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Zooplankton of the York River

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ABSTRACT

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Zooplankton are a diverse group of heterotrophic organisms that consume phytoplankton, regenerate nutrients via their metabolism, and transfer energy to higher trophic levels. Over the past 40 years, few studies have specifically targeted zooplankton communities of the York River estuary and tributaries. However, several studies targeting specific taxa, and time series of multiple taxa, provide an emerging view of York River zooplankton community composition and how zooplankton communities change seasonally, and over longer time scales. Microzooplankton communities are dominated by ciliated protozoa, and rotifers are important in fresher water regions. In the lower Bay microzooplankton abundance peaks in spring, and in mid-summer to early fall. The mesozooplankton community is dominated by calanoid copepods *Acartia tonsa*, *Acartia hudsonica*, and *Eurytemora affinis*. Mysids undergo diel vertical migrations and are important food for many fish species in the Bay. Some taxa such as chaetognaths are not endemic to the bay but are transported in from the continental shelf. Various meroplankton such as larvae of decapods, bivalves, and gastropods become abundant at times. A striking seasonal change in the zooplankton community composition occurs in spring when large gelatinous zooplankton such as the ctenophore *Mnemiopsis leidyi* and (subsequently in summer) the scyphomedusa *Chrysaora quinquecirrha* (sea nettle) "bloom." *Mnemiopsis* blooms now appear earlier in the York River compared to 40 years ago, correlated to earlier warming in spring water temperatures. Humans may be influencing zooplankton populations in the York River via introduced species and eutrophication-induced hypoxia, as well as via input of contaminants. Future research priorities and monitoring needs include long-term monitoring of zooplankton communities, increased studies of the dynamics of microozooplankton and of gelatinous zoopankton, diel and seasonal cycles and grazing rates of some of the lesser studied groups (e.g., other than copepods), and use of new technology such as underwater digital video systems.

ADDITIONAL INDEX WORDS: *Chesapeake Bay, grazing, biovolume, trophic structure, energy flow*

ABSTRACT

Introduction and Historical Perspective

The term "Plankton" means drifter (derived from the greek "planao" meaning "to wander"), thus the plankton are at the mercy of the currents more so than fish and other larger organisms. In the previous chapter the small plant drifters or phytoplankton were discussed; here we concentrate on the animal plankton or zooplankton. Zooplankton are a diverse group of heterotrophic organisms (ranging in size from unicellular flagellates one-hundredth of a millimeter in diameter to jellyfish a meter in diameter) that act to remove phytoplankton through their feeding, regenerate nutrients via their metabolism, and transfer energy to higher trophic levels. Zooplankton occupy a key position in pelagic food webs, as they transfer energy produced from phytoplankton through photosynthesis to higher trophic levels (fish) exploitable by humans. They are also key in determining the amount and composition of particles sinking to the benthos, which provides food for benthic organisms and contributes to burial of organic compounds.

Zooplankton can be grouped in many different ways, including size, habitat, depth distribution, length of planktonic life, and feeding mode. The size range is large, and can be very generally divided into microzooplankton (<200µm), mesozooplankton (200µm - 2 mm), and macrozooplankton (>2 mm). (Note- 1 µm =one-thousandth of one-millimeter.) Zooplankton are found in every aquatic habitat, from freshwater to estuarine to open ocean, and each habitat has a fairly distinct zooplankton fauna. Estuaries such as the York River are particularly interesting as the available habitat for zooplankton covers a wide salinity range. Zooplankton are also found at all depths in the water column, and some even reside in the sediments during the day and emerge into the water at night. Holoplankton spend their entire life cycle in the plankton, while meroplankton spend only a portion of their life cycle as members of the plankton. Meroplankton include many larval fishes, and larval stages of benthic invertebrates. The planktonic stage is generally used for dispersal of the young and is a very common life history strategy for estuarine invertebrates. What zooplankton feed on is not always clear, as it depends upon life stage, season, and food availability. But generally they can be grouped as herbivores which ingest only phytoplankton, omnivores which ingest both phytoplankton and zooplankton, and carnivores which ingest only other zooplankton, and detritivores which ingest detritus and bacteria.

Over the past 40 years, there have been relatively few studies specifically targeting zooplankton communities of the York River estuary and tributaries. The bulk of exploration to date has focused on the zooplankton of mainstem Chesapeake Bay, as part of several large-scale and multi-disciplinary surveys.

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For general multi-species time series reviews on microzooplankton and mesozooplankton from Chesapeake Bay see Brownlee and Jacobs (1987) and Olson (1987). Purcell et al. (1999a, 2001) and Condon and Steinberg (2008) review some of the gelatinous macrozooplankton. Grant and Olney (1983) and Grant (1977) examined mesozooplankton from the lower Chesapeake Bay. Early studies in the York River transpired during the mid 1960–early 1970 period, with a research focus on taxonomy and distribution of copepods and gelatinous zooplankton (Calder, 1968, 1971; Burrell, 1972; Burrell and van Engel, 1976), as well as decapod larvae (Sandifer, 1973, 1975), and predation by ctenophores (Burrell and van Engel, 1976). Further investigation of York River mesozooplankton includes Price (1986). In 1987, the Chesapeake Bay Program (CBP) began sampling from four stations along the York River Estuary (WE 4.2–mouth of York River; RET 4.3–upper York; and TF 4.2 and RET 4.1–Pamunkey River), in conjunction with their long-term monitoring program of Chesapeake Bay and its tributaries. To date, the majority of zooplankton measurements have been collected from station WE 4.2, and data on species composition and abundance can be downloaded via the CBP website (http://www.chesapeakebay.net). One notable publication using this data set is that of Park and Marshall (1993) who described the distribution and seasonal abundance of microzooplankton at three of the four York River CBP stations.

DIVERSITY, NATURAL HISTORY, AND ECOLOGY OF MAJOR GROUPS OF ZOOPLANKTON IN THE YORK RIVER (AND ADJACENT CHESAPEAKE BAY)

Microzooplankton

The microzooplankton mostly include protozoans (single-celled animals), rotifers, and the larval stages of invertebrates. The unicellular protozoa are mostly classified by mode of locomotion, and consist of three major groups. These include the heterotrophic flagellates (~ 5-10 μm), that move with flagella (single or many) and feed on bacteria and detritus. They are important food for other zooplankton and ciliates. Some flagellates are larger (10's -100's μm), such as the heterotrophic dinoflagellates. The ciliates (most ~10-20 μm, some >200 μm) move using cilia that is present in all but a few forms sometime during their life cycle, and feed primarily on phytoplankton (Figure 1). Many ciliates have symbiotic algae from which they receive some of their nutrition. Titinnid ciliates live in a cup- or vase-shaped shell or "lorica" secreted by the cell (thus they are called loricate ciliates, as opposed to ciliates with no shell which are called aloricate or non-loricate) and are an important component of the microzooplankton in Chesapeake Bay (Figure 2). The sarcodines are ameobae, and move and feed using "pseudopodia." Sarcodines are omnivorous, and many have symbiotic algae too. While this group is important in coastal and open ocean waters, the main sarcodines found in the Chesapeake Bay belong to the family Difflugiidae (Sawyer, 1971) and they are mostly restricted to fresher water areas (Brownlee and Jacobs, 1987). Rotifers are small, multicellular animals containing a ciliated band around the head called the "corona" that is used for locomotion and feeding. They are most common in the fresher regions of the bay, and although patchy, can be highly productive and reach high densities in some regions of the Bay (Dolan and Gallegos, 1992). Other microzooplankton include the juvenile/larval stages of zooplankton such as copepods or other invertebrates.

