Responses of infaunal populations to benthoscape structure and the potential importance of transition zones

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Abstract

Relationships between population abundance and seafloor landscape, or benthoscape, structure were examined for 16 infaunal taxa in eastern Long Island Sound. Based on analyses of a side-scan sonar mosaic, the 19.4-km² study area was comprised of six distinct large-scale ($>$ km²) benthoscape elements, with varying levels of mesoscale (km²–m²) and small-scale ($<$ m²) physical and biological habitat heterogeneity. Transition zones among elements varied from ~50 to 200 m in width, comprised ~32% of the benthoscape, and added to overall benthoscape heterogeneity. Population abundances of nine taxa varied significantly among the large-scale elements. Most species were found at high abundances only in one benthoscape element, but three had several foci of elevated abundances. Analyses of population responses to habitat heterogeneity at different spatial scales indicated that abundances of eight taxa varied significantly among spatial scales, but the significant scales were mixed among these species. Relatively large residual variations suggest significant amounts of mesoscale spatial variation were unaccounted for, varying from ~1 km² to several m². Responses to transition zones were mixed as well. Abundances of nine taxa varied significantly among transition zones and interiors of benthoscape elements, most with elevated abundances in transition zones. Our results show that infaunal populations exhibit complex and spatially varying patterns of abundance in relation to benthoscape structure and suggest that mesoscale variation may be particularly critical in this regard. Also, transition zones among benthoscape features add considerably to this variation and may be ecological important areas in seafloor environments.

The spatial patterns of benthic communities in relation to seafloor characteristics have been studied by marine ecologists since the early 1900s (e.g., Petersen 1913). Sampling along transects or grids has typically been used to explore relationships between the biological, physical, and chemical characteristics of the seafloor at various spatial scales (e.g., McCall 1978; Thrush et al. 1989). Although significant advances have been made using this approach, deep-water benthic research has historically been akin to studying a ''black box.'' The water column covers the seafloor and, as such, the benthic landscape, or benthoscape, is not readily revealed. This imparts a whole set of difficulties with respect to sampling design and data interpretation and constrains our ability to fully understand the ecological dynamics of ben-

thic communities and ecosystems. In particular, spatial distributions and characteristics of benthic habitats and communities have to be interpolated from point samples obtained from bottom grabs. The accuracy of such interpolations is clearly dependent on the number of sampling points in a defined area and the heterogeneity of the system (*see,* for example, Langton et al. 1995).

Seafloor mapping over the past several decades, using techniques such as side-scan and multibeam sonar (e.g., Knebel and Poppe 2000; Zajac et al. 2000; Valentine et al. 2001; Cochrane and Lafferty 2002), echosounders (Morrison et al. 2001), and various video and photographic instrumentation (e.g., Rhoads and Germano 1982; Robbins 1997), has revealed that coastal benthoscapes are heterogeneous and complex environments with rich and fascinating patch structures that vary over multiple spatial scales. Seafloor mapping provides benthic ecologists a gateway for the study of the structure and dynamics of benthic populations, communities, and ecosystems at multiple spatial scales within the context of a known distribution of habitat types and composition. However, until recently, detailed studies of spatial patterns in soft-sediment communities have primarily centered on smaller scale phenomena, usually ≤ 1 m^2, although patch forming processes occur over a wide range of spatial scales (Hall et al. 1994). Most studies conducted over large spatial scales have addressed broad trends in species composition and population abundance relative to sediment type, depth, etc., as noted above. There has been little explicit a priori consideration of the spatial arrangement, composition, and extent of benthoscape features.

Researchers are increasingly using the information provided via seafloor mapping to explore the structure and dynamics of benthic populations and communities in relation to benthoscape characteristics. Early efforts used towed video and camera systems and manned submersibles to characterize and assess the spatial characteristics of seafloor communities along specified transects (e.g., Grassle et al. 1975; Schneider et al. 1987) and side-scan images to relate large-scale spatial changes in benthic community structure to environmental features such as tidal regime (Warwick and Uncles 1980) and disturbances (Menzie et. al. 1982) and to address fisheries questions (Able et al. 1987). More recently, researchers are exploring, for example, impacts on benthic communities due to trawling (Thrush et al. 1998), infaunal and epifaunal responses to seafloor patch characteristics (Zajac et al. 2000; Kostylev et al. 2001; Zajac 2001; Brown et al. 2002), fisheries responses to habitat variables (Auster et. al. 2001), and classification schemes for seafloor landscapes (Greene et al. 1999). Collectively, this body of work is forming the basis for the development of a set of general working hypotheses that focus on benthos–benthoscape interactions (Zajac 1999). Similarly, landscape approaches are now also being applied to freshwater benthic habitats, including lotic (e.g., Palmer et al. 2000; Wiens 2002) and lentic (e.g., Downing and Rath 1988; Haltuch et al. 2000) systems, and are beginning to reveal the complex ways in which freshwater organisms respond to the structural characteristics of their environments over multiple spatial scales. The continued development of this area of benthic ecology, in both freshwater and marine realms, will depend on detailed stud-

ies of population and community characteristics in relation to benthoscape structure. Elucidating ecological dynamics at landscape scales is challenging owing to the difficulty or near impossibility of manipulative experiments. As such, detailed studies of structure become a critical guide to understanding process (e.g., Levin 1992) and increase our ability and confidence to extrapolate results from smaller scale, controlled studies to larger scales.

In this paper we present a study of how infaunal populations respond to benthoscape structure in eastern Long Island Sound. Previously, we have shown that community structure varied over multiple spatial scales in relation to benthoscape structure in this area of the sound (Zajac et al. 2000). Here, we address several general questions, including (a) How do infaunal populations vary within and among different patches (or elements) comprising the benthoscape in the study area? and (b) To what extent do populations vary among transition zones and the interiors of patches? Benthic community structure can vary across multiple scales (Morrisey et al. 1992), but often the underlying habitat patch structure is unknown and relationships to habitat characteristics are not necessarily evident. Transition zones in subtidal benthic environments have not been directly studied, owing to the difficulty of knowing their specific locations, extent, and characteristics (Zajac 1999). A few large-scale studies of soft-sediment environments have recognized that transitional sedimentary features can affect benthos (Yokoyama and Hayashi 1980; Dewarumez et al. 1992), and some work has been done on sea grass boundaries (e.g., Holmquist 1998). In terrestrial systems, transition zones, or ecotones, are recognized as important environments (Gosz 1991; Hansen and di Castri 1992). Following Gosz (1991), we use the terms ''ecotone'' and ''transition zone'' interchangeably, recognizing that they can be considered at different spatial scales (boundaries among landscapes and regions to edges among patches in a landscape) and are ''meaningful only relative to specific questions and specific points of reference.'' In terrestrial systems, transition zones often have elevated species diversity, can control the flow of materials and energy across landscapes, and are potentially sensitive to environmental change and, thus, may act as accurate indicators of environmental change and health (Hansen and di Castri 1992; Fagan et al. 1999, and references therein). For marine and coastal environments, the importance of benthoscape-scale transition zones is effectively unknown.

