Journal of Experimental Marine Biology and Ecology 330 (2006) 392 – 402

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Characterizing the role benthos plays in large coastal seas and estuaries: A modular approach

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Received 15 July 2005; received in revised form 13 October 2005; accepted 15 December 2005

Abstract

Ecologists studying coastal and estuarine benthic communities have long taken a macroecological view, by relating benthic community patterns to environmental factors across several spatial scales. Although many general ecological patterns have been established, often a significant amount of the spatial and temporal variation in soft-sediment communities within and among systems remains unexplained. Here we propose a framework that may aid in unraveling the complex influence of environmental factors associated with the different components of coastal systems (i.e. the terrestrial and benthic landscapes, and the hydrological seascape) on benthic communities, and use this information to assess the role played by benthos in coastal ecosystems. A primary component of the approach is the recognition of system modules (e.g. marshes, dendritic systems, tidal rivers, enclosed basins, open bays, lagoons). The modules may differentially interact with key forcing functions (e.g. temperature, salinity, currents) that influence system processes and in turn benthic responses and functions. Modules may also constrain benthic characteristics and related processes within certain ecological boundaries and help explain their overall spatio-temporal variation. We present an example of how benthic community characteristics are related to the modular structure of 14 coastal seas and estuaries, and show that benthic functional group composition is significantly related to the modular structure of these systems. We also propose a

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doi:10.1016/j.jembe.2005.12.042

framework for exploring the role of benthic communities in coastal systems using this modular approach and offer predictions of how benthic communities may vary depending on the modular composition and characteristics of a coastal system.

Keywords: Benthic; Coastal; Estuary; Functional groups; Geomorphology; Macrofauna; Modules

1. Introduction

Seeking general relationships among patterns and processes is a fundamental element of scientific progress. These generate insights into system dynamics and provide a framework for development of testable hypotheses which, in turn, act as catalysts for further increasing our knowledge of the system. In this paper, we present a set of ideas which address the potential roles played by the benthos in coastal seas and estuaries in relation to the physiognomic attributes of these systems. These relationships may give us the ability to predict benthic patterns and processes that contribute to ecosystem function in relationship to the spatial heterogeneity of these environments. The impetus for this work is grounded in the growing recognition that effective management and conservation of coastal resources necessitates understanding system structure and function at multiple spatial scales (e.g. Zajac, 1999; Hyrenbach et al., 2000). Whereas all coastal systems are rather complex, we strive to identify distinguishing attributes that coalesce pattern and process into simpler depictions that allow scientists, resource managers and the public to more easily understand these systems and expedite decisions regarding their use and protection. Soft-sediment benthic communities play critical roles in the functioning of coastal systems (e.g., Snelgrove et al., 1997; Weslawski et al., 2004), but they are difficult to study, particularly in subtidal environments which often make up the major portions of the benthic ecosystems in estuaries and coastal seas.

Our main premise is that estuaries and coastal seas can be divided into one or more geomorphological units, or modules, that are predictors of the general nature of benthic communities. As such, they may be delineated and partitioned as units for considering ecological dynamics for research, management and conservation purposes. Classifying coastal environments is certainly not new, and we first provide an overview of different approaches to coastal classification and their intent, and briefly assess efforts by others to relate large-scale coastal/estuarine characteristics to the nature of benthic communities. Because classification schemes are being developed for management and conservation at local to national and international levels (e.g. Connor et al., 1995; Digby et al., 1999; Allee et al., 2000), it is our goal to provide insights as to how the ecology of the benthos may be related to physical variables which are used in the classification schemes.

2. Coastal classifications and broad-scale relationships

2.1. Coastal classification

Coastal environments have been categorized using different sets of criteria depending on the goals of specific projects, many of which typically focus on management and research. Coastal classifications also vary with respect to the basis of classification. While many rely on an underlying geomorphological framework, classification schemes are becoming increasingly more ecologically and habitat-based (see below). In either case, the classification schemes are developed to provide a framework to organize research and management efforts, and to provide a common set of identifiers for those participating in these activities.

Classification of coastal environments based on geologic attributes and the dynamics forming specific coastal features has been ongoing since the 1800's (United States ACOE, 1995). Perhaps the most widely used classification scheme was developed by Shepard during the mid-1900s (e.g. Shepard, 1973). This system divides shorelines into two basic types; those that are shaped by marine processes and those that are not. Within each broad group there are subdivisions based on specific processes and the resultant coastal features (e.g. ria coasts formed by sub-aerial erosion and partly via post-glacial sea level rise). Geological-based classification efforts continue into the present (e.g. Fairbridge, 2004; Finkl, 2004), and indeed most coastal classification schemes, some of which are summarized below (including our own), have an underlying geomorphological framework.