Figure 1. Ciliate *Strombidium* sp. Photo by Matt Johnson.

Microzooplankton abundance in the lower Chesapeake Bay peaks in spring (March- April) and mid-summer to early fall (July-September), and reaches a minimum in winter (Dec-Jan) (Park and Marshall, 1993). This is a similar pattern seen in the rest of the Bay (Brownlee and Jacobs, 1987). The dominant groups of microzooplankton in the lower Bay are the ciliated protozoa (aloricate ciliates and tintinnids). Rotifers, copepod nauplii, and sarcodines are also important at times. A study of the lower Chesapeake Bay found non-loricate ciliates to represent 60%, tintinnids 33%, rotifers 4%, and nauplii larvae (mostly copepods) 3%, of the total microzooplankton composition (Park and Marshall, 1993). In the York River, the abundance of each of these groups was lowest in the tidal fresh region up-river, with numbers increasing in the meso- and polyhaline regions (Park and Marshall, 1993). The species diversity of tintin-

Figure 2. Tintinnid ciliate. Photo by Matt Johnson.

nids increases with decreasing salinity in the mainstem of the Bay (Dolan and Gallegos, 2001).

Mesozooplankton

Copepods

Copepods are small crustaceans approximately the size and shape of a grain of rice. They comprise the bulk of the zooplankton in the Chesapeake Bay (and all other estuarine and marine environments), and may be the most numerous multicellular animals on earth. The body is segmented, with a head with two pairs of antennae and 4 pairs of mouthparts, a mid-body with swimming legs, and a posterior that lacks appendages. They are generally omnivorous, but some are more strictly herbivorous or carnivorous, as well detritivorous. Copepods have separate sexes, and 12 stages of development (first six stages are naupliar larvae, and the last six are copepodite stages– the last of which is the adult). These early juvenile stages are considered part of the microzooplankton community described above.

The dominant copepod species in the Chesapeake Bay are the calanoid copepods *Acartia tonsa*, *Acartia hudsonica* (formerly *Acartia clausii*), and *Eurytemora affinis* (Heinle, 1966, Brownlee and Jacobs, 1987, Olson, 1987). In the lower polyhaline portion of the bay, the summer copepod assemblage is dominated by *Acartia tonsa* (Figure 3), and in winter there is a shift to *Acartia hudsonica* (Brownlee and Jacobs, 1987). In the upper mesohaline portion of the York River (station RET 4.3, CBP), *Acartia* spp. abundance peaks in August and *Eurytemora* peaks in March /April. However, while the lower York also experiences a summer *Acartia* bloom there is no winter *Eurytemora* peak (station WE 4.2, CBP, Steinberg and Brush, unpublished data). This is consistent with what is found in the rest of the lower polyhaline region of the mainstem bay, where numbers of *Eurytemora affinis* are much reduced compared to the upper, mesohaline, mainstem bay. In the lower York, *Pseudodiaptomus coronatus* can also be very abundant in summer (Price, 1986). *Acartia* exhibits diel vertical migration, with densities substantially higher in the surface waters at night in the lower York (Price, 1986) and elsewhere in the Bay (Cuker and Watson, 2002). The next most abundant copepods in the York River are the cyclopoid copepods *Oithona* spp. There are more than 60 species of copepods reported in the York River (see Appendix), but the seasonal and interannual cycles of most have yet to be investigated.

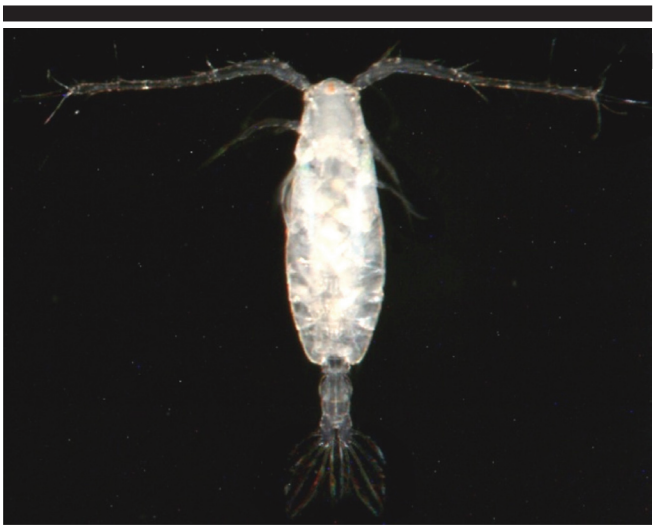

Figure 3. Copepod *Acartia tonsa*.

Cladocera

The cladocera are most abundant in freshwater, with only about 10 species that are truly marine planktonic, and in freshwater their ecological role is equivalent to copepods in marine systems. Thus cladocera are numerically and ecologically more important up-river. Cladocera have a flat body covered by a carapace, with large, compound eyes that can take up to one-third of the body. The 2nd antennae are used for swimming. Cladocera reproduce sexually or parthenogenically, and have a brood pouch inside their carapace from which young are released. They are filter feeders and generally omnivorous, consuming phytoplankton, microzooplankton, and copepod eggs.

In the Chesapeake Bay, cladocera are most abundant in warmer months and commonly occur at the extreme geographic/ salinity ranges of the bay. Freshwater cladocera can make up >50% of the zooplankton in the freshwater tributaries of the bay (Brownlee and Jacobs, 1987), while other true estuarine species, such as *Podon polyphemoides* which peaks in May, occasionally proliferate in the lower, polyhaline portion of the bay, sometimes extending the length of the estuary (Bosch and Taylor, 1967, 1973). In the tidal fresh Mattaponi tributary of the York, *Bosmina* is the most common genus and peaks in spring (April/May) (J. Hoffman, pers. comm.), while *Podon* peaks at the mouth of the York in July (CBP; Steinberg and Brush, unpublished) (Figure 4).

Figure 4. Cladocera *Podon* sp.

