Physical Energy Regimes, Seabed Dynamics, and Organism-Sediment Interactions Along an Estuarine Gradient

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Abstract: Using the muddy, microtidal York River-Lower Chesapeake Bay (YR-LCB) system as an example, we develop a conceptual framework of organism-sediment-flow interactions along an estuarine gradient. In the turbidity maximum region of the upper estuary, we found evidence for frequent, intense tidally-driven physical disturbance of the seabed. Macrofauna assemblages are impoverished, bioturbation rates are low, and macrofauna influence sediment structure primarily via pelletization. Bivalve biomass peaks at the down-estuary limit of the turbidity maximum. The middle estuary, a region characterized by reduced tidal and wave energy, periodic summertime hypoxia, and a higher potential for long-term sediment accumulation, has few large or deep-dwelling infauna but supports populations of rapidly growing suspension-feeding epifauna. Physical disturbance of the seabed of the lower estuary is minimal and is driven primarily by winter storms. Macrofauna density and non-bivalve biomass reach a maximum and the diverse faunal assemblage has major effects on seabed dynamics. Thus, our results demonstrate complex and changing organism-sediment-flow interactions along the YR-LCB estuarine gradient, with significant implications for benthic community structure and function. Future investigations of biological processes in this and other estuarine systems should explicitly consider potential interactive effects of benthic boundary layer processes, salinity, and other major environmental factors.

Introduction

The physical dynamics of aquatic systems have important implications for benthic community structure and function (Nixon 1988; Mann & Lazier 1996). Rhoads and colleagues (Rhoads et al. 1977, 1978; Rhoads & Boyer 1982; Rhoads & Germano 1982, 1986) emphasized the effects of physical processes on benthic biology when they developed a successional model relating benthic community structure and function to physical disturbance of muddy seafaths by natural or anthropogenic processes. Benthic boundary layer processes influence benthic communities through effects on feeding, growth, larval settlement and recruitment processes, population dynamics, biotic interactions, and ecosystem-level processes (Hall 1994; Ólafsson et al. 1994; Snelgrove & Butman 1994). Seabed dynamics have broader implications for benthic biology via effects on organic matter
transformations and nutrient cycling (Nixon 1988; Aller 1998), primary productivity (Monbet 1992), and pollutant transport, fate, and effects (Schaffner et al. 1997; DellaPenna et al. 1998). The net effects on benthic communities may be positive or negative (Aller 1989; Hall 1994).

Linking benthic boundary layer physical processes and seabed dynamics with estuarine benthic biology remains a challenge because estuaries exhibit high physical variability at various ecologically relevant spatial and temporal scales (Wright et al. 1987; Cloern 1996). Tides, currents, and waves can change dramatically along and across an estuary and temporally within a given region (Wright et al. 1987; Dalrymple et al. 1992). Moderate physical mixing of the water column favors benthic-pelagic coupling and the development of productive benthic communities, which enhances the potential for significant organism effects on seabed processes (Nixon 1988). But, physical processes also influence sediment disturbance regimes (Aller 1989; Hall 1994), and may limit benthic communities via effects tied to erosion and deposition processes (Rhoads et al. 1978; Rhoads & Boyer 1982; Emerson 1989; Wildish & Kristmanson 1997). The potential for complex interactions among a suite of physical and biological processes in the benthic boundary layer region of estuarine systems is very high.

Recent investigations of the York River-Lower Chesapeake Bay (YR-LCB) estuarine system provide a new framework for elucidating relationships among physical energy regimes, seabed dynamics, and benthic biology. We have used a transdisciplinary approach to identify major processes and process interactions operating along the estuarine gradient of this muddy, microtidal system. Potential implications of benthic boundary layer processes for estuarine benthic community structure and function are discussed.

Data Sources

The general environmental setting of the YR-LCB system has been detailed recently in DellaPenna et al. (1998). Specific data for the system are available as follows (or references therein):

- grain size and minor sediment structures, Schaffner et al. (1987a,b), Wright et al. (1997) DellaPenna et al. (1998), DellaPenna (1999), Hinchey (unpublished)
- benthic fauna from monitoring stations of the York River (stations RET4.3, LE4.1, LE4.3b) and lower bay (station CB7.3e), Dauer (1997)
- additional information on macrobenthos, Boesch (1977), Dauer et al. (1987), Schaffner (1990), Sagasti et al. (2000), Hinchey (unpublished)
- bioturbation processes, Schaffner et al. (1997), DellaPenna et al. (1998), DellaPenna (1999)

The Estuarine Environmental Setting

The York River, a subestuary of Chesapeake Bay, forms at the confluence of two smaller tributaries and links to the coastal ocean through the lower bay (Fig. 1). The YR-LCB system encompasses most of the estuarine salinity gradient, with average bottom salinities ranging from 5% to >25% (Fig. 2). Salinity is seasonally low during spring periods of high freshwater runoff; variations during a tidal cycle typically are less than 5% at any given location (Boesch 1977).
Fig. 1. Base map showing the location of major study areas within the York River-Lower Chesapeake Bay estuarine system.