Coastal classifications that explicitly incorporated environmental/ecological objectives became more common during the latter half of the 20th century. A significant antecedent to the presently increasing focus on the landscape ecology of coastal and near-shore aquatic systems was Turner's (1994) argument that coastal regions should be assessed at multiple spatial and temporal scales that fuse biological, physical, chemical and societal components. Cooper and McLaughlin (1998) reviewed 18 classification schemes and found that most were focused on predicting vulnerability of coastal areas to sea-level rise, coastal erosion, and potential impacts from anthropogenic disturbances such as oil spills. They noted that "few indices adequately considered the physical basis for interaction between variables used in the classification procedure." All of the approaches reviewed included geomorphological variables that could be used to assess vulnerability and/or as management units, as well hydrodynamic variables that could act on the geomorphology (Cooper and McLaughlin, 1998). Other approaches have explored using specific attributes of coastal systems. For example, Bartley et al. (2001) showed how coastline complexity could be quantified over extensive portions of a coastline in order to potentially link the level of complexity to biogeochemical patterns and coastal zone dynamics.

Increasingly, coastal classification schemes are blending ecological and geomorphological/hydrological variables for the purpose of predicting where certain habitats may be located, identifying what coastal processes shape the distribution of habitats, and how these can be used to assess environmental impacts and management scenarios. For example, Digby et al. (1999) used biologically important physical characteristics to develop a classification scheme of Australian estuaries and used it to explain variation in the distribution and proportion of mangroves and salt marshes in the estuaries. Models using the classification variables explained about 43% of the marsh and mangrove distributions in the estuaries (Digby et al., 1999). Roy et al. (2001) developed a classification system which recognized five estuary types for eastern Australia based on hydrological conditions (e.g. open bays, estuaries dominated by tides or waves) and subtypes within these that had certain types of geomorphological features (e.g. funnel shaped, macro-tidal estuaries, and drowned valley estuaries). They argued that these categories could be related to characteristic water quality, nutrient cycling/primary productivity and ecosystem attributes. Similarly, researchers working on coral reefs (Mumby and Harborne, 1999; Kendall et al., 2004) and soft-sediment environments (Greene et al., 1999) are developing classification schemes that seek to relate geomorphological habitat features to ecological processes. The melding of these is part of the growing area of coastal ecology which seeks to apply landscape ecology approaches for understanding the dynamics of these systems and managing resources within them (e.g. Ray, 1991, 1996; Zajac, 1999; Kneib, 2000; Bell et al., 2001; Paul et al., 2002).

2.2. Broad-scale relationships

A central objective of many coastal classification schemes is to enhance our understanding of relationships among different suites of biological, physical and chemical variables over different levels of spatial complexity. Such relationships have been explored both within the context of coastal classification schemes and also without reference to any classification scheme. Most attempts at drawing such relationships have focused on ecosystem properties such as nutrient levels and primary production. For example, Nixon et al. (1996) assessed various factors that can affect nutrients in coastal environments and found that the percentage of the total nitrogen and phosphorus exported from a coastal system was related to mean water residence time. Residence time can be, in part, a function of the geomorphologic attributes of the system. Welsh et al. (1982) considered similar relationships and found that geomorphological attributes, as expressed by a volume : area ratio, were highly correlated to benthic and total production, and the benthic : pelagic production ratio.