Methods

Benthoscape structure in the study area—The study was conducted in the eastern portion of Long Island Sound, south of Waterford and New London, Connecticut (Fig. 1). We used several technologies to acquire data at different spatial scales, including side-scan sonar (i.e., acoustic imaging), video, and bottom grabs. In October 1991, digital sonographs were collected in a 2.5- by 8-km area using a 100 kHz Edgerton, Germeshansen, and Grier (EG&G) side-scan sonar system, with a swath width of 200 m and a 50-m overlap. Navigation was provided by a Mini Ranger System. Subsequent processing of the digital data produced a side-
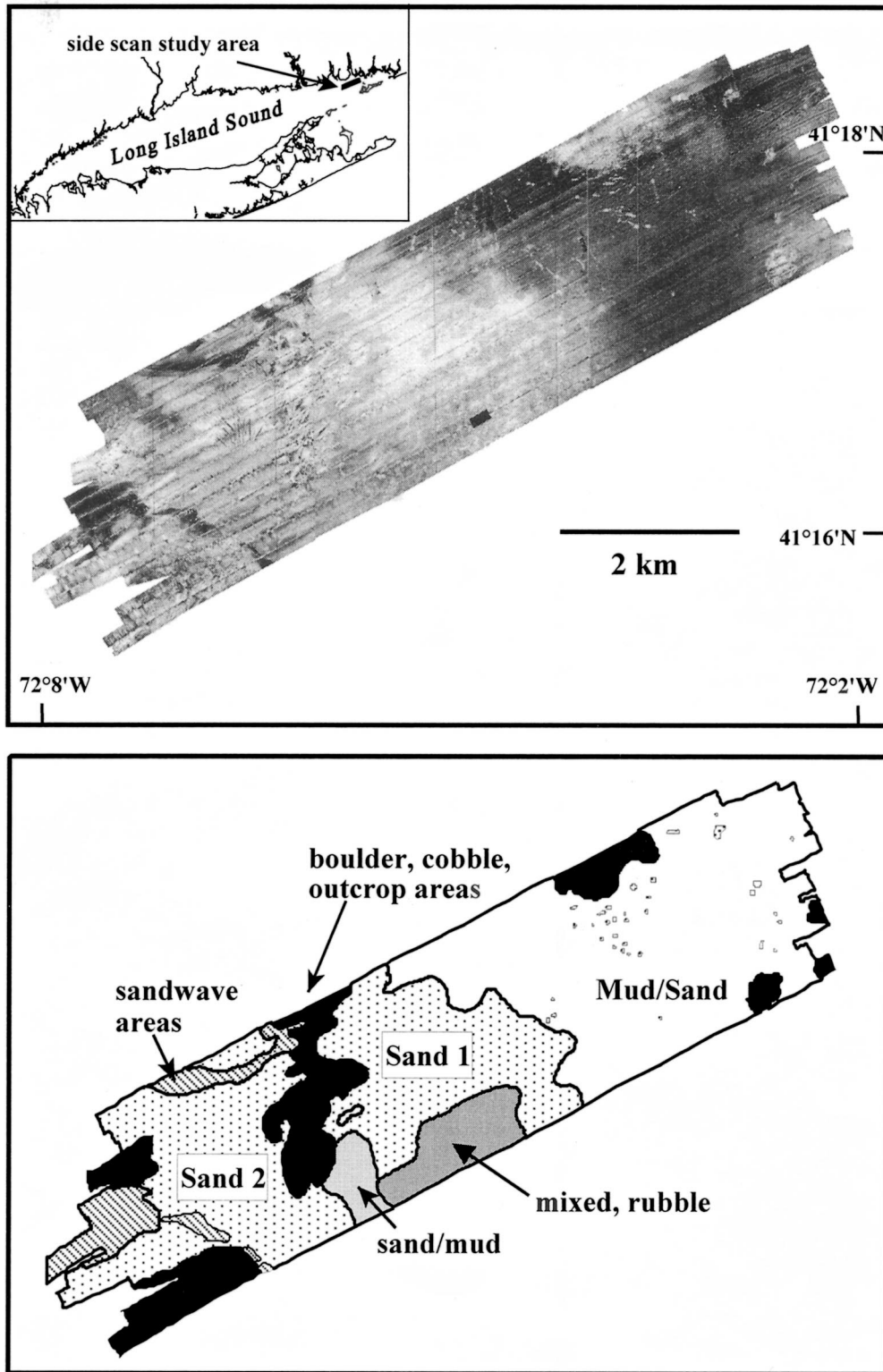
Fig. 1. Top: Sidescan mosaic of study area in eastern Long Island Sound (inset). The study area is approximately 2.5 × 8 km. Dark tones in the mosaic indicate fine sediment (fine sand, silt, and clay), and light tones indicate coarse sediment. Rough and ''grainy'' patches indicate glacial drift or bedrock outcrops. Bottom: Interpretation of general benthoscape elements comprising the study area. The three largest elements are noted by mud/sand, sand 1, and sand 2.

scan mosaic, providing a continuous image of the seafloor (Fig. 1). The mosaic was analyzed to characterize the large-scale and mesoscale benthoscape structure of the study area and to develop a benthic sampling design to assess responses of the infauna to the patch structure. The study area was sampled in June 1992 at 60 stations to collect samples for benthic and sediment analyses and video data to quantify small-scale (<1 m^2) seafloor characteristics. Details about the side-scan survey and postprocessing and benthic landscape analytical methods are given in Zajac et al. (2000). An overview of the infaunal community findings presented in Zajac et al. (2000) is given in the Results section.

The study site was found to be comprised of six distinct types of large-scale benthoscape elements (Fig. 1). The largest single element was a relatively homogenous, depositional area of muddy sands (mud/sand, or M/S) in the eastern third of the study site. A smaller area of fine sands and muds (sand/mud, or S/M) was located along the southern margin of the site. The other benthoscape elements were areas of sediment erosion or reworking (sensu Knebel and Poppe 2000). Much of the midwestern and southwestern portion of the site is comprised of two sand elements (sand 1 and sand 2, or S1 and S2, respectively). Seven boulder, cobble, and outcrop elements (B/C/O) were found, the most prominent of which separates the two sand areas. In the western portion and along the northwest margin of the site were several sand-wave fields (sandwave, or SW). Along the southern margin is an area comprised of mixed sediments and rubble (mixed/rubble, or MR), which is in a portion of a dredge disposal site. Transition zones can be seen among these elements and are distinguished by the blending of the acoustic returns. The entire mosaic area is predominantly comprised of sands, but there were statistically significant differences in the amount of gravel, sand, silt, and clay among the elements (Zajac et al. 2000).

Mesoscale variation in the study area was indicated by distinct patches within the large-scale elements and by more subtle changes in acoustic reflectance (Fig. 1). For example, the B/C/O areas were comprised of patches of boulders and lag gravel within a matrix of coarse to medium sand and gravel. In the northern portion of the M/S element, there are many patches of materials of higher reflectivity than the surrounding matrix. Based on variation in pixel intensity, seafloor heterogeneity was generally higher in the S1 and S2 elements than in the M/S element (Zajac et al. 2000). Analysis of video records indicated that small-scale habitat characteristics varied among the benthoscape elements. High amounts of biogenic features, such as pits, mounds, burrows, and tube mats, were evident in the M/S element. In the S1 and S2 elements there were fewer biogenic features and higher amounts of small cobbles, small sand waves, and accumulations of shell hash.