Mysids, isopods, and amphipods

These crustaceans belong to a group (the pericarids) that shares the diagnostic feature of brooding their young in a pouch from which they hatch as miniature adults. Mysids look much like shrimp, however they have a 'statocyst' or balance organ on their tail, which can be used to distinguish them from shrimp (Figure 5). Mysids in the York River and Chesapeake Bay (mainly *Neomysis americana*) remain near the bottom during the day and swim up into the water column at night (Price, 1986, Cuker and Watson, 2002), as is typical of this group. Mysids are omnivorous and prey on other zooplankton such as copepods (Fulton, 1982) and phytoplankton. Mysids are important food for many fish species in the Bay, including American shad, striped bass, white perch, and flounder


Figure 5. Mysid

(e.g., Walter and Olney, 2003). We know little about mysid distribution and seasonal cycles, as most studies of plankton in the Bay have sampled only in the daytime. Amphipods are familiar to most people as the small 'beach hoppers' on dead algae found on the beach. Planktonic amphipods feed on dead phytoplankton or other detritus, as well as on other animals. Amphipod bodies appear compressed laterally, as opposed to the related isopods, which are flattened dorsoventrally. Most isopods are strictly benthic, and thus they are uncommon in the plankton. There is little available information on amphipods and isopods in York River plankton, however in the adjacent lower Bay amphipods are dominated by the species *Gammarus mucronatus* in surface waters, and isopod densities are very low (Grant and Olney, 1983).

Chaetognaths

The chaetognaths or "arrow worms" are abundant and voracious predators in the plankton. They eat copepods, smaller chaetognaths, fish, and crustacean larvae. These transparent plankton have both lateral fins and tail fins, as well as large, spiny, chitinous hooks on their head used to capture and stun their prey. Chaetognaths are not endemic to the bay but are transported in from the continental shelf. The polyhaline portion of the bay near the mouth of the York River sees several species, such as the annual fall invasion of *Sagitta tenuis* (Grant, 1977).

Meroplankton and demersal zooplankton

At certain times of the year and in different salinity regimes, various meroplankton such as crab or other decapod larvae (Figure 6), bivalve (clam) and gastropod (snail) larvae, naupliar and cyprid stages of barnacles, and polychaete worm larvae (Figure 7) become numerically important in the Bay (Brownlee and Jacobs, 1987, Olson, 1987, Grant and Olney, 1983) and in the York River (e.g., Sandifer, 1973). Some of these are demersal zooplankton–residents of the benthos that emerge into the water column, especially at night. Decapod larvae are common in the York River, especially downriver. One of the most common species of decapod larvae include the Sand Shrimp, *Crangon septemspinosa*, which was found to be responsible for winter peaks in decapod abundance, and there are also a number of important crab larvae (Sandifer, 1973, 1975). Many species of decapod larvae tend to be more abundant near the bottom where net transport is upstream, likely as a mechanisms for retention within the estuary (Sandifer, 1973, 1975). In the lower Chesapeake Bay, decapod larvae become dramatically more diverse in summer months *vs*. winter (Grant and Olney, 1983). A number of bivalve and gastropod larvae occur in the lower bay, and naupliar and cyprid stages of barnacles have been noted to occur in higher densities at the surface at dawn and dusk in the lower Bay (Grant and Olney, 1983). Most polychaetes are benthic, but the larval stages of benthic polychaetes are sporadically abundant in Chesapeake Bay plankton. These segmented, bristled worms swim and can hold on to prey using their parapodia (modified 'feet'). The planktonic polychaetes are normally carnivorous or detritivorous, and may have a proboscis or jaw that everts out from the head to capture prey. The most abundant and widely distributed polychaetes in summer lower Bay samples reported by Grant and Olney (1983) were Spionid larvae.


Figure 6. Decapod (crab) larva


Figure 7. Polychaete larva

Other rare groups

Other groups such as the ostracods, also called "seed or clam shrimps," are primarily benthic in the estuarine environment, and thus rarely found in plankton samples in the York or adjacent Bay waters. Pelagic, gelatinous tunicates such as larvaceans and doliolids are also rare in estuaries, but occasionally occur in samples in the lower Bay (Grant and Olney, 1983).

Large gelatinous zooplankton

Gelatinous zooplankton is a term commonly used to describe plankton that are made up of primarily "soft," jelly-like tissue. Despite their large size, gelatinous zooplankton are not strong swimmers so their movements are primarily determined by the currents and are thus referred to as plankton. In the York River estuary, the gelatinous fauna is relatively species rich compared to other coastal regions of the world, with over 25 species. A striking seasonal change in the zooplankton community composition of the tributaries and the main stem of the mesohaline and polyhaline portions of the bay occurs in the summer when large gelatinous zooplankton "bloom" (Condon and Steinberg, 2008).

Ctenophores

Ctenophores or comb jellies are the largest animal to move by cilia, and have eight rows of 'combs' made of fused macrocilia that they use to swim (Figures 8 and 9). Some have tentacles loaded with sticky cells called colloblasts that are used to capture food. Others, such as the lobate ctenophores, use a pair of oral lobes coated with sticky mucus to trap prey items upon contact.

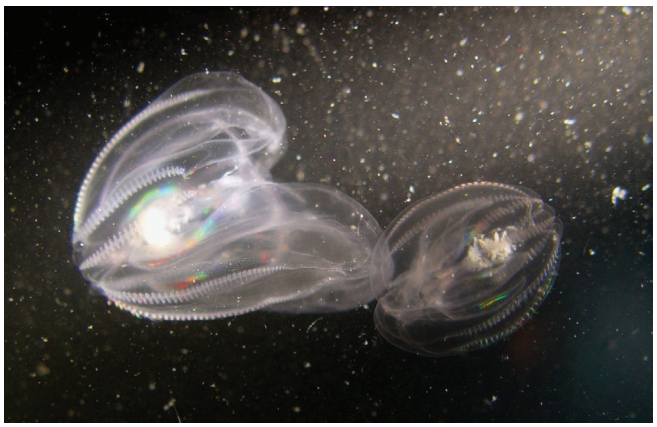

Figure 8. Ctenophore *Mnemiopsis leidyi*

Ctenophores are a very bioluminescent group, and many of the larger bioluminescent flashes one might see at night in the Bay in the wake of a boat come from them. Ctenophores are carnivorous and prey upon copepods (Condon and Steinberg, 2008), larval fish and crustaceans, and in some cases other ctenophores. Larval and smaller ctenophores also consume microzooplankton and small protozoans (Stoecker *et al.*, 1987a; Sullivan and Gifford, 2004). They have high predation rates and can drastically deplete the abundance of other planktonic species. All ctenophores are hermaphrodites and capable of self-fertilization. Sexual reproduction occurs in the water column (i.e., broadcast spawners), after which miniature (1–5 mm length) cydippid larvae form that grow rapidly into adults (>20mm length).

