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Relationships Among Sea-Floor Structure and Benthic Communities in Long Island Sound at Regional and Benthoscape Scales

Roman N. Zajac[1], Ralph S. Lewis[2], Larry J. Poppe[3], David C. Twichell[3], Joseph Vozarik[4] and Mary L. DiGiacomo-Cohen[2]

[1]Dept. Biology and Environmental Science
University of New Haven
West Haven, CT 06516, U.S.A.

[2]Long Island Sound Resource Center
Connecticut Department of Environmental Protection
1084 Shennecosett Road
Groton, CT 06340, U.S.A.

[3]U.S. Geological Survey
Center for Coastal and Marine Geology
Woods Hole, MA 02543, U.S.A.

[4]Northeast Utilities
Environmental Laboratory
Rope Ferry Road
Waterford, CT 06485, U.S.A.

ABSTRACT

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Long Island Sound is comprised of a rich and spatially heterogeneous mix of sea-floor environments which provide habitat for an equally diverse set of assemblages of soft-sediment communities. Information from recent research on the geomorphological and chemical attributes of these environments, as well as from studies of the hydrodynamics of the Sound, provide the opportunity to develop a landscape, or "benthoscape" framework for understanding the soft-sediment ecology of this estuary and for guiding future research focusing on structure and function at multiple spatial scales. This contribution reviews past research on benthic communities in Long Island Sound and addresses how they may be shaped by sea-floor characteristics at regional and benthoscape scales. At the regional scale (i.e. the entire Sound), differences in benthic community composition correspond to the distribution of general sedimentary environments. However, significant variation in community structure also occurs at the benthoscape scale (within regions) related to local variations in sediment properties, and physical and biogenic topographic features. Several topical areas in particular need further research in Long Island Sound, including temporal dynamics of benthic communities relative to sea-floor structure and the interaction between the dynamics of benthoscapes and hydrologic seascapes.

ADDITIONAL INDEX WORDS: *estuary, infauna, landscape ecology, soft-sediment, spatial scale*

INTRODUCTION

Long Island Sound (LIS) is comprised of heterogenous physical, chemical and biological environments that are structured and interact along a continuum of spatial and temporal scales. This produces a rich mosaic of habitats and processes that is challenging to decipher and understand. However, recognizing and understanding the attributes and dynamics of such mosaics are critical for managing coastal and estuarine resources (*e.g.*, LIVINGSTON, 1987, 1991), and this has been increasingly recognized in our push to restore and protect the Sound's environmental quality. For example, WELSH (1993) noted that "[the] spatial and temporal patterns [of physical oceanographic processes] and their magnitude and persistence are not well known, but their potential influence on trophic structure and eutrophication processes is great." SQUIRES (1993) argued that, in relation to developing a "comprehensive picture of how Long Island Sound works", most of the data sets available have either limited spatial or temporal resolution, or both, and they are not the "long duration and wide coverage" types needed.

Over the past 10 years, however, significant research efforts (many of which are presented in this volume) have expanded our knowledge of the LIS system and identified important characteristics and processes across a variety of spatial and temporal scales. Here, we assess how the structure of benthic communities in LIS varies relative to emerging information on the distribution of sea-floor environments and the hydrologic and geologic processes that shape these environments. This assessment takes a "benthoscape" approach, akin to landscape-level studies of terrestrial systems (*e.g.*, FORMAN, 1995). Landscape ecology focuses on the structure and dynamics of kilometers-wide areas which are comprised of mixtures of interacting ecosystems. Because of the focus on pattern and process, landscape ecology provides a particularly useful framework for investigating the responses of ecological systems to human impacts at multiple spatial and temporal scales relative to natural environmental heterogeneity.

Marine and coastal systems have long been studied at different scales in order to understand relationships between habitat structure and dynamics (*e.g.*, BARRY and DAYTON, 1991; THRUSH, 1991; ANGEL, 1994a,b). More recently, marine ecologists have begun to incorporate landscape-level approaches into their work (SHERMAN, 1991; RAY, 1991; ROBBINS and BELL, 1994; AUSTER *et al.,* 1998), and a cohesive framework for the study of marine benthic landscapes is emerging (ZAJAC, 1999). The scope of benthic landscape ecology includes the study of: a) the physical and ecological structure of the sea-floor; b) ecological dynamics in relation to sea-floor structure and dynamics; and c) and how structure and dynamics respond to disturbances and longer-term directional changes.

To understand benthoscape structure, it is imperative to determine the spatial relationships among the distinctive ecosystems, or landscape elements, that comprise a particular coastal region. This includes quantifying the distribution of species, materials and energy in relation to the sizes, shapes, numbers, kinds and configurations of the landscape elements. The boundaries, or transition zones, among the structural elements may also be ecologically important (*e.g.*, GOSZ, 1993; FORMAN, 1995). Our ability to characterize sea-floor environments and develop a benthoscape ecology has grown in concert with the use of underwater remote sensing techniques such as sidescan sonar, video, camera sleds and other technologies such as global positioning systems (GPS) and geographic information systems (GIS) (ZAJAC, 1999).

The main objectives in this paper are to apply the principles and constructs of landscape ecology to the benthic environments in LIS in order to develop a framework for understanding and addressing multi-scale patterns and processes in this system. The framework is based on relationships between sea-floor and benthic community characteristics at a regional scale (*i.e.*, across the Sound) and at the benthoscape scale (*i.e.*, within specific portions of LIS). Based on these relationships, we discuss the dynamics which may be critical in determining the patterns found and areas of research which could provide additional information critical to understanding the benthoscape ecology of the Sound and the management of this resource.

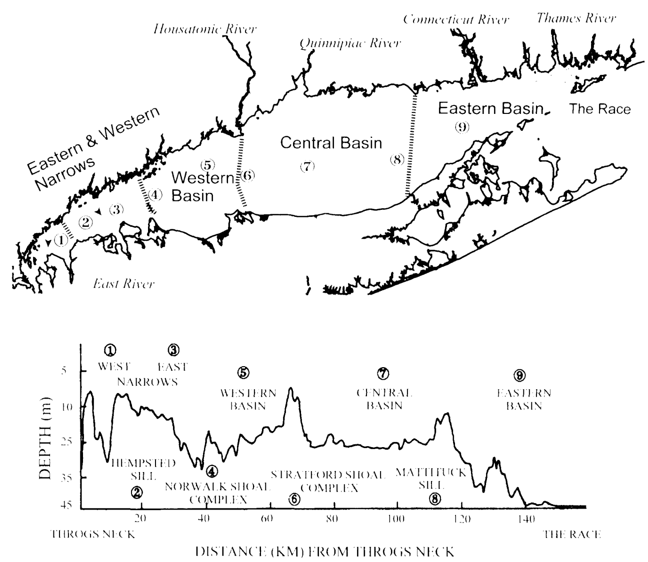

Figure 1. *Upper:* General geomorphological and ecological regions in Long Island Sound. Also shown are major rivers flowing into the Sound. The hatched area is the location of the New London sidescan mosaic study area. The circled numbers refer to features shown in lower figure. *Lower:* East-west bathymetric profile along the central axis of Long Island Sound. Redrawn from WELSH (1993).

REGIONAL-SCALE PATTERNS

Sea-Floor Environments

LIS is comprised of four main geophysical regions: the Narrows, and the western, central and eastern basins (Figure 1). These regions are separated by major bathymetric discontinuities: the Norwalk shoal complex, the Stratford shoal complex and a broad bathymetric high informally called the Mattituck Sill (Figure 1). We can further divide each region into two types of sea-floor benthoscapes: nearshore, or shallow water, and offshore, or deep water benthoscapes (see RAY (1991) for a more general discussion). The reason for this division is that sea-floor depth is a critical factor, controlling many physical, chemical and ecological benthic processes as well as the distribution of sea-floor biota. Here, we will consider nearshore benthoscapes to include sublittoral habitats in waters approximately ≤5 m deep and transitional landscape components such as intertidal flats and salt marshes. These landscapes includes the harbors, embayments and small estuaries which comprise the LIS coastline. The 5 m depth division is somewhat arbitrary as there is significant interaction between nearshore and offshore benthoscapes. However, it does reflect distinct differences in physical, chemical and biological characteristics and processes, as well as differing environmental management concerns. The focus in this paper is on the offshore, or deepwater sections of LIS, but interactions between the two types of benthoscapes are discussed as appropriate.