Benthic sampling—Sampling was conducted using a 0.1 m^2 Van Veen grab equipped with an 8-mm video camera system. Navigation was performed using a differential global positioning system and LORAN-C. The three largest benthoscape elements (M/S, S1, and S2) were divided into nested sections along roughly east–west (sites) and north–south (subsites) lines at the middle of the elements, and three to

four random samples were taken in each area (Zajac 1996). In addition, three samples were taken along transitions among seafloor elements in randomly selected sections of four transition zones among benthoscape elements. From each grab, a 6-cm diameter by 10-cm deep sample was taken for benthic infaunal analysis. A total of 60 stations were occupied; however, only 57 bottom samples were collected due to the presence of boulder fields and outcrops at three of the stations. The infaunal samples were preserved whole in 10% formalin and later washed on a 300-μm sieve; residues were transferred to 70% ethanol and sorted under a dissecting microscope. Individual specimens were identified to the lowest possible taxonomic level.

Analysis of transition zones—Image analysis was used to estimate seafloor heterogeneity across transition zones (*see also*, Goff et al. 2000; Zajac et al. 2000; Auster et al. 2001). Different seafloor features (e.g., sediment types, topographic features) generally have different acoustic properties resulting in backscatter differences and, therefore, varying pixel intensities and combinations on digital side-scan records. As such, differences in pixel intensity on these records can be used as a measure of seafloor variation. Acoustically "clean" sections across transition zones were identified in digital images, and the intensity of individual pixels (256 level grayscale) was measured using SigmaScan software along four transects across these areas. The transects were ~25-m wide and 400- to 600-m long, running parallel to the track lines used to generate the side-scan mosaic. Each pixel represented an area 43.7 m^2 (6.61 m on a side) on the mosaic images that were analyzed. The variance in pixel intensity was calculated for each transect as a measure of mesoscale habitat variation. For one of the transition zones (the M/S–S1 transition, *see Fig. 1*), an additional analysis was performed to quantify the width of the transition zone. For this analysis, pixel intensity was measured along ten 1-km long transects at points every 17 m in both directions from the line used to separate these two areas in the side-scan mosaic interpretation. At each distance, pixel intensity was measured and then averaged across all transects at each distance from the dividing line. The overall amount of transitional area among the largest benthoscape elements in the study area was estimated using a geographic information system (GIS). The side-scan mosaic interpretation was digitized and spatially registered into a GIS using PC ArcInfo. Standard GIS buffering routines were performed to define 25-m, 100-m, and 200-m wide areas spanning each transition zone, which we felt encompassed the general range of transition widths in the study area, and the total area of each buffer was calculated.

Analyses of infaunal populations relative to benthoscape structure—Differences in population abundances among the large-scale benthoscape elements were analyzed using one-way analysis of variance (ANOVA). Scale-related differences were examined in more detail based on the hierarchical sampling design in the three largest seafloor elements (M/S, S1, and S2). Differences in population abundances among the three elements were tested relative to differences within sites and subsites in each element using a nested ANOVA.

Table 1. Mean abundance (and 1 SE in italics) of the sixteen dominant taxa in each of the large-scale seafloor elements in the study area. Results of one-way ANOVA testing differences among the elements for each species are also shown. *See Fig. 1* for identification of seafloor elements. Number of stations sampled shown under each station heading. For all ANOVAs df = 6, 46.

Taxa	M/S	S1	S2	B/C/O	SW	S/M	MR	ANOVA
Polychaetes	14	10	11	6	5	4	3	
Mediomastus ambiseta	1.21	0.30	0.45	1.50	0.00	0.50	1.33	*
	0.32	*0.21*	*0.16*	*0.72*	*0.00*	*0.50*	*0.33*	
Monticellina dorsobranchialis	2.50	12.00	2.82	16.33	3.20	14.50	27.33	***
	0.78	*4.51*	*0.87*	*7.31*	*2.95*	*2.78*	*19.34*	
Tharyx acutus	0.64	1.00	1.82	2.33	0.20	1.50	1.33	ns†
	0.37	*0.37*	*0.66*	*0.84*	*0.20*	*0.65*	*1.33*	
Clymenella torquata	0.86	0.50	0.91	0.50	0.00	1.75	2.00	ns
	0.29	*0.17*	*0.34*	*0.50*	*0.00*	*1.11*	*1.15*	
Nephtys sp.	4.07	1.10	0.82	0.50	0.00	1.00	0.33	*
	2.32	*0.31*	*0.26*	*0.34*	*0.00*	*0.00*	*0.33*	
Aricidea catherinae	0.79	1.60	1.27	0.67	0.40	1.25	0.67	ns
	0.30	*0.43*	*0.57*	*0.67*	*0.25*	*0.63*	*0.33*	
Prionospio steenstrupi	135.50	126.20	118.36	81.00	9.40	176.50	266.00	**
	21.47	*26.32*	*26.74*	*26.10*	*7.92*	*55.99*	*72.51*	
Exogone hebes	0.50	2.60	0.36	2.67	1.00	0.50	1.33	ns
	0.50	*1.46*	*0.20*	*1.26*	*1.00*	*0.29*	*0.88*	
Polycirrus exumius	1.21	0.70	0.64	2.00	0.00	0.25	0.33	ns
	0.49	*0.30*	*0.39*	*1.07*	*0.00*	*0.25*	*0.33*	
Amphipods								
Ampelisca vadorum	12.79	6.90	1.55	0.17	0.20	4.50	8.67	***
	2.39	*2.15*	*0.64*	*0.17*	*0.20*	*3.52*	*6.33*	
Phoxocephalus holbolli	0.00	0.70	0.64	5.00	0.60	1.00	1.00	*
	0.00	*0.50*	*0.24*	*2.91*	*0.40*	*0.71*	*1.00*	
Unicola irrorata	6.14	2.50	0.45	0.33	0.40	1.50	1.67	***
	1.50	*0.60*	*0.28*	*0.21*	*0.40*	*1.19*	*1.67*	
Microdeutopus gryllotalpa	0.36	0.50	0.55	0.00	0.00	2.00	5.67	*
	0.29	*0.34*	*0.55*	*0.00*	*0.00*	*1.35*	*5.67*	
Other								
Nucula annulata	1.57	0.80	0.64	0.50	0.00	0.25	0.67	ns
	0.71	*0.51*	*0.24*	*0.34*	*0.00*	*0.25*	*0.33*	
Rhynchcoel sp. a	0.57	0.50	3.82	1.83	4.60	0.25	2.00	ns
	0.23	*0.17*	*2.74*	*0.83*	*3.16*	*0.25*	*1.53*	
Oligochaete sp. a	7.50	9.40	8.36	21.83	4.60	5.00	5.00	**
	1.61	*1.72*	*2.32*	*6.27*	*2.60*	*0.91*	*0.58*	

* $p<0.05$.
** $p<0.01$.
*** $p<0.001$.
† ns, not significant.

The contribution of each spatial scale to variations in infaunal abundance was examined by calculating variance components (e.g., Morrisey et al. 1992). To determine how population and community characteristics changed along the transitions zones, samples were grouped according to their position in transition zones versus the interiors of seafloor elements. Differences in population abundances in transitional versus interior portions of benthoscape elements were tested using one-way ANOVA in which each transition zone and interior area represented a separate factor in the test. This was done because interior areas were in different benthoscape elements, and the transitions among them differed as well, and structuring the ANOVA in this manner would provide an assessment of the extent to which population abundances progressively changed across the benthoscape. For all statistical analyses, normality and equality of vari-

ance assumptions were tested and if necessary the data were transformed, $\log(x + 1)$, to meet assumptions. If tests of main effects were significant, comparisons of means were performed using Fisher's least significant different (LSD) test.