There are few studies that have attempted to determine relationships between coastal elements defined via classification schemes and benthic ecological characteristics. Saintilan (2004) was able to relate the estuarine classification developed by Roy et al. (2001) for eastern Australian estuaries to commercial landings of fish and crustaceans. Dauer et al. (2000) analyzed relationships between benthic community structure, as defined by an Index of Biotic Integrity, and large-scale features in Chesapeake Bay (water quality and sediment toxicity) and factors associated with surrounding terrestrial landscapes (nutrient loads and lands use patterns). They found that benthic biotic integrity exhibited mixed levels of correlation with these factors. In particular, sites with both low and high biotic integrity were found at sites that had relatively unimpacted conditions and non-urbanized watersheds. In a similar study, Lerberg et al. (2000) considered the effects of watershed development on tidal creek benthic communities in South Carolina and found that pollution-sensitive benthic taxa decreased with increasing impervious surface in a watershed, with 42% of overall variation explained by this relationship. Pollution indicative species were positively related to the degree of urbanization, with 34% of their variation explained by this factor. However, for both pollution-sensitive and non-sensitive taxa, the percentage of each when there was little impervious surface varied by 40% to 60% (Lerberg et al., 2000). Studies such as these form an important part of the framework for exploring benthos/system relationships over multiple spatial scales, and assessing the usefulness of the suite of variables by which these systems can be classified/characterized. Interestingly, the strongest relationships appear to be in locations with the greatest levels of benthic impact, with increasingly variable relationships in areas that are less impacted. This raises two concerns. First, we still do not understand benthic communities to the extent that we can predict when certain community states occur under natural (i.e. non-disturbed) conditions. Second, at the present time we may not have indicators that are sensitive enough to accurately establish that a community or ecosystem is being degraded, although some disturbance/succession models make accurate predictions under specific types of environmental conditions (Pearson and Rosenberg, 1978; Rhoads et al., 1978). In an insightful review of eutrophication dynamics in estuaries, Cloern (2001) suggested that understanding of eutrophication dynamics is associated with the evolution and reformulation of the driving paradigms. He presented a model in which eutrophication processes were made to vary in estuaries through a suite of factors he termed "filters." Cloern (2001) suggested that these filters were system-specific attributes that could modulate responses that lead to differences among coastal and estuarine systems in their sensitivity to nutrient enrichment. The question is, "What are these filters?" We suggest that the modular system presented below may comprise a filter or filters (sensu Cloern, 2001) that captures how large-scale features of large estuaries and coastal seas shape the general characteristics of their composite benthic communities and thereby provides a research and management framework to explore benthic ecological structure and function over multiple spatial scales.

3. A modular approach

3.1. Background

There are clear indications that the geomorphological and hydrodynamic attributes of coastal systems can predict ecosystem-level dynamics. The geomorphology of a system both is shaped by and affects a suite of primary forcing factors, such as freshwater discharge, water depth, temperature and salinity, energy, disturbances and landscape characteristics, to shape a set of what we term second order processes which represent interactions among nutrient levels, primary production and food supply in the system (Fig. 1). Under certain conditions these interactions can trigger significant system events such as hypoxia and shifts in trophic structure (Carpenter, 2001; Scheffer et al., 2001). Ultimately these factors help to shape the nature of coastal benthic communities and the key functional processes they play in coastal seas and estuaries, including food chain dynamics, benthic–pelagic coupling, biogeochemical processes, and habitat engineering. The dynamics of the benthos constitute a potentially important feedback loop to the second order processes.

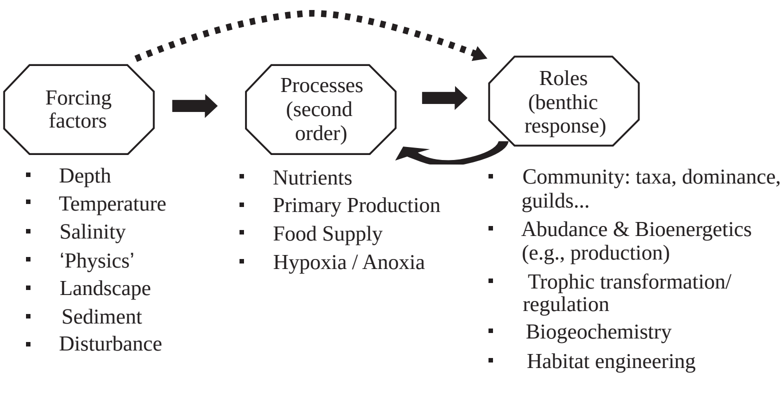

Fig. 1. Conceptual view of coastal system showing relationships among key forcing factors that interact with geomorphological/hydrodynamic attributes to shape processes that affect primary production and food supplies and ultimately the nature of benthic communities in these systems. There is a feedback from the benthic systems to the second order processes. The dotted arrow indicates that it may be possible to predict benthic communities and the roles they play directly from the forcing factors to the extent that they may be related to the geomorphological/hydrodynamic attributes of the system.

Determining the cause and effect relationships for these dynamics is a key challenge for ecologists working in the coastal zone. However, linking primary forcing factors, secondary processes and benthic functional roles is extremely difficult given the complexity of the ecological components of the systems, the details of their interactions, and natural variability that can cause signals to be masked by system noise. As argued above, it is desirable to predict the general characteristics of benthic communities and the roles they play in coastal systems directly from the primary forcing factors. The degree to which this is possible may be related to the degree of connectivity between the forcing factors and the geomorphological and hydrodynamic attributes of the system. Based on the various coastal zone classification schemes that have already been or currently are being developed (see above) it seems reasonable to assume that this relationship is strong and that some aspect of the geomorphological attributes of a large estuary or coastal sea may provide a useful indication of the nature of the benthic communities and their potential contribution to overall system dynamics. To this end we ask two basic questions: 1) Can structural characteristics of coastal seas and estuaries be identified that accurately predict benthic structure and function, and if so, 2) what are the working hypotheses that can be generated to test benthic ecosystem processes at different spatial and temporal scales relative to these characteristics?

