Ecological and Biological Setting

Habitats of North Inlet and Winyah Bay

North Inlet and Winyah Bay share many of the same intertidal and subtidal habitat types, but, because of greater freshwater contribution and the associated salinity gradient in Winyah Bay, the marshes and submerged bottom habitats vary more in Winyah Bay than in North Inlet. There are many definitions of the term habitat, but for the purposes of this document we define a habitat as a morphologically distinct subunit of the estuary wherein the depth (or extent of tidal flooding), geomorphology, sediment, vegetation, and most common animals differ from other subunits in the same estuary. For example, the intertidal salt marsh dominated by *Spartina alterniflora* is a different habitat than unvegetated intertidal mud flats. Although boundaries between adjacent habitats can be sharp, they are sometimes irregular and represent transitional stages between two or more habitat types. For instance, some intertidal flats are mosaics of mud, clumps of oyster reefs, and islands of marsh grass. Some of the more commonly encountered transitional or hybrid habitats are characterized within the descriptions of primary habitat types below.

Three major groupings of habitat types can be identified in estuaries based on tidal flooding regimes: subtidal, intertidal and supratidal. Subtidal, or permanently submerged habitats include the water column, hard and soft bottoms, shell rubble, and many man-made structures (e.g., jetties, artificial reefs). Primary intertidal habitat types shared by the two estuaries include high marsh, low marsh, intertidal creeks, mud flats, oyster reefs, low energy sandy beaches, and man-made structures (e.g. pier pilings, bulkheads). Supratidal habitats include areas of upland that periodically receive flooding during storm events. These habitats are described in further detail below.

The National Estuarine Research Reserve System's *Recommended Guidelines for Adoption and Implementation of the NERRS Comprehensive Habitat and Land Use Classification System* (Walker and Garfield, 2006) was developed to help reserves track and evaluate short-term variability and long-term changes in the extent and type of habitats within reserves and to examine how these changes are related to anthropogenic and climate stressors. The plan presents a long-term strategy to develop a standardized inventory of land use and land cover at a base year, and to measure changes over time in reserves and adjacent watersheds of influence. The NERRS has developed a land use/land cover classification scheme and mapping protocols for reserves and their watersheds, classification scheme documentation, and standard operating procedures which detail the methodology for developing and submitting habitat maps to the NERRS Centralized Data Management Office (CDMO). More information can be found at **www.nerrs.noaa.gov**.

Mapping of the North Inlet – Winyah Bay NERR began in 2007 with an inventory of available imagery, methodology and software, and discussions of the mapping boundary. Aerial photo interpretation was chosen as the most accurate method for delineating the marsh habitats within the limited budget for image and software acquisition and availability of GIS and remote sensing expertise and assistance. A total of 5,285 ha of habitat was mapped in the North Inlet estuary using color-infrared (CIR) digital orthophoto quadrangles (DOQ) with a 1-meter ground resolution from the year 2006 (Figure 65). The ten largest habitat subclasses in the North Inlet – Winyah Bay NERR are indicated in Table 4. Almost half (47%; 2,490 ha) of the area is estuarine intertidal emergent wetland (NERRS classification 2261), low marsh dominated by *Spartina alterniflora*. High marsh, including supratidal emergent wetland, and broad leaved deciduous (BLD), broad leaved evergreen (BLE) and needle leaved evergreen (NLE) scrub-shrub accounts for almost a quarter of the area (24%; 1,244 ha). Open water, including subtidal channels, intertidal channels, supratidal pools, and littoral ponds, is the third largest habitat area (11%; 587 ha). The total amount of subtidal channel edge calculated from the map is approximately 310 km. Tidal datums for a benchmark located near Oyster Landing in the NERR are provided in Table 5.

Table 4. Ten largest habitat subclasses by total area in the North Inlet-Winyah Bay NERR

Sub Class	Sub Class Name	Modifier Name	Area (ha)	% Total Area	Total Edge (km)
2261	Estuarine, Intertidal, Emergent, Persistent	Low Marsh	2489.6	47	433.9
2351	Estuarine, Supratidal, Scrub-shrub	High Marsh	665.9	13	162.4
2120	Estuarine, Subtidal, Unconsolidated	Subtidal Channel	587.4	11	309.1
2341	Estuarine, Supratidal, Emergent, Persistent	High Marsh	562.0	11	188.2
6155	Upland, Supratidal, Forested, Mixed	Maritime Forest	374.7	7	65.1
6131	Upland, Supratidal, Herbaceous, Grassland	Dune	160.8	3	56.6
2254	Estuarine, Intertidal, Unconsolidated, Mud	Intertidal Flat	125.9	2	48.2
1243	Marine, Intertidal, Unconsolidated, Sand	Beach	119.1	2	47.4
6143	Upland, Supratidal, Scrub-shrub	Maritime Shrub	51.3	1	17.1
6154	Upland, Supratidal, Forested	Pine Forest	47.0	1	3.5

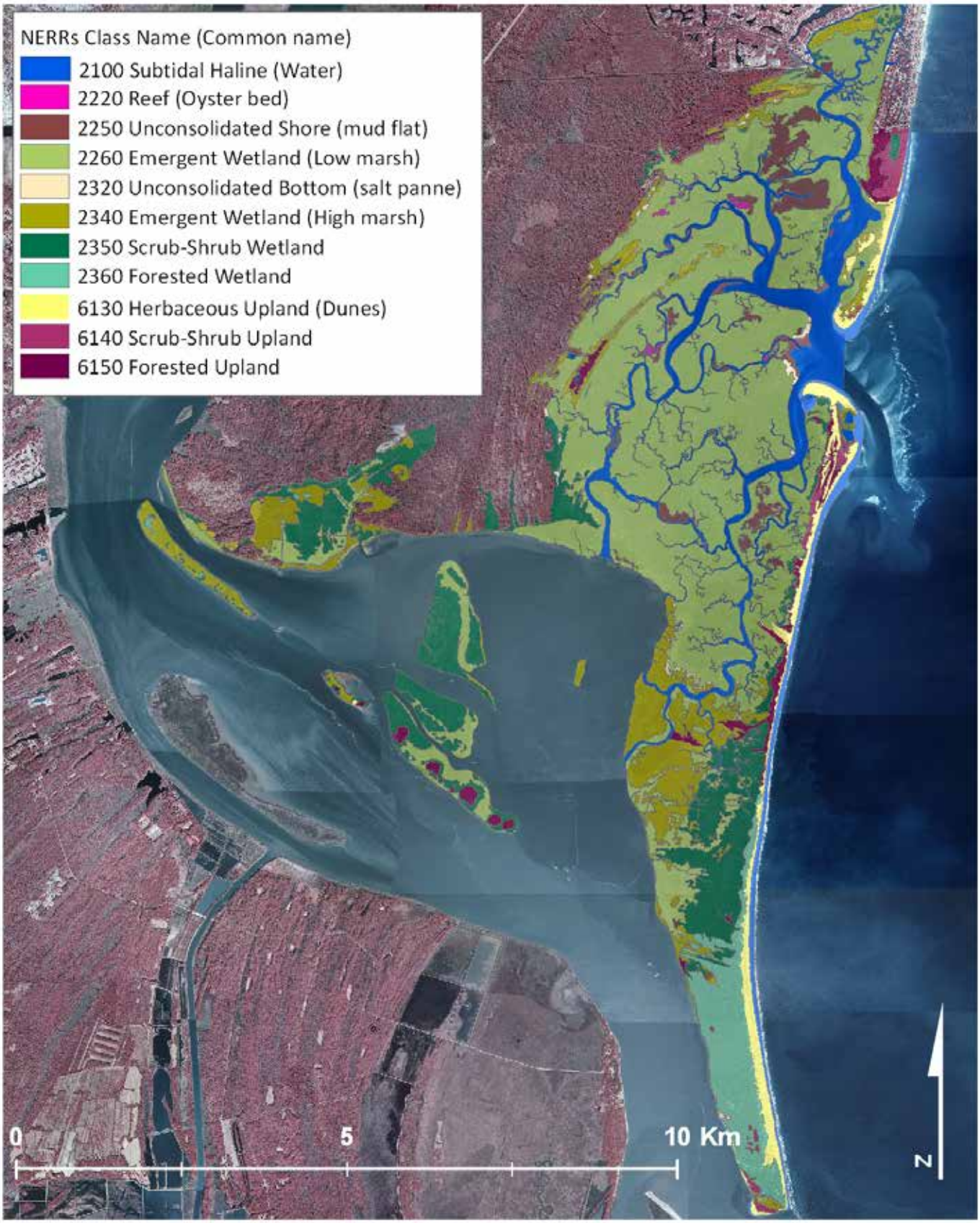


Figure 65. Habitats of the North Inlet-Winyah Bay NERR categorized by NERR class and common name.

Table 5. Tidal datums for benchmark PID DD1345 located near Oyster Landing in the North Inlet-Winyah Bay NERR. Datums are references on the 1983-2001 Epoch.

Mean Higher High Water (MHHW)	1.561 Meters
Mean High Water (MHW)	1.455 Meters
NAVD88	0.826 Meters
Mean Sea Level (MSL)	0.816 Meters
Mean Tide Level (MTL)	0.756 Meters
Mean Low Water (MLW)	0.058 Meters
Mean Lower Low Water(MLLW)	0.000 Meters

» Habitat Descriptions

ESTUARINE SUBTIDAL HABITATS

Estuarine subtidal habitats are those below mean low water (MLW) in which the substrate is continuously submerged by tidal water and the salinity is at least 0.5.

- **Subtidal Channel**

Channels that remain flooded at low tide serve as conduits of exchange of organisms and materials between the marsh and the ocean. Throughout the system, this highly dynamic habitat changes in depth, direction and rate of flow, turbidity, salinity, light penetration, and in many other ways, physically, chemically, and biologically on time scales of minutes.

In general, channel bottoms in North Inlet are composed of sands closer to the inlet and of mud closer to the upland. The most current-scoured channel bottoms are mostly sand and shell. These are generally referred to as hard (as opposed to soft) bottoms. Firm sandy and sandy–mud bottoms cover most of the lower Winyah Bay and channels in the mid- and upper Bay. These are shaped by strong tidal currents. The bottom is often highly irregular with ridges and swales being created and moved by the scouring tides. Little is known about the benthic infauna in these areas.