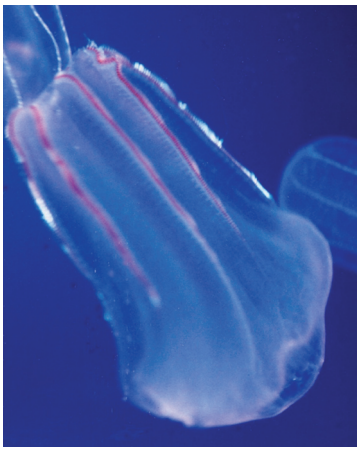

Figure 9. Ctenophore *Beroë ovata*

The dominant ctenophore in the York River and Chesapeake Bay is the lobate ctenophore, *Mnemiopsis leidyi* ('sea walnut') (Figure 8). In the York River, *M. leidyi* persists throughout the year, with two distinct bloom periods with large spikes in the population (Condon and Steinberg, 2008). During the summer months (May–August), a large biomass of ctenophores is distributed along the entire length of the estuary, occurring in salinities of 6–27.5 psu (Burrell and van Engel, 1976; Figure 10). At these times, comparable numbers of *Mnemiopsis* are also observed in the mesohaline and polyhaline regions of Chesapeake Bay (Burrell, 1968, Purcell *et al.*, 1994a, CBP). Interestingly, temperature does not limit the ability of *M. leidyi* to grow rapidly, as blooms also occur in the lower York River (salinities >15 psu) between December–March (Burrell and van Engel, 1976; Condon and Steinberg, 2008). It is unclear

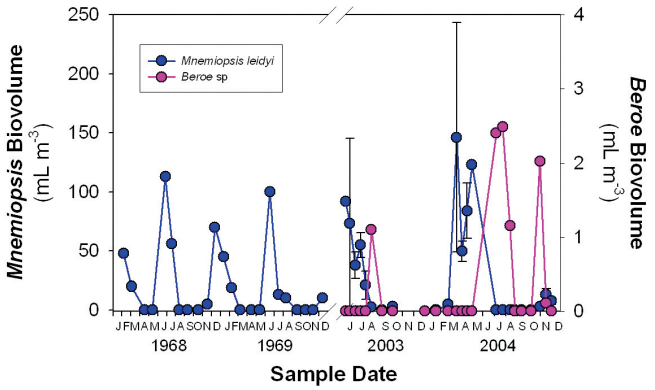

Figure 10. Seasonal cycle of ctenophores in the York River. (Data from Burrell and van Engel, 1976, and Condon and Steinberg, 2008)

whether similar abundances appear in the mainstem Chesapeake Bay during the winter. The next most abundant ctenophore in the York River is *Beroë ovata* ('pink sea jelly') (Figure 9). This football-shaped ctenophore lacks both tentacles and feeding lobes and consumes other ctenophores, particularly *M. leidyi*. Little is known about *B. ovata* feeding but some individuals can consume as many as seven *M. leidyi* at one time (Burrell, 1972). *Beroë ovata* is present mainly in the lower York River from August to early December (Burrell, 1972; Burrell and van Engel, 1976; Condon and Steinberg, 2008; Figure 10), and due to their cannibalistic behavior, *B. ovata* greatly reduces the biomass of *M. leidyi* when both species coexist. As a result, the highest numbers of *M. leidyi* in the York River during the late summer–fall period are found outside the range of *B. ovata* (Burrell and van Engel, 1976). One other ctenophore that can be found in the York during the spring is the tentaculate ctenophore or sea gooseberry, *Pleurobrachia* sp., although in general it is rare.

Scyphomedusae

Scyphomedusae (or Scyphozoan medusae), known locally as sea nettles or jellyfish, are notorious to Chesapeake Bay, primarily due to the stings they inflict to sea bathers each summer, and for their ability to form swarms. Medusae are mainly carnivorous and are major consumers of copepods, larval fish and crustaceans, ctenophores and other gelatinous zooplankton. Prey are caught using tentacles containing harpoon-like, stinging cells called nematocysts. Scyphozoan reproduction is complex, often with both a planktonic, sexual adult medusa stage, and a benthic, asexual polyp stage.

The most common scyphomedusan in the York River and lower Chesapeake Bay is the sea nettle, *Chrysaora quinquecirrha*

(Figure 11), which is found along the entire east coast of the USA. *Chrysaora* medusae are present from late May through October, with a population peak any time during July–September (Cargo and Schultz, 1966, 1967, Cargo and King, 1990; Condon and Steinberg, 2008).

Seasonal and interannual variability in medusae abundance is a function of water temperature and salinity, as well as zooplankton prey abundance (Cargo and King, 1990, Purcell *et al.*, 1999a). Using these variables and other data, NOAA have developed a sea nettle model which forecasts the distribution of medusae throughout Chesapeake Bay and its tributaries, which can be viewed at the following website: http:/www.coastwatch.noaa.gov/seanettles. In the mesohaline Chesapeake Bay and York River estuary, *C. quinquecirrha* medusae are major predators of *M. leidyi* ctenophores (Purcell and Cowan, 1995; Condon and Steinberg, 2008). The creeks and tributaries of the York River may be important nursery grounds for *C. quinquecirrha*, where large amounts of suitable hard substrate such as oyster shells/reefs exist, on which polyps develop. Two color morphs of *Chrysaora* exist in the lower Chesapeake Bay, the more common white variety and a less common red-striped variety (Figure 11), and these varieties probably represent the same species (K. Bayha, pers. comm.).

Figure 11. Sea nettle *Chrysaora quinquecirrha*. Two color morphs exist in the lower Chesapeake Bay, the more common white variety (left) and a less common red-striped variety (right).

Another scyphomedusan abundant at times in the York River is the moon jelly, *Aurelia* sp. (Figure 12). Moon jellies are present in the polyhaline regions of the lower York River and Chesapeake from June–July when they can form large swarms or aggregations (Condon and Steinberg, 2008) (Figure 12), usually determined by local hydrographic conditions such as fronts (Graham *et al*., 2001). In the winter months (January–March) the Lion's Mane jellyfish, *Cyanea* sp., can also be found in the lower York River and Chesapeake Bay (Burrell, 1972; Condon and Steinberg, 2008). This winter jelly has received little attention and consequently virtually nothing is known of the ecology and impact of *Cyanea* medusae in the York River. The cannonball jelly, *Stomolophus meleagris*, and the mushroom cap jelly, *Rhopilema verilli*, are two additional species found in the lower York River and Chesapeake Bay but both are infrequently seen.