3.2. The modular composition of estuaries and coastal seas

We suggest that coastal seas and estuaries can be characterized by a mixture of large- and meso-scale individual geomorphological elements which we term modules. At the present stage of development, we have identified six distinct types of modules; these include dendritic, insular, tidal rivers, enclosed basins, open bays and lagoons (Fig. 2) and their associated properties (Table 1). Most coastal systems and large estuaries can be characterized by one or more of these modules depending on the overall complexity of their geomorphology and coastline. For example, all six types of modules are found in San Francisco Bay, USA, each of which makes up a different percentage of the entire system (Fig. 3). In this case, the open bay and enclosed basin modules comprised most of the system with smaller portions of each of the other modules. Based on our familiarity of geographic locations that we work in, we characterized the module composition of 14 coastal systems (Table 2). For each, we identified component

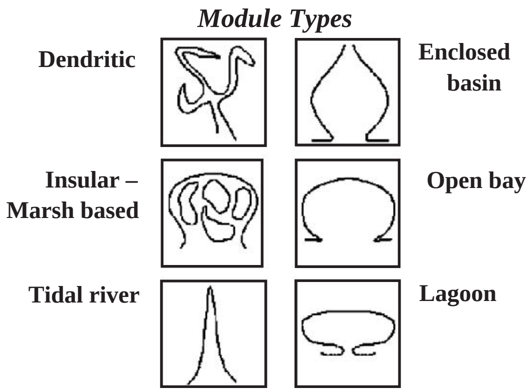

Fig. 2. Idealized module types based on system morphology that can be used to classify whole systems or portions of complex coastal seas and estuaries.

modules and estimated their percent composition by area. We used these estimates to perform a non-metric multidimensional scaling (MDS) ordination, using PRIMER software (Clarke and Warwick, 2001; Clarke and Gorley, 2001), to determine groupings of the systems examined based on module composition (Fig. 4). Based on this analysis, it is possible to distinguish systems that are primarily comprised by one or two modules. There are distinct separations among systems that are primarily lagoonal in nature (e.g., the Texas lagoons, Indian River, Ria Formosa), those that are mainly comprised of open bay modules (e.g., Narragansett Bay), those that have significant tidal river components (e.g., Chesapeake Bay, the Mira River) and those that are mostly comprised of an enclosed basin (e.g., Long Island Sound, Gullmarsfjord). Several of the systems in the center of the MDS space have variable module composition, including Chesapeake Bay and San Francisco Bay. If benthic community composition is related to module composition, then the contribution of the benthos to overall ecosystem dynamics may be quite complex in these systems, relative to those which are characterized by only a few module types (i.e. systems on the periphery of the overall distribution of the systems within the MDS plot; Fig. 4). Therefore, a critical question is, “To what extent is the benthic ecology of these rather diverse coastal systems related to system geomorphological components which we classified as modules?”

3.3. An example: relating module composition and benthic functional groups

We conducted several analyses to assess if breaking down coastal seas and estuaries into component

Table 1
General characteristics of the modules illustrated in Fig. 2

Module Type	Geomorphology	Flow patterns	Examples	Ecological features
Dendritic	Branching, sinuous, narrow	Tidal flow channeled into many hydrologic sub-systems	Large delta areas; marsh systems	Large amount of edges, shallow, depositional, nursery areas
Insular	Islands of terrestrial or marsh habitat completely surrounded by water	High degree of channelization with potentially complex water flow networks	Aaland Sea (Baltic); portions of salt marsh and mangrove systems; portions of Puget Sound	Repositories for sediments and nutrients; nursery areas for early life stages of mobile megafauna (fish and crustaceans)
Tidal rivers	Fairly direct course to adjacent sea/ocean, relatively narrow and deep?	Estuarine circulation with localized turbidity maximum; tidal cycle influence including sediment resuspension	Canal de Mira, Portugal portions of Chesapeake Bay	Often provides a link between the dendritic module and open water
Enclosed basins	Broad basin with relatively small opening to coastal waters	Dominant influence of freshwater input; estuarine circulation	Long Island Sound; Fjords; portions of San Francisco Bay; Sea of Cortez: portions of Chesapeake Bay. Mobile Bay	Physical and biological variables typically change over relatively short time periods
Open bays	Opening to open sea/ocean is large and can be wider than rest of system	Dominant influence of oceanic processes; physical and biological variables fairly stable; circulation other than 'estuarine'	Tampa Bay, USA Monterey Bay, USA Delaware Bay, USA Severn Estuary, UK	Pulsing is minimal gradients are minimal
Lagoon	Shallow, narrow system with small but potential multiple openings to sea/ocean	Significant wind-driven circulation	Lagoons along coast of Texas, USA; Laguna de Madre, Mexico	Potentially large fluctuations in environmental conditions, critical nursery habitat