Results

Overview of infaunal communities in the benthoscape—A total of 157 species/taxa were identified in the bottom samples (Zajac 1996). Benthos–benthoscape relationships were analyzed using the 16 most abundant taxa (Table 1). Classification analyses indicated that overall community composition and structure was similar among the seafloor elements, with the main differences due to shifts in the relative abundance of several species, particularly the amphipod *Am-*

pelisca vadorum and the polychaete *Monticellina dorso-branchialis* (Zajac et al. 2000). Total abundance and species richness were significantly different among the large-scale elements and exhibited significant within-element differences at mesoscales (i.e., among subsites) within the three largest elements (Zajac et al. 2000). Habitat characteristics of the benthoscape elements (sediment grain-size, geomorphologic features such as small-scale sandwaves, and biogenic features such as pits, mounds, and burrows) explained little (R^2 = 0.06–0.56, with 78% of the cases ≤0.30) of the variation in population abundances when considered irrespective of benthoscape structure (Zajac 2001). However, when the factors were grouped according to which of the elements they were found in, thus providing a spatial context, variation in population abundances explained by these characteristics increased considerably (R^2 = 0.07–0.98, with 56% of cases ≥0.70).

Population variation among benthoscape elements—Differences in population abundance among the large-scale landscape elements were statistically significant for 9 of the 16 dominant species (Table 1). Most species were found at relatively high abundances within only one benthoscape element, including *Nephtys* sp. and *Unicola irrorata* in the M/S element, *Phoxocephalus holbolli* and Oligochaete sp. a in the B/C/O elements, and *Prionospio steenstrupi* and *Microduetopus gryllotalpa* in the MR element. However, several species were found at relatively high abundances in several benthoscape elements, including *Ampelisca vadorum* in M/S and MR, *Mediomastus ambiseta* in the M/S, B/C/O, and MR elements, and *Monticellina dorsobranchialis* in the S1, B/C/O, S/M, and MR elements.

Differences in population abundance among different spatial scales in the M/S, S1, and S2 elements were mixed for the 16 species examined (Table 2). The abundances of eight species were varied significantly among scales. In all of these cases, except two, significant differences were found at only one spatial scale. Two of the most abundant species, *Prionospio steenstrupi* and *Ampelisca vadorum,* exhibited significant subsite-level differences (Fig. 2). The highest abundance of *P. steenstrupi* in the mud/sand element was found in subsite 1, in S1 in subsite 3, and in subsites 2 and 4 in the S2 (Fig. 2). *A. vadorum* was most abundant in the M/S element, but there were large differences among subsites in this element and in S1. *Exogone hebes* also exhibited significant differences in abundance among subsites. Site-level differences were found for *Monticellina dorsobranchialis* and *Unicola irrorata* (Table 2, Fig. 2). Five species exhibited significant large-scale differences, including *Tharyx acutus, Mediomastus ambiseta, Phoxocephalus holbolli, Exogone hebes,* and *Unicola irrorata.*

Variance component calculations (Table 3) indicated that for many species the residual variation was relatively large, which suggests patchiness in abundances below the subsite level. Local, small-scale, variation can obscure large-scale trends in abundance, and for species that exhibited no significant differences at the spatial scales examined, residual variation was above 90%. For species that did exhibit statistical differences, the variance components underscore the importance of particular scales. For example, 38% and 43%

Table 2. Results of nested ANOVA testing differences in population abundance at different spatial scales for the 16 most abundant infaunal species/taxa found in the study area in June 1992. For all tests df, as follows: area = 2, site = 3, subsite = 6, error = 25, total = 37.

Taxa	Area	Site	Subsite
Polychaetes			
Prionospio steenstrupi	ns†	ns	*
Monticellina dorsobranchialis	ns	MS	ns
Tharyx acutus	MS‡	ns	ns
Aricidea catherinae	ns	ns	ns
Mediomastus ambiseta	MS	ns	ns
Clymenella torquata	ns	ns	ns
Exogone hebes	MS	ns	**
Nephtys sp.	ns	ns	ns
Polycirrus eximius	ns	ns	ns
Amphipoda			
Ampelisca vadorum	ns	ns	*
Phoxocephalus holbolli	MS	ns	ns
Unicola irrorata	*	MS	ns
Microdeutopus gryllotalpa	ns	ns	ns
Oligochaetes			
Oligochaete sp. a	ns	ns	ns
Rhynchocoela			
Rhynchocoel sp. a	ns	ns	ns
Bivalvia			
Nucula annulata	ns	ns	ns

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.
† ns, not significant.
‡ MS, marginal significance ($0.10 < p < 0.05$).

of the variation in the abundance of *Prionospio steenstrupi* and *Exogone hebes,* respectively, could be accounted for at the subsite level (Table 3).

