The distribution of the total species richness across the zones shows that 98 out of the 114 taxa were found in the lower zone, 49 in the middle, and 21 in the upper (Table 5). The sand habitats had 113 taxa, while the gravel had 94 and the mud had 58. The variation in species richness among spatial blocks was large; for example, the lower sand zone segments had from 15 to 31 taxa. The gamma diversity, or average number of species per sample, was highest for the gravel (6.9) and mud (5.8) segments, but relatively low for the sand segments (3.9). So even though the total richness was highest for the sand habitats, the average number of species found per sample was lowest. Beta diversity (a measure of community heterogeneity) decreased overall with increased partitioning (geophysical homogeneity). Beta diversities at the segment level were uniformly low across all segments (mean segment beta=2.9, SD=0.8, N=38), and were considerably lower than at larger partition sizes (mean block beta=5.1, SD=1.1, N=13; mean habitat type beta=5.8, SD=0.4, N=3).

Table 5 also lists the summary statistics of data transformations for each matrix in the nested design. Although ten quadrat and ten core samples were collected from each polygon, the species matrix reflects the combined species from quadrats and cores but excludes samples (e.g., for the beta and gamma calculations) where no organisms were found. Evaluation of the descriptive statistics following data transformations showed that both double relativization and Beals transformations improved some multivariate assumptions. Each of the transformations improved the beta, skewness and CV statistics. The greatest decreases in skewness and CV while retaining abundance information came from the double relativization, but the beta was not adequately reduced because of the zero rich data. Note that the number of zeros in the raw data was up to 96%. The Beals transform performed the best overall in favorably adjusting the matrix statistics and reducing the number of zeros in the matrices. Removing the zeros from the matrices relieved the problem of false correlation among samples. However this transformation loses the most information by reducing the data to a probability form of presence/absence.

Table 5. Summary descriptive statistics for the original and the transformed data sets. Splitting the original data matrix into subsets of the major habitat types and the principal intertidal zones, reduced the row and column skewness and CV values prior to transformation. Summarized transformations are as follows: 1) raw data, 2) rare organisms < 5% frequency deleted, then relativize columns by maximum and then relativize by rows total, 3) rare organisms < 5% frequency deleted, then Beals smoothing function.

Matrix	Raw matrix size	alpha			gamma			beta			Row						Column						Percent of matrix empty		
											skew			CV			skew			CV					
		raw	double	beals	raw	double	beals	raw	double	beals	raw	double	beals	raw	double	beals	raw	double	beals	raw	double	beals	raw	double	beals
All data	114x386	114	25	25	5.2	3.9	23.5	21.9	6.4	1.1	8.8	3.7	1.6	106.7	0.0	19.7	11.7	5.3	1.4	364.4	80.7	59.3	95.5	84.3	5.9
All upper-middle	21x78	21	8	8	2.5	2.3	7.8	8.4	3.5	1.0	4.1	2.1	0.9	91.3	0.0	7.9	5.2	2.9	1.7	269.9	1.1	76.0	88.0	70.0	2.5
All lower-middle	49x110	49	29	29	7.3	6.9	29.0	6.7	4.2	1.0	5.4	3.1	1.2	85.0	0.0	8.4	5.1	4.3	1.1	321.0	98.0	89.0	85.0	76.0	0.1
All lower	98x200	98	32	32	5.2	4.3	29.1	18.8	7.4	1.1	8.1	4.0	1.9	87.5	0.0	18.4	8.9	4.9	1.6	480.0	96.2	66.8	95.0	86.7	12.2
All mud	58x115	58	24	24	5.1	4.5	23.3	11.4	5.3	1.0	6.0	3.3	1.3	90.3	0.0	13.7	5.8	4.0	1.6	243.3	71.3	61.8	91.2	81.4	3.1
Block 4 upper-middle mud	10x25	10	10	10	2.5	2.5	10.0	4.0	4.0	1.0	2.7	2.4	1.3	94.0	0.0	7.4	3.6	3.2	1.1	129.0	92.0	83.0	75.0	75.0	3.0
	194 6x9	6	6	6	2.2	2.4	5.6	2.7	2.5	1.0	2.2	1.8	0.4	103.0	0.0	12.0	2.4	1.9	0.5	162.0	103.0	59.0	63.0	60.0	4.0
	233 4x6	4	4	4	2.3	2.3	4.0	1.7	2.5	1.0	0.9	1.0	0.2	93.0	0.0	7.0	1.1	8.0	0.0	116.0	84.0	27.0	42.0	41.0	0.0
	251 8x10	8	8	8	2.6	2.8	8.0	2.9	2.9	1.0	2.3	1.8	1.0	90.0	0.0	19.3	2.5	2.7	1.3	118.0	114.0	95.0	65.0	65.0	
Block 4 lower-middle mud	27x30	27	22	22	6.1	5.9	22.0	4.4	3.7	1.0	4.2	2.6	1.2	69.7	0.0	11.6	3.4	3.0	1.0	214.0	82.6	70.0	77.0	72.8	0.3
	194 20x10	20	20	20	5.6	5.6	20.0	3.7	3.7	1.0	3.9	2.6	1.1	38.0	0.0	7.8	2.3	2.4	1.3	289.0	94.0	85.0	72.0	72.0	0.0
	233 13x10	13	13	13	4.6	4.6	13.0	2.8	2.8	1.0	2.8	2.0	0.9	61.0	0.0	18.0	2.2	2.1	1.1	211.0	111.0	75.0	65.0	65.0	0.0
	251 21x10	21	21	21	8.6	8.6	21.0	2.6	2.4	1.0	3.5	1.8	0.6	36.0	0.0	10.0	1.7	1.7	0.6	214.0	56.0	58.0	61.0	59.0	0.0
All lower mud	52x60	52	34	34	5.8	5.5	34.0	9.0	6.2	1.0	5.2	3.4	1.4	80.4	0.0	10.7	5.4	4.0	1.8	234.0	64.9	78.8	88.8	83.7	7.0
Block 1 lower mud	32x30	32	32	32	5.9	5.9	27.8	5.4	5.4	1.1	4.0	2.9	1.4	71.0	0.0	14.0	3.6	3.7	2.0	234.0	89.0	96.0	82.0	82.0	12.8
	59 19x10	19	19	19	7.3	7.3	19.0	2.6	2.6	1.0	3.3	1.4	0.8	45.2	0.0	6.2	1.9	1.8	0.8	225.0	75.0	67.0	62.0	62.0	0.0
	82 18x10	18	18	18	4.0	4.0	14.6	4.5	4.5	1.2	2.7	2.1	1.4	82.0	0.0	22.0	2.4	2.4	1.8	200.0	72.0	81.0	78.0	78.0	19.0
	93 16x10	16	16	16	6.3	6.3	16.0	2.5	2.5	1.0	2.6	1.8	0.4	64.3	0.0	7.2	2.0	2.0	0.7	168.0	63.0	59.0	61.0	61.0	0.0
Block 4 lower mud	36x30	36	36	36	5.8	5.8	34.0	6.2	6.2	1.0	4.3	3.4	1.7	75.0	0.0	14.0	3.9	4.1	2.6	257.0	106.0	113.0	84.0	84.0	4.5
	194 13x10	13	13	13	3.4	3.4	13.0	3.8	3.8	1.0	2.9	2.0	1.5	70.0	0.0	19.1	2.4	2.4	1.8	259.0	74.0	107.0	74.0	74.0	0.0
	233 25x10	18	18	18	7.6	7.6	25.0	3.3	3.3	1.0	3.1	1.6	1.0	43.0	0.0	9.0	2.1	2.3	1.3	197.0	99.0	84.0	70.0	70.0	0.0
	251 24x10	24	24	24	6.3	6.3	23.4	3.8	3.8	1.0	3.3	1.9	1.3	36.0	0.0	8.2	2.3	2.4	1.6	190.0	81.0	97.0	74.0	74.0	2.5
All sand	113x130	113	22	22	4.2	3.6	19.0	26.9	6.1	1.2	8.9	3.5	1.6	90.9	0.0	17.9	3.7	4.6	1.4	670.3	100.8	67.1	96.3	83.7	13.1
Block 4 upper-middle sand	8x10	8	8	8	1.5	1.5	3.3	5.3	5.3	2.4	2.4	2.3	1.9	123.0	0.0	3.9	2.5	2.4	1.8	116.0	91.0	60.0	81.0	81.0	58.0
	164 1x1	1	1	1	1.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	173 2x4	2	2	2	1.3	1.3	2.0	1.5	1.5	1.0	0.0	0.0	0.0	84.0	0.0	14.0	2.0	0.0	1.0	110.0	83.0	69.0	38.0	38.0	0.0
	216 7x5	7	7	7	1.8	1.8	2.0	3.9	3.9	2.3	2.1	1.8	1.6	131.0	0.0	67.0	1.9	1.9	1.6	70.0	102.0	36.0	74.0	74.0	71.0
Block 4 lower-middle sand	27x30	27	27	27	6.1	6.1	27.0	4.4	4.4	1.0	3.8	2.9	1.4	60.1	0.0	11.0	3.6	3.8	2.1	258.0	130.0	115.0	77.0	77.0	0.0
	164 8x10	8	8	8	3.5	3.5	8.0	2.3	2.3	1.0	2.1	1.9	0.7	80.3	0.0	4.5	2.1	2.1	1.0	167.0	56.0	81.0	56.0	56.0	0.0
	173 15x10	15	15	15	5.8	5.8	15.0	2.6	2.6	1.0	2.9	1.5	0.6	64.0	0.0	6.6	2.0	2.1	0.8	215.0	87.0	82.0	61.0	61.0	0.0
	216 23x10	23	23	23	9.1	9.1	23.0	2.5	2.5	1.0	2.7	1.3	0.8	39.0	0.0	5.4	1.8	1.9	1.0	194.0	78.0	81.0	60.0	60.0	0.0
All lower sand	43x90	43	21	21	3.9	3.6	21.0	11.0	5.8	1.0	5.6	3.5	1.9	82.9	0.0	19.6	6.3	4.1	1.8	495.6	138.5	91.6	90.8	83.0	0.1
Block 2 lower sand	24x30	24	24	24	3.1	3.1	17.6	7.7	7.7	1.4	4.4	3.6	2.8	64.0	0.0	55.0	4.0	4.3	2.6	428.0	240.0	111.0	87.0	87.0	27.0
	108 6x10	6	6	6	1.5	1.5	6.0	4.0	4.0	1.0	2.4	1.8	19.0	15.0	0.0	19.0	2.7	2.5	2.5	242.0	176.0	126.0	75.0	75.0	0.0
	116 20x10	20	20	20	6.4	6.4	20.0	3.1	3.1	1.0	3.2	1.6	1.0	49.0	0.0	12.0	1.9	2.1	1.1	220.0	74.0	82.0	68.0	68.0	0.0
	122 4x10	4	4	4	1.4	1.4	4.0	2.9	2.9	1.0	2.0	1.6	1.4	2.6	0.0	10.0	2.7	2.0	1.9	196.0	141.0	110.0	65.0	65.0	0.0
Block 3 lower sand	31x30	31	31	31	5.8	5.8	31.0	5.3	5.3	1.0	4.0	3.2	1.6	82.0	0.0	9.8	3.6	3.7	2.3	225.0	126.0	111.0	81.0	81.0	1.6
	128 20x10	20	20	20	8.1	8.1	20.0	2.5	2.5	1.0	3.3	1.4	0.6	36.0	0.0	4.6	1.7	1.8	0.9	218.0	62.0	74.0	60.0	60.0	0.0
	133 29x20	29	29	29	7.3	7.3	29.0	4.0	4.0	1.0	3.6	2.3	1.3	57.0	0.0	4.8	2.7	2.8	1.6	225.0	84.0	102.0	75.0	75.0	0.0
	146 9x10	9	9	9	2.6	2.6	7.8	3.5	3.5	1.2	2.3	1.9	1.0	45.0	0.0	10.0	2.4	2.2	1.2	164.0	96.0	76.0	71.0	71.0	18.0
Block 4 lower sand	15x30	15	15	15	2.9	2.9	13.9	5.2	5.2	1.1	3.5	3.1	1.7	75.0	0.0	7.9	3.9	3.8	2.3	342.0	1.6	1.9	81.0	81.0	7.6
	164 7x10	7	7	7	2.4	2.4	6.6	2.9	2.9	1.1	2.3	2.0	0.8	74.0	0.0	8.8	2.3	2.4	0.8	239.0	78.0	80.0	66.0	65.0	5.7
	173 7x10	7	7	7	3.2	3.2	7.0	2.2	2.2	1.0	1.9	1.9	0.3	110.0	0.0	4.4	2.0	1.9	0.4	172.0	43.0	42.0	54.0	54.0	0.0
	216 7x10	7	7	7	3.1	3.1	7.0	2.3	2.3	1.0	2.6	1.1	0.5	38.0	0.0	4.8	1.5	2.1	1.3	247.0	102.0	91.0	56.0	56.0	0.0
All gravel	94x201	94	30	30	6.0	5.0	29.3	15.7	6.0	1.0	7.8	3.7	1.7	110.0	0.0	10.8	8.7	5.2	1.5	368.9	90.6	77.3	93.6	83.2	1.3
All upper-middle gravel	13x43	13	6	6	2.9	2.6	6.0	4.6	2.3	1.0	3.2	1.4	0.5	74.0	0.0	5.1	4.5	2.0	0.8	279.0	93.0	71.0	78.5	57.0	1.1
Block 4 upper-middle gravel	11x23	11	11	11	2.8	2.8	8.7	3.9	3.9	1.3	2.8	2.1	1.1	75.0	0.0	17.0	3.2	3.1	1.3	205.0	111.0	95.0	74.0	74.0	21.0
	239 7x10	7	7	7	2.7	2.7	6.2	2.6	2.6	1.2	1.9	1.5	0.1	109.0	0.0	6.8	2.4	1.9	0.1	135.0	70.0	60.0	61.0	61.0	11.0
	263 3x3	3	3	3	1.3	1.3	1.7	2.3	2.3	1.8	1.7	0.8	0.2	74.6	0.0	27.0	0.8	1.3	0.3	145.0	41.0	37.0	55.0	55.0	44.0
	299 8x10	8	8	8	3.4	3.4	8.0	2.4	2.4	1.0	2.5	1.1	0.5	38.0	0.0	8.6	2.0	1.9	1.4	201.0	104.0	85.0	58.0	58.0	0.0
All lower-middle gravel	32x50	32	29	29	8.7	7.9	29.0	3.7	3.7	1.0	4.2	2.5	1.1	59.1	0.0	3.8	3.8	3.8	1.3	304.5	99.5	96.9	72.7	70.1	0.0
Block 4 middle gravel	30x30	30	30	30	8.3	8.3	30.0	3.6	3.6	1.0	3.7	2.6	1.1	63.0	0.0	5.4	3.1	3.5	1.5	235.0	100.6	100.0	72.0	72.0	0.0
	239 14x10	14	14	14	5.6	5.6	14.0	2.5	2.5	1.0	2.4	1.6	0.3	54.0	0.0	10.0	2.1	2.4	0.9	156.0	113.6	72.0	60.0	50.0	0.0
	263 20x10	20	20	20	8.8	8.8	20.0	2.3	2.3	1.0	2.8	1.2	0.4	47.0	0.0	5.0	1.5	1.5	0.3	176.0	48.0	68.0	56.0	56.0	0.0
	299 22x10	22	22	22	10.5	10.5	22.0	2.1	2.1	1.0	3.2	1.2	0.4	39.0	0.0	4.0	1.7	1.6	0.5	238.0	54.0	67.0	52.0	52.0	0.0
All lower gravel	53x50	53	35	35	6.9	6.5	35.0	7.7	5.4	1.0	6.1	3.1	1.9	61.3	0.0	4.1	4.9	3.9	2.0	431.0	81.1	114.9	86.9	81.0	1.3
Block 1 lower gravel	32x20	32	32	32	5.8	5.8	29.5	5.5	5.5	1.1	5.3	2.7	1.6	66.0	0.0	8.4	3.0	3.3	1.8	426.0	85.0	96.0	82.0	82.0	7.7
	103 20x10	20	20	20	6.7	6.7	20.0	3.0	3.0	1.0	3.8	1.6	1.1	63.0	0.0	4.6	2.1	2.1	1.4	286.0	83.0	93.0	67.0	67.0	0.0
	303 24x10	24	24	24	4.9	4.9	21.6	4.9	4.9	1.1	4.9	2.3	1.4	68.0	0.0	16.0	2.3	2.6	1.4	455.0	86.0	79.0	80.0	80.0	10.0
Block 4 lower gravel	40x30	40	40	40	7.6	7.6	40.0	5.3	5.3	1.0	4.9	3.0	1.9	52.0	0.0	4.7	3.8	4.0	2.3	329.0	99.0	128.0	81.0	81.0	0.0
	239 17x10	17	17	17	7.3	7.3	17.0	2.3	2.3	1.0	3.1	1.2	0.6	36.0	0.0	4.1	1.6	1.9	0.9	213.0	95.0	77.0	57.0	57.0	0.0
	263 23x10	23	23	23	7.5	7.5	23.0	3.1	3.1	1.0	3.6	1.8	1.1	45.0	0.0	9.1	2.2	2.3	1.3	243.0	72.0	89.0	67.0	67.0	0.0
	299 25x10	25	25	25	8.1	8.1	25.0	3.1	3.1	1.0	3.8	1.6	1.0	53.0	0.0	5.9	2.1	2.3	1.2	261.0	94.0	84.0	68.0	68.0	0.0