modules has any utility for predicting potential contributions of benthos to system dynamics. We first determined if there were any discernable differences in benthic communities among the systems and then whether any trends in benthic composition were related to differences in their modular composition. For each coastal system investigated, we assembled data on their physical attributes and the composition of the major benthic infaunal species that are found in the systems. The faunal lists for each system were then reviewed and species were assigned to functional groups using criteria developed by Fauchald and Jumars (1979) and Pearson

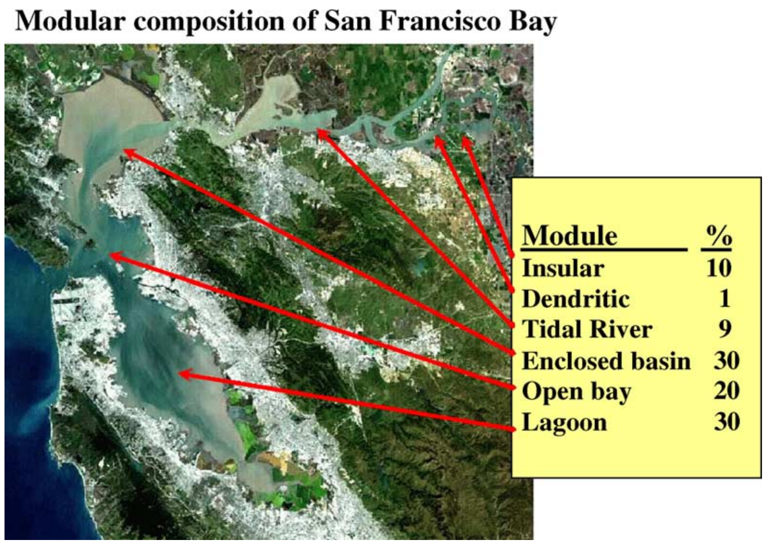

Fig. 3. Example of how a coastal system can be divided into component modules based on geomorphologic attributes. The insular module in this case is marsh-based and primarily comprised of salt marsh elements.

Table 2
Modular composition as percent coverage of several coastal seas and estuaries

System	Code	Dendritic	Insular	Tidal river	Enclosed basin	Open bay	Lagoon
Canal de Mira	CM-RA	5	10	15	30	0	40
Gullmars Fjord	GULLM	0	0	0	90	0	10
Ria de Arosa	AROSA	0	0	0	50	50	0
Ria Formosa	FORM	16	40	0	3	0	41
Narragansett Bay	NARR	0	4	8	26	62	0
Indian River Lagoon	IRL	0	9	11	34	0	46
Mobile Bay	MB	5	50	4	0	40	0
Texas Lagoons	TX	0	5	10	40	0	45
San Francisco Bay	SFB	1	10	9	30	30	20
Mira Estuary	MIRA	0	10	90	0	0	0
Puget Sound	PS	30	5	5	60	0	0
Long Island Sound	LIS	1	3	6	90	0	0
Kattagat	KAT	0	0	10	60	30	0
Chesapeake Bay	CB	1.5	1.5	48	49	0	0

(2001) (Fig. 5; Table 3). We focused our assessment on functional groups rather than species lists as these may provide a better predictor of how the benthos interacts with other system components and dynamics as outlined in Fig. 1 (see also discussions in Huryn and Wallace, 1987; Pearson, 2001).

A MDS analysis indicated that there are distinguishable trends in benthic functional group composition among the coastal systems considered (Fig. 6). For example, distinct separations occur among systems that contain more water column feeders, and those that have greater proportions of interface feeders. To assess whether trends in module composition correspond to benthic functional group composition across coastal systems we used the RELATE procedure in PRIMER.