Benthoscape transition zones—Transition zones among the large-scale elements in the study area added to the overall heterogeneity of the benthoscape. Inspection of the sidescan mosaic (Fig. 1) shows that the nature and spatial extent of the transition zones varied across the benthoscape. Some transitions, such as that between the M/S and S1 elements, were relatively broad with a high degree of backscatter variation. In contrast, others, such as that between the S2 element and the sand waves, were quite sharp. Based on variation in pixel intensity, seafloor heterogeneity was highest in transition zones between the M/S and S1 elements and between the central B/C/O and S2 elements (Fig. 3). There was relatively low heterogeneity across the S2 and sandwave elements, whereas the S1 and B/C/O transition heterogeneity was intermediate. To obtain additional information on transition zone structure, the transition zone between the M/S and S1 was examined in more detail (Fig. 4). Based on visual inspection, the change in mean pixel intensity along 1-km transects across the transition was greatest between the 400- and 600-m distance marks (Fig. 4), which indicates that the transition is approximately 200-m wide. Variation in pix-
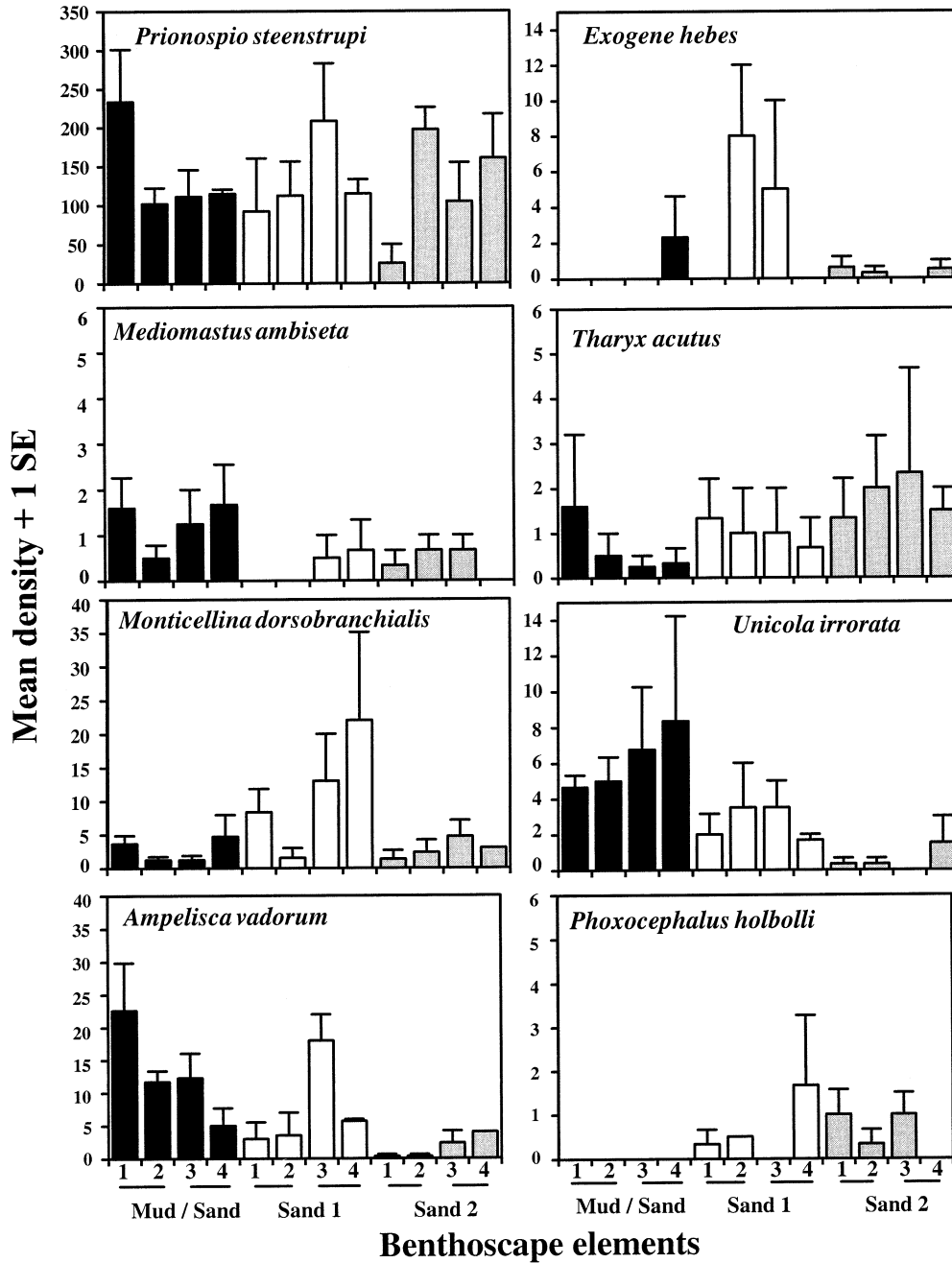
Fig. 2. Differences in the mean population density (6-cm^{-1} diameter core) of selected infaunal taxa in the benthoscape study area within subsites (noted as 1–4) and sites (marked by line under the subsite number) of and among the largest benthic landscape elements (mud/sand, sand 1, and sand 2) of the study area shown in Fig. 1.

el intensity from 0 to 400 m and beyond 600 m along the transects reflected differences in mesoscale variation in the adjoining elements (Fig. 4). Interestingly, although there was a sharp change in pixel intensity identifying the transition zone, variation at specific points within this area was relatively low. Assuming that transition zones in the study area have a maximum width of 200 m, as suggested by this analysis, and using a GIS buffer analysis, we estimated that 41% (9.2 km²) of the entire study area may be comprised of tran-

sition zones (Fig. 5). With smaller buffer sizes, the total transition areas were estimated to comprise 11.1% (2.5 km²) and 21.5% (4.8 km²) of the study area for 50- and 100-m buffers, respectively.

Both community-level characteristics and individual species population distributions varied in relation to transition zones and interiors of large-scale mosaic elements (Fig. 6). Total abundance was generally highest in the transition zones, except for the S2–sandwave transition, although these

Table 3.   Variance estimates for three different spatial scales derived from the nested ANOVAs for the numerically dominant species in the study area.

Taxa	Source of Variation			
	Area	Site	Subsite	Residual
Phoxocephalus holboli	0.13	0.00	0.00	0.98
Unicola irrorata	8.26	0.94	0.00	17.89
Thayx acutus	0.30	0.00	0.00	3.40
Mediomastus ambiseta	0.25	0.00	0.00	0.88
Ampelisca vadorum	23.84	5.81	11.61	29.45
Prionospio steenstrupi	0.00	0.00	3,253.30	5,282.66
Exogene hebes	1.22	0.00	4.89	5.15
Monticellina dorsobranchialis	14.75	18.81	0.00	61.65
Aricidea catherinae	0.00	0.06	0.02	2.11
Clymenella torquata	0.01	0.00	0.00	1.07
Nephtys sp.	2.00	0.00	0.00	32.79
Polycirrus eximius	0.00	0.00	0.21	2.10
Oligochaete sp. a	0.00	0.00	0.00	48.49
Rhynchocoel sp. a	1.86	0.00	0.23	26.87
Nucula annulata	0.04	0.00	0.09	3.86
Microduetopus gryllotalpa	0.00	0.02	0.03	1.20

were not significantly different from some of the adjacent element interiors. Differences in species richness were less pronounced, and statistical differences were primarily among different portions of the overall benthoscape. Mean species richness was highest in several of the transition zones in the central and eastern portion of the study area, but these values were similar to those for adjoining interior areas (Fig. 6).

Significant differences in population abundance among selected transition zone and element interiors were found for nine species (Fig. 6). Most of these species exhibited elevated abundances in transition zones, although several were more abundant in the interior portions of the benthoscape elements. The highest abundances of *Prionospio steenstrupi* were found in transition zones, but some of these were not significantly different to adjacent interior areas. For the other species, elevated abundances were found in only one or two of the transitions. The abundance of Rhynchocoel sp. a was significantly higher in the S2–sandwave transition zone than in any other area of the benthoscape. *Clymenella torquata* was found at elevated densities in the transition zones between the S1, B/C/O, MR, and S2 elements, but abundances were similar to the interiors of the M/S and S1 elements (Fig. 6). *Mediomastus ambiseta* exhibited a similar pattern. The abundances of *Ampelisca vadorum* were highest in the interior of the M/S element and in the M/S–S1 transition zone.
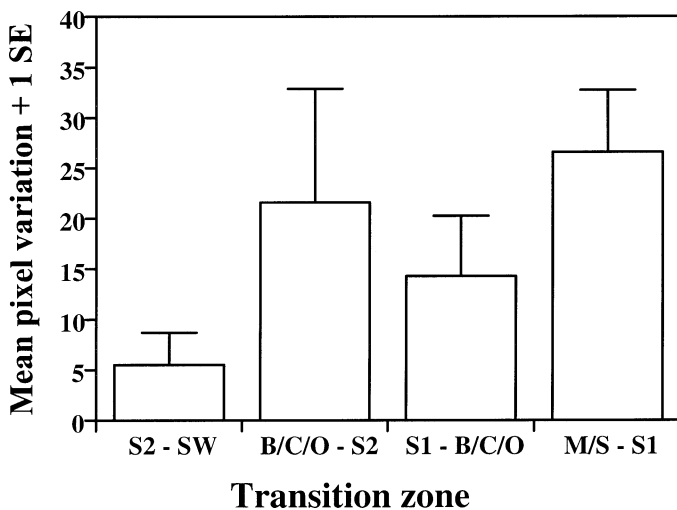