NMS and MRPP

Separate NMS ordinations were run and compared for each matrix transformation, allowing an evaluation of community differences, at each spatial scale, based on abundance and on presence/absence. The Beals transformed matrices were generally the best at evaluating differences among communities when community composition was very heterogeneous, for example when comparing all substrate types or all levels. But as community composition became more homogeneous, for example within a given level and substrate type, then evaluations based on the abundance matrices were more sensitive because more information is retained. Most results presented below thus involve the abundance matrices.

Our hypothesis was that biotic uniformity should decrease from the transect block to the spatial block level, and that communities should be statistically similar within blocks (for a given level and substrate type). For each zone, Tables 6, 7 and 8 list results from the MRPP analyses (T-statistic, R and p-values) for each aggregation and for each transformation type. The R-value indicates the average group homogeneity, or how close the data points are within a group relative to the distance expected by chance. The p-value indicates the difference among groups, or how far apart they are. When the R-values are low, the average distance among points within groups are farther apart than expected by chance, meaning that a greater distance among groups is required to get a significant p-value. If the geophysical attributes are exactly the same among samples (habitat homogeneity), and the biota are also the same, then the data points representing sampled organisms will show no discernible grouping pattern. This will result in a low R-value and a high p-value. When the groups of sampled organisms become less similar (making the data more clustered), then the R value will increase and the p-value will decrease. Graphically, the data will separate into a pattern of clouds of points with increasing separation as the communities become more different.

Figure 5 shows examples of double relativized (abundance) matrix ordination scatter plots for incremental aggregations of samples (among transect blocks, among segments, among spatial blocks) for all three substrate types. Only selections from the lower zone (the most completely sampled, Table 3) and for one representative segment

Table 6. Upper-middle zone community comparisons

	Group 1		Group 4		Group 6		Group 7	
	164		194		239		103	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	2x1		6x8		5x8		5x10	
T-Stat			-1.3216	-1.252	-1.62	-1.228	0.6291	0.3536
R	Insufficient		0.2369	0.4887	0.2483	0.2739	-0.0076	-0.0083
p-value	data		0.1014	0.0331	0.0534	0.1131	0.4997	0.4975
	173		233		263		303	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	2x4		4x6		2x1		7x10	
T-Stat			1.3050	0.0547			-1.815	-1.834
R	Insufficient		-0.2792	-0.0085	Insufficient		0.1786	0.3146
p-value	data		0.9024	0.5272	data		0.0425	0.0435
	216		251		299			
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals		
Matrix	7x4		8x10		8x10			
T-Stat			-0.1385	-0.7781	0.6347	1.021		
R	Insufficient		0.0144	-0.0672	-0.0568	-0.1152		
p-value	data		0.4237	0.6778	0.7572	0.8466		
	Block 4 Sand Total		Block 4 Mud Total		Block 4 Gravel Total		Block 1 Gravel Total	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	8x9		10x25		9x18		8x20	
T-Stat	-2.9401	-3.2621	-7.3440	-9.3060	-1.776	-3.1210	-3.2750	-2.2060
R	0.2133	0.3271	0.1970	0.4081	0.0389	0.1117	0.0761	0.0795
p-value	0.0107	0.0069	0.0000	0.0000	0.0566	0.0139	0.0107	0.0406
	Block 4 Sand Quadrats		Block 4 Mud Quadrats		Block 4 Gravel Quadrats		Block 1 Gravel Quadrats	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	6x9		9x25		6x22		5x20	
T-Stat	-3.9921	-3.3691	-7.3960	-9.3617	-4.0670	-3.2860	-1.642	-1.1400
R	0.4074	0.3711	0.2094	0.4207	0.1722	0.207	0.0471	0.0560
p-value	0.0025	0.0062	0.0000	0.0000	0.0026	0.0094	0.0703	0.1165
	Block 4 Sand Cores		Block 4 Mud Cores		Block 4 Gravel Cores		Block 1 Gravel Cores	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	2x3		1x1		4x4		3x6	
T-Stat								
R	Insufficient		Insufficient		Insufficient		Insufficient	
p-value	data		data		data		data	

ALL GROUPS

	All Upper Sand		All Upper Mud		All Upper Gravel	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	8x9		10x25		12x38	
T-Stat	-2.9401	-3.2621	-7.3440	-9.3060	-4.8370	-4.9720
R	0.2133	0.3271	0.1970	0.4081	0.0911	0.1262
p-value	0.0107	0.0069	0.0000	0.0000	0.0003	0.0004

ALL HABITAT TYPES

	All Upper	
	Dbl. Rel.	Beals
Matrix	8x75	
T-Stat	-12.8850	-19.0841
R	0.1383	0.2662
p-value	0.0000	0.0000

Table 7. Lower-middle zone community comparisons

	Group 1		Group 4		Group 6		Group 7	
	164		194		239		103	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	7x8		20x10		14x8		16x10	
T-Stat	-1.2780	-1.8490	-0.1815	-0.3941	-1.0400	0.9315	0.0625	1.4880
R	0.2257	0.4053	0.0105	0.0442	0.0952	-0.1065	-0.0038	-0.1665
p-value	0.1075	0.0491	0.4151	0.3290	0.1487	0.8236	0.5340	0.9374

	173		233		263		303	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	15x8		13x10		18x8		16x8	
T-Stat	1.025	0.9005	-0.7851	-0.9274	-0.1441	-0.0467	0.0321	1.1081
R	-0.0696	-0.1315	0.0744	0.1898	0.0112	0.0083	-0.0021	-0.1075
p-value	0.8476	0.8747	0.2097	0.1731	0.4372	0.4620	0.5054	0.8722

	216		251		299			
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals		
Matrix	23x10		21x8		22x10			
T-Stat	0.4721	-1.4320	-1.2060	-0.1601	-1.2930	-0.3379		
R	-0.0028	0.1181	0.0990	0.0285	0.0789	0.0322		
p-value	0.5169	0.0779	0.1185	0.4204	0.1046	0.3285		

	Block 4 Sand Total		Block 4 Mud Total		Block 4 Gravel Total		Block 1 Gravel Total	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	27x26		27x29		30x28		22x19	
T-Stat	-5.6740	-6.5990	-7.5150	-8.2930	-8.9290	-10.8950	-5.9480	-8.4970
R	0.0870	0.1363	0.0858	0.1669	0.1081	0.2322	0.0750	0.1809
p-value	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001	0.0000
	Block 4 Sand Quadrats		Block 4 Mud Quadrats		Block 4 Gravel Quadrats		Block 1 Gravel Quadrats	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	13x30		10x30		14x30		13x19	
T-Stat	-5.5560	-7.8770	-8.9640	-11.7190	-8.2750	-8.2180	-5.9610	-9.7970
R	0.0924	0.1937	0.1710	0.3244	0.1141	0.2066	0.1041	0.2767
p-value	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001	0.0000
	Block 4 Sand Cores		Block 4 Mud Cores		Block 4 Gravel Cores		Block 1 Gravel Cores	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	14x14		17x24		12x22		9x15	
T-Stat	0.6712	0.9059	0.3862	0.8837	-3.0420	-5.8490	-0.9281	-1.6486
R	-0.0195	-0.0315	-0.0007	-0.0188	-0.0729	0.1783	0.0314	0.0473
p-value	0.7163	0.8522	0.4739	0.8098	0.0081	0.0000	0.1619	0.0681