Fig. 2. A conceptual diagram of major physical processes, seabed dynamics, and organism-sediment interactions along the York River-Lower Chesapeake Bay estuarine gradient. The numbers 1 to 4 show the positions of major study areas. Arrows in the upper panel depict major sediment resuspension and transport pathways.
Water temperatures seasonally range between 2°C and 28°C. Short periods of bottom water hypoxia occur in the lower York during summer periods of neap tide and strong water column stratification (Pihl et al. 1991). Primary productivity is high throughout the estuary (Kemp et al. 1997; Sin et al. 1999). Through most of its length the York is characterized by a single channel (9 m to 25 m depth) flanked by narrow to broad shoals, while the lower bay channels (depths > 13 m) incise an expansive “plains” region (depths of 10–13 m), bordered by broad shoals (Fig. 2). Sediments grade from muds in the York River to sandy silts in the lower bay.

Benthic boundary layer hydrodynamic processes of the YR-LCB are driven mostly by tides and waves. Although classified as microtidal (spring tide range < 2 m; Nichols & Biggs 1985), tidal currents in the mid to upper York are strong enough to cause significant sediment resuspension (Fig. 3a). Wind wave and wind-driven current effects are minimal due to limited fetch (Dellipenna 1999), and riverine effects are low because freshwater inputs are low (Schaffner et al. unpublished). Tidal currents cause little direct sediment resuspension in the lower bay (Fig. 3b), but interactions between waves and tides enhance resuspension and are strongest during the stormy winter months (Wright et al. 1997). Physical energy is at a minimum in the broad, deep lower York River (Schaffner et al. unpublished).

Seabed Dynamics Along an Estuarine Gradient

Regional processes leading to sediment accumulation and reworking in estuaries have been well described in the literature, with numerous examples from the Chesapeake Bay system. In general, fine particles transported into an estuary from both the river and the ocean are moved toward mid-estuary by a combination of river flow, estuarine circulation, barotropic tidal asymmetry, and pumping associated with variations in stratification (Nichols et al. 1991; Dalrymple et al. 1992; Geyer 1993; Friedrichs et al. 1998). An estuary’s trapping efficiency depends on its effective volumetric capacity (manifested in water depth) in relation to sediment inputs and the energy available for sediment transport (Nichols & Biggs 1985). The Chesapeake Bay system is largely a net sediment sink because it is undergoing submergence associated with sea-level rise and it remains underfilled since the last
Benthic Processes Along an Estuarine Gradient

Fig. 4. X-radiographs of sediment cores from four study areas located along the York River-Lower Chesapeake Bay estuarine gradient. a) Area 1-channel, June 1981; b) Area 2-channel, June 1981; c) Area 3-channel flank, June 1988; d) Area 3-channel, June 1988; e) Area 4-channel flank, January 1995. Abbreviations as follows: (cp) bisected tube of the polychaete Chaetopterus pergamentaceus; (er) erosional surfaces; (im) tubes of the polychaete Loimia medusa; (mb) Macoma balthica; (ob) open burrow; (rb) relict burrow; (sl) storm layer.

Sediments accumulate in areas of reduced physical energy, such as fringing marshes and marginal embayments, and also in areas of flow convergence, such as at the head of the estuary and along channel margins (Nichols et al. 1991; Geyer et al. 1997; Friedrichs et al. 1998). Fluid mud layers and estuarine turbidity maxima develop in convergence zones when tides, wind waves, or wind-driven currents resuspend fine sediments from underconsolidated mud layers (Nichols & Biggs 1985; Geyer 1993; Uncles et al. 1994). Turbidity maxima typically are characterized by sediment concentrations 10–100 times higher than those either in the river or farther seaward in the estuary (Nichols & Biggs 1985). The frequency and depth of physical sediment disturbance in these areas depends on interactions of regional to local sediment inputs and the local physical energy regime (Nichols et al. 1991; Dellapenna et al. 1998).

The upper to middle York is characterized by a dynamic estuarine turbidity maximum and the seabed of the region records many cycles of erosion and deposition (Fig. 4a, b). Erosional surfaces separate packets of sediment a few centimeters to 10’s of centimeters in thickness. Primary sediment structures (e.g., laminations) are the dominant features. Due to significant physical reworking of the seabed, estimated decadal scale sediment accumulation rates are generally less than 1.0 cm yr⁻¹. Storms provide a mechanism for deep seabed disturbance (on order of 10’s to 100+ cm), while tides provide the major energy source for short-term (i.e., weeks to months) erosion processes within the larger storm layers, via the creation and destruction of seabed features such as erosional furrows (Dellapenna et al. 1998; Dellapenna 1999).