KNEBEL *et al.* (1999) and KNEBEL and POPPE (this volume) have reviewed the sea-floor environments in LIS based on recently acquired sets of sidescan and sediment grain-size data. Four types of large, regional scale environments are recognized which reflect dominant long-term processes that shape each region (Figure 2). In the eastern basin, there is a large-scale gradient comprised of three types of environments. From the eastern opening to the Sound, an area of erosion or non-deposition extends westward to approximately the mouth of the Connecticut River. This gives way to an extensive environment that is shaped by coarse-grained bed-load transport. Moving west, there is a transitional zone characterized by sediment sorting and reworking in the area of the Mattituck Sill. The central basin is primarily comprised of an extensive area of fine-grained deposition. There are several elongated patches of sediment sorting and reworking extending from the shallow waters in the north and other patches in the southwest portion of the basin; smaller such patches are scattered throughout the basin. The margins are a heterogenous mix of sedimentary environments in the north, but transitional, from sorting/reworking to erosion/non-deposition, along the southern rim of the central basin. The western basin is also a large area of fine-grained deposition with small patches of sediment sorting and reworking. Moving into the Narrows, sea-floor environments become het-

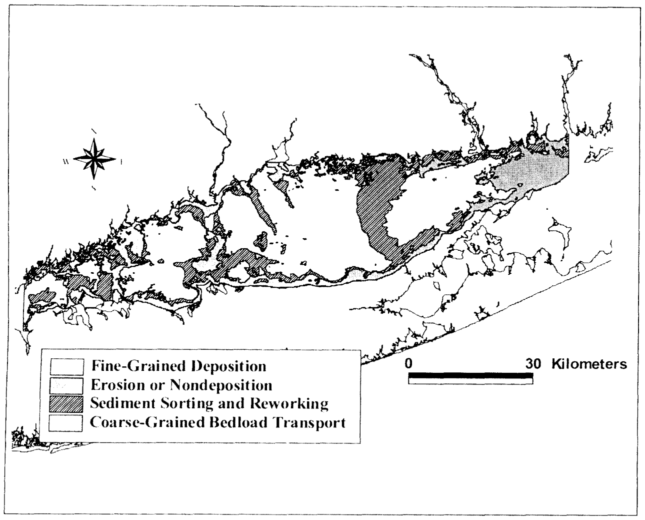

Figure 2. Sedimentary environments in Long Island Sound based on KNEBEL and POPPE (this volume). See text for details.

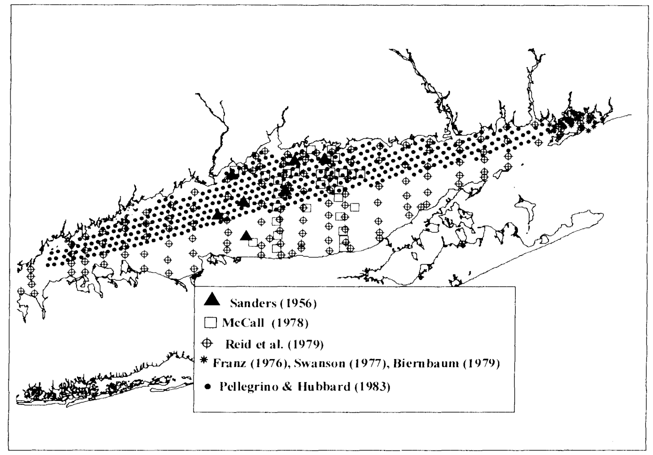

Figure 3. Station locations of deep-water benthic surveys conducted in Long Island Sound. General aspects of surveys are given in Table 1.

erogenous and spatially complex. There are deep-water areas of fine-grained deposition and sediment sorting and localized areas of erosion or non-deposition. Details on sediment grain-size distributions and physical processes associated with each type of environment are given in KNEBEL and POPPE (this volume).

Sound-Wide Structure of Benthic Communities

Relationships between the distribution and characteristics of benthic communities and sea-floor environments in LIS have been the focus of several large-scale surveys (Figure 3). These were conducted primarily during the 1970's, but SANDERS' (1956) work in the 1950's developed many of the main themes for subsequent research in the Sound, including relationships between sediment characteristics, community structure and feeding modes, and the classification of community types. Collectively, the surveys provided a reasonable view of the regional spatial variation exhibited by infaunal communities across the Sound, but they provided little information on temporal variations (Figure 3, Table 1).

Using classification analysis, REID *et al.* (1979) recognized three infaunal assemblages in the central and western basins of the Sound; no consistent groups were identified for the eastern basin (Figure 4). The three groups consisted of: (1) a muddy, deep-water assemblage distributed throughout much of the central and western basins; (2) a shallow sandy assemblage along much of the north shore of Long Island, NY, except in the western portions of the Sound; and (3) a transitional shallow-water assemblage in the western portion of the Sound, especially along the Connecticut shore. The three groups were each comprised of a mixture of species with varying life modes and life histories (REID *et al.,* 1979). Species richness was lower in the muddy, deep-water and shallow sandy groups than in the transitional group. REID *et al.* (1979) suggested that the overlap in community composition

Table 1. *Survey studies conducted on soft-sediment community structure in Long Island Sound.*

Researcher(s)	Study Dates	# Sites	Sampling Interval	Gear	Sieve Size
SANDERS (1956)	1953–1954	8	2–7 times/yr	Anchor Dredge	No. 10 No. 50
MCCALL (1975, 1977, 1978)	1971–1973 (S) 1972–1973 (E)	33 2	1–2 visits (bi) monthly	0.147 m^2 Van Veen	1.0 mm 297 μm
REID, FRAME and DRAXLER (1979)	1972–1973	142	3 sampling dates	0.1 m^2 Sm-Mc	1 mm
FRANZ (1976)	1972–1973	24	Spring, Late Summer, Winter	0.1 m^2 Peterson	1 mm
BIERNBAUM (1979)	1972–1973	24	August Jan./Feb.	0.1 m^2 Peterson	
SWANSON (1977)	1973–1974	16	July Jan./Feb.	0.1 m^2 Peterson	1 mm
RHOADS, ALLER and GOLDHABER (1977)	1974–1975	3	Summer, Fall Spring	0.045 m^2 box core (divers)	1 mm
REID (1979)	1975–1978	≈45	Yearly	0.1 m^2 Sm-Mc	1 mm
PELLEGRINO and HUBBARD (1982)	1981–1982	413	Summers, once	Van Veen	1 mm

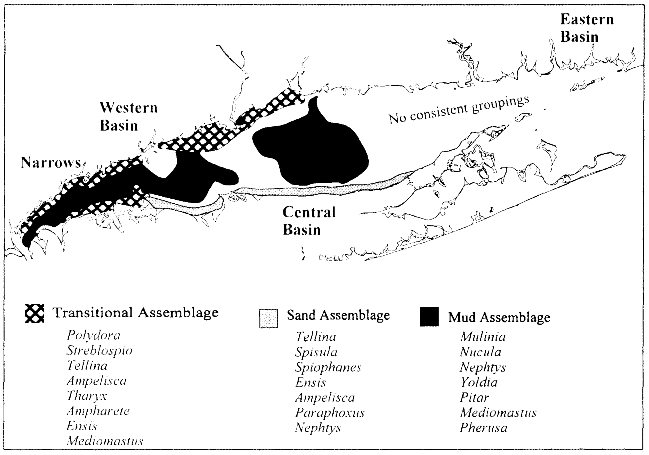

Figure 4. Infaunal community types recognized by REID *et al.* (1979) in Long Island Sound. Dominant species are given below each assemblage type in decreasing order of average abundance. Each group of species comprised 60 to 90% of the total abundance within the designated assemblage.

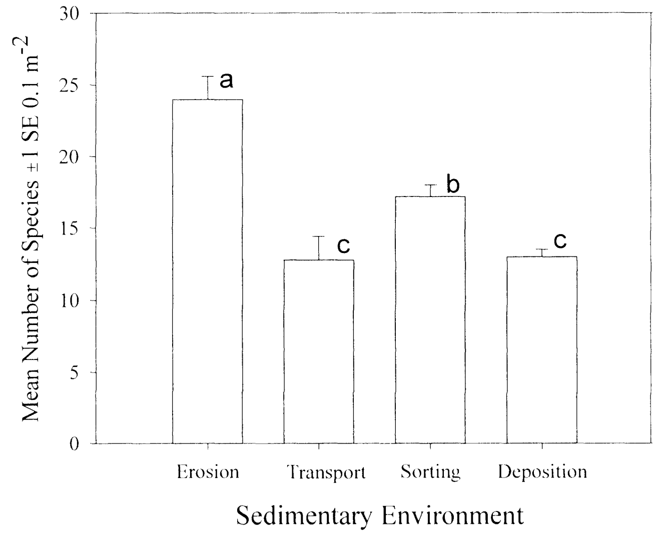

Figure 5. Mean number of species 0.1 m^{-2} in different sedimentary environments estimated from PELLEGRINO and HUBBARD's (1983) survey data. Station data were sorted by sedimentary type using a geographic information system and then analyzed using one-way analysis of variance and a post-hoc Bonferroni multiple comparison test (HINTZE, 1997). Differences among sedimentary environments were highly significant ($F_{3,395}$ = 23.81, MSE = 1.181, $p<0.0001$). Lowercase letters on data bars indicate results of post-hoc tests with matching letters indicating no significant differences ($p>0.05$) in species richness.

among the three groups indicated that benthic infauna in LIS are not distributed as discrete, well-defined communities, but rather they form a faunal continuum from one area to another.