ALL GROUPS

	All Middle Sand		All Middle Mud		All Middle Gravel	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	27x26		27x29		32x45	
T-Stat	-5.6740	-6.5990	-7.5150	-8.2930	-11.9715	-13.0054
R	0.0870	0.1363	0.0858	0.1669	0.0599	0.1195
p-value	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

ALL HABITAT TYPES

	Dbl. Rel.	Beals
Matrix	49x106	
T-Stat	-37.2840	-46.2180
R	0.1172	0.3731
p-value	0.0000	0.0000

Table 8. Lower zone community comparisons

	Group 1		Group 2		Group3		Group 4		Group 5		Group 6		Group 7	
	164		108		128		194		59		239		103	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	7x10		6x10		20x10		13x10		19x10		15x10		20x10	
T-Stat	0.9011	-1.0250	-0.1362	-0.5883	-2.7576	-2.4635	-0.9950	-0.2120	-0.8483	-0.6431	0.1165	0.3171	-2.8873	-1.7320
R	-0.0927	0.1346	0.0205	0.0434	0.1526	0.2632	0.0644	0.0357	0.0157	0.0007	-0.0106	-0.0348	0.1732	0.1799
p-value	0.8147	0.1521	0.4282	0.2738	0.0638	0.0139	0.1568	0.3826	0.4158	0.4726	0.5187	0.6043	0.0028	0.0505

	173		116		133		233		82		263		303	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	7x10		20x10		20x10		18x10		18x10		17x10		24x8	
T-Stat	-0.2499	-0.4450	0.2388	-0.2121	-5.1787	-0.1070	-1.4430	-2.0891	-0.8300	-2.1330	-1.5579	-0.6968	-0.1470	-0.6927
R	0.0300	0.0767	-0.0148	0.0224	0.0387	0.0111	0.1011	0.3035	0.0595	0.1919	0.1182	0.1217	-0.0104	0.1002
p-value	0.3545	0.3065	0.5831	0.4013	0.2930	0.4025	0.0718	0.0323	0.1983	0.0219	0.0718	0.2282	0.3931	0.2397

	216		122		146		251		93		299	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	7x10		4x10		7x8		17x10		16x10		19x10	
T-Stat	0.2815	-0.1467	-0.6569	0.1244	-1.8666	-1.4838	-1.1413	0.5044	0.5180	0.5635	-0.2739	0.3053
R	-0.0366	0.0239	0.0971	-0.0195	0.3417	0.4247	0.0857	-0.0484	-0.0319	-0.0569	0.0195	-0.0372
p-value	0.5512	0.3829	0.2433	0.4185	0.051	0.0783	0.1292	0.6769	0.6838	0.6700	0.3754	0.6038

	Block 4 Sand Total		Block 2 Sand Total		Block 3 Sand Total		Block 4 Mud Total		Block 1 Mud Total		Block 4 Gravel Total		Block 1 Gravel Total	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	15x30		24x30		31x30		36x30		30x29		39x28		32x18	
T-Stat	-7.2070	-10.5243	-10.2745	-10.2423	-8.1372	-9.2257	-10.3690	-9.6313	-7.2735	-12.1962	-6.8945	-10.2430	-6.5402	-8.8168
R	0.1302	0.3661	0.2675	0.4482	0.1116	0.1537	0.1207	0.1646	0.0897	0.3191	0.1022	0.2026	0.0883	0.2302
p-value	0.0000	0.0000	0.0035	0.0000	0.0021	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0031	0.0000
	Block 4 Sand Quadrats		Block 2 Sand Quadrats		Block 3 Sand Quadrats		Block 4 Mud Quadrats		Block 1 Mud Quadrats		Block 4 Gravel Quadrats		Block 1 Gravel Quadrats	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	6x27		6x30		12x30		8x30		4x23		16x30		13x18	
T-Stat	-1.5570	-4.9555	-11.4090	-11.5212	-5.1384	-7.2258	-11.9203	-13.1055	-6.2841	-7.2380	-6.8591	-11.1783	-6.5402	-8.8168
R	0.0475	0.1295	0.4119	0.5631	0.1019	0.1671	0.3032	0.4843	0.4556	0.5851	0.1022	0.2658	0.0883	0.2302
p-value	0.0771	0.0005	0.0000	0.0000	0.0002	0.0000	0.0000	0.0000	0.0004	0.0001	0.0000	0.0000	0.0031	0.0000
	Block 4 Sand Cores		Block 2 Sand Cores		Block 3 Sand Cores		Block 4 Mud Cores		Block 1 Mud Cores		Block 4 Gravel Cores		Block 1 Gravel Cores	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	6x15		8x13		10x27		29x28		22x30		24x29		19x17	
T-Stat	-2.0020	-2.2912	-3.8816	-4.8495	-8.3322	-7.0115	-1.2043	-2.8518	-7.8748	-4.4789	-1.9390	-4.4799	-2.2395	-2.7727
R	0.0768	0.1570	0.1679	0.1189	0.2135	0.1738	0.0126	0.0542	0.1052	0.0804	0.0277	0.0804	0.0399	0.0732
p-value	0.0401	0.0339	0.0039	0.0011	0.0000	0.0000	0.1187	0.0129	0.0000	0.0005	0.0418	0.0005	0.0300	0.0207

ALL GROUPS

	All Lower Sand		All Lower Mud		All Lower Gravel	
	Dbl. Rel.	Beals	Dbl. Rel.	Beals	Dbl. Rel.	Beals
Matrix	21x90		28x57		35x46	
T-Stat	-16.7046	-15.8171	-20.4745	-31.9658	-8.3580	-7.5562
R	0.0972	0.1343	0.0947	0.3329	0.0385	0.0544
p-value	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

ALL LOWER ZONE HABITAT TYPES

	All Lower	
	Dbl. Rel.	Beals
Matrix	98x195	
T-Stat	-56.2757	-90.1685
R	0.0858	0.3832
p-value	0.0000	0.0000

ALL ZONES AND ALL HABITAT TYPES

	All Data	
	Dbl. Rel.	Beals
Matrix	110x363	
T-Stat	-91.5903	-107.1861
R	0.0736	0.2165
p-value	0.0000	0.0000

and block are shown to conserve space. Table 9 lists the organism correlations (using both transformations) for the two NMS ordination axes that explain the most variation in the data plotted on Figure 7. Note that the Beals transformation utilizes more organisms to explain the observed variation, whereas the zero-rich double relativized data ordination has fewer correlations to explain the variation among groups.

Figures 7A, D, and G show the NMS ordinations of the aggregated matrices of transect blocks in a mud, a sand, and a gravel segment, respectively. The incremental stress reduction for three dimensions and the final stress is listed on each plot. The two axes illustrated, explain most of the variation as shown by the listed incremental r^2 and cumulative r^2. As expected for geophysically uniform habitats, all 3 plots have low R values and high p values (Table 8), and the plotted points are spread across the plot without strongly discernible patterns. This consistent within-segment homogeneity indicates that the partitioning model was successful in reducing geophysical gradients causing ecological heterogeneity. There was some spatial variation even at this very small scale; for each substrate type, a given species was seldom found in all transect blocks. However overall, communities within segments were relatively homogeneous. For the mud, the plot represents 18 organisms, but Table 9 shows that only 10 of these have r^2 values exceeding .30 for the plotted abundance transformation. This suggests that 56% of the sampled organisms explain most of the variation within this segment. For the sand, although 68% of the community variation is explained by the axes shown, only 3 out of 7 species (Dendraster, nemerteans, and Spiochaetopterus) have high individual r^2 values. For the lower zone gravel samples 92% of the variation is explained by the two axes shown, and 9 (out of 15) species had high r^2 values. Thus for each substrate type, roughly half of the species present explained the majority of the variation within the segment. Tables 6-8 list within-segment data for the other levels and segments.

Figures 7B, E, and H show the ordination plots for all segments sampled in Block 4 (ten samples from each segment, three segments within each substrate type). Summary statistics for these low-zone ordinations are given in Table 8, and for the other elevations in Tables 6 and 7. Visual comparison of the segment-level versus block-level ordinations show that the communities that were rather spread out at the segment level cluster fairly

Table 9. Lower zone organism correlations (+ or -) and r^2 values to ordination axes explaining the most variation (r^2 >.3)