Fig. 3.   Differences in the level of seafloor heterogeneity among four transition zones in the study area as measured by variation in pixel intensity on the side-scan image. The variance of pixel intensity in each of four transects was calculated, and the means of these variances (+1 standard error) are plotted. Mud/sand (M/S); sand 1 (S1); boulder, cobble, outcrop (B/C/O); sand 2 (S2); sandwave (SW). *See Fig. 5 also.*
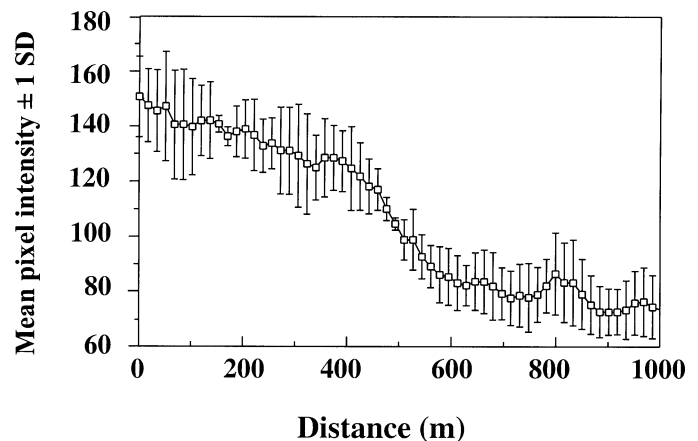

Fig. 4.   Changes in mean pixel intensity (± 1 SD) along the transition zone between the sand 1 and mud/sand elements (moving from left to right along the *x*-axis) in the side-scan mosaic image. The transition was analyzed by taking pixel intensity measurements at points approximately every 17 m along 500-m transects in each direction from the line dividing the two elements positioned as shown in Fig. 1. The 500-m point on the *x*-axis marks the position of this line.
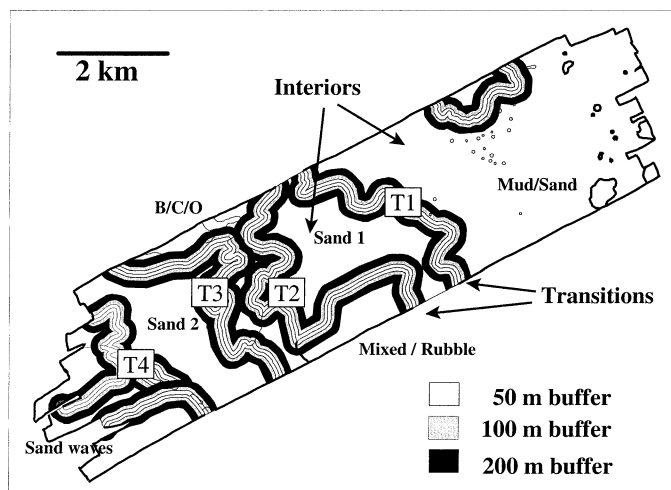
Fig. 5. Map of study area highlighting the major transition zones. Each of the transition zones are buffered to three different widths in order to calculate the relative area of transitions to overall area of the study site. Arrows indicate several transition zones and benthoscape element interiors. Specific transition zones in which population abundances were analyzed (*see Fig. 6*) are also noted: T1 = M/S–S1; T2 = S1–BCM; T3 = SM/B/M–S2; T4 = S2–SW.

Four species exhibited generally higher abundances in interior areas relative to transition zones. The abundance of *Monticellina dorsobranchialis* was highest in the central portion of the benthoscape (the S/M, MR, and S1 elements, Fig. 6). Although highly variable, the highest abundances of *Nephtys* sp. and *Unicola irrorata* were found in the interior of the M/S element. However, relatively high abundances of *U. irrorata*, were also found in several transition zones rather than in adjacent interior areas (Fig. 6). The highest abundances of *Phoxocephalus holbolli* were found in the interior portions of several seafloor elements. There were no significant differences for seven of the species examined.

Discussion

Benthoscape structure and transition zones—Previous analyses of benthoscape structure in the study area (Zajac et al. 2000) indicate that the mix and scales of habitat heterogeneity varied across the site (Fig. 1), changing with the types of seafloor elements and their locations (*see also Methods section*). This variation results from different combinations of physical and biological factors acting over varying spatial and temporal scales (e.g., Zajac 1999; Zajac et al. 2000; Knebel and Poppe 2000). Transitions zones were found to be a significant component of the benthoscape (Figs. 1 and 5) and estimated to comprise from 20% to 40% of the study area. Their structural characteristics and spatial extent varied across the benthoscape (Figs. 1 and 3). The juxtaposition of specific types of large-scale elements may be important in how geologic conditions and hydrodynamic processes shape the characteristics of transitions zones among different elements. Transition zones among the M/S and S1 elements and the S1 and central B/C/O element were fairly broad and heterogeneous (Figs. 1, 3, and 4), which

suggests that current speeds and patterns are relatively more variable along these zones. In contrast, transitions among the central B/C/O and the S2 elements and S2 and western sand-wave elements were not as extensive (Fig. 1), which suggests more uniform hydrologic conditions. The primary current direction is from east to west in this portion of Long Island Sound (Signell et al. 2000), and, as such, the central B/C/O element may act to reduce current speeds in the transition area from the S1 element, creating a wide (∼200–300 m) zone of deposition. The band of somewhat weaker backscatter on the western fringe of the S1 element (Fig. 1) may be created by this type of interaction. In contrast, currents may be accelerated across the shoal and create a more erosive and distinct transition on its western flank.

While habitat mapping (*see Introduction*) is being increasingly used as a precursor to investigating relationships between benthic environments and communities, many of these efforts thus far have focused on primarily large-scale benthoscape structure (e.g., Warwick and Uncles 1980). Few studies have attempted to quantify benthic habitat complexity at different scales. Menzie et al. (1982), using side-scan and sediment profile imaging, recognized six major topographic regions with different types of mesoscale and fine-scale variation around a disposal site in Buzzards Bay, Massachusetts. Although not directly quantified, inspection of the images in their report reveals that mesoscale variation in most of the area was high, similar to what was found in the mixed/rubble area of the study site (Fig. 1). Wright et al. (1987) found the lower Chesapeake Bay to be a mosaic of large-scale elements of varied bed morphology, with varying degrees and types of mesoscale and small-scale characteristics. For example, some areas composed of fine-grained sediments were devoid of mesoscale bedforms, but small-scale biogenic features (roughness elements) were most prevalent. This agrees with the conditions found for the M/S element in the study site. In other areas of the Chesapeake Bay, mesoscale features, such as oyster shell bioherms or physical features such as sandwaves, were the most prominent features (Wright et al. 1987). These are akin to conditions found in the S1 and S2 elements in the study area. Also, inspection of side-scan images and benthic habitat maps from other studies clearly shows that many coastal benthic environments have significant amounts of transitional areas (e.g., Valentine et al. 2001; Kostylev et al. 2001; Cochrane and Lafferty 2002). However, not many studies have addressed the physical and chemical characteristics of seafloor transition zones.