The faunal groups identified by REID *et al.* (1979) generally correspond to the sea-floor environments described previously. The extensive mud assemblage was found in the central and western basins, but also in the nondepositional and sorting/reworking environments in the Narrows. The sand assemblage was associated with the bands of sediment erosion, nondeposition and sorting along the north shore of Long Island, whereas the transitional assemblage coincides with the spatially heterogenous environments just offshore in the Narrows and along the western Connecticut shore.

PELLEGRINO and HUBBARD (1983) conducted a benthic survey of Connecticut waters in LIS that comprised 413 stations (Figure 3). They found that infaunal assemblages varied considerably throughout the Sound. Re-analysis of their data reveals large-scale differences among the four sedimentary environments described previously. Species richness differs significantly among the sedimentary environments (Figure 5), with higher numbers of species found at stations in erosional environments and areas of sediment sorting/reworking than in areas of sediment transport or deposition. Species richness was more variable in the erosion and transport environments, but ranged from 1 to over 35 species per station in all four sedimentary environments.

Benthic community structure was analyzed via classification analysis using the 35 most abundant species which PELLEGRINO and HUBBARD (1983) found throughout the Sound. Twelve community types were identified, with similarities among communities ranging between 5% and 30% (Table 2; Figure 6). The spatial distribution of these communities and the sedimentary environments were then compared to assess Sound-wide relationships (Table 3, Figure 7). ZAJAC (2000) provides a similar analysis relative to sediment grain-size characteristics throughout the Sound. Each sedimentary environment contains many of the benthic assemblages identified, but relatively distinct subsets of the benthic assemblages occur in the deposition and transport environments, whereas a larger variety of benthic assemblages are found in the erosion and sorting environments (Table 3).

Depositional environments are mainly comprised of community types B, C1 or C2. The species in these communities

Table 2. *Dominant species (based on mean abundance in the stations comprising each cluster) in each of the community types shown in Figures 6 and 7. Shown in parentheses are the number of species which were found in the community out of the 35 species used for the analysis (ZAJAC 1996, 1998).*

Community Type	Dominant Species
A)	*Mulinia, Nephtys, Cistenoides* (6)
B)	*Mulinia, Nucula, Nephtys* (16)
C1)	*Nucula, Mulinia, Nephtys* (17)
C2)	*Mulinia, Nucula, Nephtys* (13)
D)	*Cistenoids, Corophium, Mulinia* (22)
E)	*Nucula, Nephtys, Paraonis, Yoldia* (9)
F)	*Mulinia, Clymenella, Mediomastus* (21)
G)	*Cistenoids, Clymenella, Pitar, Asabellides* (10)
H1)	*Asabellides, Tellina, Spiophanes* (29)
H2)	*Ampelisca, Corophium, Spiophanes* (28)
H3)	*Unicola, Aricidea, Capitella* (14)
I)	*Cirratulis, Corophium, Prionospio* (21)
J)	*Assabelides, Polydora, Spiophanes, Leptocherius* (15)
K)	*Protohaustorius, Acanthohaustorius* (15)
L)	No Fauna

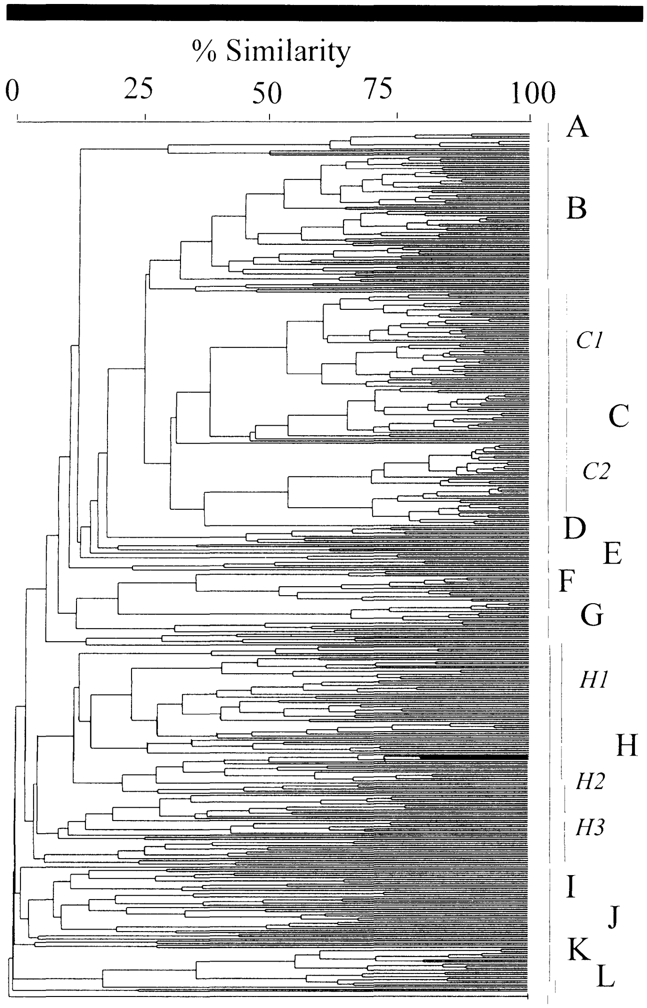

Figure 6. Dendrogram showing the results of a classification analysis of numerically dominant species in Long Island Sound based on data provided in PELLEGRINO and HUBBARD (1983). Clustering was performed using the unweighted pair-group method on a matrix of station similarities calculated using the Bray-Curtis index (ROHLF, 1993). Letters along the side of the dendrogram (A, B, C1, etc.) denote station clusters that were interpreted from the analysis and subsequently mapped (see Figure 7). Dominant species in each cluster are given in Table 2.

included *Nephtys incisa, Cistenoides gouldii, Mulinia lateralis, Nucula annulata* and *Pitar morrhuana* (Table 2) and differed primarily based on the relative number of these species, with higher numbers of *Mulinia* and *Nucula* in community C1 and C2 than in community B stations. These communities correspond to the mud assemblage identified by REID *et al.* (1979) and are similar to the *Nephtys–Yoldia* community identified by SANDERS (1956). Community type F was also found at a number of stations in the depositonal areas, especially along the transition to the area of sediment sorting in the east-central Sound (Figure 2). This community was dominated by *Clymenella zonalis,* but also included *Mulinia lateralis* and *Mediomastus ambiseta.*

Environments characterized by sediment erosion or non-deposition primarily contained community types H1 and I

Table 3. *Frequency of community types identified in Figures 6 and 7 in different types of sedimentary environments in Long Island Sound as shown in Figure 2.*

	Sedimentary Environment				
Community	Deposition	Erosion	Sorting	Transport	Grand Total
A	5	2	3		10
B	52	1	13		66
C1	62	2	8		72
C2	38		1		39
D	6	4	5	1	16
E	4	1			5
F	22	1	6		29
G	1	2	3		6
H1	2	20	38	10	70
H2	1	4	10	1	16
H3		3	1	8	12
I		20	2	8	30
J	1	1	1	1	4
K		2	3	15	20
L	1	1	1	1	4
Grand Total	195	64	95	45	399

(Table 3). Community type H1 was found in the transition between the eastern and central basins and along the bathymetric highs separating the central and western basins and Narrows (Figure 7). This assemblage was dominated by several polychaetes, *Asabelides occulata* and *Spiophanes bombyx,* and the bivalve *Tellina agilis.* Community type I was found in sediment sorting environments in the eastern basin, and dominated by the polychaetes *Cirratulis grandis, Cirratulis cirratus, Prionospio heterobranchia, Prionospio tenuis,* and the amphipod *Aeginnia longicornis.*

Areas of sediment sorting were also comprised primarily of community type H1, particularly in the transition to the central basin, over bathymetric highs, and along the northern coast of the Sound (Table 3, Figure 7). Localized areas of sediment sorting in the western and central basins contained community types B and H2. Environments characterized by coarse-grained bedload transport effectively contained only community types H1 through K (Table 3), which were dominated by several species of tubiculous amphipods and polychaetes.

These analyses suggest that although certain types of communities are associated with particular sedimentary environments in LIS, there is wide variation in community structure within each type of environment. This variation is likely due to landscape-scale variation in sea-floor structure, local differences in sediment composition and associated physical processes. These interact with biological processes such as reproduction, recruitment, and species interactions and abiotic disturbances to generate the variation in community structure. Several examples are discussed in the following section.