Organism	Sample	MUD SEGMENT 233 Dbl. Rel. Axis 1	Axis 2	Beals Axis 1	Axis 2	Block 4 MUD SEGMENTS Dbl. Rel. Axis 1	Axis 3	Beals Axis 1	Axis 2	ALL LOWER MUD Dbl. Rel. Axis 1	Axis 2	Beals Axis 1	Axis 3	SAND SEGMENT 173 Dbl. Rel. Axis 1	Axis 2	Beals Axis 1	Axis 2	Block 4 SAND SEGMENTS Dbl. Rel. Axis 1	Axis 2	Beals Axis 1	Axis 3	ALL LOWER SAND Dbl. Rel. Axis 1	Axis 3	Beals Axis 1	Axis 3	GRAVEL SEGMENT 239 Dbl. Rel. Axis 1	Axis 2	Beals Axis 1	Axis 2	Block 4 GRAVEL SEGMENTS Dbl. Rel. Axis 1	Axis 3	Beals Axis 1	Axis 3	ALL LOWER GRAVEL Dbl. Rel. Axis 1	Axis 3	Beals Axis 1	Axis 3
Acrosiphonia coalita	quadrat																									(-) 0.339	(-) 0.510	(-) 0.694	(-) 0.190			(-) 0.752	(-) 0.042			(+) 0.293	(+) 0.578
Amphipods	quadrat																			(+) .079	(+) .383							(+) 0.809	(+) 0.114			(+) 0.003	(+) 0.619			(-) 0.003	(-) 0.341
Anthopleura elegantissima	quadrat																															(+) 0.312	(-) 0.485				
Artacama conifera	core																															(+) 0.587	(-) 0.085			(-) 0.550	(-) 0.019
Axiothella rubrocincta	core																															(+) 0.737	(-) 0.287			(-) 0.570	(-) 0.060
Balanus glandula	quadrat					(+) .000	(+) .332			(-) 0.067	(-) 0.304	(-) 0.708	(+) 0.529													(-) 0.511	(+) 0.113			(+) 0.369	(-) 0.615	(+) 0.592	(+) 0.066			(-) 0.666	(-) 0.053
Callianassa californiensis	core			(-) .912	(-) .052			(-) .386	(-) .188			(-) 0.381	(+) 0.017																								
Callianassa californiensis	quadrat	(-) .007	(+) .703	(-) .321	(-) .013			(-) .576	(-) .474	(+) 0.417	(-) 0.001	(+) 0.899	(-) 0.102									(+) 0.286	(+) 0.004	(-) 0.552	(+) 0.680												
Cancer sp.	quadrat																									(+) 0.038	(-) 0.691	(-) 0.523	(-) 0.196			(-) 0.599	(-) 0.071			(+) 0.146	(+) 0.466
Capitella capitata	core	(-) .003	(-) .419	(+) .014	(+) .755							(+) 0.365	(-) 0.004																								
Chaetozone sp.	core																															(-) 0.303	(-) 0.027				
Crepidula sp.	quadrat																									(-) 0.228	(+) 0.368	(-) 0.016	(+) 0.566	(+) 0.342	(-) 0.002	(+) 0.562	(-) 0.032			(-) 0.548	(-) 0.076
Cryptomya californica	core	(-) .384	(-) .006	(-) .435	(-) .244							(-) 0.683	(+) 0.425																								
Decamastus gracilis	core									(+) 0.030	(+) 0.384																								
Dendraster excentricus	quadrat	(+) .447	(+) .145	(+) .942	(-) .027	(-) .497	(-) .147	(+) .790	(-) .083			(+) 0.412	(-) 0.098	(+) .750	(-) .007	(+) .934	(-) .004	(-) .457	(-) .053	(+) .381	(+) .001	(-) 0.609	(-) 0.153	(+) 0.433	(-) 0.750												
Edwardsia sipunculoides	core	(+) .459	(-) .063	(+) .412	(+) .393																			(-) 0.268	(+) 0.618												
Enteromorpha sp.	quadrat											(-) 0.428	(-) 0.046													(+) 0.427	(-) 0.204									(+) 0.393	(+) 0.267	(-) 0.494	(-) 0.002
Eupolymnia heterobranchia	core																							(-) 0.690	(+) 0.190												
Goniada annulata	core											(-) 0.377	(+) 0.036																								
Gracelaria sjoestedtii	quadrat	(+) .538	(+) .039	(+) .912	(+) .052							(+) 0.741	(-) 0.035											(-) 0.320	(+) 0.165												
Haminea eggs	quadrat	(+) .261	(+) .602	(+) .744	(+) .016			(-) .345	(+) .452															(-) 0.549	(+) 0.643												
Haminoea vesicula	core	(+) .444	(-) .121	(-) .811	(+) .062	(+) .026	(+) .313	(-) .689	(-) .140			(+) 0.485	(-) 0.151											(-) 0.616	(+) 0.159												
Hemigrapsus oregonensis	quadrat			(-) .395	(+) .126							(+) 0.333	(-) 0.237																								
Hemipodus borealis	core			(+) .801	(-) .128			(+) .443	(+) .222											(+) .079	(+) .383							(-) 0.008	(+) 0.865							(-) 0.143	(-) 0.520
Unidentified red crust	quadrat																							(-) 0.155	(+) 0.363	(+) 0.487	(-) 0.043					(-) 0.693	(+) 0.090				
Hippolyte clarki	core																											(-) 0.456	(-) 0.369			(-) 0.121	(+) 0.314				
Lepidonotus squamatus	core																																			(+) 0.464	(+) 0.106
Leptosynapta clarki	core							(-) .302	(-) .020															(-) 0.408	(+) 0.658												
Littorina scutulata	quadrat																																				
Lottia strigatella	quadrat																															(+) 0.462	(-) 0.409				
Macoma juv	core			(-) .190	(+) .526			(-) .635	(-) .002			(+) 0.303	(-) 0.176																								
Macoma secta	core							(-) .002	(+) .354																												
Magelona hobsonae	core															(-) .843	(+) .005			(-) .941	(-) .000			(+) 0.306	(+) 0.080												
Maldanidae	core																															(+) 0.022	(+) 0.307				
Mastocarpus papillata	quadrat																															(-) 0.226	(-) 0.413			(+) 0.467	(+) 0.219
Micropodarke dubia	core																									(-) 0.339	(-) 0.510	(-) 0.694	(-) 0.190					(-) 0.395	(-) 0.002		
Mytilus edulis	quadrat																																				
Nereis brandti	core							(-) .002	(+) .354																												
Nemertea (unidentified)	core	(-) .003	(-) .419	(+) .014	(+) .755			(-) .302	(-) .020			(-) 0.766	(+) 0.471	(+) .080	(-) .663	(+) .086	(+) .576	(+) .132	(+) .320	(-) .636	(-) .012							(+) 0.834	(-) 0.104			(-) 0.069	(+) 0.541			(+) 0.412	(-) 0.025
Notomastus lineatus	core															(+) .108	(+) .820			(-) .457	(-) .035																
Nephtys longosetosa	core							(+) .525	(-) .012							(-) .446	(-) .296			(-) .851	(+) .003			(+) 0.028	(+) 0.348												
Nereis procera	core																											(+) 0.818	(-) 0.112			(-) 0.303	(+) 0.236			(+) 0.398	(+) 0.001
Notomastus lenuis	core			(-) .399	(-) .065							(-) 0.614	(+) 0.681													(+) 0.024	(+) 0.745										
Nucella lamellosa	quadrat																																			(+) 0.127	(+) 0.316
Ophiodromus pugettensis	core																									(+) 0.396	(-) 0.052	(+) 0.172	(-) 0.514								
Pagurus sp.	quadrat																																				
Pectinaria granulata	core																															(+) 0.382	(-) 0.058			(-) 0.446	(+) 0.000
Petrocelis sp.	quadrat																															(+) 0.464	(-) 0.317				
Pinnotherid sp.	core									(-) 0.448	(-) 0.118	(-) 0.897	(+) 0.406																					(+) 0.359	(+) 0.017
Polinices lewisii	core																																				
Polynoidae	core							(-) .302	(-) .020																												
Polysiphonia sp.	quadrat																															(-) 0.585	(-) 0.004			(+) 0.307	(+) 0.172
Punctaria hesperia	quadrat																			(+) .369	(-) .000																
Pseudopythina rugifera	core											(-) 0.794	(+) 0.409																								
Scleroplax granulata	core			(-) .190	(+) .611							(-) 0.498	(+) 0.221																								
Scoloplos acmeceps	core			(-) .089	(+) .730			(-) .565	(-) .085			(+) 0.648	(-) 0.152																								
Scoloplos armiger	core							(-) .323	(-) .007											(+) .159	(-) .367			(-) 0.430	(+) 0.000			(+) 0.100	(+) 0.816			(+) 0.035	(+) 0.357			(-) 0.020	(-) 0.392
Scytosiphon lomentaria	quadrat																															(-) 0.283	(-) 0.020			(+) 0.547	(+) 0.062
Semi-balanus cariosus	quadrat																															(+) 0.546	(-) 0.323			(-) 0.397	(-) 0.131
Spionidae	core																															(+) 0.312	(-) 0.485				
Spochaetopterus costarum	core							(+) .441	(+) .000					(-) .451	(+) .497	(-) .992	(-) .040	(+) .311	(-) .369	(-) .915	(+) .020			(-) 0.222	(+) 0.898							(+) 0.382	(+) 0.058				
Spiophanes berkeleyorum	core																																				
Tapes philippinarum	core																																				
Tellina sp.	core	(-) .633	(-) .017	(-) .696	(-) .000			(-) .713	(-) .048			(+) 0.365	(-) 0.405											(-) 0.580	(+) 0.348												
Terebellides stroemii	core																																				
Ulva sp.	quadrat			(-) .765	(-) .013	(-) .441	(+) .000	(-) .391	(-) .412	(+) 0.024	(+) 0.394	(+) 0.938	(-) 0.182			(+) .976	(+) .001			(+) .897	(-) .006	(-) 0.020	(-) 0.328									(-) 0.303	(-) 0.027				
TOTALS		10		18		4		18		5		20		3		7		3		11		3		14		9		11		2		25		2		28	

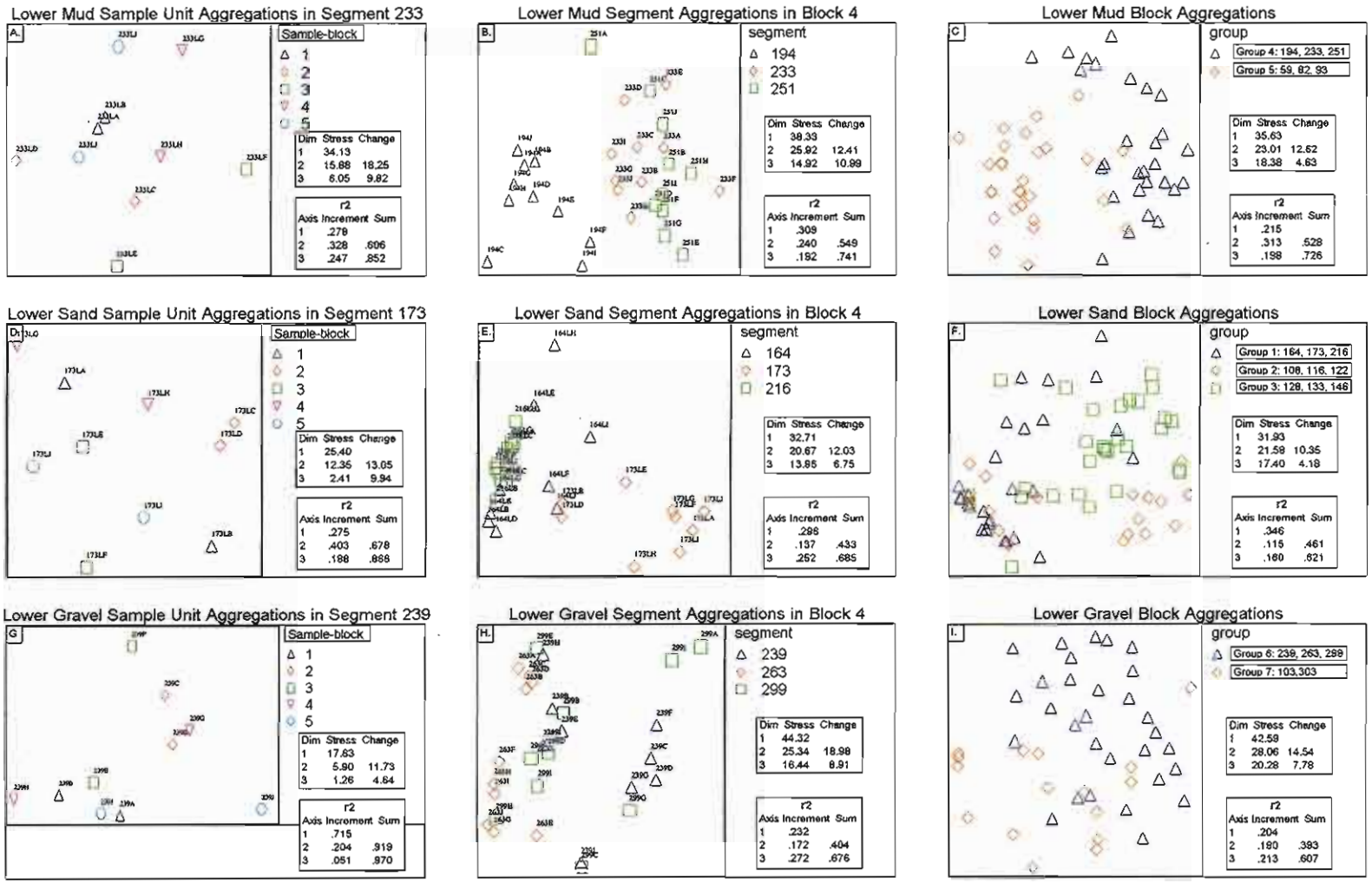


Figure 7. Non-metric multi-dimensional scaling ordination plots for samples in species abundance space. Species data was transformed by double-relativization to improve multivariate assumptions (see text).

tightly at the block level, indicating that the sampled biota have high fidelity to their respective segments. The higher R values for each substrate type give the statistical representation of this clustering. We had hypothesized that segments within a block would have similar biota, but the p values all indicate significant differences among segments. This results in part from sampling artifacts, and from our attempts to achieve homogeneity within each beach segment. Within-segment homogeneity is high, as indicated by the large p values at the segment level in Tables 6-8. In achieving this homogeneity (by sampling at a small spatial scale, in beaches lacking in geophysical gradients) we have essentially minimized overlap among beach communities because at this scale, the biota of each beach is unique. The resolution of the biotic data is greater than that of the geophysical data; had we defined the geophysical parameters much more finely (e.g., by quantifying the reduction-oxidation potential, percent silt composition) and then been able to find beaches that "matched", the biota probably would have been more similar. Proof of this lies in the geophysical differences found in the beaches with seemingly anomalous biota (see below).

Inspection of the lists of organisms on Table 9 shows that for each substrate type, only 2-10 taxa out of 20-25 explain most of the variation for the abundance ordinations. For the Beals transformations, again roughly half of the species had r^2 values over 0.3. Many of the differences among segments at this level for both the sand and the mud relate to the abundance of the sand dollar, Dendraster. These organisms bury beneath the sediment surface when exposed at low tide and then re-emerge to suspension feed at high tide, resulting in extensive daily bioturbation of the top 5-10 cm of sediment. Thus in the mud segments, for example, Segment 194 had a significant Dendraster population but few other invertebrates, while Segments 233 and 251 had no Dendraster, and other invertebrates (especially clams) dominated. Segment 194 differed physically in the higher concentration of sand in the substrate relative to the muddier and less permeable substrate of other Block 4 segments (Table 4). Separate analyses of the quadrat and core data showed that the difference between Segments 194, 233 and 251 is just with the quadrat samples (8x30, T-stat=-11.9203, R=.3032. p<.0000); the core samples were not significantly different (29x28, T-stat=-1.2043, R=.0126, p=.1187). Thus although the

surface communities (including Dendraster, which was sampled with quadrats) differ, the infauna inhabiting the substrate underneath the Dendraster are similar. Figure 5E similarly suggests a critical role for Dendraster; segment 173 had many fewer sand dollars, perhaps due to the higher fresh groundwater seepage in this segment (Table 4), and its samples clearly cluster separately from the other 2 segments. The infauna in this segment had more infaunal polychaetes and nemerteans than in the samples disturbed by sand dollars.