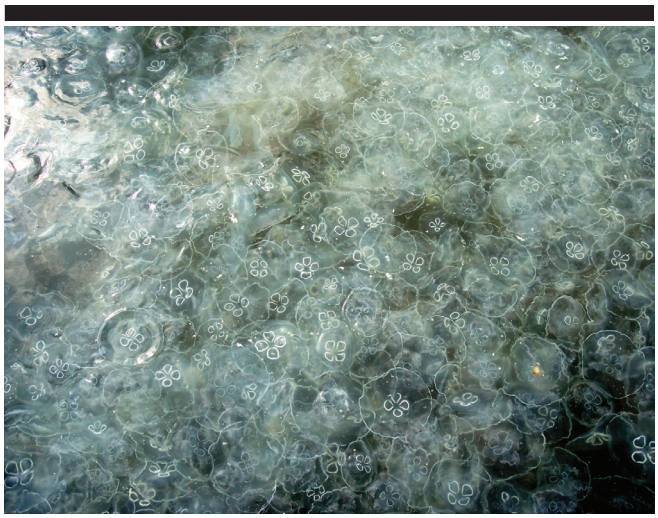

Figure 12. Moon jelly *Aurelia* sp. bloom in Mobjack Bay at the mouth of York River. Photo courtesy of Scott Kupiec.

Hydromedusae

Hydromedusae (or Hydrozoan medusae) are small (0.1mm–5mm), inconspicuous jellies, and are represented in the York River by over 20 species (Appendix I; Calder 1968, 1971). Hydromedusae are among the best described plankton groups in the world (Purcell *et al.*, 1999a), yet they have received little attention in the York River estuary. Their life cycle is similar to scyphomedusae except their benthic stage (known as hydroids) is morphologically different, and in many species the medusa stage is brief. Hydromedusae are primarily carnivorous, consuming copepodites, nauplii and other microzooplankton, and during the fall hydromedusae may be key predators in the pelagic food web in southern Chesapeake Bay (Purcell *et al.*, 1999a).

One of the most conspicuous hydromedusae in the York River and Chesapeake Bay is *Nemopsis bachei*. This euryhaline hydromedusae is found from the lower reaches of the York River and southern Chesapeake Bay (Calder, 1971) to the oligohaline regions near the Pamunkey River (< 6 psu). *Nemopsis bachei* is present in the York River throughout the year with population peaks in late spring, and during fall and early winter (September–January). During spring, *N. bachei* is the most abundant gelatinous zooplanktivore in the mesohaline Chesapeake Bay, where they consume primarily *Acartia tonsa* copepodites, and nauplii (Purcell and Nemazie, 1992), and may be partially responsible for poor fish recruitment during red drum spawning season (Cowan *et al.*, 1992). Various other hydromedusae, including *Liriope tetraphylla*, *Clytia* sp. (cf. *Clytia edwardsi*), and *Cunina* sp. (cf. *Cunina octonarina*), also appear in high numbers during October, particularly in southern Chesapeake Bay and the lower York River (Burrell, 1972; Purcell *et al.*, 1999a).

TROPHIC STRUCTURE AND ENERGY FLOW

Microzooplankton are important grazers of bacteria and small phytoplankton in the Chesapeake Bay, and are themselves important food for larger grazers such as copepods. In the Bay, phytoplankton composition changes from mainly diatoms during spring blooms to dominantly smaller cells during non-bloom periods (Ray *et al.*, 1989). These smaller cells cannot be consumed by mesozooplankton directly. Thus the microzooplankton/ microbial food web is important during much of the year and an important link for transfer of energy to higher trophic levels. Microzooplankton are important food for copepods and other grazers in Chesapeake Bay. The copepod *Acartia tonsa* feeds on ciliates and rotifers at rates higher than that for phytoplankton, an indication that microzooplankton may be an important part of the copepod diet (Stoecker and Egloff, 1987). Copepod predation can also affect diversity of some groups such as tintinnids (Dolan and Gallegos, 2001). Microzooplankton are also important food for larval ctenophores (Stoecker *et al.*, 1987a, Sullivan and Gifford, 2004) and are fed upon by the jellyfish *Aurelia aurita* (Stoecker *et al.*, 1987b). Copepods are the key grazers of phytoplankton in Chesapeake Bay, and can remove a substantial percentage of the daily phytoplankton production (White and Roman, 1992). However, estimates of Bay-wide grazing by microzooplankton and mesozooplankton combined indicate that on average zooplankton remove less than one-third of the phytoplankton biomass daily, thus much of the phytoplankton is not grazed but becomes fuel for bacterial metabolism (Sellner and Jacobs, 1993) or sinks to the benthos.

Because bloom-forming gelatinous zooplankton such as ctenophores and sea nettles are voracious consumers of mesozooplankton (primarily copepods) (Condon and Steinberg, 2008) and larval fish (Purcell, 1992, Cowan and Houde, 1993, Purcell *et al.*, 1994a,b), they are extremely important in shaping plankton and fish communities in the summer months (Baird and Ulanowicz, 1989). In the Chesapeake Bay *M. leidyi* is most abundant between June and September. *Chrysaora quinquecirrha* medusae consume ctenophores and can control *M. leidyi* populations in Chesapeake Bay (Feigenbaum and Kelly, 1984, Purcell and Cowan, 1995; Condon and Steinberg, 2008). Thus the reduction of ctenophore populations usually coincides with the seasonal appearance of *C. quinquecirrha* (in the lower bay the predatory ctenophore *Beroë* occurs in early fall and may contribute to mortality of *M. leidyi*; Burrell, 1968). Burrell and van Engel (1976) noted, however, that *Chrysaora* did not reduce ctenophores in the York River. When *M. leidyi* population growth goes unchecked by predation, zooplankton populations can be depleted (Kremer 1994). Thus, the predation of medusae on ctenophores can lead to complex food web changes that can ultimately reduce the mortality of other zooplankton and icthyoplankton (Feigenbaum and Kelly, 1984, Purcell *et al.*, 1991, Purcell and Cowan, 1995). This "trophic cascade" can result in increases in numbers of other zooplankton (e.g., copepods).

CHANGES OVER TIME

Few studies have examined long-term trends of zooplankton communities in the York River and mainstem Chesapeake Bay. Using data collected from the main stem stations of the CBP, Kimmel and Roman (2004) found no overall long-term trends for the copepods *Eurytemora affinis* and *Acartia tonsa* over a 16-year period, but concluded freshwater input and top-down control by gelatinous predators were partial factors in shaping copepod populations. More recently, Purcell and Decker (2005) correlated *Chrysaora* scyphomedusae abundance with climatic conditions in the mesohaline Chesapeake Bay, and found high medusae densities during 1987–1990, which followed a year of high salinity, warm temperature, and high solar irradiance. On a larger time scale, the North Atlantic Oscillation Index was inversely correlated with medusae numbers from 1960–1995 (Purcell and Decker, 2005). Similarly, Condon and Steinberg (2008) show that *Mnemiopsis* blooms now appear earlier in the York River estuary compared to 40 years ago, and correlate this temporal shift to the warming in spring water temperatures and the earlier release of temperature limitation on ctenophore reproduction. Whether similar trends have occurred in other York River zooplankton is yet to be determined and would necessitate continual long-term monitoring of zooplankton throughout the year.