BENTHOSCAPE-SCALE PATTERNS

Sea-Floor Environments in Eastern Long Island Sound

As an example of how benthic habitats and communities can vary at the benthoscape scale we present a study that was conducted in eastern LIS off New London, Connecticut (Figure 1). In this area, a sidescan sonar mosaic (SSM) was

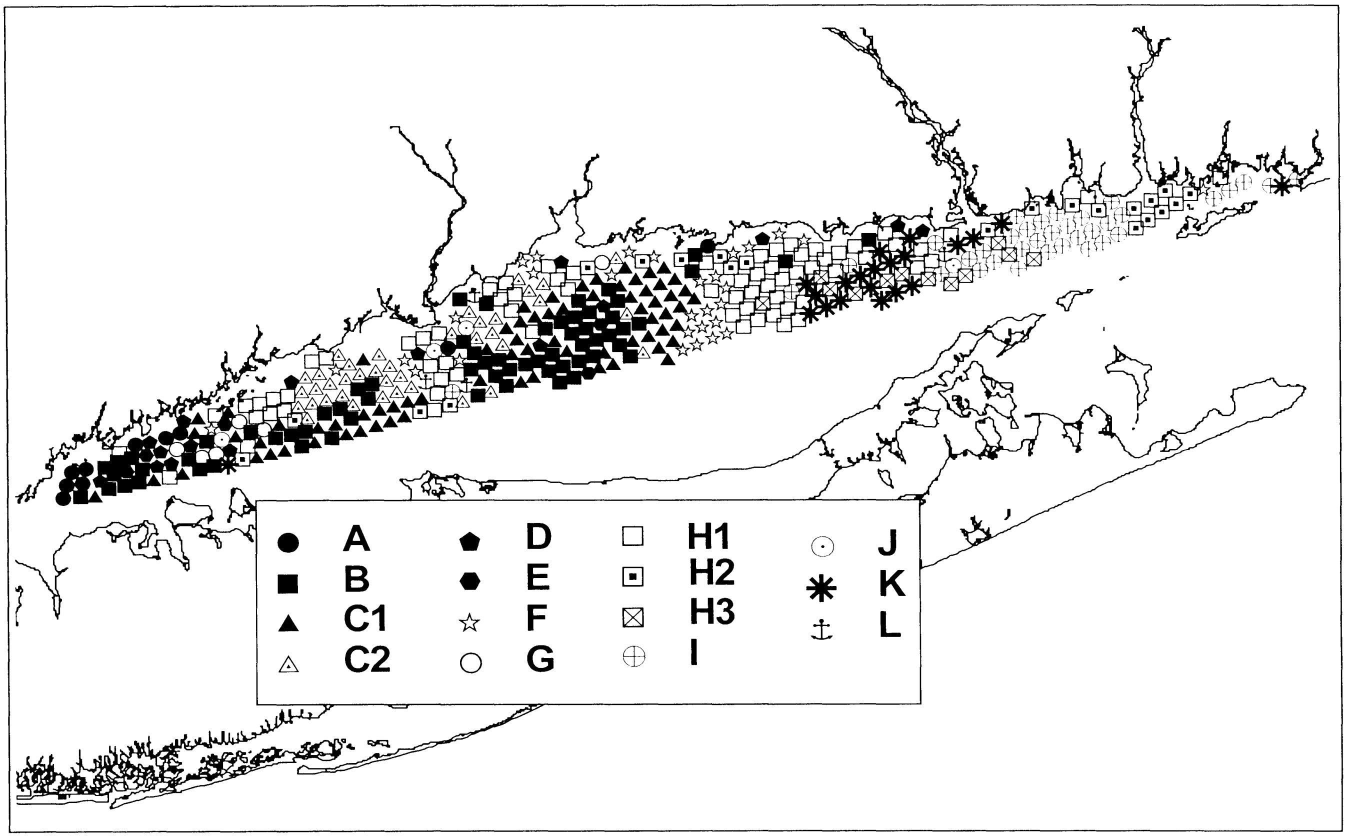

Figure 7. Spatial distribution of benthic communities identified via clustering analysis of data provided in PELLEGRINO and HUBBARD (1983). See Table 2 for general group characteristics of each cluster. Detailed information on community composition given in ZAJAC (1996, 1998).

developed and subsequently sampled to collect data on physical and biological features. The SSM (Figure 8) of the seafloor, covers approximately 19.4 km^2 (7.5 square miles) at the mouth of the Thames River from approximately 41°15.5′N, 72°08′ W to 41°18.5 N, 72°02′ W. The sea-floor is approximately 10 to 15 m deep in the northeast section of the study area, increasing to 20 to 30 m in the southwestern part.

Data for the image were collected during October 1991 aboard the RV UCONN using a 100-kHz EG&G sidescan sonar unit set for a 100-m range and towed approximately 3–4 m above the bottom. Navigation utilized DelNorte (PINSS input) and Miniranger systems. Data collection and processing was performed by Shannon Byrne and Eric Halter at the Ocean Mapping Development Center, University of Rhode Island. The mosaic was originally produced at 1:3,479-scale utilizing the U.S. Geological Survey Mini Image Processing system (MIPS) in an Equatorial Mercator Projection. Processing included: (1) bottom, ratio, and radiometry corrections; (2) sectioning the survey area; (3) "Geoming" individual map sections; (4) "stenciling" and "mosaicing"; and (5) building the final image. 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.

In June 1992, benthic samples and concurrent video were taken at 60 stations using a 0.1 m^2 Van Veen grab sampler equipped with an 8 mm video camera system and a shipboard cassette recorder. Navigational control was provided by GPS and LORAN-C. Subsamples (6 cm diameter × 10 cm deep) for infauna were taken from the grabs and preserved whole in 10% formalin. They were later washed on a 300 μm sieve and the residues were transferred to 70% ethanol. Details of how the surficial sediment samples were processed for textural analysis are given in POPPE *et al.* (1992). For the analyses presented here, sediment fractions were grouped into the following grain-size categories (percent composition by weight): gravel, >2.0 mm; sand, 2.0 mm – 0.062 mm; silt, <0.062 mm to > 0.004 mm; and silt, < 0.004 mm.

Analysis of the SSM (Figure 8) revealed five distinct types of large-scale (on the order of km^2) benthoscape elements (Figure 9). The whole mosaic area is predominantly comprised of sands, but the elements exhibited statistically significant differences in the amount of gravel, sand, silt and clay (Figure 10). There were also distinct differences in the number and types of small-scale surficial features based on analysis of video records (Figure 11).

Multivariate analysis of sediment composition and small-scale surficial features relative to the benthoscape-scale composition of elements provides a more detailed view of the potential habitat characteristics that benthic infauna help cre-