Accumulations of sloughed and degenerating oyster shell are also found on subtidal channel bottoms in North Inlet. These permanently submerged accumulations usually lie adjacent to living intertidal oyster reefs and support the growth of encrusting invertebrates and fishes, including the juveniles of many snappers, groupers, and other species that occur on similar 'live bottoms' in the coastal ocean. In Winyah Bay, shell rubble accumulations appear to be small due to limited well-developed living oyster reefs. However, re-exposed deposits of fossil shells - especially large oyster shells - may provide rubble habitat in some areas in the lower and mid-Bay.

Fine suspended sediments settle to the bottom in waterways with low velocity tidal currents, creating soft or muddy bottoms that support different infaunal benthos than sandy and shelly bottoms. Soft muddy subtidal environments are abundant in Winyah Bay, especially adjacent to the shorelines and in the large lagoonal area known as Mud Bay. These soft-bottom areas are probably maintained by the deposition of fine, river-borne sediments. Shallow subtidal bottoms are generally rich in benthic infauna and provide habitat for the commercially important species of shrimps, crabs, and fishes.

ESTUARINE INTERTIDAL HABITATS

Estuarine intertidal habitats are those in which the substrate is exposed and flooded by tides with a salinity of at least 0.5 during the period of average annual low flow. This zone extends from the mean low water mark (MLW) to the mean high water mark (MHW), but does not include the adjacent zone inundated only by storm surges.

- **Intertidal Channel**

Intertidal channels serve as conduits of exchange for water, dissolved and suspended materials, and motile animals which regularly move with the tides between the channels or pools within the channel beds and the vegetated marsh. More than 1000 intertidal channels of various sizes connect the marsh with subtidal channels in North Inlet. The mouths of intertidal channels are generally close to mean low water, and their sediments usually grade from coarse sandy-mud and shell near the mouth to soft mud further upstream. Because most of the marshes in the mid- and upper Winyah Bay were created and cultivated in the 1800's, most of the shallow channels in that system are straight, man-made canals that provided water flow and small boat access to the rice crops.

- **Intertidal Flats**

Intertidal flats are areas of unvegetated mud or sand found in low energy tidal environments that are exposed at mean low water. They are usually flanked by small subtidal channels or are mostly surrounded by salt marsh at the ends of large intertidal creeks in North Inlet. These ecologically important areas support high densities of meiofauna, macrobenthos, and benthic microalgae and serve as foraging areas for many fishes, motile invertebrates and birds. Intertidal flats are uncommon in Winyah Bay, with most of them being small fringing areas adjacent to marsh islands in the lower Bay. They tend to be composed of soft muds and likely support benthic infauna and nekton similar to those associated with mudflats in North Inlet.

- **Oyster Reef**

American Oysters, *Crassostrea virginica*, tend to grow intertidally in clusters on firm sediments and develop reefs along channel edges in North Inlet. In some locations, oyster reefs form as islands surrounded by water at low tide. Living oyster reefs are uncommon in Winyah Bay, perhaps because of the high loads of fine suspended sediments and the tendency for intertidal shorelines to accumulate mud. Some free-standing reefs occur in creeks in the lower Winyah Bay where, along the edges of some marsh islands, there are poorly-developed reefs associated with accumulations of fossil shell deposited when the ship channel was created more than a century ago. Oysters comprise the only naturally occurring hard structures in southeastern estuaries. Both living intertidal reefs and subtidal accumulations of shells provide substrate for many encrusting invertebrates (e.g., sponges, hydrozoans, soft coral, barnacles, mussels) and algae which, in turn, support small motile animals (e.g., crabs, shrimps, amphipods, polychaetes). Oyster reefs are primary feeding areas for larger motile invertebrates, fishes, and some birds.

- **Low Marsh**

Low marsh comprises the majority of habitat area in North Inlet and is dominated by salt marsh cordgrass, *Spartina alterniflora*. Regularly flooded marshes also occur in the form of *Spartina alterniflora* dominated stands in the lower Winyah Bay, *Spartina cynosuroides* in the brackish portion, and freshwater grasses in the upper Bay. Some sedges and *Typha* spp. (cattails) occur in wet marsh soils. This habitat provides cover for many species of nekton that use the marsh surface during high tide, and is an important nesting habitat for several species of birds including clapper rails, marsh wrens and willets. Snails and fiddler crabs are conspicuous invertebrates, and many shrimps, crabs, and fishes forage in low marshes when they are flooded.

ESTUARINE SUPRATIDAL HABITATS

Supratidal habitats are submerged by tidal flooding less than 5% of the time. This zone extends from the mean high water line (MHW) to the mean higher high water line (MHHW).

- **Estuarine Beach**

In contrast to the wave-influenced or high energy beaches that occur on the ocean-facing sides of barrier islands, low-energy estuarine beaches are more influenced by tidal currents. Sandy-mud

environments occur near the mouth of North Inlet and along major subtidal channels. The only low energy intertidal beaches in the Winyah Bay system are located inside of the barrier island on the south side of the inlet, specifically adjacent to the base of the south jetty on South Island. Although they support diverse assemblages of meiofauna and macrobenthos, densities of infauna are lower than in muddy environments. Large flocks of shorebirds rely on these areas during their migratory stop-overs. This habitat also provides important nesting habitat for some bird species and diamondback terrapins.

- **High Marsh**

Proximal to the upland border or surrounding upland islands are areas of marsh that are flooded for short periods of time during every tide or only sporadically. Short-form *Spartina alterniflora* dominates at the lowest end of the elevational gradient in the high marsh. *Salicornia* spp. and other salt-tolerant plants occur in the middle reaches, and *Juncus romerianus*, *Borrichia* spp., and other plants tolerant of infrequent inundation are at the upper limit of the high marsh. Large dense stands of *Phragmites australis* occur in the mid- and upper Winyah Bay. Sediments are usually firm, insect larvae are common in the sediments, and upland mammals and birds commonly forage here.

- **Pannes and Pools**

Pannes are areas of the supratidal marsh where high tide pools form and evaporate, leaving areas of high salinity soils in which few plant species can grow. These areas have not been well studied, but are frequently used as foraging areas by wading birds during flooding tides. Increased flooding due to sea level rise may decrease soil salinity, allowing plants to recolonize and eventually convert these areas to high marsh. Areas of the marsh surface that remain permanently, shallowly flooded are referred to as pools. Water salinity can range from brackish to highly saline.

UPLAND SUPRATIDAL HABITATS

Upland supratidal habitats are any coastal upland area above the highest spring tide mark that is periodically over-washed, covered, or soaked with seawater during storm events to an extent that it affects habitat structure or function.

- **Dune and Maritime Shrub**

An extensive dune system is found on North Island and to a lesser degree on Debidue Island. The dominant plant species are *Uniola paniculata*, *Panicum amarum*, *Croton punctatus*, and *Sabal minor*. This habitat is highly dynamic and is susceptible to storm-induced and long-term erosion. Hardened shoreline structures such as groins and sea walls are of concern as they may prevent the longshore drift of sediments necessary for building and maintaining dunes. Maritime shrub habitat occurs on stabilized sand dunes, dune swales, and sand flats protected from saltwater flooding and most extreme salt spray. The dominant plant species are *Myrica cerifera*, *Juniperus virginiana*, and *Sabal minor*.

- **Pine Forest and Maritime Forest**

Pine forest habitat occurs at the upland edge of North Inlet and the northern edge of Winyah Bay. The pine forest is dominated by *Pinus taeda*, but *Quercus virginiana* and *Sabal palmetto* also occur. Understory species include *Myrica cerifera*, *Sabal minor*, and *Ilex vomitoria*. Maritime forest occurs on protected parts of old, stabilized dunes and beach ridges on North Island and is dominated by *Quercus virginiana*, *Pinus taeda*, *Sabal palmetto*, *Juniperus virginiana*, and *Myrica cerifera*.

CULTURAL LAND COVER

Cultural land cover represents any area modified by mechanical or chemical manipulation more than once per growing season, regularly grazed by livestock, modified to a condition that prohibits sustained plant and animal colonization, or is dominated by built-up or residential structures (Kutcher et al., 2005).

- **Impervious Cover, Unconsolidated and Herbaceous Cover**

Very little of the land area within the Reserve boundary is in impervious cover. This classification includes the buildings of the Baruch Marine Field Laboratory and the NI-WB Reserve offices. There are no paved roads within the Reserve. Cleared land, dirt and gravel roads and parking lots, and managed turf and shrubs occur over a small area of the reserve, mostly associated with the Baruch Marine Field Lab and Reserve offices.

Few clusters of pilings (docks) exist in North Inlet other than a concentrated area of piers and bulkheads along the man-made DeBordieu canal at the extreme north end of the estuary. In Winyah Bay, dozens of piers and short bulkheads, large fields of pilings installed as erosion control structures, and ricefield water control systems and support piers built many decades ago exist along many of the shorelines in the mid- and upper Bay. Stumps and fallen logs from cypress tree stands that died in the last century provide prominent structure to the intertidal and shallow subtidal portions of these same areas.

OTHER GEOMORPHIC FEATURES

- **Hammocks and Middens**

Hammocks are areas of higher elevation surrounded by marsh where upland species can grow. These areas are either the remnants of former dunes or are Native American shell middens. Some of these predominately clam shell refuse piles are more than 30 m (100 ft) across and date to more than 2000 years before present. This habitat is dominated by upland edge species such as *Quercus virginiana* and *Juniperus virginiana*. The leaching of calcium from oyster and clam shells reduces the natural acidity of the soils in these areas and in some cases the resulting calcareous soils allow rare plant communities to develop.

- **Wrack**

Extensive wrack mats comprised primarily of *Spartina alterniflora* stems may be the most ephemeral habitat type in the intertidal and supratidal marsh. Areas of wrack accumulation may create vegetation die off areas that will either remain as intertidal flats or will eventually be re-colonized by marsh plants after the wrack has been removed. These areas may also provide cover habitat for newly hatched diamondback terrapins. Hardened structures such as causeways, retaining walls, and even temporary boardwalks to research sites affect the accumulation and movement of wrack.

- **Eroded Sod Banks**

Some edges of salt marsh are prone to current or wave scour and have nearly vertical rather than sloped profiles. Because of their instability, they do not support oyster reefs or abundances of other infauna. Living *Spartina* usually grows to the edge of these banks and root networks delay erosion of the peaty, firm muds that characterize these areas. Most of the marsh edges throughout Winyah Bay have sharp vertical profiles. The long fetch created by the large expanses of open water in the Bay probably enhances the exposure of sod banks to erosive waves. Sometimes on recently eroded banks, re-exposed, dense accumulations of white shell from a former, older oyster reef that had been buried (grown over by marsh) for decades or centuries become evident. Eroded banks also occur at the upland-marsh edge where tidal channels are migrating inland with sea level rise.