The transition from the mid to lower York River is marked by significant increases in depth and cross-sectional area, moderated physical energy near the seabed, and enhanced potential for long-term sediment accumulation (Dellapenna 1999). Sediments on the channel flanks appear nearly or completely bioturbated (Fig. 4c), but estimated bioturbation rates are relatively low (Fig. 5; Dellapenna 1999), suggesting low rates of physical disturbance of the seabed. In contrast, x-radiographs of cores
Fig. 5. Relative rates of bioturbation by macrofauna assemblages along the York River-Lower Chesapeake Bay estuarine gradient. Values are based on $^{210}$Pb profiles (Dellapenna et al. 1998; Dellapenna 1999), and therefore represents relatively long-term mixing rates. The seasonal patterns of bioturbation within the sediment are based on results presented in Schaffner et al. (1997). The upper estuary corresponds with the middle to upper York River (study areas 1 and 2), the middle estuary corresponds with the lower York (study area 3) and the lower estuary corresponds with the lower Chesapeake Bay (study area 4). See Fig. 2 for further delineation of major estuarine regions.

taken in the main channel axis reveal a greater degree of physical sediment structuring (Fig. 4d). Dellapenna (1999) reported evidence for high short-term deposition and two decadal scale mixing events in the channel of the lower York. The deeper mixing event (> 1 m) may reflect the passage of Hurricane Camille (in 1969) or Hurricane Agnes (in 1972). A mechanism for the shallower physical mixing is discussed below.

Sediment accumulation rates are low (< 0.1 cm yr$^{-1}$) and bioturbation controls seabed mixing throughout much of the lower bay (Fig. 4e). Based on $^{210}$Pb and $^{137}$Cs profiles, the estimated biological sediment mixing depths at two sites (water depths range from 11 to 15 m) studied by Dellapenna et al. (1998) were 25 cm and 40 cm and biodiffusivity ranged from 6 cm$^2$ yr$^{-1}$ to > 80 cm$^2$ yr$^{-1}$. Both Schaffner et al. (1987a) and Dellapenna et al. (1998) reported evidence for physical reworking of near-surface sediment (generally < 5 cm) at sites in the lower estuary during the winter and early spring months (Fig. 4e), but not during other seasons.

**Organism-Sediment Interactions**

Trends of increasing macrofauna abundance down-estuary, maximum biomass of bivalves near the down-estuary limit of the estuarine turbidity maximum, and increasing non-bivalve biomass toward the lower estuary are apparent in the time series monitoring data for the YR-LCB system (Figs. 6 & 7; Table 1). Species richness, measured as the total number of species collected at each monitoring station over an 11-yr period, increases down-estuary, from a low of approximately 40 species in the upper estuary to a high of approximately 150 species in the lower estuary. This is consistent with the general patterns in species richness observed for macrofauna in estuarine and other brackish water systems, worldwide.
Small annelids, peracarid crustaceans, and bivalves (Table 1) numerically dominate the upper estuary fauna. Most are active bioturbators or bioirrigators of surface sediments (Fig. 7 & Table 1). Suspension feeders and sedentary epifauna are rare, consistent with the effects of high turbidity and lack of suitable substrate in the region of the estuarine turbidity maximum (Warwick et al. 1991). Head down deposit-feeding oligochaetes reach high densities locally and may be responsible for the significant sediment pelletization observed (Fig. 8). Bioturbation is largely overshadowed by physical sediment reworking in the sediment record (Fig. 4a,b), but intense bioturbation and pelletization of surface sediments have significant implications for local sediment transport, biogeochemistry, and contaminant processes (Aller 1982; Rhoads & Boyer 1982; Karickhoff & Morris 1985). Adult clams, especially *Cyrtopleura costata*, produce burrow structures that are the only conspicuous biogenic features preserved in sediments of the upper to middle York; some have diameters exceeding 5 cm and lengths exceeding 60 cm. The presence of these large burrows may enhance local subduction of surface sediment (Dellapenna et al. 1998; Dellapenna 1999).