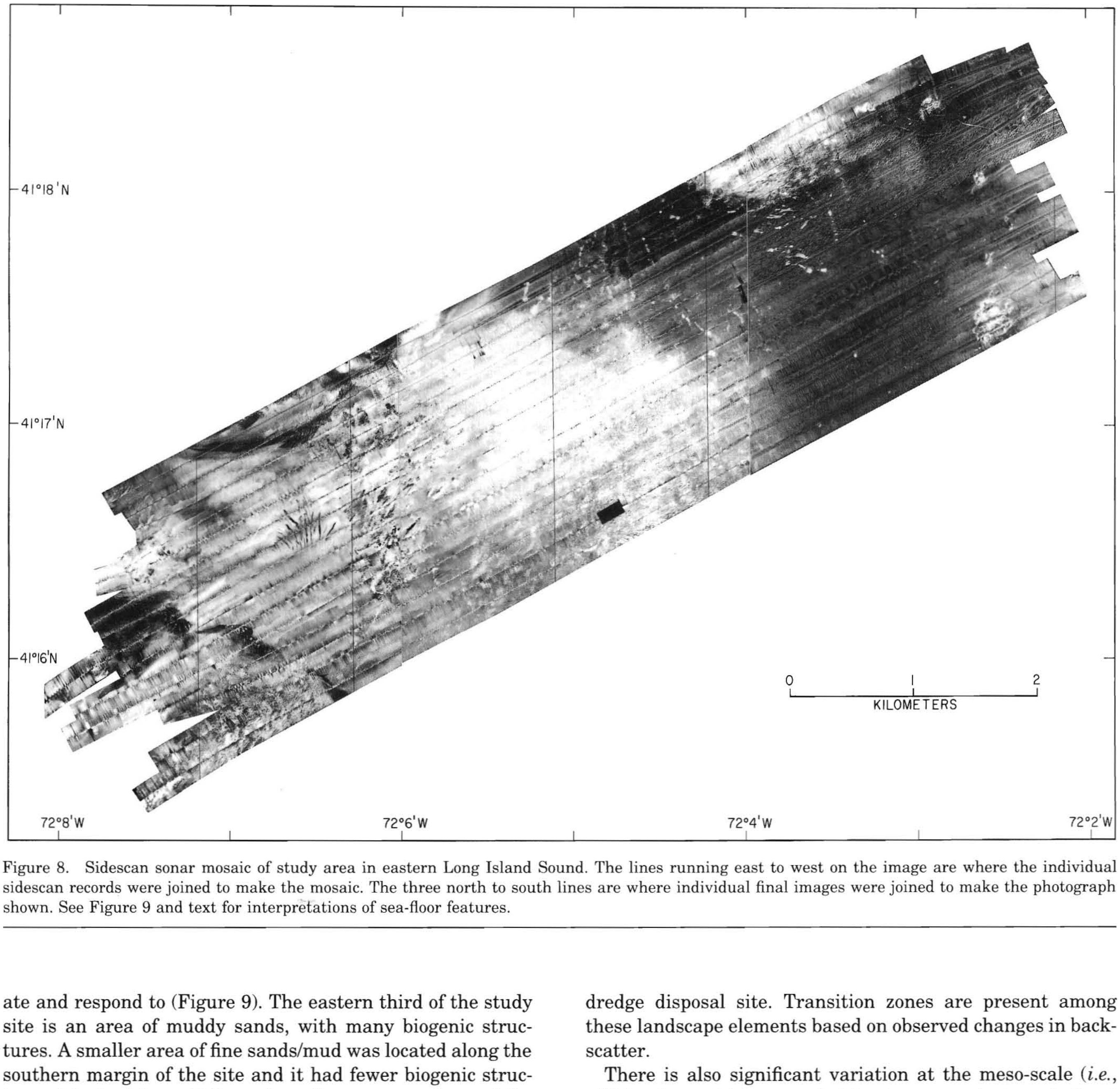

Figure 8. Sidescan sonar mosaic of study area in eastern Long Island Sound. The lines running east to west on the image are where the individual sidescan records were joined to make the mosaic. The three north to south lines are where individual final images were joined to make the photograph shown. See Figure 9 and text for interpretations of sea-floor features.

ate and respond to (Figure 9). The eastern third of the study site is an area of muddy sands, with many biogenic structures. A smaller area of fine sands/mud was located along the southern margin of the site and it had fewer biogenic structures. Much of the middle and southwestern portions of the site is comprised of two areas which were classified as sand environments. The middle element (Sand 1) had sand to mixed sediments and a relatively high number of biogenic structures. The sand area in the western portion of the study area (Sand 2) was characterized by sand and gravels, more physical small-scale features, and shell hash. Seven boulder, cobble and outcrop areas (B/C/O in Figures 10, 11) were found in the study site, the most prominent of which separates the two sand areas. Several sand-wave fields were found in the western portion and along the northwest margin of the area. Along the southern margin, is an area comprised of mixed sediments and rubble which is a portion of the New London dredge disposal site. Transition zones are present among these landscape elements based on observed changes in backscatter.

There is also significant variation at the meso-scale (*i.e.*, within elements) as revealed by image analysis and direct inspection of the SSM. Based on variations in pixel intensity, overall sea-floor heterogeneity was generally higher in the two large sand elements than in the Mud/Sand element (Figure 12). The Mud/Sand element was relatively homogeneous, but the Sand 1 and Sand 2 areas had greater within-element variation which decreased from north to south. However, in the southern portion of Sand 2, the level of meso-scale variation was similar to the Mud/Sand element. Meso-scale variations in Sand 1 are due to a combination of within-element variation, plus changes associated with the broad transitions to the Mud/Sand in the east, B/C/O in the west, and the Mixed/Rubble element to the south. The heterogeneity in

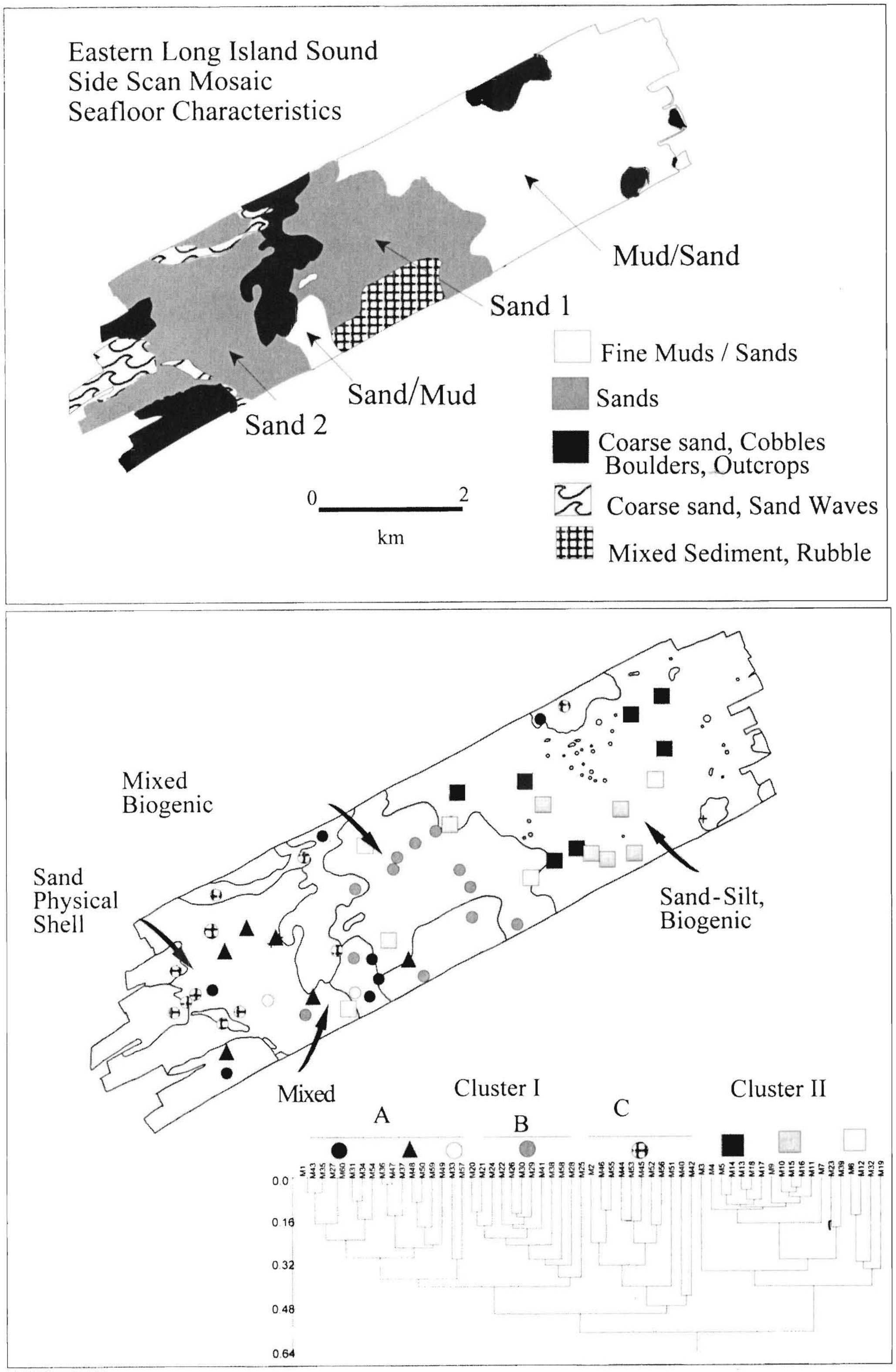

Figure 9. *Upper:* Interpretation of general benthoscape elements comprising the New London sidescan study area. The three largest elements are noted by Mud/Sand, Sand 1 and Sand 2. *Lower:* Results of multivariate analyses showing overall sea-floor habitat characteristics in the study area. The dendrogram shows identified clusters of stations with similar sediment grain-size characteristics and mix of small-scale topographic features. The spatial distribution of the clusters is shown on the map of the study area. General features of each area are noted.