- **Marsh Dieback**

Marsh dieback, also called brown marsh, is the rapid die-off and loss of marsh vegetation. It is characterized by rapid onset (1 to 2 growing seasons) and is often non-persistent. The cause of sudden marsh dieback is still under debate but may be cyclical depending on interactive climate conditions, sea level anomalies, and other biotic factors. Areas of suspected marsh dieback have been periodically observed in North Inlet, but have not been mapped or monitored.

Estuarine subtidal habitat: Subtidal channel

Estuarine intertidal habitats: (left to right) Intertidal channel, intertidal flats, oyster reef, low marsh.

Estuarine supratidal habitats: (left to right) Estuarine beach, high marsh, pannes and pools.

Upland supratidal habitats: (left to right) Dune, pine forest.

Other geomorphic features: (left to right) Hammocks, wrack, eroded sod banks, marsh dieback.

North Inlet's Major Biota

» Primary Producers

For a coastal salt marsh like North Inlet (and many others throughout the southeastern US), salt marsh cordgrass (*Spartina alterniflora*) dominates the visible landscape. Many other primary producers also contribute significantly to the salt marsh food web, including phytoplankton, microphytobenthos, macroalgae, and other vascular plants.

PHYTOPLANKTON

Chlorophyll *a* has been measured in the NI-WB NERR 20-day water chemistry program at the SWMP sites since 1994. During the summer, concentrations of 4-12 mg/L are typical for the Oyster Landing site. Diel differences in chlorophyll *a* levels usually occur with lower values being recorded during the dark period, when the primary producers are not actively synthesizing organic compounds (Figure 66). Often, in tidal creeks, a tidal signature can be observed with higher chlorophyll *a* concentrations being recorded during mid tides when the strongest currents are most likely to suspend benthic microalgae. High values around two of the three low tides on July 3 and 4 can probably be attributed to this process.

Diel and tidal variations are evident each month during 2010, but the range is greatest during the summer when phytoplankton densities are at peak annual levels. Highest concentrations were seen during mid summer and lowest values were recorded in winter and spring (Figure 67). This seasonal signature is shown in Figure 68 where summer values are consistently highest and spring is usually second highest. Mean seasonal values of chlorophyll *a* were higher in the 1990s when wetter conditions that reduced salinities and increased runoff prevailed (Figure 68). Drier conditions probably contributed to lower chlorophyll levels after 2001. A long-term decrease in chlorophyll *a* is indicated for Oyster Landing and other locations in North Inlet.

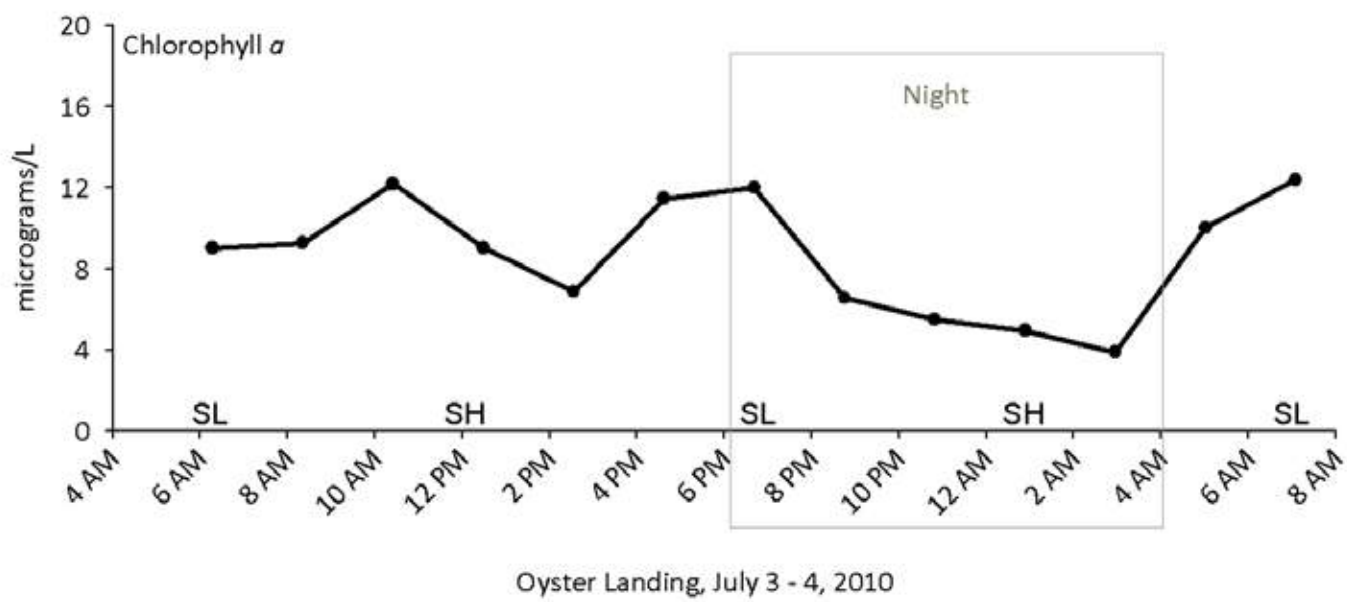


Figure 66. Chlorophyll *a* concentrations in water samples collected every hour July 3-4, 2010 at the NI-WB NERR SWMP Oyster Landing monitoring site. SL = slack low tide; SH = slack high tide.

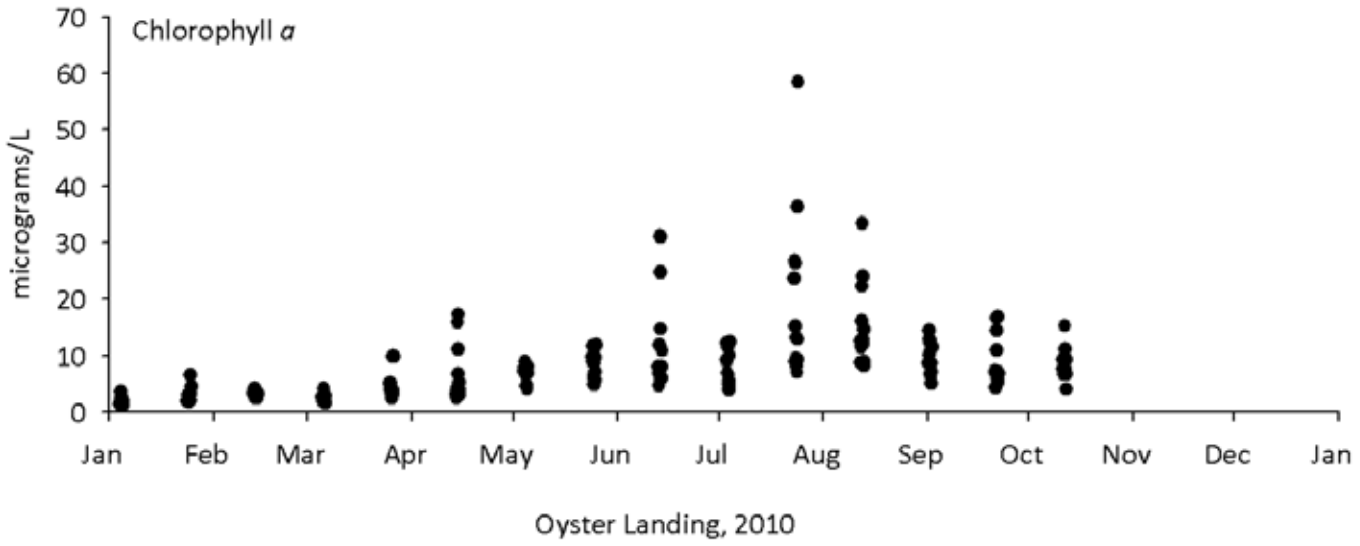


Figure 67. Chlorophyll *a* concentrations in water samples collected every hour during the 20 day samplings in 2010 at the NI-WB NERR SWMP Oyster Landing monitoring site.

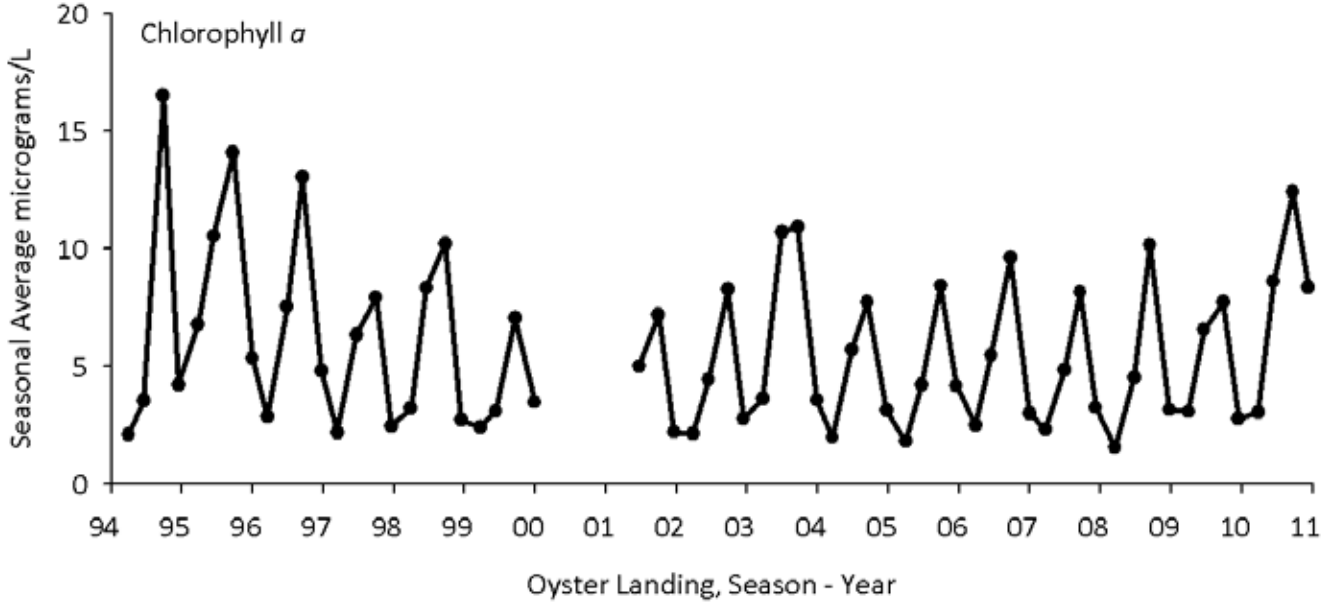


Figure 68. Mean seasonal chlorophyll *a* concentrations in water samples collected from 1994-2010 at the NI-WB NERR SWMP Oyster Landing monitoring site. Data for about 18 months starting in early 2000 were not included because of problems with the analytical processing of the water samples.