As our ability to map and obtain information on benthoscape features increases through the use of various underwater remote sensing techniques, our understanding of their contribution to benthoscape dynamics will increase. Habitat heterogeneity occurs at all scales, and the relative mix of large-scale, mesoscale, and small-scale heterogeneity can differ across a benthoscape depending on location in the benthoscape, the types and mixture of the elements, and prevailing hydrologic and geologic dynamics. While researchers have been able to generally assess large- and small-scale benthic variability using conventional approaches, seafloor mapping and the analysis of benthoscape structure provides the ability to assess variability in a continuous fashion across
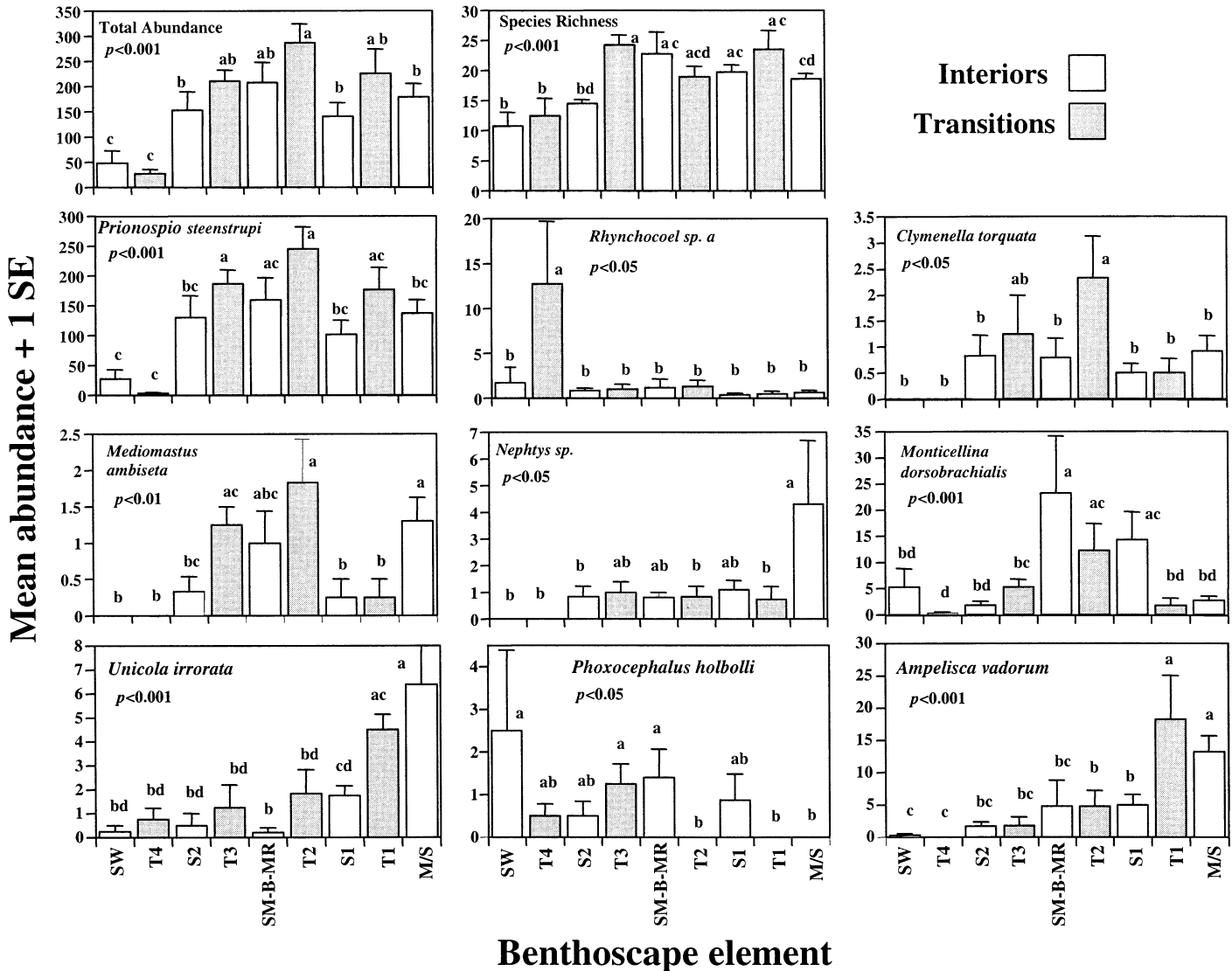
Fig. 6. Differences in total abundance, species richness, and species population densities (6-cm⁻¹ diameter core) of selected infaunal taxa among transition zones and interior portions of benthoscape elements in the side-scan study area as designated in Figs. 1 and 5. *P* values show results of one-way ANOVA testing differences among the transitions and interiors (df = 8, 45). Letters above bars indicate results of post hoc comparisons; means sharing same letter are not significantly different ($p < 0.05$). Sample size varied from four to thirteen for interiors and four to six for transition zones.

spatial scales and, in particular, to quantify mesoscale variation, which may be critical in shaping the distributions and dynamics of seafloor organisms.

Population responses to benthoscape structure—The spatial distribution of infaunal population abundances varied considerably in relation to benthoscape structure in the study area. Nine of the sixteen dominant species exhibited significant differences in abundance among the large-scale benthoscape elements (Table 1). Species that exhibited no significant differences in abundance were found at relatively low abundances, <5 individuals core⁻¹ (Table 1). Some species (*Nephtys* sp., *Prionospio steenstrupi, Phoxocepahlus holbolli, Unicola irrorata, Microduetopus gryllotalpa,* and Oligochaete sp. a) had significantly higher densities in just

one element, but others (*Mediomastus ambiseta, Monticellina dorsobrachilais, Ampelisca vadorum*) had several population foci over the scale of the benthoscape. It is also interesting to note that for species that did have high abundances in several elements, these element were generally adjacent to one another. For example, *M. dorsobranchialis* was found in high abundances in the S1, /B/C/O, S/ M, and MR elements that comprised the central portion of the benthoscape study area. Habitat characteristics in these elements were fairly different, which suggests that, at least in this case, multiple areas of high abundance may result from *M. dorsobranchialis* being able to make use of different types of habitats.

Analyses of variation in abundance among the three largest elements in the study area provides additional insights

into the spatial structure of the infaunal populations in the study area. Four species exhibited significant differences at the largest spatial scale examined (the entire element), two species exhibited a significant difference at the site level (on the order of 2–3 km^2), and significant variation was detected at the subsite level (on the order of 1 km^2) for three species (Table 2). Examination of the components of variation indicates that residual variation was high for almost all of the species (Table 3). The high residual variation suggests that significant amounts of variation in abundances remained unaccounted for. This variation may occur at scales between several m^2 and ~1 km^2. Small-scale (<1 m^2) factors in the study area, including local sediment composition and topographic features, typically accounted for only about 15%–25% of the variation in abundance across the study area for the species examined (Zajac 2001). However, higher amount of variation could be explained by small-scale factors if they were considered within a particular landscape element (Zajac 2001).