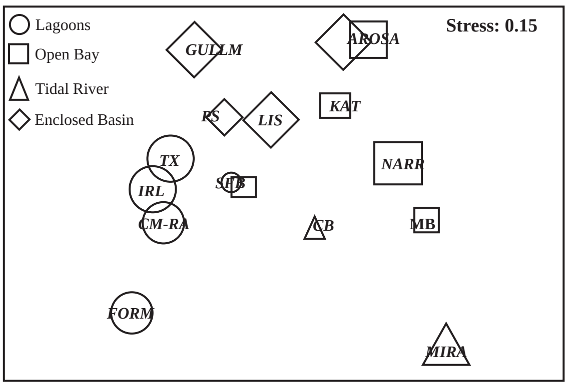

Fig. 4. Results of MDS ordination of coastal systems based on module composition. See Table 2 for system codes. Symbols are used to highlight those systems that are primarily comprised by specific modules. Size of symbol reflects the relative proportion of a particular module in the system. A Bray–Curtis similarity function was used and the data were log transformed and standardized. Stress refers to the fit of the data in the ordination (and indicates a moderately good fit in this case).

This is a Procustes-like analysis that assesses the degree of correspondence between matrices and via a randomization test provides a measure of statistical significance of the relationship (Clarke and Gorley, 2001). The results indicated that there was a significant relationship among the module and functional group compositions of the systems (Spearman rank correlation statistic (Rho) = 0.334, ($p < 0.007$) for 999 permutations). Several trends were evident (Fig. 7). In systems comprised of primarily lagoon-type modules, there are more scavengers and browsers, whereas interface feeders dominate systems which have large areas of enclosed basins and/or lagoons. In coastal systems which have large areas of open bay, functional group composition is dominated by water-column feeders. An assessment of the underlying determinants of these relationships is beyond the scope of this paper, but we can speculate that perhaps forcing factors that act on food supply for each functional group may be key variables. For example, in enclosed basins and lagoons food materials may more readily accumulate at the sediment surface that in other module types, thus supporting interface feeders. Similarly, current systems and water column dynamics in open bays may provide more food to water column feeders.

Our analyses suggest that module composition may be a good predictor of the scope and importance of particular benthic processes in coastal seas, and that the module approach may provide other insights in terms of relating benthic processes to the dynamics of coastal seas. For example, in systems that have a large proportion of enclosed areas where interface feeders dominate, benthic pelagic exchange may not be as great as in systems where suspension feeders dominate. However, our ability to draw out and eventually test any such relationships may be enhanced by a more in depth consideration of module characteristics and in

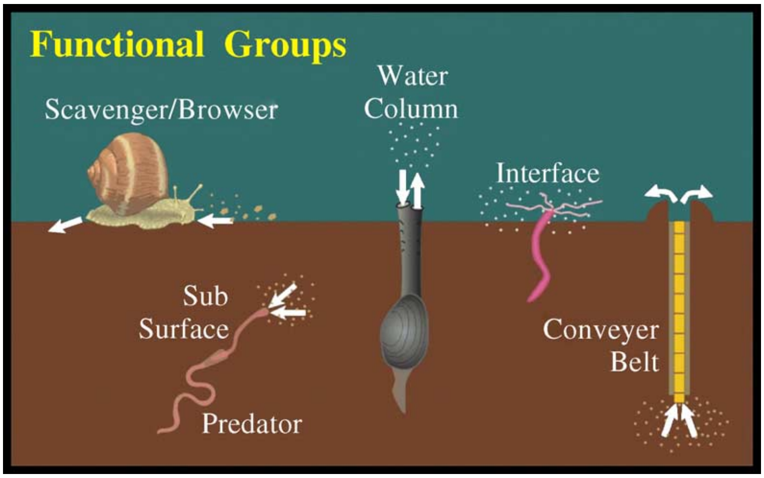

Fig. 5. Functional groups used to classify species identified as being ecologically important in the coastal systems identified in Table 2.

turn relating these to information on benthic structure and function.

4. Extending the module approach, related hypotheses, and looking forward

Coastal systems are likely to be comprised of several types of modules, and the modules have inherent characteristics such as size, shape, depth, tidal range and spatial position within a particular system. These can be quantified using established metrics that have been developed in landscape ecology and are beginning to be applied in the study of coastal systems (e.g. Bartley

Table 3
Functional group composition (percent of species identified as ecologically important in each system) estimates for coastal systems/ estuaries

	Conv	Infc	Pred	Scbrw	Subsrf	Watcol
Canal de Mira	0	67	0	13	20	0
Gullmars Fjord	11	67	0	0	0	22
Ria de Arosa	20	80	0	0	0	0
Ria Formosa	8	17	8	25	17	25
Narragansett Bay	13	38	12	0	0	37
Indian River Lagoon	20	40	0	20	20	0
Mobile Bay	22	28	17	17	5	11
Texas Lagoons	14	57	0	14	0	14
San Francisco Bay	0	56	0	0	11	33
Mira Estuary	0	25	25	0	0	50
Puget Sound	16	50	0	16	0	16
Long Island Sound	10	60	10	0	10	10
Kattagat	11	33	0	0	11	44
Chesapeake Bay	11	33	22	0	22	11

Functional groups are as follows: Conv, conveyer belt species; Infc, interface and water column feeder; Pred, predator; Scbrw, scavenger/ browser; Subsrf, sub-surface feeder; Watcol, water column feeder. A listing of ecologically important species in each system was developed by co-authors most familiar with each of the systems examined. The lists were based on the authors' knowledge of the system and available publications on each system, and strove to identify dominant taxa across the entire system. These data were then converted to percent composition by functional group.