SUMMARY OF OTHER STUDIES ON PHYTOPLANKTON IN NORTH INLET

Among the early studies of primary production (PP) were student thesis projects that characterized the phytoplankton communities occuring in the tidally-mixed waters of North Inlet (Sellner, 1973; Vennewitz, 1977; Hall, 1979). These researchers found a diverse assemblage (over 200 species) with numerical dominants that changed seasonally and year-to-year. Abundances ranged from 10^6 to 10^8 cells per liter and their concentrations varied with changes in tidal levels, possibly due to resuspension of benthic algae. Blood and Vernberg (1992) have reproduced the phytoplankton species list originally provided by Hall (1979).

Rates of PP using the C^{14} method varied from 178 to 409 gC m^{-2} y^{-1} (Sellner et al., 1976; Vennewitz, 1977; Zingmark, 1977). These rates varied according to changes in the water temperature cycle and were twice as high at some places than at others. PP in the North Inlet exit plume entering the ocean was estimated by Zeeman (1982) as 639 gC m^{-2} y^{-1}.

Erkenbrecher and Stevenson (1980) examined the effects of changing tidal levels and diel fluctuations on chlorophyll *a* and "pheophytin" concentrations in a high-marsh creek in North Inlet. They found that tidal forces controlled the chlorophyll degradation product concentration but that the chlorophyll *a* biomass changed in a complex pattern involving tides and diel photosynthetic rhythms. They cautioned that tide levels and volume fluxes must be taken into account when measuring PP and phytoplankton species composition as they change with the season in North Inlet.

Vernberg (1981) summarized many findings from the multidisciplinary Outwelling Study performed in North Inlet in the 1970s. Briefly, this study sought to determine whether (and which types of) dissolved and particulate materials, both inorganic and organic, were exported from North Inlet to the coastal ocean on an annual basis (Dame et al., 1986). Among these findings was a net import of chlorophyll *a* from offshore into North Inlet but a net loss of photosynthetic cells within the inlet. Researchers thought that this loss was due to grazing rather than to settling of cells from the water column. The general outcome of these flux studies was in support of the outwelling hypothesis that the estuary is a source of detrital outflow to the coastal ocean. By making comparisons of import/export dynamics between other estuarine systems, Vernberg sought generalities in how coastal ecosystems function. This systems approach resulted in three modeling publications: Dame et al. (1977), Summers and Kitchens (1980), and Summers and McKellar (1981), all of which pointed to gaps in our understanding of the linkages and couplings. The output from these models defined research needs for over a decade in North Inlet. Other studies soon followed with empirical data that allowed these models to be tested. For instance, Dame (1982) found that there was a regular export of macrodetritus out of the inlet, but this flux was less than 1% of the net marsh primary productivity.

Zeeman (1985) measured phytoplankton photosynthesis both just outside North Inlet and farther offshore shortly after Hurricane Dennis passed in August 1981. Using photosynthesis versus light intensity (P vs I) curves, his data showed that photosynthesis was depressed soon after the storm but was elevated at the same stations 10 days later, going from 50 to 200 inshore and from 10 to 75 mg C m^{-3} h^{-1} at the offshore station. The changes were deemed to have resulted from a change in the species composition of the community (dinoflagellates appeared in place of diatoms) and/or changes in the ambient temperature, salinity, and light regime. Nutrient levels did not change significantly over the 10-day lag between samplings.

Dame et al. (1986) calculated that phytoplankton biomass (as chlorophyll *a*) and POC (particulate organic carbon) influxed from the coastal ocean in summer and fall and outfluxed in winter and spring, with net annual export of both to the coastal ocean. The extensive data sets summarized by Dame et al. (1986) also included quantitative measurements of nitrogen and phosphorus (dissolved and particulate), microbial ATP, detrital material, zooplankton, bird biomass, and water fluxes. The conclusion reached by Dame et al. (1986) was that North Inlet is a highly productive bar-built estuary

with a strong connection to the coastal ocean that is enriched by outflow from the excess productivity that is only partially utilized within the inlet. That is, they suggested the existence of a feedback loop with offshore phytoplankton taking up nutrients before being imported by tidal flux back into North Inlet where they are consumed and remineralized.

This inflow/outflow dynamic that fuels PP in North Inlet was further investigated by Whiting et al. (1987) who measured nitrogen species (ammonium, nitrate, nitrite) in the water column. They found that North Inlet consistently exported dissolved inorganic nitrogen to the coastal ocean via tidal exchange. They suggested that nitrification within the marsh was the source of this export, thereby strongly supporting the conclusions of Dame et al. (1986).

Earlier monitoring of nutrient levels and the chl-*a* concentration in North Inlet showed that ammonia (NH_4^+) was high at the same time as chl-*a* in the summer. This unusual situation suggested that the phytoplankton were likely limited not by nitrogen as in many other estuaries studied, but by some other factor. Lewitus et al. (1998) surmised that grazing might limit the summertime growth rate of phytoplankton and devised an elegant set of experiments to test their hypothesis. They found that the summer phytoplankton consisted mostly of picoplankton, especially nanoflagellates, with the cyanobacteria *Synechococcus* spp. comprising almost all of the phototrophic picoplankton. Other dominants included the genera *Cylindrotheca*, *Nitzschia*, and *Thalassiosira*. In a series of dilution and nutrient addition bioassay experimental cultures using natural phytoplankton communities, Lewitus et al. (1998) determined that grazing by members of the microzooplankton limited summertime growth of the phytoplankton. Furthermore, they determined that, in contrast with the summer situation, wintertime phytoplankton communities were limited by available nutrients. Their seasonal samplings also showed that the size-structure of the phytoplankton community changed during the year, with smaller forms < 20 microns dominant in summer and larger forms in winter and early spring. Picoplankton (0.2-2.0 microns) and nanoplankton (2.0-20 microns) were abundant in summer, peaking in July and September, while nanoplankton and microplankton (20-200 microns) dominated the phytoplankton's summertime biomass when picoplankton comprised only 1% of the community in July. The picoplankton biovolume peaked in September. During winter the microplankton comprised 26% of the phytoplankton abundance and 77% of its biovolume. The summer-to-winter transition took place when ammonium occurs in excess in summer as nanoflagellates dominate and then becomes limiting in winter when a diatom-based phytoplankton community develops. Thus the phytoplankton community switches from one dominated by microbial loop processes in summer to one dominated by a microplankton-based food web in winter. This study raised many questions about differences in the control on water column primary production in North Inlet from offshore coastal waters where nutrient levels are lower but light intensities are higher.

Following these discoveries about the seasonal switch from microbial- to diatom-based food webs, Dame et al. (2000b) began an investigation of the impacts of oyster reefs in tidal creeks within North Inlet. In this study they examined a group of eight creeks that were to be manipulated later (by oyster removals) in a BACI (before-after control-incident) experimental design. They monitored chl-*a* in the creeks and found changes in concentrations that were consistent with those reported first by Lewitus et al. (1998), i.e., very low (near zero) in winter and highest in summer in all the creeks. Because phytoplankton did not respond appreciably to nutrient addition in their batch culture enrichment experiments in the summertime, they suggested that oyster removals would probably lead to nutrient deprivation of the phytoplankton community especially in winter. They thought that because oyster reefs are a rich source of ammonium via their excretion products, an absence of oysters might lead to nitrogen limitation of PP. Their data also suggested that nitrate and nitrite flow into the tidal creeks adjacent to the forest, an obvious source of nitrogen in these smaller creeks that are more influenced by runoff than by tidal exchanges.

Dame et al. (2002) found that oyster removals did not cause massive changes in most of the parameters they measured in the BACI design. There was elevated recruitment of oyster spat to creeks where oysters had been removed and slightly elevated growth rates of the few oysters remaining in those creeks. Their batch culture nutrient, NH_4^+ addition studies showed that chl-*a* was not usually stimulated. Their dilution experiments demonstrated that grazing was more important as a change agent for chl-*a* than nutrient limitation. Interestingly, they suggested that nekton, water column remineralization, and sediments probably supply enough ammonium to meet phytoplankton demand. There was such complete mixing of water in the creeks from tidal exchanges that removal of the oysters had a much lower impact than anticipated. They suggested that systems dominated by bivalves behave in a complex fashion and do not respond in a linear or very predictable fashion to over-fishing, pollution, or eutrophication.

To estimate the energetic demands and impact of dolphins that routinely visit North Inlet, Young and Phillips (2002) took primary productivity data from Pinckney and Zingmark (1993a, 1993b) and applied several well-established measures of trophic transfer efficiency to measure how much primary production it took to supply the energetic needs of, on average, six resident dolphins for a year. Their trophic model conservatively estimated how much fish biomass the dolphins ate and calculated that 3 to 7% of primary production (all types, not just phytoplankton) was utilized in support of dolphin biomass. Although dolphins clearly do not control primary production in North Inlet, this top-down approach provided an interesting way of thinking about how primary production is utilized in coastal marsh systems like North Inlet. Their paper illustrates many basic ecological principles about trophic transfer efficiency and would be a valuable teaching tool.

Close examination of the North Inlet phytoplankton community's pigment composition was undertaken by Noble et al. (2003) using high performance liquid chromatography (HPLC). Water samples were characterized and compared to those collected in the ACE Basin NERR (located about 150 km or 90 mi south of the NI-WB NERR) to see to what degree these communities were similarly or differentially influenced by differences in the nutrient loads in these two systems. North Inlet is more tidally-influenced than the ACE Basin where input from the surrounding forest and rivers is much greater. Cluster analysis and multivariate principal-components analyses demonstrated that the suite of pigments examined varied seasonally at the two sites and had similar diversities but different compositions. The timing, the magnitudes, and the pigment compositions of the annual summer phytoplankton blooms were quite different in these two estuaries. This pigment-based study (as opposed to one using species-based measures of community structure) makes it difficult to assume that phytoplankton communities in coastal estuaries have common community composition structuring forces. North Inlet has more autochthonous (internal, *in situ*) controls like utilization of regenerated nutrients and grazing, whereas the ACE Basin phytoplankton community was more strongly influenced by nutrient loads from river runoff and changes in light intensity with subsequent changes in turbidity.