HUMAN INFLUENCES ON ZOOPLANKTON IN THE YORK RIVER

Introduced Species

Zooplankton are easily introduced into estuarine systems because many species are tolerant of a wide range of salinity and temperature and have life cycle stages that are resilient or remain dormant (e.g., encyst) in unfavorable conditions. A good example is the invasion of the ctenophore, *M. leidyi*, in Black Sea, which ironically was likely introduced from Chesapeake Bay (Purcell *et al.*, 1999a, 2001). Subsequent population explosions of *Mnemiopsis* impacted greatly on copepod and fish populations and resulted in the closure of many commercial fishing operations in that region.

While many examples probably exist, there are few records of introduced zooplankton species to the York River and lower Chesapeake Bay. One example, however, is the inconspicuous hydrozoan, *Moerisia lyonsi*, present in the oligohaline regions of the York River during summer (Calder, 1971). *Moerisia* is thought to have been introduced from Egypt (Calder and Burrell, 1966; Purcell *et al.*, 1999b), however the long-term ecological impact of this species introduction is unknown. As *Moerisia* consume copepod adults and nauplii (Purcell *et al.*, 1999b), and probably fish larvae and eggs too, copepod abundance and fish recruitment could be affected. Further research into the feeding ecology, distribution and seasonal occurrence of *M. lyonsi* is needed in order to fully understand the impact of these hydrozoans (Purcell *et al.*, 1999b).

Eutrophication

As discussed in the paper by Reay in this Special Issue, anthropogenic eutrophication and water quality is a major is-

sue in the Chesapeake Bay. However, whether there is direct link between eutrophication and York River zooplankton is purely speculative (Purcell *et al.*, 1999a), because there is a paucity of information on zooplankton distributions prior to 1960 (Arai, 2001) when waters were relatively pristine.

Hypoxia

One major influence of eutrophication is increased bottom water hypoxia (< 2 mg O_2 l^{-1}), or in extreme circumstances anoxia (< 0.5 mg O_2 l^{-1}), resulting in an increase in oxygen deplete bottom waters in many regions of Chesapeake Bay and the York River (Taft *et al.*, 1980, Sanford *et al.*, 1990). Hypoxia can have both positive and negative effects on zooplankton survival and behavior. For example, copepod and ichthyoplankton survival, and hatching success of copepod eggs, are very low under hypoxic conditions (Roman *et al.*, 1993; Breitberg *et al.*, 1997; Decker *et al.*, 2004), and *Acartia* ceases its diel vertical migrations making these copepods vulnerable to predation by gelatinous zooplankton (Roman *et al.*, 1993). In contrast, gelatinous zooplankton such as *C. quinquecirrha* medusae and polyps, and *M. leidyi,* are tolerant of hypoxia and thus theoretically have the potential to predominate under these conditions (Purcell *et al.*, 1999a; Condon *et al.*, 2001; Decker *et al*., 2004). However in the mesohaline Chesapeake Bay and the York River these gelatinous predators appear to avoid these waters (Burrell and van Engel, 1976; Purcell *et al.*, 1999a), perhaps in response to the lack of food below the pycnocline. Further increases in hypoxia, as a direct result of eutrophication, has the potential to significantly impact zooplankton populations in the York River and thus alter the planktonic food web as a whole.

Contaminants

Assessing the degree to which contaminants affect zooplankton populations in the York River is difficult due to the lack of data from this estuary. However, as evidenced from Chesapeake Bay, it is clear that exposure to contaminants can severely impact zooplankton, particularly copepods and decapods that are sensitive and vulnerable to these pollutants (Bradley and Roberts, 1987).

Heavy metals (e.g., mercury) and pesticides (e.g., tributyltin) are two contaminant groups that pose the greatest risk to estuarine zooplankton. Their most drastic effect is death but other side effects occur, including reduced fecundity and longevity, stress and altered feeding behavior (Bradley and Roberts, 1987). Bioaccumulation of contaminants is another major problem that can cascade throughout the food chain, but this depends upon the rate of biodegradation, uptake kinetics and bioavailability of the contaminants (Bradley and Roberts, 1987). For example, in the mesohaline Chesapeake Bay, *Acartia* copepods bioaccumulate hydrophobic organic contaminants (HOC) associated with their food, but the HOC concentration is dependent on the particle size consumed (Baker *et al.*, 1994; Roman, 1994).

The York River is also home to large industry including the BP Amoco oil refinery and Virginia Electric and Power plant at Yorktown, and the West Point paper mill. Industries like power plants are major sources of heat and biocides or oxidants, like chlorine, to waterways they utilize (Bradley and Roberts, 1987). Studies into the effects of these two contaminants from Chesapeake Bay show that chlorines have a greater impact on adult and larval copepod survival than temperature (Olson, 1987).

Dredging occurs frequently in the York River to accommodate both commercial and military traffic, and while it difficult to test in the field, the potential impact on zooplankton is large in areas where toxic sediments have been disturbed or deposited (Bradley and Roberts, 1987).

RESEACH PRIORITIES AND FUTURE MONITORING NEEDS

Long-term monitoring of zooplankton communities is needed to allow us to predictively model the ecosystem of the York River. Zooplankton monitoring data is needed to increase our understanding of factors affecting fish recruitment and to support ecosystem-based fisheries management. It is also needed to examine shifts in zooplankton abundance and community composition due to effects of introduced species, increases (or reduction) in nutrients, or a change in watershed land use. Compared to the main stem Chesapeake Bay and some of the more northern tributaries of the Bay, zooplankton in the York River have been little studied. While the CBP has provided a basis for understanding interannual and seasonal abundance of the major zooplankton groups, many gaps still remain.

There are only a handful of published studies on the microozooplankton community in the York River. Members of this diverse community are rarely identified to the species level, and we know little about their trophic structure and next to nothing about their feeding rates in the York River. As the microzooplankton must certainly be major consumers of primary production in the estuary, especially during the summer months, more work is needed in characterizing this community and measuring their grazing rates and impact on the phytoplankton community.

While diel and seasonal cycles and grazing rates of some of the most common mesozooplankton such as *Acartia tonsa* are known, we still lack information on the multitudes of other species. For example, historically most sampling has occurred during the day. Many species, such as mysids and demersal zooplankton, are more abundant in surface waters at night, and feeding rates can be higher at night as well. These and other crustacean zooplankton are important prey items for larval menhaden and bay anchovy, however estimates of their abundance are poor. Future monitoring studies should thus include paired day and night sampling. Another example is that little is still known about the dynamics of larval invertebrates in the York, information which is needed to help us understand benthic invertebrate community dynamics.