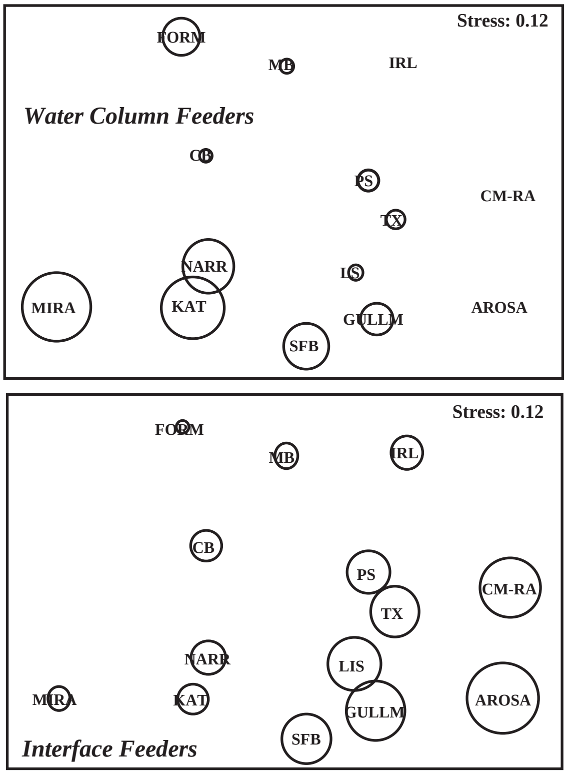

Fig. 6. Results of MDS analysis showing relationships among estuarine and coastal systems based on differences in benthic functional group composition. Shown are trends in relative proportions of water column feeders and interface feeders among the systems considered. The larger the bubble the greater proportion of that functional group in the system.

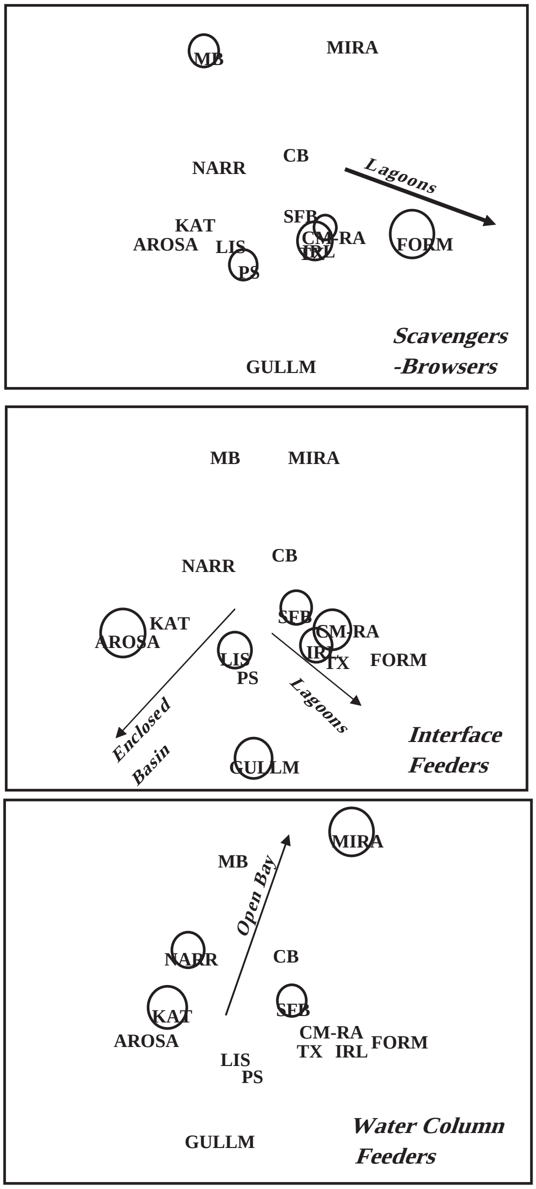

Fig. 7. Results of analyses comparing the relationships among coastal systems and estuaries based on their modular and benthic functional group compositions. The analysis was conducted using the Relate procedure in PRIMER. Shown are the relative proportions of different functional groups in each system superimposed on the separation based on modular composition. The size of the bubble at each site indicates the relative proportion of a particular functional group at that site. The arrows indicate directional trends in the MDS plot relating module composition to functional group composition.