The value of the NI-WB NERR as a pristine habitat has allowed it to serve as a natural baseline or unmanipulated control in many comparative studies. Murrells Inlet is similar to North Inlet in that both are tidally-dominated shallow systems, but Murrells Inlet has a much smaller acreage of marshland (3000 vs 9000) and is considerably more urbanized. White et al. (2004) explored the impacts of urbanization in Murrells Inlet on nutrient concentrations and chl-*a* concentrations there and in North Inlet. They found that both estuaries had similar summertime chl-*a* signals with a significantly higher maximum in Murrells Inlet and similar nutrient concentrations (orthophosphate, nitrate, ammonium, silicate, DON) except when large precipitation events occurred. Nitrate concentrations increased with the relatively larger volume of freshwater input to Murrells Inlet after these events. Because Murrells Inlet has a relatively smaller buffer of natural forest and a much greater relative volume of stormwater runoff and drainage/outfalls flowing into its waters than North Inlet, there were great differences in both quality

and quantity of nutrients entering the two systems after rainfall events. Their work illustrates the tight relationship between water quality and nutrient sources in an urbanized coastal body of water and the important role of stochastic events (storms) and tidal flushing in regulating water quality in these types of coastal ecosystems. Their results were similar to those of Wahl et al. (1997) in a similar comparative study of nutrient loading.

An additional impact of urbanization and coastal forest clear-cutting practices may be a reduction in the supply of dissolved organic matter (DOM) in runoff that reaches coastal estuaries. Components in DOM are known to bind with dissolved forms of iron, a potentially limiting micronutrient for phytoplankton communities in estuaries. Kawaguchi et al. (1997) also performed a comparative study using bioassays in Murrells Inlet and North Inlet that involved reciprocal transplants of water from each estuary into the other to test whether additions of chelated iron to cultures of natural phytoplankton or to cultures of *Cylindrotheca closterium*, a dominant in the microphytoplankton, would deplete iron and stimulate their growth. They found increased abundances in phototrophic microplankton, nanoplankton, and picoplankton when chelated iron was added to natural populations transferred to Murrells Inlet, but the same additions to North Inlet cultures enriched only the picoplanktonic *Synechococcus* spp. They concluded that iron's bioavailability to estuarine phytoplankton may be reduced by urbanization.

This study was followed later by an in depth and temporally more extensive look at iron limitation of phytoplankton, again in Murrells Inlet and in North Inlet for comparison (Lewitus et al., 2004). They found that bioavailable forms of iron may exist in limiting concentrations in both estuaries. Addition of chelating agents alone or with iron stimulated growth in most cases. In 1996, they again found that addition of chelated iron stimulated Murrells Inlet phytoplankton, but not North Inlet phytoplankton, the same response found earlier by Kawaguchi et al. (1997). Iron addition to phytoplankton cultures from Oyster Landing in North Inlet to which nitrate had also been added resulted in a shift of the community from smaller forms to larger diatoms, suggesting that iron bioavailability, nitrate (but not ammonium) and silicate concentration have an interacting effect on phytoplankton community structure in North Inlet. The authors suggested that coordinated studies of forest biochemistry and iron will be necessary to understand these interactions, especially as they are affected by weather events.

Buzzelli et al. (2004) provided analyses of correlations between chl-*a* and other water-derived measures during the 8-year period 1993 to 2001 at both the Oyster Landing (a tidal creek site) and Thousand Acre Marsh (an estuarine-influenced marsh close to Winyah Bay) monitoring sites in North Inlet. They found the lowest chl-*a* concentrations in winter, highest in summer at both sites, but the Thousand Acre Marsh site had much higher concentrations at all times of year than occurred at Oyster Landing. There were strong correlations between chl-*a* concentrations and total suspended solids and dissolved nitrogen, suggesting that the chlorophyll came from autochthanous phytoplankton production in the water column (produced within the site) rather than from allochthanous (imported to the site from elsewhere) sources in the surrounding watershed. Data from the Thousand Acre Marsh site are presented in the Winyah Bay Primary Productivity (phytoplankton) section of this chapter. These continuing data sets will foster many hypothesis-based research projects concerning controls on water quality in the future.

Gardner et al. (2006), used SWMP data on dissolved oxygen (DO) concentrations from the Oyster Landing site and calculated that North Inlet exports an insignificant amount of DO produced by phytoplankton in the inlet to the coastal ocean where oxygen demand is high. This would indicate that photosynthetic oxygen production by phytoplankton, benthic microalgae and marsh plants and diffusion of O_2 from the air into the water is mostly used to meet heterotrophic demand from organisms and chemical processes that occur within the salt marsh.

A recently developed algorithm, CHEMTAX, is a program for describing the relative abundance of taxonomic groups of phytoplankton based

on their expected pigment ratios. Lewitus et al. (2005) used CHEMTAX to characterize a variety of cultured cells and natural phytoplankton samples using waters from both Murrells Inlet and North Inlet. Microscopically unidentifiable flagellates and their diverse pigment make-up created problems for the taxonomic characterizations produced by CHEMTAX, and ground-truthing comparisons were problematic when dinoflagellates were present. Despite these and other issues, their modifications to the CHEMTAX methods using complementary microscope verifications resulted in an improvement of our abilities to assess the taxonomic composition of phytoplankton communities in estuarine waters.

The spectral fluorescence technique is another method for characterizing the composition of phytoplankton assemblages based on the fact that photosynthetic components ("antennae") and accessory pigments fluoresce differently when excited by light. Richardson et al. (2010) characterized natural phytoplankton from both North Inlet and the Neuse River Estuary, North Carolina, using spectral fluorescence measured with the Algae Online Analyser (AOA) in discrete sample mode (for North Inlet samples) and continuous flow mode (on a passenger vehicle ferry in the Neuse River estuary) and compared their results with data using the CHEMTAX methodology. Because the AOA can be used as a community composition monitoring tool, Richardson et al. (2010) were interested to see whether the instrument could be used as an early warning system to alert investigators to the presence of noxious algae or other precursors to eventual harmful algal blooms. Comparisons between the AOA system and the HPLC-based CHEMTAX method showed significant differences, with the AOA providing better (higher) estimates of total chl-*a* in the water. Despite inherent uncertainties in both methods, the authors felt that the AOA could be used reliably as a HAB monitor, especially if it was supplemented with direct microscopic examinations of cells for calibration.

There are many questions left to be answered about phytoplankton communities in the NI-WB NERR and these will need to be studied using multidisciplinary approaches and a variety of technologies. For example, with recent satellite imaging advances, additional analyses of the spectral qualities of phytoplankton will need to be studied in conjunction with estimates of how various other factors affect these qualities, including water turbidity, dissolved organic matter concentrations, and weather patterns. Continued urbanization of our nation's coastlines makes analyses of natural habitats like the NI-WB NERR an integral part of future ecological comparisons related to phytoplankton at the base of the estuarine food web.

In summary, phytoplankton biomass is highest in North Inlet during summer and lowest in winter. The Outwelling Study found that chl-*a* is, on average, inwelled from offshore. These imported cells are lost to grazing and sinking inside the inlet and chl-*a* is exported offshore in winter and spring. Primary productivity is about 400-500 g C $m^{-2}yr^{-1}$. Microzooplankton grazing limits phytoplankton communities in summer when small cells and microbial loop processes dominate the system. Nutrient limitation in winter results in larger cells dominating the community at that time of year. The surrounding forested watershed supplies inorganic nutrients to North Inlet. Comparative studies of phytoplankton in areas nearby North Inlet show that urbanization reduces the availability of iron to phytoplankton. Several new approaches have been used to characterize phytoplankton communities in recent years.

BENTHIC MICROALGAE

Holland et al. (1974) compared the sediment stabilization abilities of six species of benthic diatoms grown in flask culture in a laboratory setting with that of a natural community of sediment microbiota from North Inlet. Several species grown in unialgal culture with sediment produced mucilaginous coatings that prevented sediment resuspension, but three species did not. Control natural sediments incubated under similar conditions also inhibited resuspension of sediments. Although unable to extrapolate these results directly to field situations, the authors suggested that sediment stabilization properties of benthic microalgae (BMA, or microphytobenthos)

could have significant impacts on organisms that feed at the sediment-water interface as well as on animal-sediment relationships for meiofauna.

Pearse (1977) used the ^{14}C method to measure vertical migration of benthic diatoms in cores. When more diatoms were on the sediment surface, more radioactivity was present in that layer. When surface diatoms migrated deeper into the sediment, there was less radioactivity present at the sediment surface. Benthic diatoms came to the surface mostly during low tide.

Montagna (1984a) measured the grazing rates of meiobenthic organisms on sediment microbes, including bacteria and microalgae. He used radioactive ^{14}C-glucose to label autotrophs and added them to small cores that were incubated undisturbed for 4 hours. Meiofaunal polychaetes grazed on benthic diatoms more than other meiobenthic taxa. The meiofauna removed about 1% of the benthic diatom community per hour, yielding a turnover time for the benthic diatoms of 6.5 days. He suggested that meiofaunal grazing had a stimulatory effect on the benthic microbial community.

Because of the known rhythmic migratory behavior of members of the BMA, Pinckney and Zingmark (1991) sought to examine how tide stage and sun angle affected BMA productivity in the muddy low intertidal regions of North Inlet. They measured productivity in cores using an oxygen microelectrode and found an endogenous rhythmic variation in productivity that was correlated with diurnal and tidal periodicities. Production values could differ by as much as an order of magnitude over a 12-hr period and were found to range between 28 and 460 micromoles of oxygen per milligram chlorophyll *a* per hour, with the highest values occurring during mid-afternoon low tides. Much lower values were obtained during afternoon high tides. The interacting effects of tidal stage and sun angle caused this high variability. They suggested that other physiological and abiotic variables also can influence BMA productivity and cautioned that large errors can result from extrapolating single short-term estimates to longer time periods. Their results were similar over all seasons of the year.