Small capitellid and spionid polychaetes dominate the lower York fauna, mid-way along the estuarine salinity gradient (Fig. 7 & Table 1). The occasional biomass dominant, *Mercenaria mercenaria*, is a sedentary suspension feeder (Table 1), which tends to be more common in shallow water. Deep-dwelling infauna are rare in the channel-flank subenvironments, consistent with the effects of summertime hypoxia. Juveniles of the head-down deposit-feeding polychaete *Pectinaria gouldii* reach high densities locally, but adults are rare. Bioturbation is subdued, except at the sediment-water interface (Fig. 5). Although not well-documented in monitoring surveys, suspension-feeding epifauna are surprisingly abundant in the lower York. Side-scan sonar records and direct diver observations, made in various seasons and years, indicate that these organisms form conspicuous, sediment-laden mounds in a range of water depths. The mounds can be quite large, exceeding 10 m or more in length and 1 m in width, with elevations of 10's of centimeters above the
Table 1. Region of abundance, depth distribution, living position and biogenic sediment alteration for the characteristic taxa of the YR-LCB study area. Major taxa are as follows: (A) Amphipoda; (An) Anthozoa; (B) Bivalvia; (C) Cumacea; (D) Decapoda; (H) Hydrozoa; (O) Oligochaeta; (Op) Ophiuroidea; (P) Polychaeta; (St) Stomatopoda; (U) Urochordata. Region of abundance categories are (U) upper estuary, (M) middle estuary, (L) lower estuary. Living positions as follows: E, epifaunal; TE, tubiculous, epifaunal; TI, tubiculous, infaunal; MB, mobile burrowing, infaunal; SB, sedentary burrower, infaunal.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Region of abundance</th>
<th>Depth range (cm)</th>
<th>Living position/ Motility</th>
<th>Biogenic sediment alteration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leptocheirus plumulosus Shoemaker, 1932 (A)</td>
<td>X</td>
<td>0–5</td>
<td>SB, MB</td>
<td>pellets, burrows</td>
</tr>
<tr>
<td>Tubificoides spp. (O)</td>
<td>X</td>
<td>0–5</td>
<td>MB</td>
<td>pellets, advective bioturbation</td>
</tr>
<tr>
<td>Macoma balthica (Linnaeus, 1758), M. mitchelli Dall, 1895 (B)</td>
<td>X</td>
<td>0–40</td>
<td>SB, MB</td>
<td>pellets, burrows</td>
</tr>
<tr>
<td>Cyrtopleura costata (Linnaeus, 1758) (B)</td>
<td>X</td>
<td>0–60+</td>
<td>SB</td>
<td>pellets, burrows</td>
</tr>
<tr>
<td>Leucon americanus Zimmer, 1943 (C)</td>
<td>X</td>
<td>0+</td>
<td>E</td>
<td>bioturbation, biosuspension</td>
</tr>
<tr>
<td>Streblospio benedicti Webster, 1879 (P)</td>
<td>X</td>
<td>0–5</td>
<td>TI</td>
<td>pellets</td>
</tr>
<tr>
<td>Mogula manhattensis (DeKay, 1843) (U)</td>
<td>X</td>
<td>0+</td>
<td>E</td>
<td>biodeposition, pellets</td>
</tr>
<tr>
<td>Asabellides oculata (Webster, 1879) (P)</td>
<td>X</td>
<td>0–2</td>
<td>TI</td>
<td>tubes, pellets</td>
</tr>
<tr>
<td>Mercenaria mercenaria (Linnaeus, 1758) (B)</td>
<td>X</td>
<td>0–10</td>
<td>SB</td>
<td>biodeposition, pellets</td>
</tr>
<tr>
<td>Corophium tuberculatum Shoemaker, 1934 (A)</td>
<td>X X</td>
<td>0–5</td>
<td>TE</td>
<td>tubes, pellets</td>
</tr>
<tr>
<td>Pectinaria gouldi (Verrill, 1873) (P)</td>
<td>X X</td>
<td>0–5</td>
<td>TI</td>
<td>advective bioturbation, biosuspension</td>
</tr>
<tr>
<td>Cirratulidae (P)</td>
<td>X X</td>
<td>0–10</td>
<td>SB</td>
<td>burrows, pellets</td>
</tr>
<tr>
<td>Paraprionospio pinnata (Ehlers, 1901) (P)</td>
<td>X X</td>
<td>0–10</td>
<td>TI</td>
<td>pellets</td>
</tr>
<tr>
<td>Region of abundance</td>
<td>Depth range (cm)</td>
<td>Living position/ Motility</td>
<td>Biogenic sediment alteration</td>
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<tr>
<td>Sertularia argentea Linnaeus, 1758 (H)</td>
<td>X</td>
<td>X</td>
<td>0+</td>
<td>E</td>
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<tr>
<td>Mediomastus ambiseta (Hartman, 1947) (P)</td>
<td>X</td>
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<td>0-5</td>
<td>TI</td>
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<tr>
<td>Loimia medusa (Savigny, 1818) (P)</td>
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<td>X</td>
<td>0-10</td>
<td>TI</td>
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<tr>
<td>Mytilus edulis Linnaeus, 1785 (B)</td>
<td>X</td>
<td></td>
<td>0+</td>
<td>E</td>
</tr>
<tr>
<td>Tellina agilis Stimpson, 1858 (B)</td>
<td>X</td>
<td></td>
<td>0-5</td>
<td>SB</td>
</tr>
<tr>
<td>Macroclymene zonalis (Verrill, 1874) (P)</td>
<td>X</td>
<td></td>
<td>0-15</td>
<td>TI</td>
</tr>
<tr>
<td>Cerianthidae (An)</td>
<td>X</td>
<td></td>
<td>0-15</td>
<td>TI</td>
</tr>
<tr>
<td>Chaetopterus sp.* (P)</td>
<td>X</td>
<td></td>
<td>0-15</td>
<td>TI</td>
</tr>
<tr>
<td>Ensis directus Conrad, 1843 (B)</td>
<td>X</td>
<td></td>
<td>0-20</td>
<td>MB</td>
</tr>
<tr>
<td>Microphiopholus atra (Stimpson, 1852) (Op)</td>
<td>X</td>
<td></td>
<td>0-15</td>
<td>SB</td>
</tr>
<tr>
<td>Squilla empusa Say, 1818 (St)</td>
<td>X</td>
<td></td>
<td>0-60</td>
<td>MB</td>
</tr>
<tr>
<td>Callianassa spp. (D)</td>
<td>X</td>
<td></td>
<td>0-60</td>
<td>MB</td>
</tr>
</tbody>
</table>