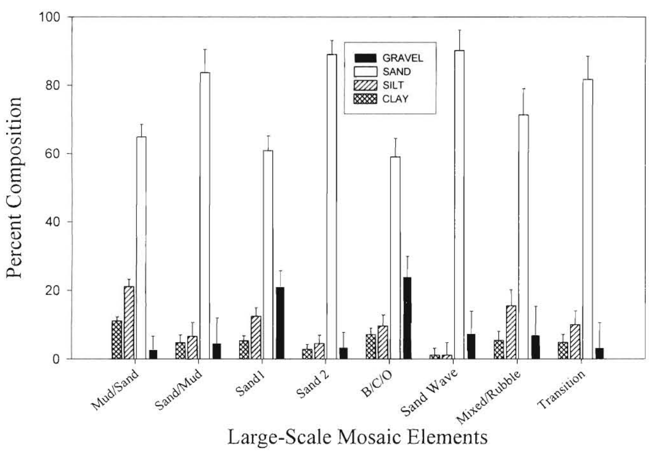

Figure 10. Sediment grain-size composition (mean % ± 1 SE) in the benthoscape elements of the sidescan mosaic study area. Differences among elements for sediment grain-size classes were assessed using one-way analysis of variance and in each case the test was significant (Gravel: $F = 2.64$, $MSE = 553.1$, $p<0.0211$; Sand: $F = 6.73$, $MSE = 1{,}229.9$, $p<0.0001$; Silt: $F = 5.72$, $MSE = 362.0$, $p<0.0001$; Clay: $F = 4.29$, $MSE = 87.0$, $p<0.009$; $df = 7{,}49$ for each test).

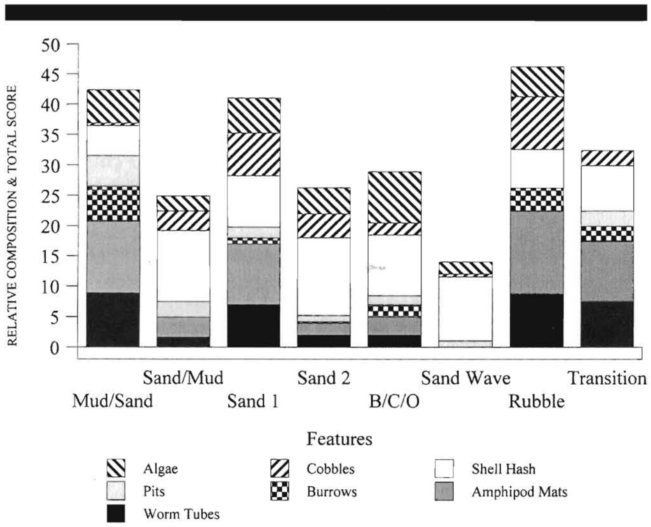

Figure 11. Small-scale (< 1 m^2) sea-floor features in each of the benthoscape elements of the New London sidescan mosaic study area based on analysis of video records. The height of the bar is the total of mean incidence scores which are shown within the bar for each feature type. Video records were analyzed to determine the relative amounts of various biogenic and geologic features including pits, mounds, tubes, burrows, algae, shell hash, cobbles and boulders. At each station, one minute of video was scored as to whether each of the features noted was present, and, if present, whether it occurred at low, medium, or high amounts with respect to coverage of the bottom (e.g. shell hash) or incidence (e.g. burrows). These qualitative scores were then assigned a numerical value of 0, 5, 10 or 15, respectively. Video from each station was analyzed twice by two different people and the two scores were averaged.

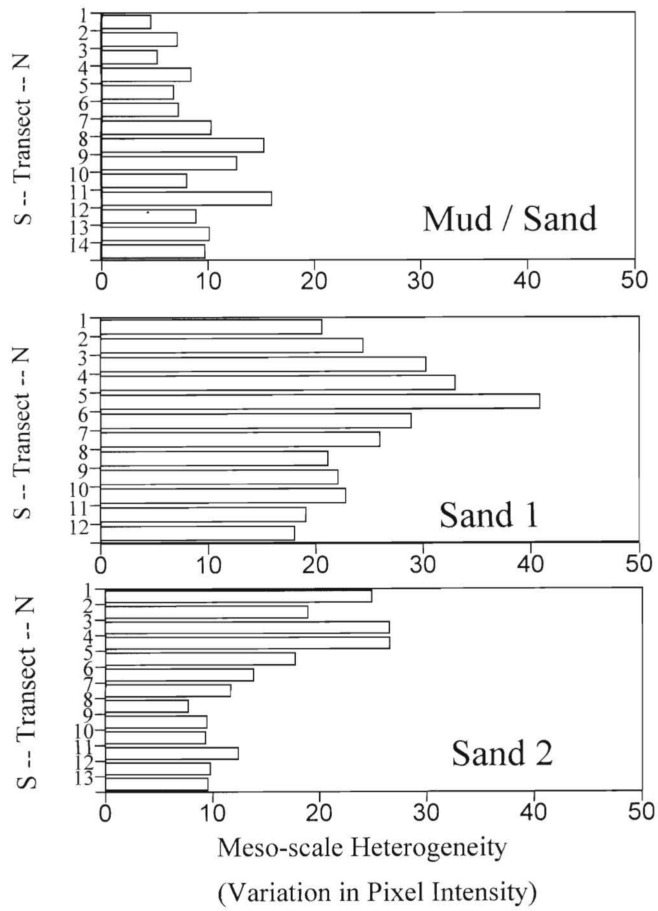

Figure 12. Sea-floor heterogeneity in the three largest benthoscape elements shown in Figure 9 as measured by pixel variation. "Transects" were placed along acoustically clean sections of a digital image of each section of the mosaic, running parallel to the track lines. The transect swaths along which pixel intensity (256 level gray scale) was measured were approximately 55 m wide by 500 to 2000 m long. Each pixel was 6.61 m on a side in the image used for the analysis. Variation in pixel intensity is the standard deviation of gray scale levels among all pixels in the transect. The transect numbers are in a north (N) to south (S) direction.

Sand 2 is due to the presence of several distinct within-element patches in the northern portion of the element, including, for example, the finger-like patches visible in the mosaic (Figure 8). Meso-scale habitat variation is also evident in the results of the multivariate analysis (Figure 9) as stations from several sub-clusters were found within the larger elements of the benthoscape.

Only the western half of the New London SSM study area falls within the area surveyed to delineate sedimentary environments (Figures 2 and 9). Two sedimentary environments were identified, an area of sorting coinciding with Sand 2 and a portion of the Sand 1 element, and an area of erosion or nondeposition which covers the western end of the mosaic area, the large B/C/O area in the center of the mosaic area and another part of the Sand 1 area. It is interesting to note that even at a reconnaissance scale, KNEBEL *et al.* (1999)

Table 4. *Species found at the New London side scan mosaic study area at the highest abundances and used in analyses of community structure.*

	Feeding, Motility, Sediment Modification
Polychaetes	
Prionospio steenstrupi	Surface deposit-feeding, Filter feeding, Discretely motile, Tubiculous
Tharyx dorsobranchialis	Surface deposit-feeding, Discretely motile/motile, Sediment bioturbating?
Chaetozone sp. a	Surface deposit feeder, Discretely motile
Aricidea catherinae	Herbivore, Surface deposit feeder, Motile, Burrower
Polycirrus exumis	Surface deposit feeder, Discretely motile
Nephtys sp.	Carnivorous, Burrowing deposite feeder, Motile, Burrows
Clymenella torquata	Subsurface deposit feeder, Sessile, Tubiculous, Bioturbation, Oxygenation
Mediomastus ambiseta	Burrowing deposit feeder, Motile Pelletization
Amphipods	
Ampelisca vadorum	Surface deposit/suspension feeder, Tubiculous
Unicola irrorata	Surface deposit/suspension feeder, Tubiculous
Microduetopus gryllotalpa	Surface deposit/suspension feeder, Tubiculous
Phoxocephalus holboli	Surface deposit/suspension feeder, Tubiculous
Exogenes hebes	Herbivore, Surface deposit feeder, Carnivore, Motile, Burrower, Non-tubiculous
Bivalve	
Nucula annulata	Subsurface deposit feeder, Discretely motile
Other	
Nemertean	Carnivore, Burrowing
Oligochaete sp. a	Burrowing deposit feeder, Motile

found meso-scale differences within the erosion or nondeposition environments in the B/C/O portions of the SSM study area.

Infaunal Community Variation at the Benthoscape Scale

A total of 157 species/taxa were identified in the bottom grab samples. Relationships between community structure, individual species populations, and benthoscape structure in the SSM study area were analyzed using the 16 most abundant taxa (Table 4). Mean abundance per core of the 16 dominant species and the mean number of species per core (based on all 157 species), varied significantly among the benthoscape elements (Figure 13). The lowest abundances and numbers of species were found in the sand-wave elements, whereas the highest values were found in the Mixed/Rubble, Sand/Mud and transition elements. Mean species richness and total density per core were similar among most other elements (Figure 13). However, analyses of total abundance and species richness at varying spatial scales within and among the Mud/Sand, Sand 1 and Sand 2 elements indicated significant differences at meso-scales within these elements but not at larger spatial scales among the elements (Table 5).