Dynamics of gelatinous zooplankton, especially that of the larger medusae (sea nettles, moon jellies), is still poorly known and sampled in the York. More sampling of the tributaries of the York River is needed to investigate early life history stages of medusae. We also know nothing of the fate of these remarkable gelatinous zooplankton blooms–do they

sink out or are they consumed? While plankton nets sample the ctenophores adequately, sampling of the larger medusae is more difficult. Larger nets are needed but often prohibitive as monitoring normally takes place off of smaller boats from which such nets are difficult to deploy. Alternatively, new technology such as camera systems that can see large volumes of water could be used to obtain reliable estimates of the abundance and distribution of this very important component of the zooplankton community.

New technology should be an important part of future monitoring studies. Olney and Houde (1993) used silhouette photography with some success to monitor zooplankton communities in the Chesapeake Bay. Another possibility is the video plankton recorder or VPR. The VPR is an underwater digital video microscope designed for high resolution imaging of plankton (Davis *et al.*, 1996). Upon retrieval, data and images can be analyzed by an image recognition software package that automatically identifies and counts organisms. If instruments such as the VPR can be modified for use in high particle load environments such as the York River, there is potential to map zooplankton species abundance over large spatial scales.

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APPENDIX

Species List of Zooplankton for the York River Estuary

The catalog of species found within the York River are recorded in chronological order with the initial reference listed first and the most recent last.

Key for references:
1 = Park and Marshall, 1993
2 = Burrell, 1972
3 = Burrell and van Engel, 1976
4 = Sandifer, 1973
5 = Sandifer, 1975
6 = Price, 1986
7 = Chesapeake Bay Program (data from Stations CB 6.4, WE 4.2, RET 4.1 and 4.3, and TF 4.2)
8 = Calder, 1968
9 = Calder, 1971
10 = Calder and Burrell, 1966
11 = Purcell, Malej and Benovic, 1999
12 = Grant and Olney, 1983

\+ indicates species predominately found in southern Chesapeake Bay
* indicates species predominately found in the Pamunkey River and the freshwater tributaries.
^ indicates species is non native to the York River
R indicates species are rare or infrequently observed
L indicates species represented in plankton by larval or egg stage

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Phylum Ciliophora (Ciliates)

Class Litostomatea
Order Haptorida
Didinium sp. 1

Class Spirotrichea
Order Stombidiida
Strombidium sp. 1

Order Choreotrichida
Strobilidium sp. 1

Order Tintinnida (Loricate ciliates)
Eutintinnus sp. 1
Tintinnopsis sp. 1
Tintinnidium sp. 1

Phylum Foraminifera

Globorotalia sp. 7

Phylum Rotifera

Brachionus sp. 1
Branchionus calyciflorus 7
Branchionus havanaensis 7
Filinia sp. 1
Keratella sp. 1
Synchaeta sp. 1
Trichocerca sp. 1

Phylum Cnidaria

Class Scyphozoa (True jellyfish or Scyphomedusae)
Order Semaeostomeae
Aurelia sp. (Moon jelly) 2,7
Chrysaora quinquecirrha (Sea nettle) 2,3,7
Cyanea sp. (Lion's mane jelly) 2

Order Rhisostomeae
Rhopilema verrilli[R] (Mushroom cap jelly) unpub. data
Stomolophus meleagris[R] (Cannonball jelly) unpub. data

Class Hydrozoa (Hydromedusae)
Order Anthomedusae
Bougainvillia rugosa 8,9,7
Dipurena strangulate 8,9
Ectopleura dumortieri 8,9
Halocordyle tiarella 8,9
Hydractinia arge 8,9
Hydra carnea 7
Linvillea agassizi 8,9
Moerisia lyonsi^ 8,9,10
Nemopsis bachei 8,7,9
Podocoryne minima 8,9
Proboscidactyla ornate 8,9
Rathkea octopunctata 8,9
Sarsia tubulosa 8,9
Turritopsis nutricula 8,9

Order Leptomedusae
Aglantha digitale 8,9

"Campanulina" sp.	8
Clytia edwardsi	8,9,11
Cunina octonarina	8,9,11
Eucheilota ventricularis	8,9,7
Lovenella gracilis	8,9
Liriope tetraphylla	8,9,11
Obelia spp.	8,9
Phialicium carolinae	8,9

Phylum Ctenophora (Comb jellies)

Class Tentaculata

Order Lobata

Mnemiopsis leidyi (Sea walnut)	2,3,7

Order Cydipidda

Pleurobrachia sp. (Sea gooseberry)	7

Class Nuda

Order Beroida

Beroe ovata (Pink sea jelly)	2,3,7

Phylum Platyhelminthes (Flat worms)

Turbellaria sp.	7

Phylum Chaetognatha (Arrow worms)

Sagitta tenuis	2
Sagitta elegans	2,7
Sagitta enflata	7

Phylum Polychaeta (Bristle worms)

Autolytus sp.	7
Polydora ligni	7
Polydora sp.	2

Phylum Phoronida (Horseshoe worms)

Phoronis architecta	7
Phoronis sp.	7

Phylum Mollusca[L]

Class Bivalvia

Crassostrea virginica (American oyster)	7
Mercenaria mercenaria (Quahog or Hard clam)	unpub. data
Mytilus edulis (Blue mussel)	7

Class Cephalopoda

Loligo sp.	7
Lolliguncula brevis	7

Phylum Arthropoda

Subphylum Crustacea

Class Maxillopoda

Order Siphonostomatoida

Caligus sp.	7

Subclass Copepoda (Copepods)

Order Calanoida (Calanoid Copepods)

Acartia hudsonica	2,3,7
Acartia longiremis	7
Acartia tonsa	2,3,7
Calanus finmarchicus[+]	2,7
Centropages furcatus[+]	2,7
Centropages hamatus	2,3,7
Centropages typicus	2,7
Diaptomus sp.	7
*Eucalanus pileatus**	2,7
Eurytemora affinis	2,7
*Eurytemora americana**	2,7
Eurytemora hirundoides	7
Labidocera aestiva	2,3,7
*Mecynocera clause**	2
Metridia lucens	7
Paracalanus crassirostris	2,7
Paracalanus fimbriatus	7
*Paracalanus indicus**	2,7
*Paracalanus quasimodo**	2
Pseudocalanus minutus	2,7
Pseudocyclops sp.*	2,7
Pseudodiaptomus coronatus	2,3,7
Rhincalanus nastus[R]	7
Temora longicornis	2,7
*Temora stylifera**	2,7
*Temora turbinat**	2,7
*Tortanus discaudatus**	2,7

Order Cyclopoida (Cyclopoid copepods)