* Chaetopterus variopedatus sensu Enders 1909, not C. variopedatus (Renier, 1804); Mary Petersen, Zoological Museum, University of Copenhagen, personal communication.
Fig. 7. A generalized illustration depicting the composition, abundance, size, and living positions of macrofauna assemblages found along the York River-Lower Chesapeake Bay estuarine gradient. The upper estuary corresponds with the middle to upper York River (study areas 1 and 2), the middle estuary corresponds with the lower York (study area 3), and the lower estuary corresponds with the lower Chesapeake Bay (study area 4). See Fig. 2 for further delineation of major estuarine regions.

The lower estuary, bay region supports structurally and functionally diverse benthic assemblages, dominated by polychaetes (Fig. 7 & Table 1). Bioturbation rates reach a maximum for the estuary (Fig. 5), but faunal activities are highly seasonal (Schaffner et al. 1997). An important bioturbator of the lower estuary is the head-down deposit-feeding polychaete Macrocythere zonallis, which produces extensive networks of feeding voids at sediment depths of 10 to 20 cm (Schaffner 1990). Subsurface feeding and surface deposition of fecal mounds (Fig. 11) enhances deep sediment-mixing. Other more sparsely distributed crustaceans and brittlestars contribute to this deep bioturbation (Schaffner 1990; Dellapenna et al. 1998). While sediment resuspension by physical processes
is uncommon, fecal materials deposited at the sediment-water interface are readily transported as bedload during strong spring tides (Wright et al. 1997). An epifaunal suspension-feeding assemblage associated with the tubes of the large, infaunal suspension-feeding polychaete *Chaetopterus* sp. enhances the potential for biodeposition of material from suspension near the bed (Schaffner 1990;

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**Fig. 8.** Biogenic structures of the upper to middle York River estuary (study areas 1 and 2). a) profile image showing a recently eroded sediment-water interface (er), February 1995; b) profile image showing a mobile mud layer (ml) at the sediment-water interface, February 1995; c) fecal pellets (63–125 µm) from a surface sediment sample (0–1 cm) collected in May 1998; intact pellets comprised approximately 20% of the total sample, by weight.

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**Fig. 9.** Biogenic structures of the lower York River estuary (study area 3). a) profile image showing a sediment-water interface with tubes of the polychaete *Asabelides oculata* (as) and an oxygenated burrow (b) of an unidentified organism, February 1995; b) profile image of the hydroid *Sertularia argentea* (sa), February 1995; c) profile image showing a clump of the urochordate *Molgula manhattensis* (mm), February 1995.
Fig. 10. Side-scan sonar image of mounds, consisting of epifauna and sediment, in the channel of the lower York during February 1995. The thin black line bisecting the image is the trackline of the side-scan towfish. The survey transect was perpendicular to the main axis of the channel. The long axes of the mounds are perpendicular to the channel. Each mound has a white “acoustic shadow” on the side that is distant from the towfish. The dark, channel-normal “trails” represent areas of higher acoustic reflectance, relative to the background condition, and are due to the presence of rougher or harder substrate.

Wright et al. 1997). Direct biosuspension of particulate material due to the ejection of feces and pseudofeces produced by polychaetes and bivalves has been observed.

Implications for Benthic Community Structure and Function

In both ecological and evolutionary time frames, estuarine and coastal environments provide a fundamental tradeoff to organisms between the effects of high environmental stress and high resource availability (Bambach 1977; Deeton & Greenberg 1986; Jablonski & Bottjer 1991). High nutrient availability in estuaries leads to high primary and secondary production (Nixon 1988), but the ability of local populations to utilize nutrient resources also depends on the mechanisms, magnitude, and periodicity of environmental stresses (Grime 1977; Menge & Sutherland 1987; Huston 1994). Estuaries are dominated by the relatively few organisms that have the complex adaptations necessary to survive high levels of environmental stress (Deeton & Greenberg 1986).
The fundamental shifts in physical energy regimes and seabed dynamics described above have important implications for benthic community structure and function. While distributions and diversity of estuarine macroinvertebrates and fishes have been shown in many studies to follow primary salinity gradients, these gradients often correlate with variations in other environmental factors, such as turbidity and dissolved oxygen (Boesch 1977; Deeton & Greenberg 1986; Wagner 1999). The relative importance of benthic boundary layer processes, seabed dynamics, and physical sediment disturbance regimes for benthic community structure and function along estuarine gradients remains poorly resolved. Regions of high turbidity associated with sediment trapping and resuspension have been reported for many estuaries around the world (Nichols & Biggs 1985), so it is surprising that effects of turbidity and sediment disturbance processes on estuarine benthic community structure and function are not better documented. In part, this may reflect the difficulties of separating sediment-related effects from salinity effects and the difficulties associated with characterizing the near-bed regime with respect to seabed dynamics and turbidity. Improving technology, the availability of relatively low-cost instrumentation packages and the move to transdisciplinary approaches in science are helping to alleviate these problems.

In a classic paper on estuarine benthos, Boesch (1977) emphasized the role that salinity stress plays in limiting the regional species pool of the middle to upper York. He documented major changes in macrofauna community composition near the 15‰ isohaline (corresponding with the transition from the middle to lower York) and another region of accelerated change in community composition at the transition from the lower York to the lower bay. He attributed the shift at the 15‰ isohaline to a rapid decline of marine euryhaline species, driven primarily by physiological intolerance of low salinity, while the down-estuary shift was attributed to a change in the sedimentary environment. We now know that both regions are characterized by major shifts in physical energy regimes and seabed dynamics. Salinity certainly plays a major role in determining species distribution patterns along the YR-LCB estuarine gradient, but the potential role of benthic boundary layer physical processes and potential interactions with the salinity gradient are now readily apparent. For the YR-LCB system, physical disturbance of the seabed increases concordant with decreases in salinity, making the effects of each stress more difficult to separate, especially without a priori knowledge of benthic boundary layer processes.

In previous studies of other estuarine systems, comparisons of relatively quiescent versus highly energetic subenvironments within a salinity regime have provided some insights into the effects of physical sediment disturbance processes while controlling (somewhat) for salinity effects. For example, in the highly dynamic Columbia River system, the estuarine zone is characterized by both a turbidity maximum and a highly variable salinity regime. Density and standing stocks of benthic infauna are high in protected tidal flat habitats but are comparatively impoverished in the energetic channels (Jones et al. 1990). McLusky et al. (1993) documented a relative impoverishment of subtidal faunas in a comparison of intertidal and subtidal benthic communities in the upper Forth estuary, eastern Scotland, UK. They attributed this to a much greater degree of sediment instability in the estuary’s main channel. Negative effects of strong tidal currents on benthic community structure and function also have been noted by comparing subenvironments within high salinity estuarine and coastal regions. In the macro (hyper) tidal Bay of Fundy estuarine system, low biomass and production, and a predominance of specialized deposit-feeders, usually deep burrowers, characterize the impoverished macrofauna assemblages found in the highest energy areas, where mean current speeds at 1–2 m above the bed exceed 30 cm s⁻¹ (Wildish & Kristmanson 1997). For this system, suspension-feeder biomass peaks in areas characterized by mean current speeds in the range of
Fig. 11. Biogenic structures of the lower bay (study area 4). a) a profile image showing well-bioturbated sediment with feeding voids (fv) of the polychaete *Macroclymene zonalis*, a bisected *Chaetopterus* sp. (cp), and unidentified epifauna (ep). September 1994; b) a plan image showing a burrow of the stomatopod *Squilla empusa* (sq), tube tops of *Chaetopterus* sp. (cp), and fecal coils (fc) of *Macroclymene zonalis*, May 1985; c) a plan image showing clumps of the urochordate *Molgula manhattensis* (mm) and a colony of the hydroid *Sertularia argentea* (sa), all attached to tube tops of *Chaetopterus* sp., April 1985.

10–30 cm s⁻¹, while deposit feeder biomass increases steadily with decreasing current speeds to a maximum in areas where current speeds drop to about 10 cm s⁻¹. Warwick & Uncles (1980) found impoverished benthic communities associated with regions of very high bed stress in the Bristol Channel.

Warwick et al. (1991) argued for substantial effects of sediment instability and high turbidity on estuarine biota by comparing macrobenthic communities among estuaries of southwest Britain. They found clear differences in the faunal composition and the abundance and biomass of individual invertebrate species between the Severn River estuary and five other estuaries studied. The Severn is a large macro (hyper) tidal estuary (tide range > 4 m) characterized by high levels of sediment instability and turbidity (values typically exceed 500 mg l⁻¹) throughout its length, while the other estuaries studied are smaller, have restricted to moderate tidal ranges, and are generally far less turbid. High levels of turbidity occur in the smaller estuaries only at the estuarine turbidity maximum and for only brief periods during summer months when run-off is low. Suspension-feeding invertebrates are absent from the Severn and the dominant species are primarily motile forms, whereas suspension feeders and sedentary species are abundant in the less dynamic estuaries.

Emerson (1989) found negative relationships between benthic secondary production and wind stress for 201 widely distributed coastal sites. Multiple regression analysis demonstrated that wind stress, tidal height, shelter indices, and water temperature explained approximately 90% of the variance in total benthic secondary production (including micro-, meio-, and macrobenthos), and that neither benthic or pelagic primary production contributed to a significant reduction in the variance
in benthic secondary production. Emerson argued that the effects of wind stress on benthic secondary production are mediated largely by sediment transport and that smaller organisms living near the sediment-water interface are likely to be the most susceptible. Removal of food supply, inhibition of feeding, injury from abrasion, and direct mortality will translate a higher susceptibility to sediment transport into lower secondary production.

Some of the most dramatic examples of faunal impoverishment due to high physical disturbance of muddy seabeds have been recorded for the inner shelf regions off the mouths of large rivers such as the Changjiang and Amazon, where both physical energy and rates of delivery of fine sediments are very high (Rhoads et al. 1985; Aller & Aller 1986; Aller & Stupakoff 1996). These regions are characterized by high turbidity and dynamic seabeds. Areas of highest physical disturbance exhibit reductions in the size, abundance, and reproductive output of macrofauna, increases in the prevalence of shallow-dwelling opportunistic species, decreases in macrofauna diversity, and enhancement of microbial over metazoan productivity. Given that these regions are associated with large river plumes, the faunas may also be influenced to some degree by salinity stress. Benthic habitats in these regions tend to develop more persistent and diverse populations of macrofauna as physical disturbance decreases in space or time.

The success of a few species of bivalves, especially *Macoma balthica* and *Cyrtopleura costata*, in the upper to middle York River estuary is interesting, given the high degree of physical disturbance documented for the seabed. Juvenile *M. balthica* are highly motile and use physical transport processes to facilitate dispersal (Beukema & de Vlas 1989). In both the York and James River subestuaries of lower Chesapeake Bay, the burrowing depths of *M. balthica* increase as they grow; juveniles of 1 cm width are found at ~10 cm and adults of 4 cm width can be found as much as 40 cm below the sediment-water interface (Schaffner et al. 1987a; Hinchey unpublished). Deep burrowing provides a predator refuge for adult clams (Blundon & Kennedy 1982), but in the YR-LCB system it also makes them far less susceptible to physical disturbance, which is most intense in surface sediments.

While a paucity of large or deep-dwelling infauna in the lower York is consistent with effects of physiological stresses due to hypoxia (Diaz & Rosenberg 1995), sediment trapping associated with mounds of epifauna and subsequent transport of these mounds along the seabed might also limit infauna. Given their abundance, the dynamics of successful epifauna and the mounds they form warrant further investigation. Our results demonstrate that side-scan sonar and underwater profile cameras provide rapid and effective means to identify and map the distributions of epifauna assemblages in turbid estuarine waters.

Resident biota of the lower estuary, bay environment experience minimal physical disturbance of the seabed and relatively low physiological stress. This is the region of the estuary where the structural and functional diversity of benthic macrofauna assemblages are highest (Schaffner 1990). Many of the dominant species have maximum life spans that exceed a year and their high standing stocks and relatively high growth rates lead to high secondary production (Diaz & Schaffner 1990; Thompson & Schaffner in press). During the spring and early summer months, following the period when the upper few centimeters of the seabed are disturbed by physical processes, the lower estuary also supports high densities of small, fast-growing species (Schaffner 1990). Both the high standing stock of suspension feeders and high productivity of the macrofauna in this region of the estuary argue for efficient benthic-pelagic coupling (Thompson-Neubauer 2000). The moderate tidal currents observed near the bed in the lower bay can be expected to affect efficient delivery of primary production and removal of waste materials, thereby serving as a source of auxiliary energy (sensu
Mann & Lazier 1996; see also Nixon 1988; Wildish & Kristmanson 1997) to enhance secondary productivity.