For the gravel, as with the Block 4 aggregations for the other habitat types, the low p-values (Table 8) indicate the segment samples are again more different than hypothesized. Separate analyses of quadrat and core matrices for both types of transformations (and for Block 1 as well as Block 4) suggest that the infauna communities (in the cores) are more similar among segments than are the surface fauna (quadrat data: Table 8). A similar pattern is seen in the lower-middle zone (upper-middle cores were almost completely depauperate) and this trend extends to the other substrate types; in general, the major differences seen among segments within a block were driven by the surface quadrat data, while the infauna are less unique at the beach segment scale.

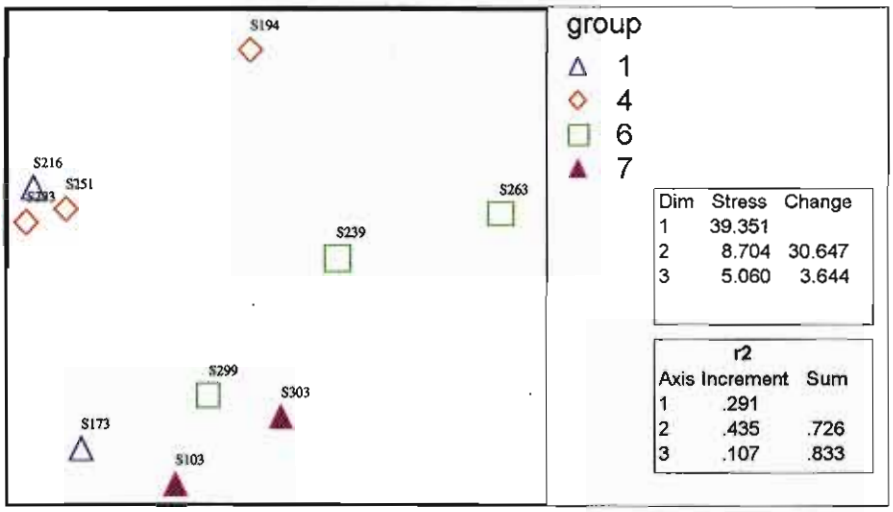
Figures 7C, F, and I show the plots for segments aggregated by spatial block (each Group represents a subset of clustered polygons from within one quadrant of Carr Inlet, see Table 3) for each substrate type. In each case, once again the segments that appeared scattered at the within-block level (Figures 7B, E, and H) appear as a relatively tight cluster of points when compared with segments from other parts of the inlet; at each level, the ordinations illustrate *relative* similarity. The R values (Table 8) are lower than those at the within-block level, indicating the reduced homogeneity or increased variance at this increased spatial scale, and the p values are very low, illustrating the significant differences among blocks in community composition and abundance. For each substrate type, there were taxa that were found in one Block/Group but seldom in another. In the mud, for example, the red alga Gracelaria, green ulvoid algae, and the opisthobranch Haminoea were found primarily in Group 4. Nemertean worms and various commensals with ghost shrimp (Cryptomya, Pseudopythina, and Scleroplax) were only found in Group 5. Similarly, in the sand segments the burrowing anemone Edwardsia and the ghost

shrimp Callianassa were found in Group 3 but not in the other two sand groups. In the gravel, Acrosiphonia, Crepidula, Enteromorpha, and Ophiodromus were found largely in Group 6.

Upper and middle zone comparisons among blocks are summarized in Tables 6 and 7. The patterns are consistent with the lower zone analyses, with highly significant differences among blocks. The R values for the lower-middle zone are similar to those for the low zone, reflecting the relatively high variance among samples when looking at communities from the whole inlet. R values for the upper-middle zone, however, are quite high, suggesting greater homogeneity within blocks; this is a statistical artifact, reflecting the depauperate nature of these high samples. At most sites there were only occasional barnacles on the surfaces of cobbles and occasional amphipods in the substrate.

Indicator Organisms

Dufrene and Legendre "indicator values" were calculated for each species in each segment to obtain a measure of organism reliability to habitat type. Identification of species with high indicator values both aids in interpretation of the ordination plots (because these species help explain the heterogeneity of the grouped samples at the various spatial scales), and suggests species that might serve as good habitat-indicators in monitoring programs. Figures 8-10 show the NMS ordination plots of the indicator species values for the upper-middle, lower-middle, and lower zones respectively. Analysis of indicator organisms was done by segment groups (see Table 3 for group membership) to determine the relative similarity within groups compared to among groups. Since each species has a single indicator value per segment (i.e., the value averages across the individual samples), each segment ends up as one point whose position in the ordination space is driven by the species with the highest indicator values. The correlations and r^2 values listed on each figure for the two illustrated axes help to identify the organisms that drive the differences among groups, and to some extent within groups when the differences among segments are large. There were insufficient data to do MRPP analyses for the middle zones, but R and p values were calculated for the low

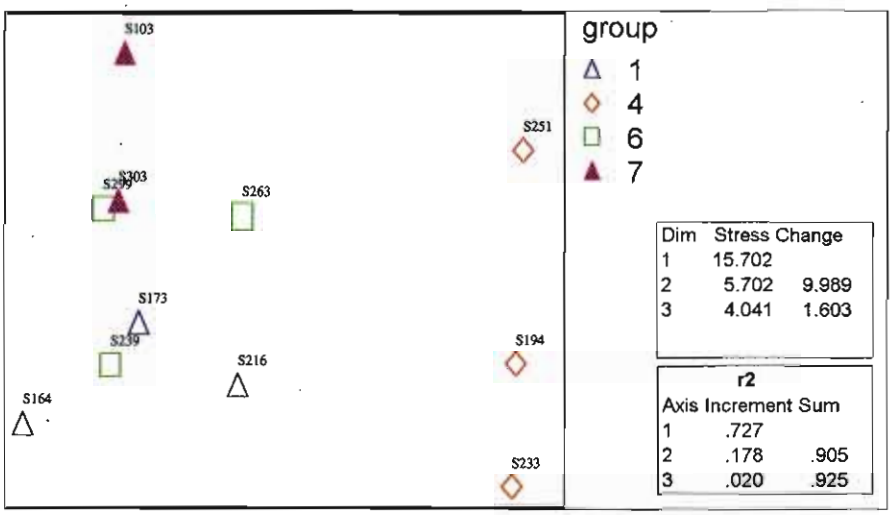


Upper Zone Indicator Species

Organism	Sample	Axis 1	Axis 2
Amphipods	core	(+) .641	(+) .049
Balanus glandula	quadrat	(-) .144	(-) .691
Callianassa californiensis	quadrat	(+) .016	(+) .360
Enteromorpha sp.	quadrat	(-) .492	(+) .526
Littorina scutulata	quadrat	(+) .035	(-) .473
Tapes philippinarum	core	(+) .542	(-) .002

Total = 6

Figure 8. Upper-middle zone indicator species analysis

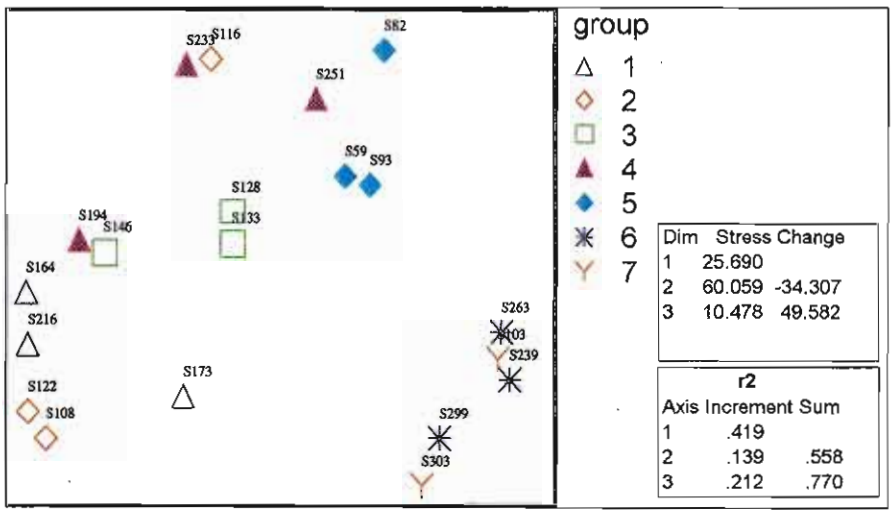


Lower-Middle Zone Indicator Species

Organism	Sample	Axis 1	Axis 2
Anthopleura elegantissima	quadrat	(-) .064	(+) .412
Balanus glandula	quadrat	(-) .735	(-) .038
Callianassa californiensis	core	(+) .573	(-) .071
Callianassa californiensis	quadrat	(+) .582	(-) .320
Capitellids (unidentified)	core	(+) .200	(+) .286
Cryptomya californica	core	(+) .360	(-) .096
Fucus gardneri	quadrat	(+) .383	(-) .151
Gracelaria sjoestedtii	quadrat	(+) .258	(+) .116
Hemigrapsus oregonensis	core	(-) .157	(+) .251
Hemipodus borealis	core	(+) .623	(-) .001
Unidentified red crust	quadrat	(-) .091	(+) .423
Lottia strigatella	quadrat	(-) .367	(+) .066
Littorina scutulata	quadrat	(-) .624	(+) .005
Macoma juv	core	(+) .893	(-) .057
Mastocarpus papillata	quadrat	(-) .231	(+) .419
Mytilus edulis	quadrat	(-) .249	(-) .325
Notomastus tenuis	core	(+) .438	(+) .001
Nereis vexillosa	core	(-) .417	(-) .055
Ulva sp.	quadrat	(+) .251	(+) .124

Total = 18

Figure 9. Lower-Middle Zone Indicator Species



Lower Zone Indicator Species

Organism	Sample	Axis 1	Axis 3
Balanus glandula	quadrat	(+) .487	(-) .082
Callianassa californiensis	core	(+) .005	(+) .262
Callianassa californiensis	quadrat	(-) .019	(+) .406
Crepidula sp.	quadrat	(+) .279	(-) .058
Dendraster excentricus	quadrat	(-) .520	(-) .177
Enteromorpha sp.	quadrat	(+) .490	(-) .109
Eupolymnia heterobranchia	core	(+) .000	(+) .255
Goniada annulata	core	(+) .262	(+) .084
Gracelaria sjoestedtii	quadrat	(-) .016	(+) .287
Haminoea vesicula	core	(-) .007	(+) .369
Hemigrapsus oregonensis	quadrat	(+) .379	(-) .001
Unidentified red crust	quadrat	(+) .270	(-) .080
Macoma juv	core	(+) .003	(-) .253
Micropodarke dubia	core	(+) .287	(-) .237
Notomastus tenuis	core	(+) .352	(-) .186
Tellina sp.	core	(+) .001	(+) .397
Ulva sp.	quadrat	(-) .365	(+) .010

Total = 17

Figure 10. Lower zone indicator species analysis

zone ordinations. Table 10 summarizes the indicator species by segment group and tidal zone.

Figure 8 shows a generally clear separation in indicator species among segment groups in the upper-middle zone. Group 1 are the sand segments from Block 4, Group 4 are the mud segments from Block 4, Group 6 are the gravel segments from Block 4, and Group 7 are the gravel segments from Block 1. Much of the distribution of points is explained by the abundant amphipods, Tapes, and Littorina in the gravel segment (Groups 6 and 7) but not in Group 1 (sand) or 4 (mud). Higher values for Callianassa and Enteromorpha in Group 4 separate the mud segments from the sand on the vertical axis. The sand segments were relatively depauperate in this zone, but Balanus glandula was found in all segment groups.