Pinckney and Zingmark (1993a) collected sediment cores at bi-monthly intervals for 18 months at five different sediment/light habitats in North Inlet to measure BMA biomass and productivity. They found the highest biomass (chl-*a*, averaged over time) in the tall *Spartina* zone and lowest in the shallow subtidal habitat. BMA biomass generally increased in late winter and early spring with lower, relatively constant, levels during the rest of the year. Pheopigments followed roughly similar temporal trends. BMA production tracked the biomass trends and was highest in the intertidal mudflat (2.48 mg C [mg chl-*a*]$^{-1}$ h^{-1}) and lowest in the shallow subtidal and sandy intertidal habitats (1.25 and 1.07), respectively. The highest productivity on an areal basis was in the short *Spartina* zone at 234.2 g C m^{-2} y^{-1}.

Pinckney and Zingmark (1993b) constructed a model of primary production by the BMA community. They concluded that on an annual basis, the short *Spartina* zone provided 45%, intertidal mudflats 22%, tall *Spartina* zones 18%, shallow subtidal 13%, and intertidal sandflat 3% of benthic microalgal production which equaled 3.4 x 10^{9} g C y^{-1} as the sum of all five habitats. This annual rate is higher than phytoplankton and macroalgal production but lower than that of *Spartina*. They performed a sensitivity analysis of the model and found that all factors affecting the amount of light received by BMA were important but varied in their relative importance between the five habitats. Their paper includes an extensive list of other habitats in which BMA production has been measured worldwide.

Pinckney and Zingmark (1993c), reported measurements of photosynthesis vs light (P versus I) curves, for intertidal benthic microalgal communities. Because highest rates of oxygen production had been found during afternoon low tides, they measured gross primary production at that time and compared three different methods of calculating productivity. Cores were collected in bare low intertidal areas as well as in the short and tall *Spartina* areas of the marsh, obtaining depth-integrated areal estimates of gross primary production in these areas of the marsh. They regressed P_{max} versus BMA biomass (as chl-*a* in the

uppermost 2 mm of the cores). These variables were significantly positively correlated at all three of the study areas (mudflat, tall, short *Spartina*) and chl-*a* specific production rates were three times higher on the mudflat than at either of the other two locations which had similar rates. Comparisons of P versus I curves from these three different light environments showed that BMA were equally efficient and responded similarly to changes in incident radiation. In contrast to the community measures, when photosynthesis production rates are expressed as a percentage of maximum rates over the range of irradiances used, it was clear that the BMA in tall *Spartina* habitats were more efficient at low light levels and least efficient in the short *Spartina* at low light levels.

Additional study of the vertical distribution of BMA biomass was conducted by Pinckney et al. (1994a). Vertical diatom migration occurred mostly within the uppermost 3 mm of the sediment column and may explain much of the short-term variability observed in primary productivity in marine sediments. These dynamics may also be important in the foraging strategies of benthic organisms that are surface deposit feeders. Pinckney et al. (1994b) showed that standard spectrophotometric methods for measuring BMA biomass (as chl-*a*) in sediments overestimated concentrations by about 16% compared to HPLC pigment extractions.

Jackson et al. (2006) examined changes in the biomass of epiphytic BMA on *Spartina* stems over time at two different stem heights (bottom, middle) on three growth forms of the plant (tall, medium, short), for both living and standing dead plants. Standing dead stems harbored more biomass than living stems on both tall and medium growth forms. Differences were less evident for short *Spartina* plants. Generally the bottom portion of the stem had more epiphytic chlorophyll *a* than the middle of the stem, no matter whether live or standing dead plants were examined. Seasonal changes were evident, with more biomass found in spring, though variance over time was high. Tidal currents affected epiphytic biomass as well, but variability from low tide to the next high tide was too great to suggest a consistent effect of flowing water on the epiphytic community. Dead forms held 4-5 times more biomass per square meter of marsh, especially in winter and early spring. Highest epiphytic biomass occurred on tall plants, but compared to sediment biomasses found by Pinckney (1992), even tall forms had about three times less biomass than found in BMA in the surrounding sediments. The importance of epiphytic algae to the marsh's food web cannot be discounted, as many other investigators have found them in the guts of grazers of many types, e.g., periwinkle snails, grass shrimp, amphipods, and meiofauna. However, estimating the productivity of the epiphytic community presented challenges that were addressed later by Jackson et al. (2009).

Earlier compositional characterization of the epiphytic community by Jackson (2004) led to the biomass studies above and to a community productivity modeling effort. Jackson et al. (2009) deduced that the epiphytic community is an energy sink, existing not as a net autotrophic assemblage but as a net heterotrophic community using more energy or carbon than it is able to produce over the year. This was a surprising result, given that so many heterotropic organisms ingest members of this attached microalgal community. Annual production was greater on short forms of *Spartina* than on tall forms, but both were negative for the year. They also found photoinhibition was present at all times of the year, suggesting that these cells are adapted to the low light environment of the plant canopy.

Sullivan and Currin (2000) reviewed the status of research on the community structure and dynamics of BMA in salt marshes, and the pioneering studies of Pinckney and Zingmark and others are cited prominently in that document.

In summary, the benthic microalgal community of North Inlet is, on a per square meter basis, approximately half as productive as phytoplankton communities, but its rate of productivity is highly variable among different habitats. Well-documented vertical migration of BMA contributes to short-term variability in the production rate. Microphytobenthic communities are currently under-sampled in North Inlet.

MACROALGAE

Dame (1982) measured the amount of macrodetritus, some portion of which contained material sloughed off from macroalgae, exported from North Inlet. Export happened on a regular basis but varied seasonally with maximum values in summer. The amount of material exported, however, was small (only about 1%) compared to the salt marsh's net aboveground primary productivity.

Ebeling (1982) characterized benthic macroalgae at three locations in North Inlet (Oyster Landing, Clambank dock, Town Creek from Clambank south towards Winyah Bay) and found 14 species. Five species dominated (*Enteromorpha* sp., *E. siliculosus*, *Ulva lactuca*, *Bryopsis plumose*, and *Porphyra leucosticta*) during the winter months. She determined ash-free dry weights and caloric content of these five species.

Coutinho (1987) examined the spatial and temporal distribution of macroalgae in North Inlet from 1983 to 1987. Eighteen species of greens, 8 browns, and 28 species of red macroalgae were documented. Many species had productions of 1 g C m^{-2} y^{-1} in winter and less than that during summer. One-third of annual production occurred in March, with 84% occurring between December and April. Average net annual production for macroalgae was calculated as 200 g C m^{-2} y^{-1}, being greatest on the flood tidal delta and lowest in the high marsh.

Ulva lactuca is found in North Inlet mainly in the winter months.

Coutinho and Zingmark (1987) measured P versus I curves on 4 species of green macroalgae (Chlorophyta), one brown species (Phaeophyta), and one red species (Rhodophyta) to test whether there was any variability in the shape of these curves during the day. Using three different curve-fitting models on data collected in February and March, most curves exhibited photoinhibition at the higher light levels. They also found no evidence of any endogenous photosynthetic rhythms in these species. Illumination was the largest source of variation for calculating production rates. Additional details of this study can be found in Coutinho's 1987 dissertation.

The only study of macroalgal recruitment was performed by Flavier and Zingmark (1993) who used marble tiles as settlement substrates submerged over a range of depths in a tidal creek. Month-long deployments were recovered during all four seasons of the year, with highest recruitment occurring in spring and summer, lowest in winter. Propagule densities varied significantly with depth and with season, with highest densities generally at zero and -15 cm depths relative to MLW. Most of the settlement took place between winter and the start of spring. Comparisons were made to calculate survivorship and mortalities of the different types of macroalgae found on the tiles. Ulvoids and ectocarps were prominent settlers and generally settled where they were most abundant as juveniles, suggesting that natural densities were set by factors influencing settlement and early post-settlement rather than later in the life history of the algae. Macroalgae may contribute more to summertime productivity in the estuary than was previously thought, based on the presence of high numbers of propagules found on tiles in this season.

In summary, the diverse macroalgal community in North Inlet is less productive than phytoplankton, BMA, or vascular plants. It gains prominence in winter when water clarity is highest and contributes regularly to the macrodetritus inventory of the inlet throughout the year. Macroalgal communities are severely understudied in North Inlet.

VASCULAR PLANTS

Vascular plant research began at the Clambank Landing area of Hobcaw Barony in the late 1960s and was followed by survey and census work that listed species known in the area (Tiner, 1977; Conservation Foundation, 1980: both cited in Blood and Vernberg, 1992; and Zingmark, 1978). The uplands regions of Hobcaw Barony harbor typical maritime low country stands of pines and hardwoods, but there is not very much forested upland acreage within the actual NI-WB NERR boundary lines. Trees and shrubs will not be mentioned here, but a vascular plant list for Hobcaw Barony and adjacent estuarine habitats is in **Appendix C**. Freshwater marshes are also not abundant area wise, but plant communities in old abandoned rice fields (worked in the 1920s) that have converted to freshwater marshes were followed by Baden et al. (1975) and then re-censused 20 years later by Stalter and Baden (1994). They found that the species composition there had changed little over that time. Please consult the Belle W. Baruch Institute of Coastal Ecology and Forest Science of Clemson University for information on uplands forestry studies on Hobcaw Barony proper. Vascular plant research in the North Inlet - Winyah Bay NERR area has included numerous topics, broadly categorized below.

- **Salt Tolerance and Osmotic Stress**

Stalter and Batson (1969) performed reciprocal transplantation experiments in the salt marsh at Clambank Landing. They identified four vegetation zones according to their elevation above sea level: High high marsh (HHM), Low high marsh (LHM), High low marsh (HLM), and Low low marsh (LLM). Each zone had a nearly unique set of plant species present: HHM = I*va frutescens*, *Baccharis halimifolia*, *Spartina patens*; LHM = *Salicornia* spp., *Spartina alterniflora*, *Borrichia frutescens*, *Limonium carolinianum*, *Distichlis spicata*; HLM = dwarf *Spartina alterniflora*; LLM = tall *S. alterniflora.* Thirty plants of each species were transplanted in winter from each zone into each of the other three zones, with re-transplantation into the same zone serving as a control. By 6 months later, most plants did not tolerate transplantation well, but *Salicornia* from the LHM tolerated HLM and LLM, while *Limonium carolinianum* from the LHM tolerated HLM transplantation. Their data also suggested that the dwarf and tall forms of *Spartina alterniflora* were distinct, or "inherent". Follow-up examination of the transplants two years later found that *Salicornia virginica* from the LHM lasted a year in the Upper LM and that *S. patens* from the Upper HM had only a 10% survival rate after two years in the LHM (Stalter, 1973).