et al., 2001; Liu and Cameron, 2001). Furthermore, any individual module of a coastal system is comprised of a surrounding terrestrial landscape, the overlying water column seascape and the sea floor benthic landscape (or benthoscape). To explore relationships between modules and benthic pattern and process, the characteristics of the modules and their component 'scapes" can be quantified by using a set of metrics for both the modules themselves and their component "scapes." For example, modules can be characterized in detail by their size, shape, hypsography and tidal regimes (e.g. Roy et al., 2001; Saintilan, 2004), whereas component elements of the "scapes" can be characterized by patch composition (e.g. sediment type, patch size and spatial arrangement) (e.g., Zajac, 1999; Bell et al., 2001). It is likely that there will be some subset of metrics that best captures their characteristics, similar to those found for terrestrial landscapes (Ritters et al., 1995).

Extending the application of decomposing complex systems into their component modules may also help in generating testable hypotheses relating module and "scape" characteristics to the role benthic communities play in coastal seas and estuaries. For example, we might expect that certain attributes of the benthos and relationships to surrounding landscape features may change as individual module size increases. Fig. 8 illustrates two such possibilities. In one case we hypothesize that as module size increases, benthoscape and seascape variation across the module increases, potentially indicating more complex roles played by the benthos in system functioning. We can also hypothesize that as module size increases the relative influence of the bounding landscape on the module decreases (note, we do not mean watersheds draining into a module, but rather the landscape directly bounding the module).

Our objective was not to develop a new coastal classification scheme per se, but rather to explore relationships between simple geomorphological topologies typically found in coastal environments and relate these to ecological characteristics and dynamics of the

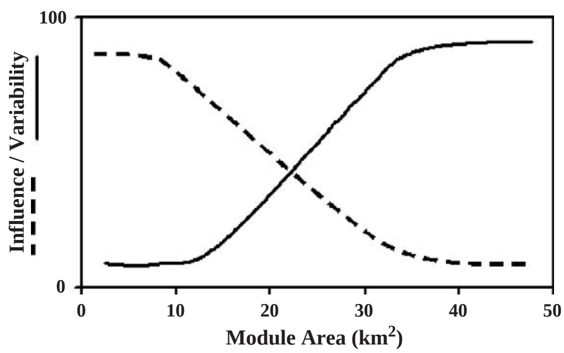

Fig. 8. Hypothesized relationships between module area and a) the variability of benthic characteristics in the module (solid line) and b) the influence of the landscape directly bounding the module (dotted line). The module area scale is illustrative only; the y axis is relative with 0 denoting low variability/influence and 100 denoting high variability/influence.

sea floor. Looking at habitats and ecosystems in new ways to gain better insights into fundamental ecological problems has long been a mainstay of ecological research. The general relationships we have described here might be incorporated into more detailed classification schemes as outlined above, or coupled with other approaches (e.g., Bartley et al., 2001), to decipher relationships among classification variables and benthic communities and populations. In addition, they can be used to identify how key functional roles of benthic systems may differ across a variety of coastal systems, and what are the factors that cause them to differ. It is also possible that the modular approach might be used to further partition component modules in a system into smaller elements, and apply the concept on smaller spatial scales. In the future we may be able to make connections over multiple spatial and temporal scales, including regional and global-scales and eventually build up an ecological geography of the sea floor and link it to water-column patterns that we see (e.g. Longhurst, 1998). Modules may be an efficient way of making these linkages and to develop testable predictions regarding the importance of the benthos to coastal dynamics across space and time.

Acknowledgments

The ideas expressed in this paper were developed as part of the Navigator Project, the goal of which is to develop a framework for studying and understanding the roles benthos plays in coastal seas and estuaries. Workshops were held in Lisbon Portugal in March 2000, and in December 2000 at the Department of Marine Sciences, University of Connecticut. Funding was provided by the Luso–American Development Foundation (FLAD) and United States National Science Foundation. We express our warmest thanks to Charles Buchanan, FLAD, for his extensive support and hospitality. Fig. 5 was illustrated by Fran Younger at the Chesapeake Biological Laboratory. Comments and suggestions by Erik Bonsdorff and an anonymous reviewer greatly enhanced the manuscript. We also wish to express our deep sadness at the untimely passing of our co-author Martin Sprung. **[SS]**

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