The NMS ordination for the lower-middle zone indicators is illustrated on Figure 9, along with the organism correlations for this more diverse level. The distinct separation of Group 4 (mud) on the plot is explained by a variety of species (with high positive correlation to axis 1), especially Macoma, Hemipodus, and Callianassa, all found primarily in these muddy habitats. The sand Group 1, and the gravel Groups 6 and 7 both had cobble as their primary substrate type at this level (Table 4), and they share the epifaunal species Balanus, Lottia, Littorina, and Mytilus. The separation between the sand group and the gravel groups is explained by the latter having common amphipods, Protothaca, Mastocarpus, and Hemigrapsus oregonensis. The sand group is distinct only in that Haminoea eggs were found in abundance in this habitat only.

Since the low zone was more fully sampled, Figure 10 shows the NMS ordination plot for all seven groups (3 sand, and 2 each of gravel and mud). MRPP analyses found that each of the substrate types was significantly different from the others using these indicator values (all p values were $< .01$). Sand and mud were the most similar ($R = .06$, $p = .006$), while both are quite different from the gravel (mud-gravel comparison $R = .13$, $p = .001$; sand-gravel $R = .15$, $p = .0001$). There were no significant differences between pairs of groups within any of the substrate types, i.e. all the sand groups were basically the same in terms of indicator species, as were the two mud groups. There were insufficient data to test for differences among the gravel groups, although the ordination

Table 10. Indicator species list for sampled segment groups and zones (see Table 4 for group and segment descriptions).

Upper-middle zone indicators

Mud (Group 4)	Sand (Group 1)	Gravel (Groups 6 and 7)
Balanus glandula	Balanus glandula	Balanus glandula
Callianassa sp.		Littorina sp.
Enteromorpha sp.		Tapes sp.
		Gravel (Group 6)
		Amphipods

Lower-middle zone indicators

Mud (Group 4)	Sand (Group 1)	Gravel (Group 6 and 7)
Callianassa sp.	Haminea eggs	Balanus glandula
Capitella sp.		Hemigrapsus nudus
Crytomya sp.		Hemigrapsus oregonesis
Fucus gardneri		Hildenbrandia sp.
Gracelaria sp.		Masticarpus sp.
Hemipodus sp.		Protothaca sp.
Macoma sp.		
Ulva sp.		
		Gravel (Group 6)
		Amphipods

Lower zone indicators

Mud (Groups (4 and 5)	Sand (Groups 1 and 3)	Gravel (Groups 6 and 7)
Callianassa sp.	Nemerteans	Balanus glandula
Goniada sp.	Porphyra sp.	Enteromorpha sp.
Tellina sp.	Spiochaetopterus sp.	Hemipodus sp.
	Ulva sp.	Lottia sp.
		Micropodarke sp.
		Mastocarpus sp.
		Notomastus sp.
		Hildenbrandia sp.
Group 4	Groups 1 and 2	Group 6
Gracelaria sp.	Dendraster sp.	Acrosiphonia sp.
Macoma sp.	Scoloplos sp.	Crepidula sp.
		Ophiodromus sp.
		Piddock siphons
Group 5	Group 3	
Cryptomya sp.	Edwardsia sp.	
Pinnotherid sp.	Haminea eggs	
Scleroplax sp.	Neomolgus sp.	
	Group 2	
	Eupolymnia sp.	

plot suggests very high similarity. The gravel groups have their patterns driven especially by the epifaunal Balanus glandula and Enteromorpha, and the infaunal polychaetes Micropodarke and Notomastus (other indicator species listed in Table 11). Group 6 (in a slightly higher-energy area) is distinct from Group 7 by having Acrosiphonia, Crepidula, Ophiodromus, and Piddock siphons. Mud Groups 4 and 5 are separated from the rest by having abundant populations of Callianassa, Goniada (which is also present in Groups 6 and 7 but in lower abundances), and Tellina. Mud Group 4 (a slightly cooler, higher-salinity region) is distinct from Group 5 in having Gracelaria and Macoma, while Group 5 has more of the ghost shrimp associates Cryptomya, Pinnixia spp., and Scleroplax. The sand Groups 1, 2, and 3 share nemerteans (not common, but present in all groups),Punctaria, Spiochaetoperus, and ulvoids. Only Groups 1 and 2 have significant populations of Dendraster and Scoloplos, and only Group 3 (warmer, lower salinity) has Edwardsia, Haminoea eggs, and Notomastus lineatus sp. Only Group 2 had Eupolymnia sp. as an indicator organism.

Nested ANOVA

For each organism sampled in the three different habitat types, sources of variation in abundance were examined at increasing spatial scales of segment aggregation using a three-way nested ANOVA. For each analysis, the effect of scale was tested by using the mean square of the next lowest factor as the error term (e.g., the effect of within-groups was tested with the MS of within-segments, with 4 and 24 degrees of freedom for the low zone mud samples, Table 112). If the effect was significant, then the next higher spatial increment is not listed. Since we are interested in retaining statistical sensitivity to detect change, the level of spatial aggregation where variability becomes significant is the terminal level of effective scaling for that particular organism. Thus the columns in Table 11 for segment and group list only those organisms found to have non-significant variation at the preceding scale. The statistics in bold face are for the indicator organisms. The summary at the bottom of the table lists for each scale the number of taxa analyzed, how many were found non-significant, and the number of indicator taxa and how many of them were found non-significant.

Table 11. Evaluation of the effect of transect-block, segment, and group on lower zone organism abundance. * indicator organisms in bold

		Lower Mud Source of Variation						Lower Sand Source of Variation						Lower Gravel Source of Variation					
		Within segment (df=24)		Within group (df=4)		Among groups (df=1)		Within segment (df=36)		Within group (df=6)		Among groups (df=2)		Within segment (df=16)		Within group (df=12)		Among groups (df=1)	
Organism	Sample	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Acrosiphonia coalita	quadrat													2.96	0.012				
Amphipods	quadrat							1.00	0.495	0.57	0.755	2.38	0.174	0.79	0.684	0.02	0.978	209.99	0.005
Artacama conifera	core													0.75	0.715	2.64	0.102	1.00	0.423
Axiothella rubrocincta	core													0.35	0.980				
Balanus glandula	quadrat	0.71	0.804	5.26	0.003									1.78	0.111	6.88	0.007		
Callianassa californiensis	core	1.30	0.244	2.36	0.682	0.02	0.899												
Callianassa californiensis	quadrat	1.38	0.201	2.11	0.111	12.51	0.024	1.49	0.103	3.37	0.010								
Cancer sp.	quadrat													0.82	0.650	2.08	0.158	1.00	0.423
Capitella capitata	core	1.00	0.486	0.05	0.993	58.53	0.002												
Crepidula sp.	quadrat													1.12	0.401	0.55	0.540	39.19	0.032
Cryptomya californica	core	0.97	0.530	3.53	0.021														
Decamastus gracilis	core							0.59	0.948	11.94	0.000								
Dendraster excentricus	quadrat	0.77	0.743	14.42	0.000			1.33	0.183	18.24	0.000								
Edwardsia sipunculoides	core	0.77	0.743	14.42	0.000			0.78	0.777	6.19	0.000								
Enteromorpha sp.	quadrat	1.78	0.068	3.94	0.014									3.80	0.003				
Eudymene zonalis	core													0.87	0.608	0.27	0.768	12.12	0.074
Eupolymnia heterobranchia	core	1.92	0.045					0.58	0.951	17.84	0.000								
Gelidium sp.	quadrat													1.00	0.493	0.03	0.973	71.63	0.014
Goniada annulata	core	0.85	0.651	0.49	0.741	2.24	0.209							0.77	0.701	2.51	0.113	0.01	0.945
Gracilaria sjoestedtii	quadrat	1.10	0.396	0.33	0.855	8.75	0.042	2.57	0.001										
Haminoea vesicula	core	0.94	0.555	1.78	0.166	0.60	0.483	0.71	0.850	10.08	0.000								
Hemigrapsus oregonensis	quadrat	387.00	0.634	0.36	0.832	12.45	0.024												
Hemipodus borealis	core	0.75	0.765	1.28	0.765	1.24	0.328							2.53	0.026				
Unidentified red crust	quadrat													1.39	0.240	13.56	0.000		
Hippolyte clarki	core													0.77	0.700	2.50	0.114	1.00	0.423
Lepidonotus squamatus	core													1.00	0.493	1.00	0.390	1.00	0.423
Leptosynapta clarki	core							2.99	0.000										
Littorina scutulata	quadrat													1.00	0.493	1.00	0.390	0.48	0.560
Lottia singatella	quadrat													1.03	0.467	0.79	0.472	0.71	0.488
Macoma secta	core	1.18	0.331	1.17	0.348	5.16	0.086												
Magelona hobsonae	core							0.46	0.991	8.34	0.000								
Mastocarpus papillata	quadrat													0.92	0.565	1.46	0.263	0.95	0.433
Micropodarke dubia	core													1.32	0.277	0.60	0.561	3.78	0.191
Haminea eggs	quadrat	3.07	0.002					0.68	0.881	15.12	0.000								
Mytilus edulis	quadrat																		
Nemertea (unidentified)	core	0.79	0.721	3.46	0.023			0.63	0.920	5.33	0.001			0.71	0.750	4.32	0.032		
Notomastus lineatus	core							0.70	0.868	3.22	0.012			1.00	0.493	0.30	0.742	5.58	0.142
Nephtys longosetosa	core							1.69	0.022										
Neries procera	core													0.84	0.633	1.94	0.176	0.35	0.616
Notomastus tenuis	core	1.33	0.227	5.75	0.002									0.67	0.787	0.65	0.523	10.36	0.085
Nucella lamellosa	quadrat													0.82	0.648	1.07	0.367	2.86	0.233
Unidentified Oligochaeta	core													0.78	0.693	2.44	0.119	1.00	0.423
Ophiodromus pugettensis	core													0.44	0.952	6.26	0.010		
Pectinaria granulata	core													1.00	0.493	1.00	0.390	0.06	0.829
Petrocelis sp.	quadrat													1.03	0.470	1.27	0.309	0.62	0.513
Unidentified clam siphons	core	0.67	0.839	2.03	0.122	3.08	0.154												
Pinnotherid sp.	core	3.13	0.002											0.75	0.715	2.64	0.102	1.00	0.423
Polysiphonia sp.	quadrat							0.91	0.607	4.52	0.002			0.77	0.697	0.28	0.757	16.43	0.056
Punctaria hesperia	quadrat							1.88	0.023										
Protothaca staminea	core	0.98	0.513	0.82	0.524	0.75	0.437												
Pseudopythina rugifera	core	5.03	0.000																
Saccoglossus sp.	core	0.89	0.613	1.63	0.200	0.05	0.837												
Scleroplax granulata	core	2.67	0.006																
Scolelepis acmeceps	core	0.44	0.979	7.37	0.001			0.68	0.883	2.27	0.059	1.00	0.422						
Scolelepis armiger	core													1.00	0.493	0.02	0.985	132.17	0.007
Scytosiphon lomentaria	quadrat													1.00	0.493	1.00	0.390	1.00	0.423
Semibalanus cariosus	quadrat													1.33	0.271	2.65	0.101	1.00	0.423
Spionidae	core													1.00	0.493	1.00	0.390	0.21	0.691
Spiochaetopterus costarum	core							0.96	0.547	1.94	0.102	1.84	0.238						
Spiophanes berkeleyorum	core	12.36	0.000																
Tellina sp.	core	0.02	0.907	2.58	0.063	0.02	0.907												
Ulva sp.	quadrat	0.51	0.952	12.00	0.000			1.40	0.141	0.90	0.509	6.19	0.005						

	Lower Mud			Lower Sand			Lower Gravel		
Lower Zone Summary	Within segment	Within group	Among groups	Within segment	Within group	Among groups	Within segment	Within group	Among groups
Total number of organisms	28	22	13	19	15	4	34	31	26
Number of organisms with p>.05	22 (79%)	13 (46%)	9 (32%)	15 (79%)	4 (20%)	3 (15%)	31 (91%)	26 (76%)	22 (65%)
Total number of quadrat organisms	8	8	4	9	7	2	18	16	14
Number of quadrat organisms with p>.05	8 (89%)	4 (44%)	1 (11%)	7 (78%)	2 (22%)	1 (11%)	16 (94%)	14 (78%)	11 (61%)
Total number of core organisms	20	14	9	10	8	2	16	15	12
Number of core organisms with p>.05	14 (74%)	9 (47%)	8 (42%)	8 (80%)	2 (20%)	2 (20%)	15 (94%)	12 (75%)	11 (69%)
Total indicator organisms	8	6	5	10	9	3	11	8	5
Number of indicator organisms with p>.05	6 (75%)	5 (63%)	4 (50%)	8 (80%)	3 (30%)	2 (20%)	8 (73%)	5 (45%)	4 (36%)

The lower mud habitat type had 28 taxa analyzed for within-segment effects, with 22 (79% of the total) that showed no significant variation at that scale (Table 11). This suggests that relatively homogeneous segments were sampled. Of the 6 taxa that were significantly variable within segments, all were infauna (sampled by cores). The 22 organisms with no variation at the within-segment scale were then analyzed at the within-group scale, where 13 still showed no effect. At this scale, both infauna and epifauna showed significant variability in about half their species. Of the original 8 indicator organisms, 5 remained non-variable at this scale. At the among-group scale (i.e., among spatial blocks in Carr Inlet), only 9 of the original 28 taxa, and 4 of the original 8 indicators remained non-significant.