Physiological work on salt marsh plants by Cavalieri and Huang (1977) examined the activity of NAD-malate dehydrogenase (MDH) under various salt (NaCl) concentrations. They took six species from the North Inlet marsh for laboratory experiments. *Borrichia frutescens* differed from the other species by being much more salt-tolerant, particularly in its cytosol MDH, but not in its mitochondrial MDH. This succulent was thus better adapted to life in the middle-to-high marsh where soil salinities can become quite high. Follow-up physiological work on enzyme activities (leucine aminopeptidase, peroxidase, and MDH) was done by Gettys et al. (1980) on leaf extracts from *Spartina alterniflora* and *S. patens* collected in North Inlet. They found evidence, based on the activities of this suite of enzymes in response to changes in salinity, that correlated well with the greater salt-tolerance of *S. alterniflora* in the low marsh over that of *S. patens* from the high marsh.

To better understand how salt marsh plants adapt to high soil salinities, salt marsh plants in North Inlet were measured for their proline content in the field and transplants were placed into growth chambers where their exposures to NaCl and polyethelene glycol were manipulated (Cavalieri and Huang, 1979). Proline is an amino acid known to have an osmoregulatory function in plant cell cytoplasm. These researchers measured the buildup of proline at threshold levels of salinity in the C4 plants (*Spartina alterniflora*, *Spartina patens*, *Disticlis spicata*), but the succulents did not exhibit such an adaptation to salinity levels normally reached in their habitat.

An examination of the nutrient status of *Spartina* was performed on short and tall forms of the plant by Cavalieri and Huang (1981). They measured the

concentrations of proline and glycinebetain and found that tall plants in the low marsh had sufficient nitrogen for metabolism, osmoregulation, and growth, whereas short plants had to allocate more of their limited nitrogen supply to osmoregulation and hence had reduced growth. Cavalieri (1983) grew plants hydroponically under controlled conditions with varying salt and N concentrations and followed the amounts of these same two osmolytes in the plants as they responded to the nutrient and salinity manipulations. This study confirmed their earlier field observations concerning reduced plant growth at high salinities and greater growth with nitrogen fertilization.

Over a range of salinities, Bradley and Morris (1991b) again used lab culture of *Spartina* collected from North Inlet to examine how the plant managed to thrive under osmotic stress. They measured evaporation from control chambers, plant growth as volume of water taken up during a time interval and incorporated as wet tissue weight, and, by difference, whole plant transpiration. They found that plant growth declined as simulated soil salinities increased. Plant height, leaf area, and total plant biomass were considerably lower at a salinity of 40 compared to 10. Higher salinity thus reduced transpiration by reducing plant biomass. Measures of the rate of ion exclusion by root secretion also increased at increased salinities. This plant manages salt stress by minimizing uptake of salts through its roots and by excreting about half the salt it takes in through its leaves, a remarkable and successful adaptation to harsh, if not sometimes lethal, salt gradients often encountered in the salt marsh.

Morris (1995) studied the dynamics and mass balance of porewater salinity by modeling the movement of both water and salt using a variety of data on rainfall, tidal floodwater salinity, evaporation, evapotranspiration, diffusion, plant excretion of salts, and drainage by gravity. His model ignored any groundwater inputs and assumed that water movement was strictly vertical within the sediment. The model was run for both exposed and flooded sediments. Generally the salinity of porewater remains constant in the upper 30 cm of the sediment, with a salinity drop of only about 2 during rain events in the uppermost centimeter. Porewater salinities were almost 4 units lower at the Oyster Landing site than at the Goat Island site, mostly because of Oyster Landing's closer proximity to freshwater forest runoff. His Figure 1 illustrates the mass balance of salt and water during exposure and during flood tides. Infiltration was also higher at Oyster Landing due to the greater permeability of the soil there. Salt that builds up in sediments from evaporative water loss is lost primarily by drainage, as plant-mediated losses are much less significant. Porewater salinities were always highest in summer and lowest in winter, reaching maxima of about 40 and 50 at Oyster Landing and Goat Island, respectively. Elevation and tidal flood frequency are the major determinants of porewater salinity, however. This modeling effort closely matched empirical data collected at both sites and provided valuable insights about seasonal and interannual changes in marsh productivity.

- **Sediment Aeration and Bioturbation**

Sediment aeration is necessary for *Spartina* roots. Gardner (1973a) studied the drainage characteristics of mid-marsh areas and later (Gardner et al., 1987) estimated the influence of bioturbation by fiddler crabs whose burrowing activities on the creek banks of North Inlet can turn over 7 cm^3 of sediment per square centimeter per year. King (1988) studied bacterial sulfate reduction in creek bank sediments, another process involved in the mechanics of sediment aeration. Following earlier work by Morris and Whiting (1985) on the movement of air into and gases out of sediments of the high marsh, short *Spartina* zone, Bradley and Morris (1990a) measured sediment compressibility in four sediment types in North Inlet and found that the entry of air into the sediments was sufficient to oxidize reduced sulfur compounds like pyrite. Water loss from sediments via evapotranspiration was important in this aeration process during low tide.

Gardner et al. (1988) pursued additional studies on sediment sulfur species in the salt marsh along transects that included short, medium, and tall plants. Their discussion of the roles played by belowground *Spartina* production,

evapotranspiration, fiddler crab burrowing, and porewater movement on sulfur chemistry explains much about the variable presence of sulfides and pyrites and iron oxides in the salt marsh. Fiddler crab activities bring sulfides up to the surface that are replaced by iron oxides moving from surface sediments down into their burrows. Sharma et al. (1987) provided strong evidence for the role that bioturbation plays, especially at creek banks, in making iron oxide-rich sediments available to react with any hydrogen sulfide produced by sulfate reduction.

- **DMSP and Grazing Stressors**

Adaptations that limit the adverse effects of high soil salinity help make *Spartina* a salt marsh dominant, but this plant must also cope with reducing sulfidic conditions in the soil. Another plant compound, dimethylsulphoniopropionate (DMSP), was thought to help *Spartina* detoxify excess sulfur. Following earlier studies of DMSP in *Spartina* by Otte and Morris (1994) and Morris et al. (1996), Otte et al. (2004) found that concentrations of DMSP did not respond to changes in salinity or sulphide concentrations in soil, suggesting that DMSP plays neither an osmolytic nor a sulphide detoxification role in *Spartina*. However, Kiehn and Morris (2010) suggested that changes in the DMSP content of *Spartina* under stress may be used by periwinkle snails, *Littoraria irrorata*, as a trophic trigger or signal that attracts snails to plants. The incidence of salt marsh diebacks in the southeast in the past decade has increased, and there is intense debate about whether this is due to top-down (grazing) control or bottom-up (nutrients and edaphic factors). Kiehn and Morris (2009) in a 40-month transect survey found that *Spartina* stem density correlated positively rather than negatively with the density of periwinkle snails in North Inlet and that the snails were more abundant in long-term fertilized plots of *Spartina*. The absence of evidence for any top-down controls on *Spartina alterniflora* biomass or productivity at three locations in North Inlet as well as a low incidence of blue crab predation on snails found by Long (2006) suggests that significant snail grazing impacts are likely greater only on plants that have become stressed in isolated areas.

- **Sediment Composition and Supply Effects**

Part of the slow buildup of salt marsh sediments is due to incorporation of organic matter (OM) as part of the sediment structure. This organic matter comes from several sources, including vascular plants (roots, detritus), terrestrial litter, benthic micro- and macroalgae, bacteria, and settled phytoplankton. The remains of burrowing and other types of animals may also contribute to the sediment's OM content. To examine the various sources of organic matter that get buried in saltmarsh sediments, Ember et al. (1987) took core samples to depths of 40 cm in tall and short *Spartina* areas and also deployed litter bags both above- and belowground. The core samples and litterbag contents (aged for 15 months) were analyzed for their carbon and nitrogen content and for their carbon stable isotope signatures. They found that diagenesis of sedimentary OM takes place deep within the sediment, below the depth to which *Spartina* roots and rhizomes extend (about 25 cm or 10 inches). *Spartina* biomass was not a major contributor to buried OM in the marsh, but the refractory components of this biomass (e.g., lignocelluloses and humins), and the carbon:nitrogen ratios and stable isotope fractionation signatures were consistent with the enhanced presence of these decay-resistant components. Ember et al. (1987) were also able to rule out bacteria as a contributor to the isotope signatures occurring at depth despite the fact that diagenesis of plant material eventually resembles the isotopic signature of bacteria. Bioturbation was implicated as the mechanism by which OM is mixed into sediments, especially in the tall *Spartina* zone along creekbanks. Carbon isotope analyses alone were insufficient for uniquely identifying the various possible sources and types of sedimentary organic matter found in the salt marsh habitat.

Because of their relevance to how the *Spartina*- and *Juncus*-dominated saltmarsh plant communities in the NI-WB NERR will evolve, several studies of sediment supply and redistribution in North Inlet and/or Winyah Bay should be consulted. These include Settlemyre and Gardner (1975, 1977), Wolaver et al. (1986), Wolaver et al. (1988a,b), Gardner et al. (1989), Pillay et al. (1992), Childers

et al. (1993a), Hutchinson et al. (1995), Vogel et al. (1996), Goni and Thomas (2000), Mwamba and Torres (2002), Torres et al. (2003, 2004), Voulgaris and Meyers (2004 a,b), Patchineelam and Kjerfve (2004), Goni et al. (2005), Gardner and Kjerfve (2006), Murphy and Voulgaris (2006), and Goni et al. (2009). An important aspect of this sedimentation issue is the erosion impact that major coastal storms and hurricanes may have on North Inlet, Winyah Bay, and similar coastal habitats [see Gardner et al. (1991), Gardner et al. (1992a),and Kjerfve et al. (1994) regarding the impact of Hurricane Hugo in September 1989].