Although composite community characteristics, such as

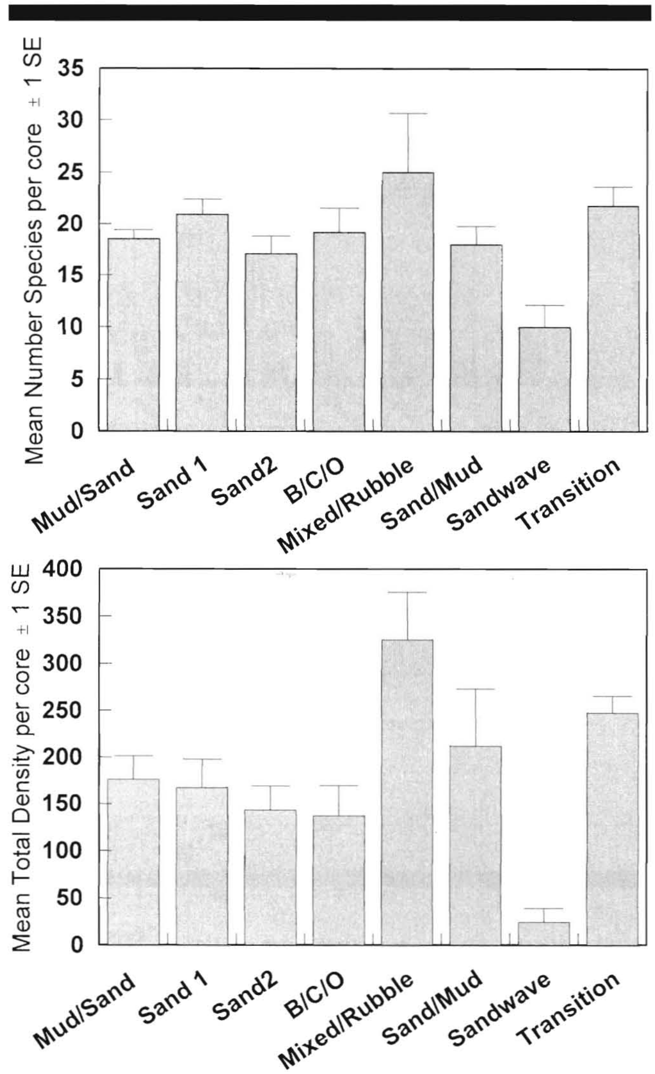

Figure 13. Mean (± 1 standard error) total species per core and total abundance in each of the large-scale sea-floor elements in the sidescan mosaic study area. Differences among elements were significant for both total abundance ($F_{7,49}$ = 4.23, MSE = 7554.2, P<0.001) and species richness ($F_{7,49}$ = 3.56, MSE = 24.6, p<0.01).

species richness and total abundance, did not vary greatly among the benthoscape elements, there was more variation in community structure across the study area at different spatial scales. Twelve station clusters were identified (Figure 14). The main groups were Clusters III, IV and IV, which comprised stations within the largest benthoscape elements. Stations in Cluster III were primarily found in the Mud/Sand element, but also in Sand 1 and in the western and eastern portions of the Mixed/Rubble and Sand/Mud elements, respectively (Figure 15). These stations were characterized by relatively high densities of *Ampelisca vadorum,* Oligochaete sp. a, *Unicola irrorata* and *Tharyx dorsobranchialis.* Stations in Clusters IV were almost exclusively found in the western portion of the SSM study area either in Sand 2 or in adjacent elements (Figure 15). This cluster was characterized by high

Table 5. *Results of nested analysis of variance of differences in total density and species richness per core among the three largest landscape elements (AREA) in the mosaic study area (Mud/Sand, Sand 1 and Sand 2, see Figure 9). The terms SITE and SUBSITE refer to two successively smaller subdivisions of each landscape element (AREA). The SITE subdivision divided each element into halves roughly along the middle axis of the study area (running from the southwest to the northeast), and the SUBSITE division into quarters by a line perpendicular to the SITE line down the middle of each element.*

Source of Variation	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level
Total Abundance					
Area	2	15888.5	7944.3	0.97	0.4746
Site (A)	3	24692.3	8230.8	0.41	0.7497
Subsite (S(A))	6	119449.2	19908.2	3.39	0.0139*
Error	25	146974.2	5879.0		
Total (Adjusted)	36	307004.3			
Total 37					
Species Richness					
Area	2	126.4	63.2	1.22	0.4102
Site (A)	3	155.7	52.0	1.05	0.4369
Subsite (S(A))	6	297.0	49.5	3.29	0.0158*
Error	25	375.8	15.0		
Total (Adjusted)	36	954.9			
Total 37					

* Term significant at alpha = 0.05.

densities of Oligochaete sp. a. and elevated abundances of Nemertean sp.a, *Chaetozone* sp. a, *Aricidia catherinae* and *Ampelisca vadorum*. Stations comprising Cluster V were found as small spatial groups in several elements. These included groups of three stations in the northern portion of Sand 1, in Sand/Mud and in the sand-wave elements along the western end of the study site (Figure 15). These stations were characterized by high densities Oligochaete sp. a and *Tharyx dorsobranchialis* and moderate densities of *Exogone hebes, Chaetozone* sp. a, *Phoxocephalus holbolli* and *Aricidia catherinae.*

Clusters III, IV and V had a fairly high level of similarity and can be interpreted as characterizing the primary community types found in the study area. The main difference appears to have been a shift in dominance from *Ampelisca vadorum* in Cluster III to *Tharyx dorsobranchialis* and/or Oligochaete sp. a in Clusters IV and V. The remaining clusters were comprised of two to three stations distributed across the study area (Figure 15), where community structure varied from the general patterns noted for Clusters III, IV and V by having high abundances of one or two of the dominant species.

CONCLUSIONS AND RECOMMENDATIONS

Sea-floor environments and associated infaunal communities in LIS exhibit varying degrees of congruity at different spatial scales. At the regional scale, geologic and hydrologic processes interact and form a gradient of sedimentary environments from the eastern entrance of the Sound to the Stratford Shoal complex at the western limit of the central basin. To the west of the Stratford Shoal complex, in the western basin and Narrows of LIS, sedimentary environments form a heterogenous mosaic. To a large extent regional-scale shifts in benthic assemblages in LIS follow these spatial trends, and particular sets of assemblages tend to associated with particular sediment types (ZAJAC, 2000) and regions (Table 3). Eight types of assemblages (Clusters A–G) are primarily found in the central and western basins of LIS, whereas six assemblages (Clusters H–K) are generally found in the eastern end of the Sound (Figure 7). Most assemblages had one geographical "hot spot" where a particular assemblage was found at a relative high number of neighboring stations. However, some assemblages had smaller spatial clusters and were distributed over large areas of the Sound (*e.g.*, assemblage H1), whereas others had only one cluster of stations (*e.g.*, assemblage K). Several assemblages were found spread throughout LIS (*e.g.*, assemblages D, E, and H2) in a variety of sedimentary environments.

The regional distribution of benthic communities in LIS reflects the influence of processes which shape the sedimentary environments. At the core of these dynamics is the interaction between sediment characteristics, geomorphology and hydrodynamics (*e.g.*, KNEBEL and POPPE, this volume), and the resulting influence on the ecology of the benthic organisms via dispersal and settlement, resource availability and feeding, and modifications of local habitat conditions (*e.g.*, RHOADS, 1974; GRAY, 1974; SNELGROVE and BUTMAN, 1994). The species comprising the communities are adapted to different sediment types and hydrodynamic regimes via their resource requirements and feeding modes (*e.g.*, WHITLATCH, 1980; SNELGROVE and BUTMAN 1994), and these appear to set the regional limits of the assemblages in LIS (ZAJAC, 2000). For example, in the western portion of LIS, relatively sharp breaks in benthic community structure occur in the areas of bathymetric highs, specifically the Norwalk and Stratford Shoal complexes. In the central basin, two less distinct faunal breaks (the core area of community type B and the change from community type C1 to F; Figure 7) appear

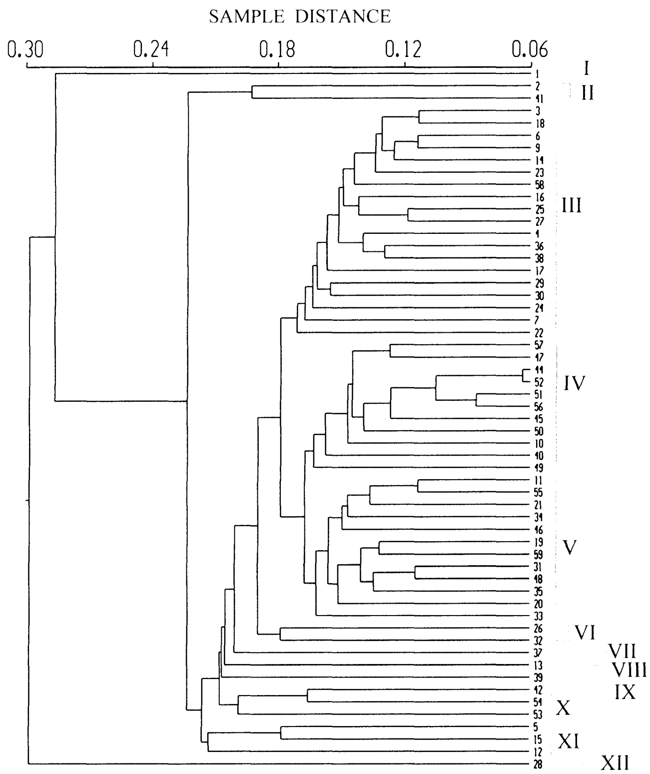

Figure 14. Dendrogram showing results of clustering analysis of stations in the New London study area based on the abundances of the 16 dominant species of infauna. Clusters of stations comprising similar types of infaunal communities are given along the vertical axis (I, II, III etc.), as well as individual stations (1,2, 3 etc.). Clustering was performed using the unweighted pair-group method on a matrix of station similarities calculated using the average distance coefficient (ROHLF, 1993). Increasing sample distance indicates less similarity among stations and clusters of stations. Clusters were selected based on sample distance threshold of 0.15.

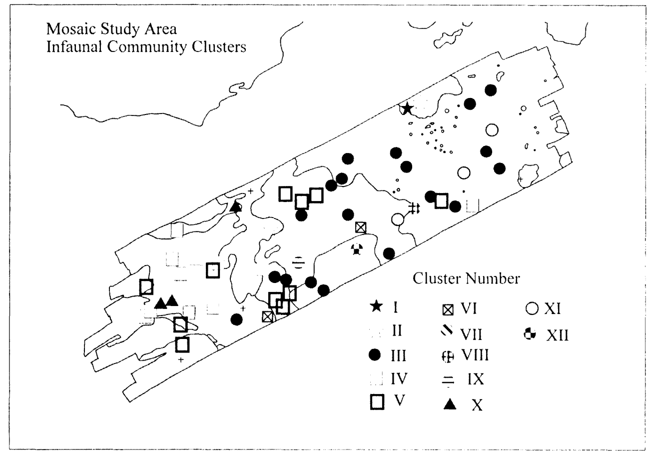

Figure 15. Spatial distribution of stations comprising each infaunal community cluster in the New London sidescan mosaic study area. Cluster structure is shown in Figure 14.

to be associated with meso-scale circulation patterns (ZAJAC, 2000), specifically a system of gyres that may occur in this part of the basin (SCHMALZ, 1994). Distinct faunal breaks also occur to the west of the Connecticut and Thames Rivers (Figure 7), where bottom substrates are complex and characterized by a mixture of coarse to fine-grained habitats.

Although Sound-wide trends in community structure corresponding to the distribution of sedimentary environments are evident, varying degrees of community variation are found within regions at the benthoscape scale. In the western basin and Narrows, assemblages changed over smaller spatial scales and there was a higher diversity of community types (Figure 7). Community shifts appear to occur at larger spatial scales in the eastern basin, and these communities were more dissimilar to one another than those found in the central basin. Although community variation is present within the central basin, the changes there are less distinct (Figure 6). These differences appear to be directly related to differences in sea-floor complexity among regions.

The eastern basin is a dynamic region of the Sound, and benthoscape-scale sea-floor structure can be quite complex as seen for the New London SSM study area (Figure 8). Meso-scale variations within the main elements of this benthoscape (e.g. Figure 12) appeared to be an important structuring factor as community variation was comprised of relative shifts in abundance of a common species pool in response to meso-scale variation (Figure 15). The coarse-grained bedload transport environment (Figure 2) is a complex area of sand waves and sand ribbons (KNEBEL *et al.,* 1999) and community changes appear to be related, in part, to the position of these features (Figure 7). In contrast, much of the central basin is a depositional area containing muddy sediments. Here, benthoscape variation is relatively low, and is likely most prevalent at small scales, similar to that found in the Mud/Sand area in the New London SSM study area (Figures 9, 11 and 12).

At the present time, we have a basic understanding of the spatial distribution of soft-sediment communities in LIS and the possible range of infaunal assemblages. These represent ecological communities to the extent that they are temporally consistent. However, many portions of the LIS sea-floor have been sampled only once to characterize benthic communities and, therefore, it is difficult to assess their temporal dynamics. Consistent sampling over time is especially critical for detecting long-term trends and for assessing changes that may result from management activities.

A few studies have looked at temporal changes in community and population characteristics at selected sites. MCCALL (1978) analyzed survey data collected over two years in the central basin to partition the effects of disturbance, substratum type and other factors which may affect species distributions and population abundances. He found that while faunal differences among bottom types did exist, differences in population abundance (and variation) associated with depth were more pronounced. During the survey (1971–1973), a significant reduction in the abundance of infaunal populations was observed in this portion of LIS (MCCALL, 1977; REID *et al.,* 1979). MCCALL (1978) found that many of the affected species were bivalves and other species with long-lived planktotrophic larvae. Seventy-five percent of the species having lecithotrophic larvae or larvae which are brooded for some period of time were unaffected. Large-scale changes in the water column (e.g. suspended load, increased turbulence) may have affected planktotrophic larvae and the adults of filter-feeding species. Overall, McCall (1978) suggested that "Benthos distribution will be patchy depending on the frequency and distribution of . . . disturbance and initial heterogeneity of the substratum" and that other patterns may be "most clearly related to plankton phenomena." Similarly, Zajac and Whitlatch (1988, 1989) found fluctuations in the abundance of *Nephtys incisa,* a dominant polychaete species in the central basin, over periods of several years that may be related to poor recruitment in some years.

The results of the survey studies can also be compared to explore the possibility of temporal changes over longer periods of time. The *Nephtys–Yoldia* community that Sanders (1956) recognized was generally present at the time Reid *et al.* (1979) and McCall (1977 and 1978) did their sampling in this area of the Sound, although both of the latter studies did find different relative species abundances. Likewise, the species groupings identified in the re-analysis of Pellegrino and Hubbard's (1983) data indicate that the community types in the central basin are generally dominated by *Nephtys incisa, Nucula annulata* and *Mulinia lateralis. Yoldia limatula* was found at high densities only in one community type identified via the classification analyses (C1). This community type was found at just three stations in the central basin (Figure 7). Thus, general community types appear to be consistent, but longer-term changes may have occurred in populations of some of the dominant organisms. For example, in SANDERS' (1956) study, the abundance of *Mulinia lateralis* was generally low, but subsequent surveys indicated that this was a numerically dominant species in various areas of the Sound.

Although there is a substantive body of scientific research on LIS, a comprehensive understanding of the spatial and temporal structure and dynamics of biological communities associated with sea-floor environments is yet to emerge. Detailed investigations on several scales may help in this regard. As shown for the New London SSM study area, meso-scale variations in benthoscape structure can have an important influence on the structure and potentially the dynamics of infaunal communities. Meso-scale features observed in sidescan mosaic study areas in the western basin (Twichell *et al.,* 1997) and in the central basin (Twichell *et al.,* 1998) also appear to be associated with differences in benthic community structure (Zajac 1998, 1999). Moreover, transition zones between benthoscape elements can comprise a large proportion of coastal sea-floor habitats (e.g in the western end of LIS) and may be a key meso-scale feature (Zajac, 2000).

Another critical area of research is elucidating the links between benthoscape dynamics and those of the water-column. The dynamics of benthoscapes are a function of within- and among-patch population dynamics as mediated by the hydrographic seascape. The structure and dynamics of the water column are important determinants of several aspects of benthic dynamics such as production and distribution of food resources and dispersal of larvae and adults. The water-column also shapes various types of disturbances that impact bottom communities. The water-column seascape itself is a mosaic of different physical and biological patches spanning multiple scales (Steele, 1989; Barry and Dayton, 1991). Understanding the relationships between water-column and benthic processes has long been a focus of coastal research, and significant insights have been made over the past decade (Barry and Dayton, 1991; Angel, 1994a,b). This work continues, but surprisingly few studies have attempted to explicitly compare the patch structure and dynamics of the water-column with that of benthoscapes. Research on this topic may lead to important insights with regards to the distribution of communities via hydrodynamic effects on the sea-floor (Warwick and Uncles, 1980) and provide information for building metapopulaton models for key species in LIS (Zajac, 1999). These additional types of information will allow us to develop a better framework for assessing both ecological interactions (*e.g.,* food web dynamics) in LIS and changes due to natural and human disturbances. This may be especially critical for the western basin and Narrows region where there is a significant management effort in response to hypoxia and contaminant problems but a lack of comprehensive data on benthic communities and environments. A better understanding of the structure and dynamics of benthic environments across multiple spatial and temporal scales is critical to advance our understanding of LIS and thereby more effectively manage the resources it provides.

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