These data suggest that for about half the taxa, and 5 out of the 8 indicator taxa, we can validly extrapolate their abundances from site-scale transect data to other segments within groups of geophysically similar segments. In this case the segments consist of very low and low energy, mud and sandy mud beaches. Furthermore, 9 out of 28 taxa (4 out of 8 indicators) can be scaled up across 2 levels, i.e. from the within-beach to the within-inlet scale. The indicators include ghost shrimp, two clam species, and the predatory polychaete Goniada. The muddy habitat type represented here spans substrates from low energy sandy mud (Segments 233 and 251, Group 4), to very low energy all mud (all of Group 5), to very low energy muddy sand (Segment 194, Group 4).

The analysis of scaling effects for low zone sand organisms (Table 11) showed few significant differences at the transect-block scale, again suggesting homogeneity within segments. However, at the within-group scale only 4 of the original 19 organisms (3 of 9 indicators) remained non-variable. Both infauna and epifauna tended to have high segment to segment variability. Interestingly, relatively few additional organisms appeared variable at the among group scale. The 3 organisms remaining (two of which were sand indicators) appear to be robust to environmental diversity; these were amphipods and the polychaetes Spiochaetopterus and Scoloplos.

A relatively large percentage of the gravel organisms showed no effects of spatial scaling on variability; at the among-group level, 65% of the taxa remained non-variable (versus 32% in mud and 15% in sand, Table 11). This may relate to the geophysical

similarity of both groups of gravel segments compared to the mud and sand habitats. Table 4 shows that all the gravel low zone polygons, from both groups, were cobbles, pebbles and sand, with differences among groups primarily in wave energy. The homogeneity of organism abundances across spatial scales can therefore be attributed to either the geophysical homogeneity among the segments, or niche breadth of the organisms sampled from this habitat type. Two of the remaining indicator species, Lottia strigatella and Mastocarpus, both live on rocky substrates over a wide range of wave exposures.

Table 13 and 14 list the nested ANOVA comparisons for the Block 4 lower-middle and upper-middle zone organisms. No among-group comparisons were possible since only the lower zones of these substrate types were sampled in multiple blocks (Table 3). In the lower-middle zone (Table 12), homogeneity was again high at the within-segment scale (as expected), but remained very high at the among-segment scale in contrast with the low zone data. Species richness was similar in the two zones, but over 80% of the taxa remained non-variable among segments in most comparisons for all three substrates, in contrast with the 20-47% for the low sand and mud. Homogeneity was seen in both the surface (quadrat) and infaunal (core) species. If anything, physical characters (including seepage) were more variable among segments in this zone than low, so geophysical similarity is unlikely to account for this pattern. It is possible that again these hardy, mid-intertidal organisms are tolerant of a range of physical conditions.

Species richness is so low in the middle-upper zone (Table 13) that it is difficult to discern patterns in the variability at different scales. Within-segment homogeneity is still very high. Among-segment variability was high for the mud, probably because geophysical characters were poorly matched among segments at this level, and the primary substrate type ranged from silt to pebbles (Table 4). In contrast, geophysical characters matched well in the 'sand' habitat (Table 4), and all 3 taxa remained similar among segments. The gravel segments were well matched, yet 2 of the 6 taxa (Balanus and Mastocarpus) were different among them.

Table 12. Evaluation of the effect of transect-block, segment, and group on lower-middle zone organism abundance.

* indicator organisms in bold

		Lower-middle Mud Source of Variation				Lower-middle Sand Source of Variation				Lower-middle Gravel Source of Variation			
		Within segment (df=12)		Within group (df=2)		Within segment (df=12)		Within group (df=2)		Within segment (df=12)		Within group (df=2)	
Organism	Sample	F	p	F	p	F	p	F	p	F	p	F	p
Amphipods	quadrat					0.97	0.513	0.65	0.542	**2.86**	0.029		
Artacama conifera	core									2.53	0.046		
Balanus glandula	quadrat	4.76	0.003			0.57	0.831	2.78	0.102	**0.87**	**0.592**	1.46	0.271
Callianassa californiensis	core	**0.91**	0.563	0.25	0.784	0.88	0.584	0.86	0.447				
Callianassa californiensis	quadrat	0.35	0.964	16.25	0.000	0.86	0.757	0.28	0.595				
Capitella capitata	core	**0.64**	0.779	2.83	0.099								
Crassostrea gigas	quadrat									0.75	0.688	2.66	0.111
Cryptomya californica	core	0.64	0.778	2.16	0.158					0.52	0.867	5.53	0.020
Endocladia muricata	quadrat									0.76	0.683	2.61	0.114
Enteromorpha sp.	quadrat					0.80	0.649	2.26	0.146				
Freemania litoricola	core									0.82	0.630	1.05	0.379
Fucus gardneri	core	**1.81**	**0.138**	2.22	**0.157**								
Gnorimosphaeroma oregonense	core	5.18	0.002			72.72	0.000						
Goniada annulata	core	0.86	0.598	1.00	0.397								
Gracelaria sjoestedtii	quadrat	**0.87**	**0.587**	1.91	**0.190**								
Hemigrapsus nudus	quadrat									**0.96**	**0.524**	0.71	**0.510**
Hemigrapsus oregonensis	quadrat	1.13	0.406	2.87	0.096	0.78	0.666	5.36	0.022	**1.13**	**0.408**	0.29	**0.755**
Hemipodus borealis	core	**1.52**	0.221	0.15	**0.864**	0.78	0.668	2.20	0.154	0.66	0.766	2.42	0.131
Unidentified red crust	quadrat									**2.44**	**0.052**	3.30	**0.072**
Littorina scutulata	quadrat	0.93	0.545	1.39	0.287	0.72	0.711	5.84	0.017	0.77	0.672	7.87	0.007
Lottia strigatella	quadrat					0.74	0.697	9.09	0.004	2.84	0.030		
Macoma juveniles	core	**1.44**	**0.250**	0.21	**0.814**								
Macoma nasuta	core	0.75	0.688	2.67	0.110								
Macoma secta	core					0.75	0.685	2.63	0.113				
Mastocarpus papillata	quadrat					0.76	0.682	1.46	0.272	**1.27**	**0.324**	1.29	0.311
Haminea eggs	quadrat					**5.45**	**0.001**						
Mytilus edulis	quadrat	0.79	0.653	2.31	0.142	0.96	0.524	0.54	0.594	1.93	0.115	2.66	0.111
Nemertea (unidentified)	core	2.25	0.070	1.28	0.314								
Notomastus lineatus	core	2.39	0.057	2.16	0.158								
Nereis vexillosa	core					1.00	0.492	0.74	0.477	0.96	0.523	0.18	0.837
Notomastus tenuis	core	1.54	0.213	0.85	0.452					0.62	0.794	4.18	0.042
Pagurus sp.	quadrat									1.35	0.286	0.74	0.496
Unidentified clam siphons	core									1.21	0.356	1.37	0.291
Polydora brachycephala	core					2.25	0.070	1.00	0.397	0.76	0.684	2.62	0.114
Polydora columbiana	core									0.92	0.550	1.42	0.279
Polydora socialis	core									1219.50	0.000		
Polysiphonia sp.	quadrat					237.21	0.000						
Punctaria hesperia	quadrat	1.73	0.157	1.14	0.352								
Prototheca staminea	core									**1.53**	**0.215**	**2.94**	**0.092**
Spiophanes berkelyorum	core	0.82	0.634	0.89	0.435	0.87	0.540	0.88	0.441				
Tapes philippinarum	core									0.77	0.675	2.52	0.122
Tellina sp.	core	0.29	0.982	20.35	0.000								
Ulva sp.	quadrat	1.00	0.492	0.70	0.514					0.55	0.850	7.64	0.007

	Lower-Middle Mud		Lower-Middle Sand		Lower-Middle Gravel	
Lower-MiddleZone Summary	Within segment	Within group	Within segment	Within group	Within segment	Within group
Total number of organisms	22	20	18	15	25	21
Number of organisms with p>.05	20 (91%)	18 (90%)	15 (83%)	12 (80%)	21 (84%)	17 (81%)
Total number of quadrat organisms	8	7	11	10	13	11
Number of quadrat organisms with p>.05	7 (86%)	6 (86%)	10 (91%)	6 (60%)	11 (85%)	9 (82%)
Total number of core organisms	14	13	6	6	12	10
Number of core organisms with p>.05	13 (93%)	12 (92%)	6 (100%)	6 (100%)	10 (83%)	8 (80%)
Total indicator organisms	8	8	1	0	7	6
Number of indicator organisms with p>.05	8 (100%)	8 (100%)	0	0	6 (86%)	6 (100%)

Table 13. Evaluation of the effect of transect-block, segment, and group on upper-middle zone organism abundance.
* indicator organisms in bold

		Upper-middle Mud Source of Variation				Upper-middle Sand Source of Variation				Upper-middle Gravel Source of Variation			
		Within segment (df=12)		Within group (df=2)		Within segment (df=12)		Within group (df=2)		Within segment (df=12)		Within group (df=2)	
Organism	Sample	F	p	F	p	F	p	F	p	F	p	F	p
Amphipods	quadrat	0.59	0.821	4.51	0.035					0.91	0.558	1.02	0.391
Balanus glandula	quadrat	1.34	0.292	6.00	0.016	3.52	0.012			1.31	0.306	11.70	0.002
Callianassa californiensis	quadrat	2.36	0.059	4.14	0.043								
Capitella capitata	core									1.00	0.492	0.80	0.473
Enteromorpha sp.	quadrat	1.09	0.429	2.31	0.142	0.80	0.647	2.25	0.148				
Fucus gardneri	core	0.87	0.592	1.31	0.308								
Hemigrapsus oregonensis	quadrat	1.73	0.157	6.85	0.010					0.70	0.732	1.23	0.328
Littorina scutulata	quadrat	1.01	0.483	0.58	0.574					2.04	0.096	2.44	0.129
Lottia strigatella	quadrat					0.75	0.688	2.67	0.110				
Mastocarpus papillata	quadrat									0.45	0.916	8.21	0.006
Notomastus lineatus	core									8.32	0.000		
Tellina sp.	core					1.00	0.492	0.51	0.614				

	Upper-Middle Mud		Upper-Middle Sand		Upper-Middle Gravel	
Upper-Middle Zone Summary	Within segment	Within group	Within segment	Within group	Within segment	Within group
Total number of organisms	7	7	4	3	7	6
Number of organisms with p>.05	7 (100%)	3 (43%)	3 (75%)	3 (100%)	6 (86%)	4 (67%)
Total number of quadrat organisms	6	6	3	2	5	5
Number of quadrat organisms with p>.05	6 (100%)	2 (33%)	2 (67%)	2 (100%)	5 (100%)	3 (60%)
Total number of core organisms	1	1	1	1	2	1
Number of core organisms with p>.05	1 (100%)	1 (100%)	1 (100%)	1 (100%)	1 (50%)	1 (100%)
Total indicator organisms	3	3	1	0	3	3
Number of indicator organisms with p>.05	3	1	0	0	3	2

1.4 Discussion

Overview

Our results show that it is possible to partition and classify intertidal shorelines such that geophysical homogeneity is minimized within a given segment of the shore, and that with this geophysical homogeneity comes biological homogeneity. Reducing physical and chemical differences among sites thus reduces the environmental variation that inevitably results in biotic variation. By reducing biotic variation, this methodology should help to solve the problems of change detection and scaling up that plague both basic and applied ecological studies.