- **Carbon Transformations and Dynamics**

Understanding how carbon moves through ecosystems is fundamental for making predictions about how these systems might change over time. Carbon uptake, transformation, storage, and loss rates occur throughout the salt marsh, but little work has been done to quantify these processes. Morris and Whiting (1986) measured fluxes of carbon dioxide gas from unvegetated portions of sediment in the high marsh and also from the low marsh adjacent to tidal creeks when sediments are exposed at low tide. Loss of carbon dioxide from sediments to the atmosphere varied seasonally (i.e., with temperature), being greater in summer than in winter. Loss was greater from the high than from the low marsh as well. When the marsh sediments are covered by the tide, carbon is lost to overlying waters as dissolved inorganic carbon. The complexities involving microbial respiration in the sediments, living root gas exchanges during *Spartina* photosynthesis and belowground plant production, presence/absence of suitable buried organic substrates for microbial metabolism, porewater turnover, diffusional losses, changes in temperature, etc., make these measurements very difficult both technically and interpretationally. These investigators felt that carbon dioxide loss and fluxes from sediments accounted for a significant, though small, portion of total plant photosynthesis in the salt marsh as *Spartina* fixes carbon taken up from below ground through hollow spaces in its stems.

The question of where *Spartina* gets the inorganic carbon that it fixes during photosynthesis prompted Hwang and Morris (1992) to grow plants from North Inlet in pots in the laboratory under gas-tight conditions. This technique was developed previously by Hwang and Morris (1991) in an investigation of how *Spartina* moves atmospheric oxygen hygrometrically to its roots in anoxic sediments. Huang and Morris (1992) utilized the radioactive ^{14}C method to label gases in the lacunar spaces of the plant (via injection) and then followed the radioactivity's path through the plant. In short, they found that uptake and utilization of dissolved inorganic carbon from interstitial water in the sediment was quite small compared to the amount of atmospheric carbon dioxide taken up and fixed by the plant's leaves.

- **Productivity**

Dame and Kenny (1986) undertook the laborious harvest method of measuring both aboveground and belowground productivity of short, tall, and intermediate forms of *Spartina alterniflora* at three sites (creekside, mid-marsh, high marsh) in North Inlet over 5 years, 1981-1985. They used 0.25 m^2 plots and collected cores to 40 cm depth to measure living and dead root biomass for calculations of net belowground primary production. Leaf litter decomposition was also taken into account using small mesh cages aboveground. They measured highest aboveground biomass in late summer at all three sites, with highest amounts of dead biomass in winter. There was a gradient in mean stem height as well, with the tallest plants creekside and shortest in the high marsh. Variation from year-to-year in above ground biomass was high at all sampling sites. Creekside plants had higher growth during years when precipitation was high and salinity was lowered. Summer rates of decomposition were higher than in winter. Belowground live biomass was highest at the high marsh site. So-called "root-to-shoot" biomass ratios, indicative of the stress a plant is under, varied between 2 and 76 depending on season and site but generally reflected an adaptation to high salinities. Belowground primary production was about the same as aboveground primary production for the creekside site but greatly exceeded aboveground production at the

high marsh site. Aboveground average net primary production (g m^{-2} y^{-1}) was 2188 creekside, 724 midmarsh, and 1295 in the high marsh. Average net belowground primary production (same units) was 2363 creekside and 5445 in the high marsh. Their measurements of productivity, among the highest reported for salt marshes, revealed great variability both within sites, between sites, and between years within sites. They also calculated biomass turnover rates as high as 5 y^{-1} for the aboveground portion of tall plants at the high marsh site. This variability suggests that models which incorporate saltmarsh primary production values must take this uncertainty into account. Accuracy of the harvest method utilized here has been criticized by Morris and Haskin (1990) and other investigators cited therein, but this harvest-based study still serves as a comparator for other similar harvest-based studies.

Measuring the aboveground productivity of *Spartina alterniflora* in North Inlet, Morris and Haskin (1990) used a non-destructive method that took into account stem and leaf turnover in permanent plots for more than 5 years. This data record length was sufficient to examine reasons why there was a two-fold interannual variation in production. Their method utilized regression equations of stem height versus stem biomass and monthly measures of stem height of tagged stems on permanent plots. Leaves on stems were also tagged to estimate leaf turnover. Net aboveground production was calculated on both a monthly and annual basis. For plants older than 10 months, leaf loss was a significant part of its annual production. Plants lived for about 18 months, on average. Stem density was greater in the older marsh at Goat Island than in the younger marsh at Oyster Landing by a factor of two or more, with peak density occurring in fall-winter and lowest in June-July. Interestingly, maximum stem density occurred several months after calculated peak biomass. Plant growth rates were highest when stem densities were lowest at both sites. Despite the two-fold difference in stem density, net aboveground production per unit area of marsh surface was the same, suggesting that plants had different strategies for growth allocation at the two locations. Goat Island plants allocated more to vegetative reproduction than to increased stem growth. They also found positive correlations between annual productivity and both rainfall and sea level anomalies, and that both had greatest effects in summer. Thus future variations in the rate of sea level rise could have significant impacts on marsh productivity and subsequent secondary productivity (Morris et al., 1990). Annual aboveground dry biomass productivity ranged between 402 and 1042 g m^{-2} over the 5-yr period from 1984 to 1988. Morris and Haskin (1990) also raised questions about harvest methods for estimating annual production and the effects of spatial variability in standing biomass for examining temporal trends in productivity. Morris has continued long-term monitoring of *Spartina* at Oyster Landing and Goat Island using this non-destructive method. Figure 69 shows the mean annual aboveground productivity of high marsh *Spartina alterniflora* from 1984 to 2008 at Goat Island and Oyster Landing. He has found evidence of an 18.6-yr cycle of productivity, corresponding to the lunar nodal cycle, and an upward trend. The upward trend suggests that the marsh is not keeping pace with sea-level rise.

- **Chemical Composition and Stable Isotopes**

Ornes and Kaplan (1989) analyzed the macronutrient chemical composition (N, P, K, Ca, Mg, and S) of live plants and live roots harvested by Dame and Kenny (1986). They also collected soil samples at intervals down to a depth of 27.5 cm in each season for a year and analyzed them for redox potential (Eh), sulfide, P, Ca, Mg, Fe, orthophosphate, ammonium, total dissolved nitrogen and total dissolved phosphorus. Concentrations of shoot N peaked in winter and decreased to a minimum in July as the increase in shoot biomass at this time caused a dilution of the N concentration. Monthly root N concentrations did not change appreciably during the year but were, on average, higher in the tall form of *Spartina* than in the short form, whereas shoot and root P was higher in the short form than in the tall form. Root N concentrations did not change over time in either plant form. Soil concentrations of ammonium were sufficiently high that they were not limiting to plant growth, leading to the conclusion that other factors limit

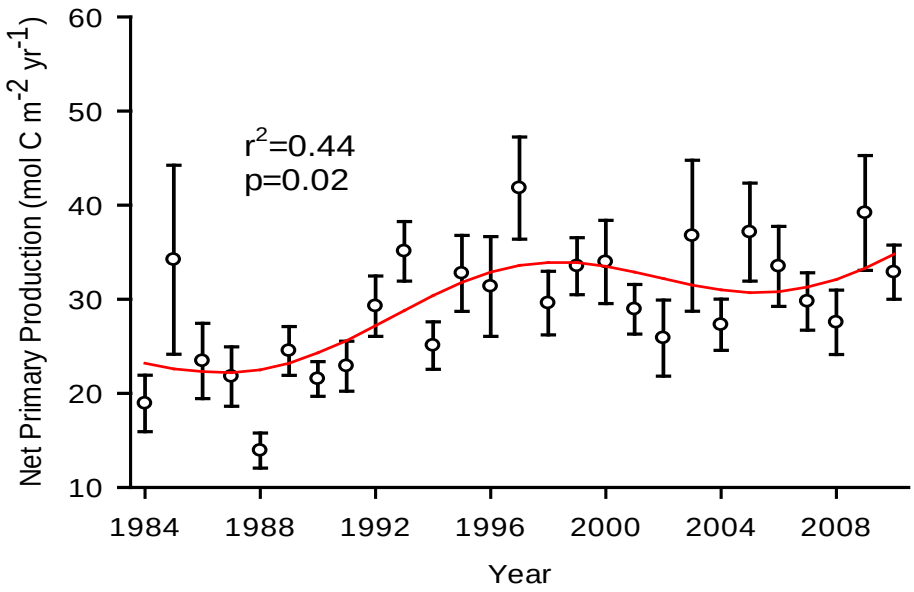


Figure 69. North Inlet mean annual aboveground production of *Spartina alterniflora* as derived by the non-destructive census technique of Morris and Haskin (1990). The red line is the result of an harmonic regression with a period length of 18.6-yr, corresponding to the lunar nodal cycle, and with an upward trend.

the growth of the plant, especially in the high marsh. Interactions between iron and sulfide were implicated as moderators of N limitation. Although N, P, and S changed, Ca, Mg, and K generally did not change over time in shoot tissues.

Following work begun by Ember et al. (1987), Bernot et al. (2008) also measured the stable isotopes of carbon and nitrogen in the roots and stems of intertidal short *Spartina* that had undergone long-term fertilization for between 10 and 20 years, a manipulation started by Morris and his students [see Sundareshwar and Morris (1999), Morris (2000), and Morris et al. (2002)]. Bernot et al. (2008) found that fertilizer-amended plots showed evidence of nitrogen limitation as well as changes in phosphorus uptake that, based on the stable isotope values and their mild fractionation, was due to chronic nutrient inputs from coastal development over time. The impacts of these inputs were confined to the uppermost 5 cm of the sediment column.

- **Nitrogen and Phosphorus Dynamics**

Sundareshwar et al. (2001) looked closely at the role of phosphorus compounds in salt marsh ecology. Because standard methods for measuring bioavailable forms (e.g., soluble reactive phosphorus) do not detect polyphosphates, they used nuclear magnetic resonance spectrometric methods to measure pyrophospahate (Ppi) in a variety of coastal wetlands, including North Inlet as an undeveloped control site. They found that Ppi concentrations were higher where coastal development was higher. They also demonstrated that microbial utilization of Ppi can supplement other forms of bioavailable P by making additional orthophosphate available for plant uptake.

It has been generally believed that *Spartina alterniflora*'s growth is limited by the amounts of available nitrogen. However, observations that salt marshes export nitrogen and that ammonium is abundant in the areas where short forms of this species grow prompted Bradley and Morris (1990b) to examine what factors might be limiting the ability of *Spartina* to uptake nitrogenous nutrients. They examined the uptake kinetics of ammonium as influenced by pH, sulfide, and oxygen concentrations. