Benthos of the York River

David J. Gillett and Linda C. Schaffner

Virginia Institute of Marine Science
Gloucester Point, VA 23061 U.S.A.

ABSTRACT

Benthic organisms and their communities are key components of estuarine systems. We provide an overview of the biology and key ecological features of benthic communities of York River Estuary (YRE), which is the site of the Chesapeake Bay National Estuarine Research Reserve in Virginia (CBNERRVA). Major subtidal benthic habitats in YRE include soft mud and sand bottoms, with only limited distribution of submerged aquatic vegetation and oyster shell. Major taxonomic groups of macrofauna dominating muds and sands of YRE include annelids, molluscs and crustaceans; similar to those found in other temperate estuaries of the US Mid-Atlantic. Meiofaunal assemblages of YRE soft bottoms are dominated by nematodes and copepods. Species distribution patterns in YRE are strongly correlated with salinity and bottom type, while other factors such as eutrophication and hypoxia may be growing in importance. Much of the YRE benthos fails to meet the restoration goals set by the Chesapeake Bay Program. The poor condition of the benthos is expressed as low biomass and abundance and may be associated with degraded water quality, hypoxia and sediment disturbance processes. No comprehensive inventory of the benthic biota of the CBNERRS sites is available, which will make it difficult to assess future changes due to human impacts such as climate change or the introduction of exotic species. Given this paucity of data, a systemic cataloging of the benthic resources of the reserve sites and any potential invasive species is a much needed avenue of future research for CBNERRVA.

INTRODUCTION TO THE BENTHOS

The soft mud and sand habitats of the York River Estuary, as well as the interspersed patches of aquatic vegetation and oyster shell, support a wide variety of fauna and flora and are an important part of this productive coastal ecosystem. These bottom habitats and their resident organisms are called the benthos, derived from the Greek for "bottom of the sea." The animals comprising benthic communities, the zoobenthos[1], include almost every known phylum and exclusively encompass a number of them. For the purposes of this paper we have limited ourselves to a discussion of the benthic invertebrate residents and their communities of the York River Estuary. This is not to slight the countless numbers of bacteria, Archea, and protozoans that comprise the microbenthos, or the bottom-dwelling fish and crustaceans of the estuary, all of which are discussed in other papers in this issue.

Most benthic invertebrates are quite small and can be clearly distinguished only with the aid of magnification. They are classified into three major groups based on adult size. The smallest are the meiobenthos, which pass through a 500-µm mesh, but are retained on a 63-µm screen. Important taxa of meiobenthos include harpactacoid copepods, nematodes, ostracods and Foraminfera (see Higgins and Thiel, 1988). Macrobenthos are retained on a 500-µm mesh screen and are not readily identifiable without magnification. Annelid worms, bivalves, gastropods, crustaceans, tunicates, and insect larvae are commonly encountered macrobenthos in estuaries. The largest size-based category, the megabenthos, can be identified without magnification because individuals are typically multiple centimeters in size. This group includes animals such as crabs, bivalves, gastropods, sponges, colonial entoprocts and hydrozoans. Benthic organisms may progress through different categories as they grow. Many animals classified as macrobenthos start off as meiobenthic juveniles and are known as "temporary meiobenthos."

Beyond size, the mobility of an animal (motile versus sessile) and how it associates with the sediment or hard substrate (infaunal versus epibenthic) are other common ways benthic organisms are classified. Epibenthic animals live on or just above the substrate. They may be firmly attached (sessile), relatively sedentary, or fully motile. Animals such as barnacles, oysters, sponges, tunicates, entoprocts, gastropods, anthozoans, mud crabs, and certain species of amphipods are common representatives of the epibenthos. Animals that live within the substrate are called infauna and include most species of annelids and bivalves, larval insects, phoronids, as well as some species of amphipods and anthozoans.

MAJOR TAXONOMIC GROUPS OF BENTHIC FAUNA IN THE YORK ESTUARY

A comprehensive checklist of benthic animals in the York River Estuary and the greater Chesapeake Bay was published by Wass (1972). It provides frequency of occurrence and habitat preferences of those animals known at the time. There is no complete benthic invertebrate species list exclusively for the York River system; however, most of the benthic fauna found in the York River Estuary are listed in the regularly updated checklist available for the Chesapeake Bay Benthic

[1]The generic terms *benthos* and *benthic*, which are used to describe the bottom realm, have also been variously used to describe any and all of the organisms, from bacteria and microalgae to seagrasses and demersal predators, that are associated with benthic habitats. Use of the term *zoobenthos* provides more clarity, but in practice is rarely used by benthic ecologists working in the U.S.

Monitoring Program (Llansó, 2005). A partial checklist of benthic organisms in the York River Estuary developed from these and other sources is provided in the Appendix.

Poriferans

Sponges are colonial macro- to megabenthic-sized organisms. They filter feed by pumping water through inhalant and exhalent pores called ostia, trapping particles along the body wall, and ingesting them by phagocytosis (Brusca and Brusca, 1990). Most sponges in the York River Estuary are limited to the meso- to polyhaline reaches. Among the most conspicuous are the red beard (*Microciona prolifera*) and brown (*Haliclona* spp.) sponges, both of which grow attached to hard substrate (Figure 1). *M. prolifera* is frequently seen on pier pilings, while *Haliclona loosanoffi* is commonly found on the blades of submerged aquatic vegetation (SAV). The boring sponges, *Cliona* spp., erode galleries of passageways through calcareous shell of molluscs, which provides protection from predators. These types of sponges are considered nuisance species by commercial shellfish harvesters because the erosion of shell material is detrimental to living molluscs. All of the sponges found in the York River Estuary are capable of both sexual and asexual reproduction. Fragments of a sponge can grow an entire new sponge, given an appropriate substrate. Sexual reproduction in sponges is through broadcast spawning with most species thought to be hermaphroditic, which means that they switch between the production of male and female gametes during different parts of their lives (Brusca and Brusca, 1990).

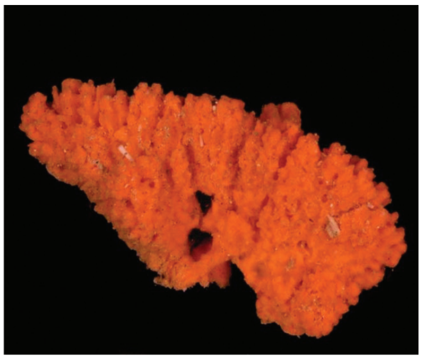

Figure 1. Unidentified red sponge. (Image courtesy of Southeastern Regional Taxonomic Center/South Carolina Department of Natural Resources)

Cnidarians

Representatives of all three classes of cnidarians (Hydrozoa, Anthozoa, and Scyphozoa) have been observed among the macrobenthic fauna of the York River Estuary. All cnidarians possess nematocysts, responsible for the familiar stinging sensation of jellyfish, which they use for both defensive and prey capturing purposes. Hydrozoans, the most conspicuous benthic cnidarians found in the York River Estuary, settle and grow on myriad substrates along the full salinity gradient. As passive filter feeders, hydroids rely on water currents to bring food particles to their feeding tentacles. Hydromedusae are found as solitary individuals and, more commonly, as colonies of many individuals or zooids that can create substantial colonies, extending several centimeters in to the water column. Colonial hydroids are abundant in the lower York River, where the large mounds they form on the bottom support a variety of other macrobenthic organisms (Figure 2) (Schaffner *et al.,* 2001). Hydrozoans have both sexual and asexual reproduction during different stages of their life cycle. Asexually, new hydroid zooids can be budded off an adult in an expansion of the colony, or as separate individuals in the non-colonial forms. Sexual reproduction in hydrozoans, much like the other types of cnidarians, is somewhat more complex. A free-swimming male or female medusa (jellyfish-like) stage is budded off of the benthic adult form, which in turn, releases gametes into the water column that when fertilized, form asexual, benthic individuals (Brusca and Brusca, 1990).

Figure 2. Colonial hydroids from the lower York River. (Image courtesy of Robert Diaz, VIMS)

Though less abundant and less diverse in the York River Estuary than hydrozoans, anthozoan (sea anemones) and scyphozoan (jelly fish) cnidarians are also found within the benthic communities. Like the hydrozoans, benthic anthozoans are passive filter feeders capable of both sexual and asexual reproduction. Anthozoans are non-simultaneous hermaphrodites that can bud off new individuals from the adult form, as well as produce male or female gametes. Anthozoans have lost the free-swimming medusa-stage of other cnidarians. The benthic adults directly release gametes to the water column, where they combine to form planular larvae that settle out of the water to from new benthic adults. Common anthozoans include epibenthic species (e.g., *Diadumene leucolena*) and infaunal species (*Ceriantheopsis americanus*, *Actiniaria* sp. or *Edwardsia elegans*) (Sagasti *et al.*, 2001; Llansó 2005). Scyphozoans are only ephemeral benthic organisms, but the benthic stage is an essential part of their reproductive lifestyle that occurs at various times of the year depending upon the species (see Steinberg and Condon this S.I.). This benthic stage is referred to as a scyphistoma and is an asexual from that buds off the familiar, pelagic medusae seen in the estuary.

Platyhelminthes

Flatworms are a small, relatively obscure component of the benthic community that can be found all along the estuarine salinity gradient. Free-living turbellarian flatworms can be macro- or meiobenthic in size and typically live within the upper few centimeters of sandy or muddy sediments, or on hard substrate (Martens and Schockaert, 1986). The most common estuarine turbellarians prey or scavenge upon the smaller benthos they encounter, such as meiobenthic harpactacoid copepods or nematodes, larger protozoans like Foraminifera, as well as macrobenthic oligochaetes and chironomids (Armitage and Young, 1990). Although living oysters are now uncommon in the York River Estuary, the oyster flatworm *Stylochus ellipticus* remains an important component of the ecosystem's hard substrate benthic community (Sagasti *et al.*, 2000). Parasitic flatworms (trematodes, monogenetic flukes, and cestodes) are also found within the estuary. They live on or within a variety of estuarine fauna, including fish, gastropods, or annelids. Most of the free-living species of turbellarians are hermaphroditic and are capable of both asexual (fission) and sexual (cross-fertilization) reproduction (Brusca and Brusca, 1990).

Nemerteans

Nemerteans are highly mobile, flat, non-segmented worms, commonly referred to as "ribbon worms." They are an ecologically important, though relatively poorly studied, taxonomic group within the benthic community of the York River. Nemerteans (Figure 3) can be quite large (often many centimeters in length) and move through the sediment by ciliary or peristaltic motion in larger species. Some of the largest nemerteans are burrowing predators (e.g., *Cerebratulus lacteus*), which move up from below to capture their prey with an eversible pharynx, which may be armed with a toxin-delivering stylet (Bourque *et al.*, 2002). Some species have quite advanced chemosensory detection capabilities and have been observed tracking potential prey items for some distance before striking (Brusca and Brusca, 1990). These chemosensory capabilities are also used to by nemerteans to track and locate mates for reproduction. Most nemerteans undergo sexual reproduction, with external or internal fertilization depending upon the species. Additionally, some species of the genus *Lineus*, a few species of which are observed in the York River Estuary (Wass, 1972), are also capable of asexual reproduction via fragmentation of the posterior end of the worm.

Figure 3. Unidentified nemertean. (Image courtesy Southeastern Regional Taxonomic Center/South Carolina Department of Natural Resources)

Nematodes

Meiobenthic nematodes are among the most numerically abundant benthic fauna in the York River Estuary (Alongi *et al.*, 1982; Metcalfe, 2005), though given their small size and somewhat obscure taxonomy, little species-specific research has been done on local nematode communities. These small, non-segmented round worms move through the interstitial spaces of sandy and muddy sediments. Nematodes encompass a wide variety of feeding styles, including deposit feeding, grazing, carnivory, interstitial filter-feeding, and parasitism, all of which, excluding the parasitic species, reproduce sexually with internal fertilization.

Entoprocts

Another example of a colonial filter-feeder, entoprocts (formally known as bryozoans) are epibenthos that will attach to almost any hard surface in the poly- and euhaline portions of the York River and other estuaries. Composed of numerous individual zooids, species commonly found in the York River Estuary such as *Pedicellina cernua* (Sagasti *et al.*, 2000), passively feed on passing plankton using ciliated tentacles (Figure 4). Entoprocts will undergo asexual budding within a given colony, but also periodically undergo sexual reproduction, broadcasting larvae into the water column to start new colonies (Brusca and Brusca, 1990). The zooids of entoprocts do not develop specialized functions like those of hydroids, but each individual is a protandric hermaphrodite, capable of both feeding and reproduction.

Figure 4. Unidentified branching, colonial entoproct. (Image courtesy of Southeastern Regional Taxonomic Center/ South Carolina Department of Natural Resources)

Annelids

This group of truly segmented worms includes the polychaetes, oligochaetes, and leeches. The annelids are a numerically abundant and ecologically important component of all benthic communities, including those of the York River Estuary. Within the estuary, annelids range in size from meiobenthic juveniles to megabenthic chaetopterid polychaetes and encompass all major feeding types and living positions.

Polychaetes are the most diverse group of annelids in the saline portions of the York River Estuary, with different species dominating in different salinity zones. *Polydora cornuta* and *Sabellaria vulgaris* are tube building, epibenthos commonly found on SAV or other hard substrates throughout the York River (Orth, 1973; Sagasti *et al.*, 2000). There are also highly mobile carnivores (e.g., *Eteone heteropoda* and *Glycinde solitaria*) with well-developed parapodia and cirri for mobility and sensory organs for tracking prey items (Figure 5). Many species of polychaetes are sessile infauna, living with their heads and feeding appendages at the sediment-water interface (e.g., *Loimia medusa*), or head down in the sediment with their tails at the surface (e.g., *Clymenella torquata*). Deposit feeders ingest bacteria, microalgae and organic matter associated with sediment particles and are common among the polychaetes. Filter-feeding is also common in the sessile

Figure 5. A common polychaete annelid *Neanthes succinea*. (Image courtesy of Southeastern Regional Taxonomic Center/South Carolina Department of Natural Resources)

polychaetes. Some species actively pump water into their tubes/burrows with their parapodia (e.g., *Spiochaetopterus costarum*), while others are capable of switching between passive filter-feeding and surface deposit-feeding with the anterior palps (e.g., *Streblospio benedicti*) (Fauchald and Jumars, 1979). Polychaetes primarily reproduce via sexual reproduction, wherein some species undergo internal fertilization and brood their larvae, while others are broadcast spawners with distinctive planktonic trochophore larvae.

Oligochaete annelids are also found throughout the York River Estuary, but are far less diverse than the polychaetes. They lack parapodia and typically have simple heads, without sensory palps or antennae, though some freshwater taxa have a proboscis for feeding (e.g., family Naidae). All of the oligochaetes found in the York River Estuary are motile, deposit feeders. Members of the genus *Tubificoides*, the naid *Paranais litoralis* and some species of the family Enchytraeidae are found in brackish and saline portions of the estuary. The tidal freshwater region contains a much more diverse assemblage of oligochaetes (e.g., *Limnodrilus hoffmeisteri*, *Aulodrilus templetoni*, *Dero digitata*). This pattern of higher diversity up-estuary reflects the radiation of oligochaetes into the estuary from freshwater systems (Stephenson, 1972). This contrasts with the pattern of diversity increasing with salinity in the estuary seen in many of the other estuarine invertebrates, which are descended from marine forms. All oligochaetes found in the estuary are simultaneously hermaphroditic and reproduce sexually, depositing cocoons into the mud or sand that contain a varied number of zygotes that grow and disperse after release. Some genera of oligochaetes, notably the naids, also reproduce asexually by budding offspring from their posterior regions (Stephenson, 1972). Asexual reproduction is a common means of reproduction during periods of favorable environmental conditions (food availability, temperature, etc.), but most species will switch to sexual reproduction when conditions become unfavorable (Stephenson, 1972).

The last sub-class of annelids found in the York River Estuary is the Hirudinae (leeches). Leeches are closely related to oligochaetes and are likewise simultaneous hermaphrodites with a reduced body structure devoid of parapodia or complex setae. Unlike oligochaetes, leeches reproduce strictly through sexual reproduction, producing cocoons they deposit into the environment. Most species of Hirudinae are exoparasites (e.g., *Myzobdella lugubris*, *Calliobdella vivida*) of other animals, though a few species (e.g., *Helobdella elongata*, *H. stagnalis*) are free-living predators of smaller invertebrates such as nematodes, copepods, or oligochaetes (Wass, 1972; Brusca and Brusca, 1990). Within the York River Estuary, these free-living species are primarily limited to the tidal freshwater and oligohaline waters (J. Williams, pers. comm.).

Echiurans

Echiurans are a phylum of non-segmented, worm-like animals that live in the high mesohaline to polyhaline parts of the estuary. Wass (1972) lists *Thallasema hartmani* as the only species commonly found in the estuary. Echiurans are sessile, surface deposit feeders. They build a tube in the sediment and feed with a long a proboscis that pulls sediment below the surface to the mouth. Echiurans have separate sexes and reproduce sexually in mass spawning events where gametes are released to the water column.

Arthropods

In terms of phylogeny and body form, arthropods are possibly the most diverse group of benthic organisms in the York River. These segmented animals have hard exoskeletons and jointed appendages, but range in form from barnacles to crabs. Arthropods of the estuarine benthic community reproduce via sexual reproduction, typically with external fertilization. Most arthropods are highly motile animals capable of swimming and walking, though barnacles are a notable, sessile exception.

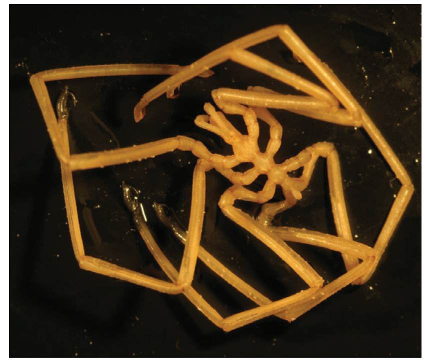

Figure 6. The pycnogonid *Pallenopsis schmitti*. (Image courtesy of D. Gillett)

Pycnogonids, or sea spiders (Class Chelicerata), are epifaunal arthropods (Figure 6) most commonly observed in fouling communities; among tunicates or sponges in the polyhaline and high mesohaline portions of the York River Estuary (e.g., *Anoplodactylus pygmaeus*, *Tanystylum orbiculare*, etc.) (Wass, 1972; Sagasti *et al.*, 2000). These mobile, spider-like arthropods are mostly carnivores, which feed upon other epifauna. There are some herbivores though, which feed on the algae growing in fouling communities (Brusca and Brusca, 1990).

Though they spend only a portion of their lives as benthic fauna, larval insects, predominantly of the Orders Diptera (flies and midges) and Trichoptera (caddis flies), are an important component of the tidal freshwater and oligohaline portions of the York River Estuary. Most families of insect larvae found living within the sediments span a range of feeding modes, from carnivore/scavengers (e.g., *Tanypus* sp.) to grazers (e.g., *Cryptochironomus* sp.). After a few weeks to months in the benthos, chironomid insect larvae metamorphose into adult dipterid and trichopterid flies and leave the system.

Crustaceans are the most taxonomically and trophically diverse group of benthic animals found in the estuary, as well the best known by the general public. Crustacean arthropods encompass the range of feeding types, including grazing, filter feeding, and deposit feeding. Macrobenthic crustaceans in the York River Estuary include sessile, filtering epifaunal organisms such as barnacles (*Balanus eburneus* and *B. improvisus*), motile, shrimp-like (peracarid) taxa like cumaceans (e.g., *Leucon americanus* or *Cyclaspis varians*) and mysids (e.g., *Neomysis americana*) that live on the sediment surface, mobile burrowing isopods (e.g., *Cyathura polita* or *Edotea triloba*), and amphipods (e.g., *Leptocheirus plumulosus*, *Protohaustorius deichmannae*, or *Caprella penantis*) (Figure 7). Decapod crustaceans include one the most famous benthic organisms of the estuary, the blue crab (*Callinectes sapidus*), as well as some smaller less well-known members, such as xanthid mud crabs (e.g., *Rhithropanopeus harrisii*). Many of the small crabs that populate the estuary are relatively cryptic, living among shells and other structured benthic habitats such as sponges. Fiddler crabs (*Uca* spp.), which live in the intertidal salt marshes that line the banks of the estuary, are a common sight to most people. The most abundant crustaceans in the York River Estuary, meiobenthic harpactacoid copepods (e.g., *Euterpina acutifrons* or *Canuella canadensis*), reside near the sediment-water interface among sediment grains of the estuarine bottom and are important grazers of bacteria and micro-algae.

Figure 7. *Leptocheirus plumulosus*, a common amphipod in the York River Estuary. (Image courtesy of D. Gillett)

Molluscs

Benthic molluscs in the York River Estuary include the conspicuous and familiar clams and snails that can live multiple years and in some cases, e.g., oysters and mussels, are capable of creating complex, hard bottom habitats that provide living space and refugia for other benthic organisms. The most common molluscs of the York River Estuary can be divided into two groups based on the shape and number of shells they have: bivalves, with two relative concave shells, e.g., clams (*Macoma balthica* or *Mya arenaria*), oysters (*Crassostrea virginica*), and mussels (*Geukensia dermissa*); or gastropod snails, which have a single, typically spiraled shell that includes whelks (*Busycon canaliculatum*) and mud snails (*Littorina littorea* or *Hydrobia* sp.).

Bivalves are found along the length of the York River Estuary in all of the salinity zones and typically comprise a significant amount of the total biomass of the infaunal benthic communities (Diaz and Schaffner, 1990; Schaffner *et al.,* 2001). All of the bivalves found in the York River Estuary reproduce sexually, broadcasting their gametes into the water column, creating planktonic larvae. Most are filter feeders (Figure 8), though one of the dominant genera in the meso- and polyhaline portions of the estuary, *Macoma*, is a functional deposit-feeder that can switch from filter feeding to deposit feeding depending upon the water currents and food availability (Pohlo, 1982). Large reefs of the eastern oyster *C. virginica* were once dominant benthic features of the York River, but overfishing, habitat destruction and disease have lead to their demise (Figure 9.) (Hargis and Haven, 1999) and the ecological importance of the oyster has been drastically reduced (Pomeroy *et al.*, 2006; Coen *et al.*, 2007).

Figure 8. *Macoma balthica*, one of the most common infaunal bivalve molluscs in the York River Estuary. Note the incurrent and excurrent siphons protruding from the top of the shell. (Image courtesy of Heidi Mahon, Old Dominion University)

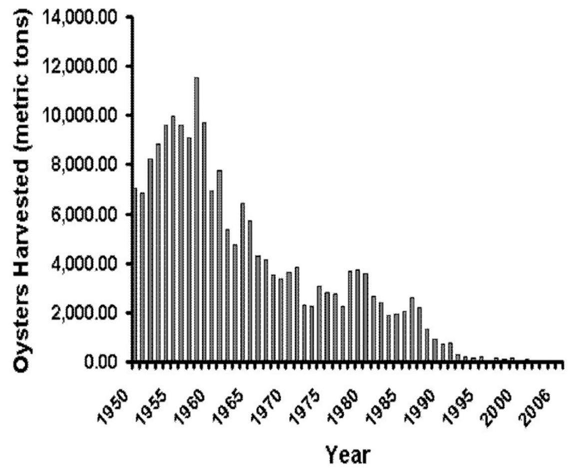

Figure 9. Commercial landings of the Eastern Oyster *Crassostrea virginica* in Virginia from 1950 – 2006. Data from the National Marine Fisheries Service (NMFS)

Gastropods are among the most voracious predators in the benthos. Large whelks, such as the channeled whelk *B. canaliculatum* and the non-native veined rapa whelk *Rapana venosa,* are a considerable problem for commercial bivalve aquaculture operations (J. Harding, pers. comm.). Other gastropods feed on benthic microalgae in the shallow subtidal and intertidal flats of the estuary (e.g., *Hydrobia* sp. or *Narssarius obsoletus*) or on the epiphytic microbes found on the stalks of intertidal marsh grass (e.g. the marsh periwinkle *Littorina littorea*). Gastropods reproduce sexually, undergoing internal fertilization, with the females attaching their egg cases the sediment surface or some hard structure in the environment (e.g., shell material or SAV blades,).

STUDIES OF BENTHIC FAUNA IN THE YORK RIVER

Because of the economic importance of the oyster fishery and the feared decline in the resource, significant effort was put into quantifying the abundance and spatial extent of eastern oyster (*C. virginica*) reefs in the York River by the state of Virginia from at least the mid 1800's, (Wheatley, 1959; Hargis and Haven, 1999). These works, most notably the Baylor survey of 1900, represented the first surveys of benthic biota within the York River Estuary; even in light of their focus on one organism and the delineation of fishing rights. The quantitative study of the complete benthic communities of the York River Estuary began in earnest in the mid-1960's, led by scientists of the Virginia Institute of Marine Science (VIMS). Notable early studies include those of Wass (1965), Haven *et al.* (1981) [*note: Haven* et al. *collected data in 1965-1966, but did not published until 1981*], and Boesch (1971). Initial studies focused on describing benthic community composition of major York River habitats. Based on a review of the early literature for Chesapeake Bay and the major sub-estuaries, distribution and abundance patterns of dominant macrobenthic organisms of soft sediment habitats were summarized by Diaz and Schaffner (1990) (Table 1). Marsh (1970) and Orth (1973) identified the epifaunal and infaunal communities of sea grass beds in the lower York River Estuary.

Table 1. Physical and benthic community characteristics of the major benthic habitats of the York River estuary. Modified from DIAZ and SCHAFFNER, 1990.

Salinity/Habitat Type	Reserve Site(s)	Physical Characteristics	Macrobenthic Community Characteristics	Macrofauna Density / Taxa of Note	Macrofauna Biomass / Taxa of Note
Tidal Freshwater					
Shoals	Sweet Hall Marsh	Shallow depths Mud to sand sediments Wave- and tide-dominated High turbidity Low to moderate light penetration	Stenohaline freshwater fauna Deposit and suspension feeders Infaunal predators Many ephemeral fauna Moderate to low diversity	Low to moderate *Limnodrilus* spp., *Illydrilus templetoni, Stephensonia trivandrana, Coelotanypus* spp.	Oligochaetes and bivalves high Others low *Limnodrilus* spp., *Illydrilus templetoni,* and *Rangia cuneata*
Channels		Intermediate depths Mud to sand sediments Fluid mud possible Tide dominated High turbidity No light penetration	Stenohaline freshwater fauna Deposit and Suspension feeders Moderate to low diversity	Low, especially in areas of fluid mud	Bivalves high Others low
Oligohaline					
Shoals	Taskinas Creek	Shallow depths Mud and sand sediments Wave- and tide-dominated Region of estuarine turbidity maximum (ETM) High deposition Low to moderate light penetration	Euryhaline estuarine fauna Deposit and suspension feeders Some ephemeral fauna Low diversity	Low to high *Tubificoides heterochaetus, Tubificoides brownae, Leptocheirus plumulosus*	Bivalves high Others low *Marenzelleria viridis* , *Macoma balthica* , *Cyathura polita*
Channels		Moderate depths Mud sediments Fluid mud possible Tide-dominated Region of ETM High deposition No light penetration Occasional low oxygen	Euryhaline estuarine fauna Deposit and suspension feeders Low diversity	Low to high *Marenzelleria viridis, Leucon americanus*	Bivalves high Others low *Macoma balthica*
Mesohaline					
Shoals	Cattlet Islands Timberneck Creek	Shallow depths Sand and mud sediments Wave- and tide-dominated Low to moderate turbidity Moderate light penetration Occasional low oxygen	Euryhaline estuarine fauna All feeding types Moderate diversity	Moderate to high *Streblospio benedicti* , *Mediomastus ambiseta* , *Leptocheirus plumulosus*	Bivalves high Others moderate *Macoma balthica* , *Loimia medusa* , *Clymenella torquata* , *Paraprionospio pinnata*
Channels		Intermediate to deep depths Mud sediments Fluid mud possible Tide-dominated High turbidity, related to secondary ETM No light penetration Seasonal low oxygen	Euryhaline estuarine fauna All feeding types Moderate diversity*	Moderate to high* *Streblospio benedicti* , *Mediomastus ambiseta*	Bivalves high* Others moderate* *Macoma balthica* , *Paraprionospio pinnata*
Polyhaline					
Shoals	Goodwin Islands	Shallow depths Sand sediments Wave- and tide dominated High light penetration	Stenohaline estuarine/marine fauna All feeding types Moderate diversity	Low to moderate *Streblospio benedicti* , *Spiochaetopterus oculatus*	Low to moderate *Mercenaria mercenaria* , *Mya arenaria*
Channels		Moderate to deep depths Mud to sand sediments Tide-dominated Moderate turbidity No light penetration Seasonal low oxygen	Stenohaline estuarine/marine fauna All feeding types Moderate to high diversity*	Moderate* *Acteocina canaliculata* , *Heteromastus filiformis*	Low to high *Mercenaria mercenaria* , *Chaetopterus variopedatus*

* Except when low oxygen conditions prevail.

Studies to assess the potential impact of anthropogenic disturbances in the York River Estuary were conducted by scientists at VIMS beginning in the 1970's (e.g., Jordan *et al.*, 1975; Boesch and Rosenberg, 1981; Alongi *et al.*, 1982). Monitoring of macrobenthic communities in the York River began in the 1980's as part of a larger monitoring program coordinated by the Chesapeake Bay Program (CBP), which is funded by USEPA (United States Environmental Protection Agency), NOAA (National Oceanographic and Atmospheric Association) and the states in the Chesapeake Bay watershed. Samples for infaunal macrobenthos (non-colonial forms only) of soft sediment habitats have been collected at a series of fixed and random stations throughout the Chesapeake Bay, including four fixed stations in the York and Pamunkey Rivers. The four fixed stations, all located in the main channel of the estuary, were sampled quarterly between 1984 and 1994 and subsequently reduced to the present schedule of once a year. Beginning in 1996 the sampling design was changed and 25 samples are now collected in the York-Pamunkey estuarine system each summer (July 15 – September 30) based on a probabilistic sampling design that stratifies the estuary by salinity regime and water depth (Llansó *et al.*, 2006). These monitoring studies provide a wealth of information about the infauna of the York River Estuary, much of which is now available online www.chesapeakebay.net/baybio.htm. Some of the major studies describing the monitoring program and its findings are presented in Weisberg *et al.* (1997), Dauer *et al.* (2000), Alden *et al.* (2002) and Llansó *et al.* (2003).

DISTRIBUTION OF MACROBENTHIC COMMUNITIES ALONG THE ESTUARINE GRADIENT

Benthic studies of the York, James and mainstem Chesapeake Bay regions have clearly demonstrated the strong relationship between benthic community structure and salinity regime (see review by Diaz and Schaffner, 1990). For ease of comparison, the salinity regime of estuarine waters is typically referred to within the Venice salinity classification system (International Association of Limnology, 1958). Salinity in the York is relatively stable, with typical daily changes of less than 5 psu (practical salinity units) at a given location (Boesch, 1977; Schaffner *et al.*, 2001). Freshwater flow is from the Pamunkey and Mattaponi Rivers, but is relatively low overall, with the York receiving only about 6% of the freshwater entering the Chesapeake Bay from the watershed each year.

Salinity affects osmotic balance and ion regulation of most aquatic organisms. Given the variability of salinity in most estuaries, resident invertebrates must be relatively tolerant. Although some benthic organisms have a wider range of salinity tolerance than others, few species of benthic invertebrates are capable of maintaining physiological function over the full salinity range observed in an estuary, even when local populations become acclimated. Rapid changes in salinity are especially problematic and pulses of fresher water, due to major spring freshets and hurricanes, can act as disturbances to the benthic community (e.g., Boesch and Rosenberg, 1981; Dauer *et al.*, 2000; Holland *et al.*, 2004).

A classic pattern observed for macrobenthic communities of estuarine and other brackish water environments is the relationship between salinity and species diversity (Remane and Schlieper, 1971; Gainey and Greenberg, 1977; Deaton and Greenberg, 1986). In large brackish water systems such as the Baltic, or in estuaries that are relatively homeohaline, diversity has been shown to decrease when moving from higher salinity waters to a minimum in at 2 - 7 PSU and then increases again moving into freshwater (Attrill, 2002). The pattern of declining diversity with declining salinity is observed in the York River Estuary (Boesch, 1971; Boesch *et al.*, 1976; Schaffner *et al.*, 2001), but the pattern in oligohaline to tidal freshwater is not well defined due to limited sampling. Diaz (1989, 1994) found that species diversity did not increase substantially in the tidal freshwater region of the nearby James River estuary and attributed it to the highly variable and physically stressful nature of the region.

Distribution and abundance of benthic species in soft sediment habitats of the York River Estuary is further correlated with bottom type, hydrodynamics, oxygen regime, and other variables that may covary with salinity along the estuarine gradient (see review by Schaffner *et al.*, 2001). Bottom types in the estuary range from cohesive silts and clays to well-sorted sands (Figure 10) (Schaffner *et al.*, 2001; Schaffner unpublished). In the broad lower York, wave energy is a major factor determining sediment distribution patterns. Fine sediment is winnowed away and the bottom is floored mostly by sand and shell in shallow areas (< 10 m depth), while muds tend to accumulate in the channel. In the middle to upper estuary, upstream of Gloucester Point, tidal energy and estuarine circulation become the more important determinants of sediment distribution. Estuarine circulation processes lead to trapping of fine particles, particularly during periods of high freshwater input. Relatively strong tidal scouring of the channel bottom, and strong wave energy on the shoals during some seasons, but not others, results in significant resuspension of sediment and physical disturbance of the bottom (Dellapenna *et al.*, 1998, 2003; Schaffner *et al.*, 2001), which influences the structure and productivity of subtidal benthic communities in this region of the estuary (Schaffner *et al.*, 2001; Hinchey, 2002.).

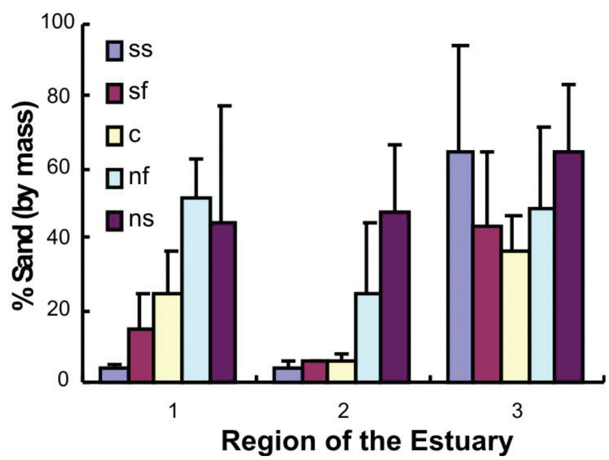

Figure 10. Mean grain size of sediment distributed throughout the York River + 1 standard error. Regions of the Estuary: 1= upper York River, 2 = mid-York River, 3 = lower York River. ss = southwest shoal, sf = southwest flank, c = channel, nf = northeast flank, and ns = northeast shoal.

Benthic fauna exhibit sediment preferences that are reflected in their living positions and feeding mechanisms. As noted above, meiobenthic fauna such as harpactacoid copepods, nematodes, and ostracods live within the spaces between individual sediment grains (the interstitial spaces), ingesting individual particles or filtering the porewater. Sediment with high clay content may become compacted and rich in sulfides, which limits habitat for meiofauna (Higgins and Thiel, 1988). For larger benthic organisms, feeding type may determine the suitability of a given sediment type. Highly mobile, non-selective deposit feeders (e.g. capitellid polychaetes and oligochaetes) tend to be more abundant in depositional areas where organic rich sediment particles accumulate and higher sediment water content makes burrowing easier (Lopez and Levinton, 1987; Rice and Rhoades, 1989). Sandier sediment provides favorable habitat for filter feeders, which have passive collection mechanisms (e.g., phoronids, bryozoans, or hydroids) or limited ability to sort captured particles (e.g., venerid bivalves or chaetopterid polychaetes). In turbid, soft sediment areas of the estuary, smaller silt or clay particles may clog these delicate filtering structures (Lopez and Levinton, 1987; Rice and Rhoades, 1989). Many benthic taxa of estuaries live equally well in the middle ground of muddy-sands and sandy-muds, particularly those that are capable of switching between deposit feeding and filter feeding as water flow conditions change (e.g., tellinid bivalves or spionid polychaetes) (Taghon *et al.*, 1980; Pohlo, 1982; Dauer, 1983**)**. In the deeper waters of the York, bivalves, including both filter and surface deposit feeders, are especially abundant downstream of the estuarine turbidity maximum, which is an area high phytoplankton production (Sin *et al.*, 1999; Schaffner *et al.*, 2001).

Hypoxia and anoxia are common during summer months in the deep channel of the lower York River Estuary, whereas the shallow shoals almost always remain well mixed and oxygenated. Low oxygen events, which typically last a week or less, occur primarily during periods of summer neap tides, when stratification of the water column tends to be strong and respiration is high (Haas, 1977; Diaz *et al.*, 1992). Oxygen is replenished to bottom waters during periods of spring tide due to physical mixing. Episodes of hypoxia or anoxia result in mortality of sensitive taxa (e.g., forams, most species of crustaceans, and some families of polychaetes) and create communities dominated by stress-resistant taxa that tolerate the events, or opportunistic taxa that are able to quickly able recolonize disturbed areas (Diaz and Rosenberg, 1995; Sagasti *et al.*, 2000; Sagasti *et al.*, 2001; Metcalfe, 2005).

Physical structure within estuarine habitats also influences the composition and abundance of macrobenthic communities. Oyster reefs were once a predominant feature of estuaries like the York River (Hargis and Haven, 1999). Reefs provide important ecosystem services, including substrate for sessile forms, such as sponges, entoprocts, and barnacles, shelter for motile species, such xanthid crabs, and filtration by the oyster reef community contributes to improving water clarity, which may benefit nearby sea grass meadows (Coen *et al.*, 1999; Harwell, 2004; Cerco and Noel, 2007). Due to over-harvest, disease, and declining water quality there are no longer large oyster reefs in the York River estuary (Hargis and Haven, 1999), though shell clusters may still provide a habitat for other macrobenthos (Figure 11) (Schaffner, unpublished). The proliferation of other structures in the estuary (e.g., piers, bridges, hardened shore lines, stake arrays that support fishing nets, and even ghost crab pots) have created hard substrate habitat that is used by these epifaunal macroinvertebrates, though possibly not to the same degree as oyster reefs did in the past (Pomeroy *et al.*, 2006).

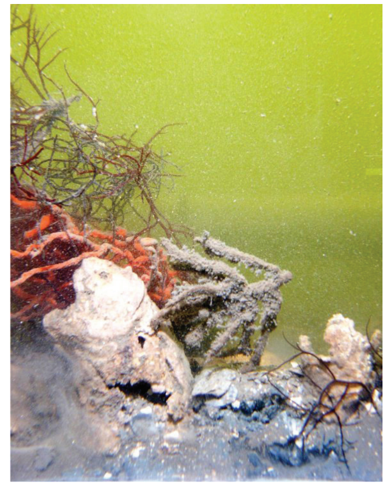

Figure 11. An epifaunal community of sponges, hydroids, entoprocts, and other fauna attached to shell rubble at Catlett Islands in the York River. (Image courtesy of Robert Diaz, VIMS)

Submerged aquatic vegetation (SAV) also increases habitat complexity, and its presence results in the formation of unique assemblages of macrobenthos in shallow estuarine waters. Orth (1973) characterized the macrobenthic infauna associated with *Zostera marina* beds in the high-mesohaline and polyhaline portions of the York River. He found a community very similar in composition to that which has been found in unvegetated habitats within the same salinity zone (e.g., Boesch, 1971; Bender, 1972; Jordan *et al.*, 1975). Wass (1972) provided some cataloging of the fauna attached to SAV (e.g., sponges, tunicates, etc.) and Orth and Van Montfrans (1984) and Duffy and Harvilicz (2001) have discussed the composition of the motile epifaunal grazing communities of SAV beds in the higher salinity, including amphipods, isopods and snails. Although none of the macroinvertebrates found in beds of SAV are unique to those environments, some of them may be more abundant in SAV than they are in other benthic habitats. Unfortunately, much like oyster reefs, the occurrence of SAV meadows within the York River Estuary has precipitously declined from historical levels in recent decades, due in large part to anthropogenic alterations to the estuary (Moore *et al.*, 1996; Orth and Moore, 1983; Moore, this S.I.).

Imposed upon the large-scale changes in community structure along the length of the York River Estuary, there are also changes in community structure with depth (Diaz and Schaffner, 1990; Table 1). The York River Estuary consists of a relatively deep channel (9 – 25 m) flanked by shallow (2-3 m), sometimes quite broad shoals and tidal creeks (Schaffner *et al.*, 2001). In the shallow areas, light may penetrate to the sediment surface where it provides energy for the growth of microphytobenthos, an energy-rich food source for benthic fauna (MacIntyre *et al.*, 1996; Cahoon, 1999). Phytoplankton production can also have a greater influence on the macrobenthic community in the shallow portions of the estuary, where filter feeding animals have access to the entire overlying water column and living phytoplankton, as opposed to those animals in deeper parts of the estuary that are isolated from the photic zone by stratification of the water column (Gerritsen *et al.*, 1994). Relatively labile detrital materials may also be available due to the proximity to marshes and SAV beds. These additional food sources allow for higher productivity of the benthic community in areas where recruitment and growth are not limited by other factors (Beukema and Cadee, 1997).

While food availability may enhance the potential for high secondary productivity in shallow water areas, other factors may be limiting. Physical disturbance due to waves, strong predation, temperature extremes and other factors alter benthic community structure and may limit productivity in shallow water areas despite high food availability (Emerson, 1989; Beukema and Cadee, 1997; Harley *et al.*, 2006). Predation on meio- and macrobenthos is often intense in shallow water areas due to the juxtaposition of highly productive shallow water benthic habitats with marsh and SAV beds that provide smaller predators of benthic infauna, such as juvenile fish, crabs, and large infauna, refuge from larger predators (Kneib, 1997; Seitz *et al.*, 2005; Seitz *et al.*, 2006). Benthic invertebrates living in shallow subtidal and intertidal zones are also subject to predation by birds (Kiviat, 1989).

THE IMPORTANCE OF BENTHIC FAUNA

Despite their relatively small size and cryptic lifestyle, macro and meiobenthos are important components of the estuarine ecosystem, serving as critical links between the variety of organic matter sources in estuaries (e.g., phytoplankton, benthic micro- and macroalgae, detritus) and the economically, ecological, and recreationally important finfish and crustaceans that live there (Cicchetti, 1998). Baird & Ulanowicz (1989) estimated that approximately 50% of the fish production in Chesapeake Bay is directly linked to a benthic food web. Diaz and Schaffner (1990) estimated that 194,000 metric tons of carbon is produced by benthic macrofauna in Chesapeake Bay each year (70% of which occurs in high mesohaline and polyhaline habitats) and supports a fisheries yield of 27,500 metric tons of carbon. Commercial fisheries of benthic feeding and demersal nekton (e.g., spot, croaker, blue crabs) in the Virginia portion of Chesapeake Bay yielded an annual average of 39.8 million dollars of revenue between 1998 and 2002 (NMFS, Fisheries Statistics and Economics Division, 2004). Direct harvest of benthic species, especially the oysters and other bivalves, were historically important fisheries in the York River Estuary (Wheatley, 1959; Bender, 1987; Hargis and Haven, 1999), though now they constitute less than one million dollars in landings Bay-wide (NMFS, Fisheries Statistics and Economics Division, 2004) (Figure 9). Commercial aquaculture of bivalve molluscs, particularly the hard clam *Mercenaria mercenaria*, has become an important economic force in the Chesapeake Bay as a whole (Camara, 2001; VA Sea Grant, 2007), though there are no large-scale operations within the York River Estuary. Benthic communities also provide a variety of ecosystem services that affect water and sediment quality in the estuaries. In relatively shallow areas, filter feeders may effectively remove particles from the water column, which leads to deposition of organic matter from the overlying water at rates greater than natural sinking and physical mixing would allow. This can result in enhanced water clarity, which may increase the success of SAV (Newell and Koch, 2004). SAV may also enhance particle deposition due to a baffling effect. Biodeposition by filter feeders also serves to shunt water column production to the sediment bed where transport, transformation and fates are then governed by benthic rather than pelagic processes (Cohen *et al.*, 1984; Gerritsen *et al.,* 1994; Neubauer, 2000). Some of this organic matter will fuel the production of benthic invertebrates and their predators. Organic matter that is not assimilated by macro and meiobenthic organisms may be buried, but more likely, it will be processed by microbes. The released nutrients and breakdown products may be retained in sediment pore waters or fluxed across the sediment-water interface.

Microbial processes generally control the rates of most important biogeochemical processes in the sediment, while meio- and macrobenthos control the mixing of constituents such as oxygen and organic matter that settles or is deposited to the estuary floor. Bioturbation and biogenic structuring of the bottom by benthic organisms has been show to have major effects on carbon, nitrogen, phosphorus, and contaminant cycling and fate (Diaz and Schaffner, 1990). The degradation of organic matter and some contaminants is generally enhanced in the presence of infaunal organisms, due to stimulation of microbial processes, which leads to enhanced rates of mineralization (Aller and Aller, 1998; Kristensen, 2000). Bioturbation and sediment ventilation by larger benthic organisms tend to enhance the diffusivity of dissolved constituents such as ammonium into the water column (Rice and Rhoades, 1989; Michaud *et al.*, 2005; Michaud *et al.,* 2006). Simultaneously, reduction/oxidation sensitive processes, such as nitrification-denitrification, may be enhanced in the presence of macrofauna whose tubes and burrows increase the surface area of the sediment-water interface and the depth of oxygen penetration into the sediment. The enhanced coupling of nitrification-denitrification in the presence of benthic macrofauna can lead to the production of nitrogen gas, which escapes to the atmosphere, thereby reducing the nitrogen load in the estuary (Mayer *et al.*, 1995).

THE BENTHIC FAUNA OF CBNEERVA

As noted above, the shallow waters of the York River Estuary historically contained a variety of different habitat types, with extensive SAV beds and oyster reefs interspersed with open areas of mud and sand flats. At present, the estuary is floored mostly by unvegetated mud or sand sediments with very limited, narrow bands of SAV beds in some areas. As such, soft sediment communities have been the most well-studied, both temporally and spatially (see Studies of the Benthic Fauna of the York River, above). These habitats provide the best characterization the benthic communities throughout the whole estuary and within each of the salinity zones where the different parts of the CBNERRS VA reserve are located (Table 1). Within these generalized benthic communities though, there is almost always a considerable amount of patchiness in space for most species and in time for others, particularly those with strongly seasonal recruitment (e.g., bivalves and polychaetes) (Kravitz, 1983; Zobrist, 1988; Hinchey, 2002).

INVASIVE/NON-NATIVE ORGANISMS IN THE YORK RIVER ESTUARY

The presence or distribution of invasive benthic fauna in the York River Estuary remains poorly studies. Invasive taxa have been found in other parts of Chesapeake Bay. The Asian clams *Corbicula manilensis* and *C. fluminea*, which are thought to have invaded other tributaries of the Chesapeake Bay around 1968 (Wass, 1972; Diaz, 1974; Phelps, 1994), were not historically observed in the York River Estuary (Boesch, 1971), but have recently been collected in the Chesapeake Bay Benthic Monitoring Program (Chesapeake Bay Program, 2009). There are regular observations of the veined rapa whelk *Ra-*

pana venosa (Figure 12), an invasive gastropod accidentally introduced to the high mesohaline/polyhaline York River in the mid-1990's. This species may severely impacts bivalve fisheries via predation (Harding and Mann, 2005). Additionally, the history of colonial activity in the York River increases the likelihood that some of the species considered to be natives were introduced before scientific surveys began.

Figure 12. The invasive gastropod *Rapana venosa* collected from the York River. (Image courtesy of Juliana Harding, VIMS)

There are also examples of deliberate introduction of non-native species, most notably the non-native oysters *Crasostrea gigas* and *C. ariakensis*. These species that have been introduced to the mesohaline and polyhaline portions of the York River in the interest of supplementing/replacing the oyster fishing industry, which traditionally was based upon the native *C. virginica*. Introduced non-native species may directly compete with native fauna for resources and serve as means for unintentional introductions of parasites and other cryptic fauna associated the non-natives (Dobson and May, 1986; Carlton, 1992). In recognition of these potential problems, only sterilized, non-reproductive *C. ariakensis* have been introduced to date into the York River in experimental deployments by VIMS and the Virginia Seafood Council. In the end, the true abundance and distribution of invasive benthic taxa in estuaries like the York River and its tributaries will remain difficult to definitively quantify due to the size of the estuary, the cryptic nature of native and non-native benthic organisms, and the ephemeral and stochastic nature of most invasions (Carlton, 1996).

HUMAN PERTURBATIONS OF BENTHIC FAUNA

The annual benthic monitoring program of the Chesapeake Bay Program assesses the quality and degree of benthic habitat degradation in the Chesapeake Bay and its tributaries using the macrobenthos and the Chesapeake Bay Benthic Index of Biotic Integrity (B-IBI) (Weisberg *et al.*, 1997). Based upon randomly selected sites in 2005 (the most currently available data) and the B-IBI assessment approach, 73% of the area of the York River Estuary failed to meet the restoration goals set by the Chesapeake Bay Program, due in large part to low macrobenthic abundance and biomass (Llansó *et al.*, 2006). The distribution of habitat quality is not uniform along the length of the estuary (Figure 13). Most of the degraded sites fall within the polyhaline and mesohaline portions of the York River, areas known to be affected by low dissolved oxygen (Llansó *et al.*, 2006). In contrast, benthic communities of sites sampled in the oligohaline and tidal freshwater parts of the York River were assessed as non-degraded (Llansó *et al.*, 2006).

The hypoxic and anoxic waters observed in the York River Estuary are the end product of a complex process created by excessive nutrient inputs into Chesapeake Bay and human development and alteration of the Bay's watershed (Reay and Moore, this S.I.; Dauer *et al.*, 2000). Hypoxic episodes in the York River are periodic in nature, lasting from hours to over a week at a time during late summer (Haas, 1977; Diaz *et al.*, 1992). Direct mortality of benthic fauna via suffocation will occur during persistent, multi-day episodes of hypoxia/anoxia, though the length of time an organism can survive without oxygen will vary from species to species (Holland *et al.*, 1977; Diaz and Rosenberg, 1995; Sagasti *et al.*, 2001; Sagasti *et al.*, 2003). Relatively low levels of dissolved oxygen are always present in the sediment of estuaries given the abundance of organic matter and the subsequent respiration of heterotrophic bacteria. These processes result in the accumulation of reduced compounds in the sediment pore waters (e.g., sulphides, ammonia) that are toxic to benthic organisms (Theede *et al.*, 1973; Pearson and Rosenberg, 1978; Shin *et al.*, 2006). Water column hypoxia exacerbates the sediment system, increasing the concentrations of reduced chemicals and preventing a source of oxygen to oxidize and remove these

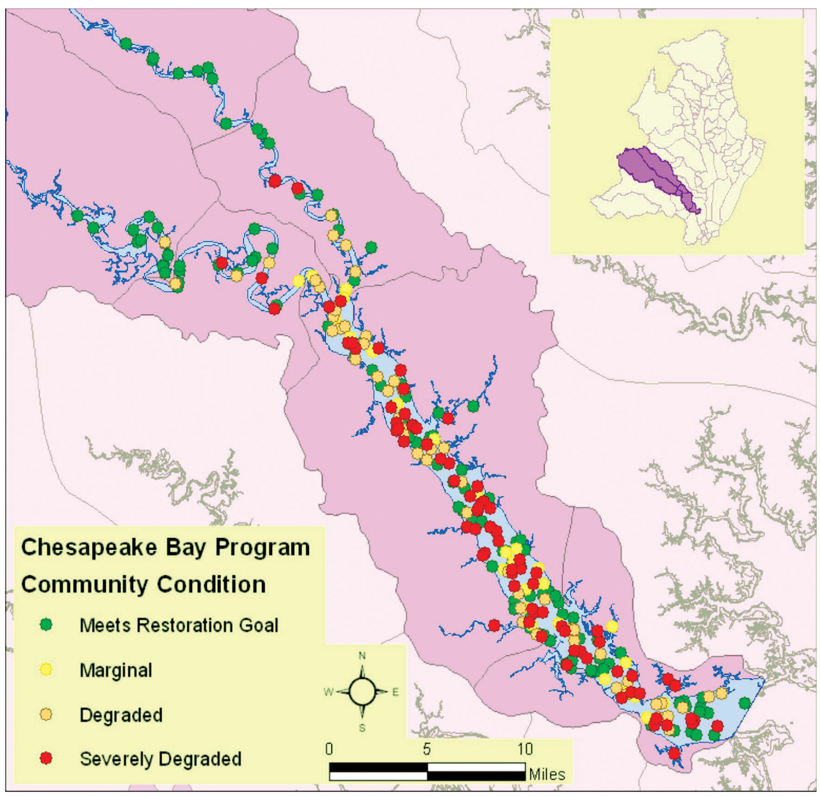

Figure 13. Benthic habitat condition at randomly selected sites within the York River Estuary from 1996 – 2006. Benthic habitat condition was assessed using the Chesapeake Bay Benthic Index of Biotic Integrity (B-IBI) and graded using the Chesapeake Bay Program's restoration guidelines: B-IBI ≥ 3.0 = Meets Restoration Guidelines; 2.7 – 2.9 = Marginal; 2.1 - 2.6 = Degraded; and ≤ 2.0 = Severely Degraded, as noted in the legend. (Data from CBP database and figure created by David Parrish, CBNERRSVA)

toxic chemicals (Gaston *et al*., 1985; Diaz and Rosenberg, 1995; Levin, 2003).

By most accounts, the York River Estuary is not systemically affected by chemically contaminated sediments, unlike more developed parts of Chesapeake Bay (e.g., Elizabeth River, Baltimore Harbor, etc.) (Llansó *et al*., 2006). That said, there are inevitably instances of local contamination in areas surrounding the various marinas along the length of the estuary, the U.S. Navy installations in the mesohaline estuary, and the coal-fired power plant and petroleum refinery in the polyhaline parts of the estuary. Fuels spills that contain toxic polycyclic aromatic hydrocarbons (PAHs) occur, older military landfills leach a variety of toxic compounds (e.g., chlorinated compounds or asbestos), and anti-fouling compounds with heavy metals leach from ships into the water column, all of which can bind to sediments and negatively impact the benthic fauna of the estuary (e.g., Jordon *et al*., 1975; Lynch and Bull, 2007; USEPA 2007).

AREAS OF FUTURE RESEARCH

One of the strategic goals of the National Estuarine Research Reserve System program is to characterize and monitor the biological and community conditions of the reserves, to establish reference conditions, and to quantify change (NERRS 2005). Thus, an understanding of the composition of the benthic community should be of primary concern to the CB NERRS VA program. A comprehensive baseline inventory of the benthic fauna at each of the reserve sites, from the sand and mud flats of the Goodwin Islands to the tidal creeks of Sweet Hall Marsh. Recent research projects conducted at different parts of the reserve system will provide some insight into the macro- and meiobenthic community structure (Gillett, unpublished; Schaffner and Gillett, unpublished) and serve as a good starting point, but these studies were not designed to catalog the entire benthic community. Without knowledge of the fauna of different parts of the York River Estuary, it will be impossible to track future invasions, or to assess the role of anthropogenic factors such as development or climate change, in the alteration of benthic community structure and function. Benthic community data is most acutely lacking in the tidal freshwater and oligohaline portions of the York River Estuary. The reserve would benefit significantly by beginning a benthic community investigation at the Sweet Hall Marsh and Taskinas Creek portions of the reserve system before the further development of the watershed begins to degrade the habitat quality in those regions.

In addition to establishing the resident fauna for each portion of the reserve, habitat mapping and inter-habitat comparisons should be completed. Comparisons of the communities in the unvegetated sediment, natural and artificial hard bottom, and SAV meadows will allow the reserve managers to better assess the ecological complexity and ecosystem services rendered within the different parts of the reserve and along the salinity gradient of the York River Estuary. This is key information needed for developing restoration and mitigation plans, which will become increasingly important as human pressures on the estuary continue to grow.

Finally, very little is known concerning the spatial and temporal extent of hypoxic and anoxic conditions in the small tributaries of the York River Estuary. There is anecdotal evidence that low oxygen conditions occur in the tributaries and creeks of the estuary that can severely impact and degrade the benthic community (Gillett personal observation), but there is little direct, quantitative evidence. Given the spatial extent of these shallow tributaries and their high primary and secondary productivity, the impact of hypoxia-induced mortality on these areas could drastically reduce the ecosystem productivity of the estuary. The CBNERRS VA program would be well equipped to investigate these areas.

FINAL OBSERVATIONS ON THE BENTHOS OF THE YORK RIVER

The York River Estuary and the component NERRS sites comprise a large, complex ecosystem. The resident benthic fauna represent a wide array of trophic and taxonomic diversity. From well-known taxa like the eastern oyster *Crassostrea virginica* or the hard clam *Mercenaria mercenaria* to the relatively obscure harpactacoid copepods or capitellid polychaetes, benthic organisms play a vital role the functioning of the estuarine system. The benthic fauna of the York, Pamunkey, and Mattaponi rivers, like all of their biological resources, are still relatively non-disturbed compared to many parts of the Chesapeake Bay. That said, the benthic communities of the estuary will change and lose their ecological and economic value as the continuing developmental pressure within the estuarine watershed continues to increase, as it has in the coastal zone around the country (Beach, 2000; Pew Ocean Commission, 2003). The preservation and research of a diversity of benthic habitats by the Virginia CBNERRS program has been, and will continue to act as, part of the counterbalance to the forces of development in and along the York River Estuary. We have a rudimentary understanding of the functioning of the hidden and fascinating world of benthic fauna, but there is still much more for us to learn there.

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APPENDIX

A Partial Species List of Benthic Fauna Collected in the York River Estuary

Scientific name and the corresponding Integrated Taxonomic Information System Serial Code (TSN) where available.

Annelids

Aglaophamus verrilli	0066052
Almyracuma proximoculi	0066052
Amastigos caperatus	
Ampharetidae	0067718
Amphicteis floridus	0067753
Amphicteis gunneri	0067747
Ancistrosyllis commensalis	0065548
Ancistrosyllis hartmanae	0065543
Ancistrosyllis jonesi	0065544
Ancistrosyllis sp.	0065541
Asabellides oculata	0067786
Aulodrilus limnobius	0068682
Aulodrilus pigueti	0068680
Bhawania goodei	0065158
Bhawania heteroseta	0065159
Boccardiella ligerica	0067012
Branchiura sowerbyi	0068621
Brania wellfleetensis	0065762
Bratislavia unidentata	0069023
Cabira incerta	0065565
Calliobdella vivida	0069351
Capitella capitata	0067415
Capitella jonesi	
Capitellidae	0067413
Capitomastus aciculatus	0204558
Carazziella hobsonae	0067003
Caulleriella killariensis	0067131
Chaetopterus variopedatus	0067097
Cirratulidae	0067116
Clymenella torquata	0067528
Cossura longocirrata	0067207
Demonax microphthalmus	0068222
Dero digitata	0068904
Dero obtusa	0068907
Dero sp.	0068898
Diopatra cuprea	0066180
Dorvillea rudolphi	0066525
Drilonereis longa	0066426
Drilonereis sp.	0066423
Eteone heteropoda	0065266
Eteone lactea	0065267
Eumida sanguinea	0065343
Glycera americana	0066106
Glycera dibranchiata	0066107
Glycera sp.	0066102
Glycinde solitaria	0066132
Gyptis sp.	0065468
Gyptis vittata	0065470
Haber speciosus	0068745
Harmothoe extenuata	0064509
Harmothoe sp.	0064502
Helobdella elongata	0069397
Helobdella stagnalis	0069398
Heteromastus filiformis	0067420
Hirudinea	0069290
Hobsonia florida	0067755

Hydroides dianthus	0068282
Ilyodrilus templetoni	0068662
Isochaetides freyi	0068810
Laeonereis culveri	0065965
Leitoscoloplos fragilis	0066656
Leitoscoloplos robustus	0182728
Leitoscoloplos sp.	0066653
Lepidametria commensalis	0064703
Lepidonotus sublevis	0064610
Lepidonotus variabils	0064611
Levinsenia gracilis	0066729
Limnodriloides anxius	0158432
Limnodrilus hoffmeisteri	0068639
Limnodrilus profundicola	0068649
Limnodrilus sp.	0068638
Linopherus paucibracnchiata	0065175
Loimia medusa	0068015
Macroclymene zonalis	0067632
Maldanidae	0067515
Malmgreniella taylori	BAY0335
Manayunkia aestuarina	0068171
Marenzelleria viridis	0573739
Mediomastus ambiseta	0067439
Melinna maculata	0067766
Microphthalmus sczelkowii	0065477
Microphthalmus sp.	0065476
Monticellina dorsobrancialis	0204530
Mystides borealis	0065307
Myzobdella lugubris	0069316
Nais communis	0068950
Nais variabilis	0068959
Neanthes succinea	0065918
Nephtys incisa	0066028
Nephtys picta	0066030
Nephtys sp.	0066011
Nereidae	0065870
Nereis acuminata	0065926
Notomastus sp.	0067423
Oligochaeta	0068422
Orbiniidae	0066570
Paleanotus heteroseta	0065152
Parahesione luteola	0065493
Paranais frici	0068865
Paranaitis speciosa	0065321
Paraprionospio pinnata	0066937
Pectinaria gouldi	0067709
Phyllodoce arenae	0065366
Phyllodoce fragilis	0065337
Podarke obscura	0065517
Podarkeopsis brevipalpa	0065532
Podarkeopsis sp.	0065530
Pokarkeopsis levifuscina	0555698
Polycirrus eximius	0067963
Polydora cornuta	0204501
Polydora ligni	0066801
Polydora socialis	0066791
Polydora websteri	0066802
Prionospio perkinsi	0066854
Pristina breviseta	0068880
Pristinella jenkinae	0069030
Pristinella osborni	0069026
Pristinella sima	0069028
Pseudeurythoe paucibranchiata	0065176
Pseudeurythoe sp.	0065174
Quistradrilus multisetosus	0068794
Sabaco elongatus	BAY0341
Sabella microphthalma	0068223
Sabellaria vulgaris	0067671
Samythella elongata	0067802
Schistomeringos rudolphi	0066523
Scolelepis bousfieldi	0066944
Scolelepis sp.	0066942
Scolelepis squamata	0066943
Scolelepis texana	0066949
Scoloplos rubra	0066603
Sigambra bassi	0065554
Sigambra tentaculata	0065552
Spio setosa	0066868
Spiochaetopterus costarum	0067107
Spiochaetopterus oculatus	0067110
Spiophanes bombyx	0066897
Spirosperma ferox	0068610
Stephensoniana trivandrana	0069018
Sthenelais boa	0065084
Streblospio benedicti	0066939
Terebellidae	0067899
Tharyx acutus	0067147
Tharyx setigera	0067145
Tubifex sp.	0068622
Tubificidae	0068585
Tubificoides benedeni	0068592
Tubificoides brownae	0068688
Tubificoides diazi	0068689
Tubificoides gabriellae	0068590
Tubificoides heterochaetus	0068595
Tubificoides motei	
Tubificoides sp.	0068687
Tubificoides wasselli	0068692

Ascidians

Ascidiacea	0158854
Botryllus schlosseri	0159373
Molgula lutulenta	0159581
Molgula manhattensis	0159557

Chordates

Branchiostoma caribaeum	0159682
Branchiostoma virginiae	0206924

Cnidarians

Actiniaria sp.	0052485
Anthozoa	0051938
Ceriantheopsis americanus	0051992
Cerianthus americanus	0051987
Clytia cylindrica	
Diadumene leucolena	0052749
Ectopleura dumortieri	0719102
Edwardsia elegans	0052489
Haliplanella luciae	0204191
Halopteris tenella	
Hydrozoa	0048739
Obelia bidentata	0049532
Sertularia argentea	0049914

Crustaceans

Aegathoa medialis	0092440
Americamysis bigelowi	0682618
Ameroculodes sp.	0656551
Ampelisca abdita	0093329
Ampelisca macrocephala	0093322
Ampelisca sp.	0093321
Ampelisca vadorum	0093330
Ampelisca verrilli	0093331
Amphiodia atra	0157649
Amphitoidae	0093408
Balanoglossus aurantiacus	0158629
Balanus eburneus	0089621
Balanus improvisus	0089622
Batea catharinensis	0093528
Callinectes sapidus	0098696
Campylapsis rubicunda	
Caprella penantis	0095419
Cassidinidea lunifrons	0092347
Cerapus tubularis	0093587
Chiridotea almyra	0092638
Chiridotea coeca	0092640
Chiridotea nigrescens	0092642
Corophium acherusicum	0093590
Corophium insidiosum	0093600
Corophium lacustre	0093594
Corophium simile	0093595
Corophium sp.	0093589
Corophium tuberculatum	0093596
Corophium volutator	0093601
Cyathura burbancki	0092150
Cyathura polita	0092149
Cyclaspis varians	0091033
Cymadusa compta	0093430
Decapoda	0095599
Diastylis polita	0090858
Dyspanopeus sayi	0098901
Edotea triloba	0092627
Elasmopus laevis	0093761
Erichsonella attenuata	0092618
Erichsonella filiformis	0092619
Erichthoneus brasiliensis	0093613
Eurypanopeus depressus	0098759
Exosphaeroma	0092301
Gammarus daiberi	0093779
Gammarus mucronatus	0093783
Gammarus palustris	0093782
Gammarus sp.	0093773
Gammarus tigrinus	0093781
Gilvossius setimanus	0552843
Hargeria rapax	0092068
Harpactocoida	
Hutchinoniella taylori	0083682
Hyalella azteca	0094026
Idoteidae	0092564
Idunella smithii	BAY0133
Lepidactylus dytiscus	0093998
Leptocheirus plumulosus	0093486
Leucon americanus	0090790
Listriella barnardi	0094213
Listriella clymenellae	0094214
Melita appendiculata	0093813
Melita nitida	0093812
Microprotopus raneyi	0094122
Monocorophium tuberculatum	0656762
Monoculodes edwardsi	0094539
Monoculodes intermedius	0094536
Neomysis americana	0090062
Ogyrides alphaerostris	0096737
Oxyurostylis smithi	0090923
Palaeomonetes pugio	0096390
Panopeus herbstii	0098778
Paracaprella tenuis	0095434
Parametopella cypris	0094927
Paraphoxus spinosus	0094756
Parapleustes estuarius	BAY0199
Pinnixa chaetopterana	0098998
Pinnixa retinens	0099001
Pinnixa sayana	0099002
Pinnixa sp.	0098993
Pleusymtes glaber	0094797
Polyonyx gibbesi	0098083
Ptilanthura tenuis	0092155
Rhithropanopeus harrisi	0098790
Sarsiella texana	0084276
Sarsiella zostericola	0084277
Sphaeroma quadridentatum	0092339
Squilla empusa	0099143
Stenothoe minuta	0094936
Unciola irrorata	0093632
Unciola serrata	0093633
Unciola sp.	0093629
Unionicola	0083073
Upogebia affinis	0098209
Xanthidae	0098748

Echinoderms

Holothuroidea	0158140
Leptosynapta tenuis	0158432
Microphiopholis atra	BAY0347

Echiurians

Echiura	0154972
Thalassema hartmani	0155119
Thalassema sp.	0155118

Ectoprocts

Anguinella palmata	0155542
Bowerbankia gracilis	0155559
Conopeum tenuissimum	
Ectoprocta	0155470
Membranipora tenuis	0155827
Pedicellina cernua	0156740

Foraminifera

Miliammina fusca	0044215

Hemichordates

Hemichordata	0158616
Saccoglossus kowalevskii	0158626

Insects

Ablabesmyia annulata	0128081
Ablabesmyia parajanta	0128112
Bezzia sp.	0012778
Ceratopogonidae	0127076
Chaoborus albatus	0125905
Chaoborus punctipennis	0125923
Chaoborus sp.	0125904
Chironomidae	0127917
Chironomini sp.	0129229
Chironomus sp.	0129254
Cladopelma sp.	
Cladotanytarsus mancus	
Cladotanytarsus sp.	
Clinotanypus pinguis	0127998
Coelotanypus sp.	0128010
Coleoptera sp.	0109216
Cricotopus sp.	0128575
Cryptochironomus fulvus	0129376
Cryptochironomus parafulvus	0129382
Cryptochironomus sp.	0129368
Cryptotendipes sp.	0129394
Demicryptochironomus	0129421
Dicrotendipes nervosus	0129452
Ephemeroptera	0100502
Epoicocladius sp.	0128682
Glyptotendipes sp.	0129483
Gomphidae	0101664
Harnischia sp.	0129516
Hexagenia limbata	0101552
Hexagenia sp.	0101537
Nanocladius sp.	0128844
Oecetis inconspicua	0116613
Oecetis sp.	0116607
Palpomyia sp.	0127859
Paralauterborniella sp.	0129616
Paratendipes sp.	0129623
Polypedilum convictum	0129671
Polypedilum fallax	0129676
Polypedilum flavum	
Polypedilum halterale	0129684
Polypedilum illinoense	0129686
Polypedilum scalaenum	0129708
Polypedilum sp.	0129657
Polypedilum sp.	0129657
Probezzia sp.	0127729
Procladius sp.	0128277
Procladius sublettei	0128316
Pseudochironomus fulviventris	0129858
Pseudochironomus sp.	0129851
Sialis sp.	0115002
Simulium sp.	0126774
Sphaeromias	0127761
Stictochironomus devinctus	0129790
Stictochironomus sp.	0129785
Tanypodinae	0127994
Tanypus neopunctipennis	0128329
Tanypus sp.	0128324
Tanytarsini sp.	0129872
Tanytarsus sp.	0129978
Trichoptera	0115095
Xenochironomus festivus	0129841
Xenochironomus sp.	0129837
Zygoptera	0102042

Molluscs

Acteocina canaliculata	0076117
Aligena elevata	0080685
Anachis obesa	0073622
Anadara ovalis	0079342
Anadara transversa	0079340
Anomia simplex	0079798
Barnea truncata	0081798
Bivalvia	0079118
Boonea bisuturalis	0075987
Busycon canaliculatum	0074097
Corbicula fluminea	0081387
Corbicula manilensis	0081386
Crassispira ostrearum	0074901
Crassostrea virginica	0079872
Cratena kaoruae	0078714
Crepidula convexa	0072624
Crepidula fornicata	0072623
Cylichna alba	0076148
Cyrtopleura costata	0081796
Doridella obscura	0078439
Ensis directus	0081022
Epitonium multistriatum	0072247
Epitonium rupicola	0072249
Epitonium sp.	0072233
Eupleura caudata	0073300
Gastropoda	0069459
Gemma gemma	0081511
Geukensia demissa	0079555
Haminoea solitaria	0076258
Hydrobia	0070494
Littoridinops tenuipes	0070528
Littorina littorea	0070419
Lucina multilineata	0080389
Lyonsia hyalina	0081926
Macoma baltica	0081052
Macoma mitchelli	0081054
Macoma sp.	0081033
Macoma tenta	0081055
Mangelia plicosa	0074568
Mercenaria mercenaria	0081496
Mitrella lunata	0073552
Mulinia lateralis	0080959
Musculium	0081427
Mya arenaria	0081692
Nassarius obsoletus	0074111
Nassarius vibex	0074107
Nucula proxima	0079132
Nuculana messanensis	0079212
Nudibranchia	0078156
Odonata	0101593
Odostomia bisuturalis	0075988
Odostomia engonia	0075504
Odostomia sp.	0075447
Parvilucina multilineata	0080388
Petricola pholadiformis	0081627
Pisidium sp.	0081400

Polinices duplicatus	0072918
Polymesoda caroliniana	0081383
Pyramidella candida	0075948
Rangia cuneata	0080962
Rapana venosa	
Rictaxis punctostriatus	0076083
Sayella chesapeakea	0070946
Sphaeriidae	0112737
Sphaerium sp.	0081391
Tagelus divisus	0081274
Tagelus plebeius	0081272
Tellina agilis	0081088
Tellina versicolor	0081100
Tellinidae	0081032
Tenellia sp.	0078547
Turbonilla interrupta	0075687
Turbonilla sp.	0053964
Turridae	0074555
Unionidae	0079913
Urosalpinx cinerea	0073264
Yoldia limatula	0079273

Nematodes

Anticoma litoris	0062032
Axonolaimus spinosus	0059512
Cylindrotheristus oxyuroides	0060433
Desmodora sp.	0060744
Euchromadora sp.	0061205
Mesotheristus setosus	0060526
Metachromadora parasitifera	0060715
Metalinhomeus retrosetosus	
Metalinhomeus typicus	
Nematoda	0059490
Neotonchus punctatus	0061519
Oncholaimus sp.	0062449
Pamponema sp.	
Paracanthonchus sp.	0061480
Paramonhystera proteus	
Parodontophora brevamphida	0059569
Ptycholaimellus ponticus	0061468
Sabatieria pulchra	0061095
Sphaerolaimus balticus	
Steineria sp.	0191219
Thalassoalaimus sp.	0062146

Nemerteans

Carinomidae	0057427
Cerebratulus sp.	0057446
Nemertea	0057411

Ostracods

Ostracoda	0084195

Phoronids

Phoronida	0155456
Phoronis psammophila	0155467
Phoronis sp.	0155462

Platyhelminthes

Euplana gracilis	0054139
Stylochus ellipticus	0054089

Poriferans

Cliona sp.	0048523
Halichondria bowerbanki	0048398
Haliclona loosanoffi	0047774
Haliclona spp.	0047771
Lissodendoryx carolinesis	0048072
Microciona prolifera	0047997

Pycnogonids

Anoplodactylus lentus	0083644
Pycnogonida	*0083545*

Sipunculids

Sipuncula	0154520