The method of partitioning shorelines using quantitative and qualitative geophysical parameters is conceptually straightforward. But when large spatial scales are considered, the large number of potentially interacting spatial and temporal gradients can increase system complexity. Any attempt to force natural phenomena into discrete categories is going to encounter problems since ecosystems are multidimensional continua; beach types, for example, rarely change abruptly (in time or space) from one to another. However, much of what ecologists do requires such categorizing, and some 'noise' in our categories is inevitable. The nested partitioning (i.e., dividing a large region first into blocks differing in large-scale physical features such as wave action, then into smaller blocks) resulted in categories of increasing biotic homogeneity with decreasing spatial scale, as predicted. This can be seen both in the beta diversities (a measure of community heterogeneity: Table 5) and with the R values in the ordinations. Homogeneity is high within a beach (at the smallest spatial scale) and low among all the beaches within the whole inlet (the largest spatial scale).

The close tie between organisms and their sediment type is a well-known phenomenon (refs. in Introduction), although mechanisms are poorly understood. Our research strengthens data on organism-environment linkages, but still is only correlative. However, some of the clearly defined spatial patterns found (e.g., the burrowing anemone Edwardsia occurring only in low-salinity sandy beaches) suggest profitable avenues for further mechanism-level research. Some of our work also illustrates the positive feedbacks between soft-sediment organisms and their environment, i.e. the effects that

some of the biota have on the substrate itself. The two clearest examples in our study area were: the sand dollar Dendraster, which extensively bioturbates surface sediments, excluding other biota and probably keeping fine particles from remaining within the sand; and the ghost shrimp Callianassa, which excavates deep burrows in mud, oxygenating the sediment and creating habitat for a host of commensal species. Other, smaller organisms such as the capitellids that reached huge densities in the sediment of gravel beaches also affect their environment both by burrowing and by consuming organics.

The organism-environment link is perhaps best seen in the cases where the infauna did not "match" the habitat type as defined by measured geophysical features; in several cases errors in beach classification were 'pointed out to us' by the organisms. For example, mud segment 194 'should' not have had Dendraster (as predicted by the fauna in the other members of this mud group) but it did, probably because of the relatively high proportion of subsurface sand there. Sand segment 173, in contrast, 'should' have had high Dendraster populations, but an area of extensive freshwater seepage (not noted during beach classification) probably excluded these echinoderms. And since sand dollars alter their habitat so extensively, their unexpected presence or absence in those anomalous segments introduced substantial variability in the biotic data. Future mapping efforts will thus be careful to note both subsurface sediment and seepage characteristics, which were not in the original model.

Interpretation of Ordinations

Examining whole communities in different beach segments using non-metric multivariate analyses clearly illustrated the trends in decreasing biotic similarity with increasing spatial scale, as discussed above. Ordinations at each spatial scale show *relative* similarity of sample units, such that groups of samples that seem to be quite variable (i.e., heterogeneously scattered on the two-dimensional plots) at small spatial scales (segments within a block) show up as tightly clustered groups of samples at larger spatial scales (blocks of segments within the whole inlet). The MRPP statistical tests, however, suggested greater (i.e. significant) differences among groups of samples at the within-group level than we expected, or than was suggested by the graphs. We believe

this is at least in part a statistical artifact caused by the large numbers of organisms sampled compared to the relatively small number of samples at transect and segment spatial scales. We found that within-segment homogeneity is high, as indicated by the large (non-significant) p values at the segment level in Tables 6-8. In achieving this homogeneity (by sampling at a small spatial scale, in beaches lacking in geophysical gradients) we have essentially minimized overlap among beach communities; at this scale, the biota of each beach is unique. Thus any test comparing beaches is likely to find significant differences. This artifact results from the resolution of the biotic data being greater than that of the geophysical data; had we defined the geophysical parameters much more finely (by quantifying organic content, percent silt composition, O_2 levels, etc.) and then been able to find beaches that "matched", the biota probably would have been more similar. Proof of this lies in the geophysical differences found (a posteriori) in the beaches with seemingly anomalous biota, discussed above.

The two transformations applied to the data prior to ordination proved to be effective in handling these non-normal, zero-rich data, although in different ways. The double-relativizations retained abundance information and thus gave a more realistic view of the biota of each area, but statistical comparisons were severely biased by the high percentage of zeros in the data matrices. The Beals transformation lost the abundance information but, because it is strongly affected by the relative frequencies of species in the samples, was very effective at illustrating what species are most consistent at separating the beach segments from each other biotically. This utility can be seen in the long list of species with high r^2 values for the Beals ordinations (Table 9), i.e. those that correlated well with the two principal axes explaining the ordinations. The abundance transformation left relatively few species with high correlation values, and thus it was less easy to discover the taxa driving the community differences when only this transformation was used. Not surprisingly, then, the species viewed as most "important" in separating groups using the relativization transformation were the abundant ones, while some of the high-r^2 Beals species were not necessarily abundant but nonetheless characteristic (i.e. frequent) in a given group.

Further analyses of these data are examining the ability of higher taxonomic groupings (e.g., families) to distinguish differences among beach segments and groups. Preliminary data suggest, as in several pollution studies (Warwick 1988, Heip et al. 1988, James et al. 1995, Olsgard et al. 1997), that family-level analyses are still quite effective at detecting differences, in this case among geophysically different beaches (Dethier and Schoch, in prep.). This result could allow substantial savings in effort and therefore cost for mapping and monitoring work in these soft-sediment habitats.

Interpretation of Indicator Values

Species found to have large indicator values, i.e. those with either even abundances or high frequencies (or both) in a given set of samples, can serve two functions in helping to detect change and extrapolate biotic data. First, because these species are important to a given habitat type, they are likely to be ones on which to focus monitoring or change detection efforts. These are the species that should most predictably be found in a given substrate type or region, and therefore their absence would be indicative of unusual conditions. The capitellid polychaete Notomastus tenuis, for example, was both frequent and abundant in all the gravel samples but uncommon elsewhere (other capitellids were found in other beach types) and is thus an excellent indicator of 'normal' for this substrate in Carr Inlet. Indicator species are also logical ones on which to focus further mechanism-level research, e.g. figuring out why a given animal is characteristic of a given set of physical conditions, and how it interacts with others in the community. The tradeoff in using these organisms may be in their sensitivity to "change"; organisms with a weaker presence in a segment may also be more responsive to perturbations. Second, when we are trying to understand the variation seen at different spatial scales, for example between segments within a group that we expected to be similar, examining the species that had high indicator values for each segment gives the best overall summary of the biotic character of that site. For example, in interpreting the ordination in Figure 10, segment 116 clearly is separate from the other sand segments. Species with high indicator values for this segment include ghost shrimp, a terebellid polychaete, and others more characteristic of mud than of sand. Table 4 shows that in

fact this segment was slightly misclassified, since its substrate contained more mud than the other Group 2 members.

When we used nested ANOVAS to analyze the spatial scales at which each indicator species was most variable, we could then pick out the taxa that would be best at detecting change at any given scale. Indicator species that are homogeneous at small spatial scales but become heterogeneous at the within-group scale (e.g., the brown alga Punctaria in the low sand, Table 11) would be poor choices for monitoring on an inlet-wide (or presumably wider) scale because their natural variability would result in low statistical power to detect change. Indicators that still show low variability among groups (e.g., the clam Tellina in the mud) are predictably found in most beach segments of that type in the whole inlet, and thus would be good choices for comparisons with other regions. Species that are good indicators only of one, narrowly defined group of physical conditions (e.g. the anemone Edwardsia in low, Group 3 sand, Table 11) would be interesting to seek in parallel shores in other regions; if consistent there, they could become excellent choices for monitoring the health of that particular bio-physical community.

Applications

The shoreline partitioning model tested here has a wide variety of potential applications, both for basic and applied research. First, the methodology should be usable to perform detailed mapping of shorelines, with each beach segment (or whatever minimum mapping unit is feasible) delineated by its distinct geophysical features. With appropriate testing in each region, the biota associated with each group of geophysical units should be able to be characterized based on a limited series of randomly located transects. Such maps could then be used to: 1) identify matched sites for field research, e.g. basic ecological studies. Reducing site to site variation is a critical design component of any ecological study, and this could provide an objective and systematic method; 2) identify 'reference' sites for monitoring programs, again geophysically matched and randomly selected. Nested biotic sampling designs such as ours can then help choose 'reference species' with manageable levels of spatial variation; 3) denote sensitive

habitats, e.g. mud flats or other low-energy habitats that are particularly vulnerable to long-term damage from oil spills; 4) denote resource-rich habitats, or habitat types that should be suitable for species of concern, e.g. wildlife or commercially valuable organisms. Since economically important or 'charismatic' species tend to use certain habitat types (e.g. oysters grow best on certain types of mud flats), potentially valuable sites should be readily identifiable. This approach has certain advantages over the current effort by many state agencies to map 'vegetated areas' in the marine realm; important habitat-forming species such as eelgrass or kelp come and go unpredictably through time, and thus may not be found in a given location when a map is made. Mapping physical regions suitable for those species (e.g., low shore sandy mud areas for eelgrass) gives a much longer-term picture of *potential* habitat; 5) choose regions for conservation efforts. Since biota, including rare species, are likely to be linked to particular physical habitats, preserves can be designed by choosing areas that have those habitats, or that encompass the range of habitats in an area.

Second, as discussed in the Introduction, change detection in nature can only be accomplished if environmental variation can be factored out, and this model provides one mechanism. We have not yet studied temporal variation in our sites at Carr Inlet, and our model was not designed for this. However, many monitoring and impact-detection programs have run afoul of the problem of confounding spatial and temporal variation, i.e. of assuming that change has occurred at an impacted site because it is different from a control site, when really the sites were not adequately matched to begin with. Controlling for environmental variables and minimizing physical gradients are critical before change detection can even be attempted. Change detection in the marine realm is needed for quantifying the effects of controlled ecological experiments, of the introduction of alien species, of chronic or catastrophic pollution events, or even of positive efforts such as cleanup or habitat restoration. For many of these applications that involve looking at the responses of multiple species, the multivariate procedures we described would probably be useful as well.

Finally, marine (and other) ecologists need to be able to scale up their research results in order to answer questions about critical processes affecting natural communites

at large spatial scales, including broad anthropogenic effects. At small spatial scales, it is relatively easy to find similar, low-variation habitats for making comparisons or running experiments. But there is increasing pressure to be able to extrapolate our local findings to larger regions: when is this justifiable? Our model has been tested extensively in Carr Inlet but not in other parts of Puget Sound; thus we cannot yet determine if geophysically similar beach segments in an adjacent inlet or an inlet 100 km to the north will have similar biota. Our studies within the inlet, however, have demonstrated a phenomenon that is likely to be true at these larger spatial scales: whenever we scale up our observations (whether from a beach to the inlet, or from the inlet to the sound) we are adding new sources of variation to the data. Geophysical and presumably biotic heterogeneity are likely to be greater among all the sandy low-energy beach segments in Puget Sound than among just those within Carr Inlet. At some point in this scaling process, the communities in 'similar' beaches are likely to become so different (e.g., as one moves into a different oceanic mixing regime or biogeographic province) that comparisons are not meaningful. What ecologists (and regulators) must decide is how much variation we are willing to accept.

Our ability to scale up, or generalize our results, has led to some acrimonious debate in the literature. For example, Foster (1990) pointed out that community structure along much of the rocky coast of N. California does not follow some of the patterns described by previous researchers in Washington, and thus that we cannot assume that ecological processes are parallel, either. Paine (1991) responded that the sites Foster examined may be physically very different, and that ecological experiments are necessary to test what ecological processes are acting at those sites. We suspect that both are correct. Our data suggest that without matching the physical regime (e.g., extreme wave action, strong upwelling) of Paine's study sites, it is unlikely that other regions would have identical biota, and thus that processes could also differ. Scaling up to shores xx km down the coast is likely to add in much ecological variation. Known ecological processes (e.g., the role of predation) in one region should provide a good starting point for experiments in another, but if sites are clearly different geophysically then we should not attempt to make ecological generalizations to them.