Overall, our analyses indicate that patterns of spatial variation of infaunal populations in relation to habitat characteristics can be quite varied across a benthoscape at several spatial scales. In particular, although there are significant large-scale trends in population abundances, it appears that mesoscale habitat characteristics (~1–2 km^2 to 10s of m^2) may play an important role in shaping infaunal population distributions across the seafloor. Analyses of community structure also indicated that community variation was a function of mesoscale variation, as changes in community structure generally coincided with mesoscale differences in habitat structure (Zajac et al. 2000). The existence of large-scale patterns (on the order of tens to hundreds of kilometers) in infaunal community structure in coastal areas is well known, as is the spatial variation that can occur at small spatial scales (Hall et al. 1994). However, few studies have noted the importance of mesoscale structure and pattern of benthic communities. For example, Thrush et al. (1989) showed that polychaetes and bivalves form patches of elevated abundances at scales of 1 to 100 m in an intertidal sand flat, with varying types of spatial pattern. Hodda (1990) found that 52% of the variation in nematode abundances could be accounted for by mesoscale (among sites within estuaries) differences in habitat characteristics (e.g., sediment grain size and organic content, availability of certain types of food, surface topography). In a similar study, Morrisey et al. (1992) compared differences in macrofaunal abundances at five spatial scales ranging from 1 m to 3.5 km. They found significant spatial variation at spatial scales from 10 m to 3.5 km, with taxonomic groups exhibiting variation at several, and in some cases different, spatial scales, similar to species differences observed in this study (Table 2, Fig. 2). McArdle and Blackwell (1989) found that physical characteristics ranging from a kilometer to tens of meters significantly affected the density of the bivalve *Chione stutchburyi,* and that locally elevated abundances of the bivalve were like due to factors operating on a scale ≤600 m^2.

The presence of significant mesoscale variation in benthoscape structure and coinciding patterns of infaunal spatial variation has potentially interesting implications for population dynamics. The metapopulation (e.g., Hanski and Gil-

pin 1997) characteristics of infaunal populations are virtually unknown, but this study and those noted above suggest that infaunal populations have a complex spatial structure, and this may influence their dynamics and maintenance in a particular environment. The taxa studied here were generally found throughout the benthoscape, but some had elevated abundances in only one element or area within an element, whereas others had several population foci (areas of elevated abundances) (Table 1, Fig. 2). Populations also varied among the interiors of and transitions between benthoscape elements (Fig. 6). Species with single population foci may potentially be more sensitive to disturbances than species that have high population abundances in several different benthoscape elements. The latter may be more resilient to disturbances because populations in nondisturbed elements, and portions of elements, can be a source of individuals to recolonize disturbed habitats. The demographic dynamics of infaunal populations can vary at mesoscales. For example, populations of the polychaete *Nephtys incisa* in central Long Island Sound exhibited significant variation in individual growth, size-structure, and fecundity among sites 200 to 3 km apart, but had similar population growth rates (Zajac and Whitlatch 1989). There are few studies of infaunal population dynamics over extended spatial scales in relation to benthoscape structure, and it is not clear whether the populations form metapopulations and can be studied within a metapopulation framework. Benthic ecologists are beginning to understand processes that link populations by transport of larvae and/or adults (e.g., Dobbs and Vozarik 1983; Committo et al. 1995; Bradbury and Snelgrove 2001). Larval mixing and the degree to which populations interact via larval transport can differ depending on the type of coastal environment (Keough and Black 1996). The heterogeneity of benthoscapes at multiple scales adds another level of complexity to these dynamics, interacting with varying patterns of transport and behaviors of meroplankton that influence the eventual recruitment of individuals into extant populations. In turn, biological and physiochemical processes in the benthoscape shape juvenile and adult portions of the demographic dynamics, which results in differences in the abundance and structure of populations at varying spatial scales.

Population responses to transition zones among benthoscape elements—Another, potentially ecologically important, mesoscale to large-scale feature of benthoscapes is transition zones among large-scale elements. Benthic community structure has been shown to change in the area of well-defined transitions such as rock outcrops and adjacent soft sediments (Posey and Ambrose 1994), and transitional changes in benthic communities have been found associated with water column fronts (Josefson and Conley 1997). In freshwater systems, most of the focus has been on land/aquatic boundaries, but within-system transitions are being increasingly recognized as critical to the dynamics of these environments (Ward and Wiens 2001; Wiens 2002). For the most part, benthic communities have not been studied across marine soft-sediment transitions directly, and the location, extent, and attributes of transition zones are usually not known or are extrapolated. Habitat mapping allowed us to directly compare infaunal community structure within the interior

portions of specific seafloor elements and the transition zones between them. Nine species exhibited significant differences among transition zones and interior areas, with most of these having higher abundances in the transition zones (Fig. 6). This included the most abundant species in the study, *Prionospio steenstrupi,* as well as *Mediomastus ambiseta, Ampelisca vadorumm, Clymenella torquata,* and Rhynchocoel sp. a. In many cases elevated abundances spanned both interior portions of a particular element and the adjacent transition zone, and although not statistically significant, mean abundances were higher in the transition zones. In the case of *Prionospio steenstrupi,* the population was comprised of mostly newly recruited individuals at the time of sampling, which suggests that higher abundances in the transitions may be the result of factors affecting recruitment. These may include, for example, changes in hydrodynamics across the transition that may enhance larval settlement and/or active habitat selection processes. Several species, including *Monticellina dorsobranchialis, Nephtys* sp., and *Phoxocephalus holbolli,* had higher abundances in the interior portions of specific elements. The highest abundance of *Unicola irrorata* was found in the interior of the M/S element, but abundances in the other portions of the benthoscape were higher in transition zones.

The transition zones appear to make a significant contribution to overall infaunal variation in the study area. Although several community types remained consistent across certain transition zones, in other areas infaunal communities in the transitions zones were less similar to all others identified across the benthoscape (Zajac et al. 2000). Total abundance was somewhat higher in transitions, but species richness was similar among most transitions and interiors (Fig. 6). Population-level responses to transition zones varied among taxa, and when considered on an overall basis, our results underscore the potential complexity of pattern and process in benthoscape transition zones. The characteristics of transition zones, such as topography, sediment composition, and hydrodynamics, change across the benthoscape, resulting in variable, large-scale and mesoscale species responses to these habitats. Certain species may reach higher abundances in transition zones as a result of increased habitat heterogeneity and levels of food resources. If, for example, benthoscape transition zones are associated with hydrodynamic changes and fronts, then these areas may have elevated food levels (e.g., Chl *a,* phaeopigments, particulate organ carbon) in association with elevated levels of benthic biomass and abundance (Josefson and Conley 1997). The general importance of transition zones in marine and coastal benthoscapes is basically unknown, and the range of potential dynamics that may be occurring across these zones remains to be explored.

Studies of soft-sediment environments are increasingly addressing spatial variation in the structure and dynamics of benthic communities and populations (e.g., Thrush et al. 1997; Bell et al. 1999; Kneib 2000) and show that significant spatial variation can occur at several scales. However, only a few studies have considered spatial patterns in detail over benthoscape scales more than several square kilometers in deep-water environments (e.g., Thrush et al. 1998, 2001; Zajac et al. 2000; Kostylev et al. 2001; Brown et al. 2002). In this study, logistical constraints precluded a sampling design that would have allowed us to assess how the spatial patterns found may change over time, and it will be critical to do so in future studies given that infaunal populations can exhibit considerable seasonal, and sometimes longer term, variation. However, we have been able to show that significant degrees of population variation can be associated with large, and in particular mesoscale, benthoscape spatial structure. The results also suggest that transition zones may add considerably to overall benthoscape complexity, which in turn affects the distribution and dynamics of infaunal populations and communities.

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