Conclusions and Recommendations for Future Work

How representative is the YR-LCB estuarine gradient, and how useful are the results presented here for understanding processes in other estuaries or other marine systems? It can always be argued that, to some extent, each estuary is unique. Our work-in-progress suggests that even the subestuaries of the Chesapeake Bay system vary with respect to physical energy regimes (Schaffner et al. unpublished). Nonetheless, we are encouraged that the organism-sediment-flow interactions we report for the YR-LCB system are consistent with the results reported previously for coastal systems as diverse as the Severn River estuary, Bay of Fundy, and Amazon River shelf environment. Benthic macrofauna assemblages become impoverished when physical energy regimes are sufficient to cause frequent, intense physical disturbance of muddy seabeds. As in many of the studies discussed above, we observed increases in the structural and functional diversity of the macrofauna, increased densities of macrofauna and increased standing stocks of suspension feeders as physical disturbance of the seabed declined. Given that the Chesapeake Bay and its subestuaries are microtidal, we were somewhat surprised by our findings regarding the dynamic nature of seabed processes in the upper York River. Thus, we offer a caveat to those working in muddy, coastal environments. Convergent transport processes operate to enhance the trapping of fine sediment in many estuarine environments. Thus, it can not be assumed that sediment grain size and physical energy regime will correlate in these systems. Underconsolidated muddy sediments may be found in relatively high energy areas where they will be easily mobilized by physical processes.

For the YR-LCB system, the physical sediment disturbance gradient is correlated with the estuarine salinity gradient. This is significant because the size of the regional species pool in estuaries and other bodies of brackish water declines with decreasing salinity, usually reaching a minimum at 5–8‰ (Deeton & Greenberg 1986). Most estuarine organisms are derived from marine species and their up-estuary limits often are set by physiological tolerances of low salinity (Vernberg & Vernberg 1972). The potential for synergistic effects of salinity stress and physical disturbance on macrofauna seems high based on studies of the responses of individuals to multiple physiological stresses (Vernberg & Vernberg 1972). Physical sediment disturbance processes imposed in addition to salinity stress might have greater effects on individuals or populations living near their physiological tolerance limits in the upper estuary than those observed for individuals or populations residing at higher salinities in the middle to lower estuary.

A variety of approaches will be needed to separate the effects of near-bed flow regimes and sediment disturbance processes from the effects of other environmental factors, such as salinity, oxygen, and food availability, that influence the structure and function of estuarine benthic communities. Experimental manipulations of bed disturbance regimes offer the potential for significant control over some variables; however, it will be difficult to reproduce fully the disturbance environment experienced by resident biota, and scaling issues will be a concern. “Natural” physical disturbance events, such as the formation of furrows in the upper middle York, may provide significant insights if effects can be followed in time and space. Comparisons of distinct estuarine subenvironments characterized by different physical energy and salinity regimes (e.g., protected versus exposed areas, high salinity versus low salinity) within single estuaries will provide control over regional differences in the environmental setting (e.g., nutrient or sediment loadings). Following
faunal responses to "natural" disturbance events or comparing subenvironments within a single system offers no control over the regional disturbance regime. The regional disturbance regime has important implications for community dynamics following disturbance events because it influences the size and characteristics of the regional species pool available as potential colonizers (Huston 1994; Palmer et al. 1996). Comparisons among a variety of estuarine systems, particularly those that represent "endmembers" along a gradient of physical energy regimes, can be expected to provide insights regarding the relative importance of disturbance versus other factors that vary among the systems. This approach has been successfully employed to examine the relationships among nutrient loading, tidal energy regime, and primary production in microtidal versus macrotidal estuaries (Monbet 1992).

We urge further investigations of the linkages between physical and biological processes in the benthic boundary layer of estuarine environments using the approaches outlined above. We can envision many interesting and fruitful comparisons with other physically dynamic environments. Estuaries provide a sharp contrast to rocky intertidal environments because of the differences in the nature of the substrates, the mechanisms by which physical disturbance influences the substrate, the nature of the geochemical setting, and differences in taxonomic composition of dominant resident organisms. Characteristics of estuaries, such as high physical variability, high productivity, relatively small size, and ephemeral nature, could make for interesting comparisons with deep-sea vent habitats. Finally, the well-documented effects of physical seabed disturbance processes on biology and chemistry of continental shelf benthic habitats off large river systems have provided important insights for the interpretation of processes operating in a much smaller estuarine system. We predict that a better understanding of processes operating in the benthic boundary layers of estuaries will enhance general understanding of muddy seabed dynamics and help us to understand the ramifications of seabed processes for ecosystem structure and function in a wide variety of marine settings.

Acknowledgments

The Office of Naval Research, Harbor Processes Program (grant N00014-93-1-0986) and the Virginia Institute of Marine Science funded this study. Two anonymous reviewers provided very useful comments that helped us improve the manuscript. We thank Dr. Joseph Kravitz of the Office of Naval Research and Dr. Don Wright of Virginia Institute of Marine Science for their support and guidance during our investigations. The field work that formed the basis of our insights could not have been accomplished without the untiring efforts (and strong backs) of many students, technicians, and vessel operations support staff at the Virginia Institute of Marine Science. We thank them all! Contribution number 2231 of the Virginia Institute of Marine Science.

Literature Cited


**Sources of Unpublished Materials**