Acanthocyclops vernalis	7
*Corycaeus amazonicus**	2,7
Corycaeus speciosus	7
Corycaeus venustus	7
Cyclops vernalis	2,7
Diacyclops thomasi	7
Ectocyclops phaleratus	7
*Eucyclops agilis**	2,7
Halicyclops fosteri	2,7
*Hemicyclops adherans**	2
*Leptinogaster major**	2
Mesocyclops edax	2,7
*Mesocyclops leukarti**	2
Mesocyclops obsoletus	7
Oithona brevicornis	2
Oithona colcava	7
Oithona similis	2
*Oncaea mediterranea**	2,7
Paracyclops affinis	7
Paracyclops sp.	7

Saphirella sp.	7
Troprcyclops sp. (cf. *T. prafinus mexicanus)*	7
Order Harpacticoida (Harpacticoid copepods)	
*Alteutha oblongata**	2
Canuella canadensis	2
*Canthocamptus**	7
Canuella elongata	7
Clytemnestra rostrata[+]	7
Diosaccus tenuicornis	7
*Euterpina acutifrons**	2,7
Paralaophonte brevirostris	7
Harpacticus chelifer	7
Harpacticus gracilis	7
Tisbe furcata	7
*Zausodes arenicolus**[,R]	7
Order Poecilostomatoida	
Ergasilus cerastes	2
Ergasilus versicolor	7
Farranula gracilis	2
Class Branchiopoda	
Order Cladocera (Cladocerans)	
*Alona guttata**	7
*Alona quadrangularis**	7
*Alonella rostrata**	7
Bosmina coregoni maritime	7
Bosmina longirostris	7
*Ceriodaphnia reticulata**	7
*Chydorus**	7
*Daphnia ambigua**	7
*Daphnia longispina**	7
*Daphnia pulex**	7
Diaphanosoma brachyurum	7
*Eurycercus lamellatus**	7
Evadne nordmanni	7
Evadne tergestina	7
Holopedium sp.	7
*Ilyocryptus spinifer**	7
Latonopsis fasciculate*	7
*Leptodora kindtii**	2,7
*Leydigia quadrangularis**	7
*Moina brachiata**	7
Penilia avirostris	7
Pleuroxus striatus[R]	7
*Pseudosida bidentata**	7
*Scapholeberis kingi**[,R]	7
*Simocephalus**	7
*Sida crystalline**	7
Podon intermedius	7
Podon polyphemoides	7
Podon sp.	2
Class Malacostraca	
Order Decapoda (Crab and shrimp larvae)[L]	
Acetes americanus	7
Alpheus cf *heterochaelis*[+,R]	4,7
Alpheus normanni[+,R]	4,7
Callinassa cf. *atlantica*[+]	4,7
Callianassa cf. *biformis*[R]	4,7
Callinectes sapidus (Blue crab zoea)	2,4,5,7
Cancer irroratus[+]	4,5,7
Crangon septemspinosa (Sand shrimp zoea)	2,4,5,7
Dissodactylus mellitae[+,R]	4
Emerita talpoida[+] (Sand crab larvae)	4,7
Euceramus praelongus	4,7
Eurypanopeus depressus [R]	4,7
Hexapanopeus augustifrons	4,5,7
Hippolyte pleuracantha	4,5,7
Lepidopa cf. *websteri*[+]	4,7
Libinia spp.[R]	4,7
Libinia emarginata	7
Lucifer faxoni[+]	4,7
Macrobrachium ohione	7
Naushonia crangonoides[+]	7
Neopanope sayi (cf. *N. texana sayi)*	4,5,7
Ogyirides limicola	4,5,7
Ovalipes ocellatus	4,5,7
Pagurus longicarpus	4,7
Pagurus pollicaris[+,R]	4,7
Palaemonetes spp.	2,4,5,7
Palaemonetes pugio	7
Panopeus herbstii	4,7
Penaeus spp.[+,R]	4
Penaeus aztecus	7
Pinnixa chaetopterana	5,7
Pinnixa cylindra[+]	4,7
Pinnixa sayana	4,5,7
Pinnotheres maculates	4,5,7
Pinnotheres ostreum	4,5,7
Polyonyx gibbesi	4,7
Portunus gibbesii	7
Portunus spinicarpus	7
Rhithropanopeus harrisii	2,3,4,5,7
Rhithropanopeus hermandii	7
Sesarma cinereum[R]	4
Sesarma reticulatum	4,5,7
Uca spp.	5,7
Uca minax	7
Upogebia affinis	4,7
Order Mysidacea (Mysids)	
Bowmaniella dissimilis	7
Mysidopsis bigelowi	7
Neomysis americana	6,7
Order Cumacea	
Leucon americanus	6
Order Stomatopoda	
Squilla empusa (Mantis shrimp)	7
Order Amphipoda (Amphipods)	
Caprella geometrica	7
Corophium lacustre	7
Cymadusa compta	3

Gammarus fasciatus 7
Gammarus mucronatus+ 12
Monoculodes sp.* 7

Order Isopoda
Edotea sp. 7

Class Insecta
Order Diptera
*Chaoborus punctipennis**,L 7
Ephydra sp. 7
Odonata sp.*,R 7
*Pentaneura monilis** 7

Subclass Branchiura
Order Argulidea
Argulus sp. (Common fish lice) 7

Subclass Cirripedia
Order Thoracica
Balanus sp.L (Barnacle) 7

Phylum Chordata (Icthyplankton)

Class Osteichthyes (Bony fishes)L
Order Atheriniformes
Menidia beryllina (Inland silverside) 7
Menidia menidia (Atlantic silverside) 7
Membras martinica (Rough silverside) 7

Order Clupeiformes
Alosa mediocris (Hickory Shad) 7
Anchoa hepsetus+ (Striped Anchovy) 7
Anchoa mitchelli (Bay Anchovy) 7

Order Gobiesociformes
*Gobiesox strumosus** (Skilletfish)

Order Perciformes
Cynoscion nebulosus (Weakfish) 7
Cynoscion regalis (Gray weakfish) 7
Ammodytes americanus+,R 7
(American sandlance)
Bairdiella chrysoura (Silver perch) 7
Gobiosoma bosc (Naked goby) 7
*Gobiosoma ginsburgi** (Seaboard goby) 7
Leiostomus xanthurus (Spot) 7
Hypsoblennius hentzi (Feather blenny) 7
Menticirrhus saxatilis 7
(Northern kingcroaker)
Micropogonias undulatus 7
(Atlantic croaker)
Morone americana (White perch) 7
Morone saxatilis (Striped bass) 7
Peprilus paru (American harvestfish) 7
Perca flavescens (Yellow perch) 7
Pogonias cromis (Black Drum) 7

Order Pleuronectiformes
Pseudopleuronectes americanus 7
(Winter flounder)
Scophthalmus aquosus (Widowpane) 7
Trinectes maculates (Hogchoaker) 7

Order Sygnathiformes
Hippocampus erectus (Lined seahorse) 7
Syngnathus fuscus (Northern pipefish) 7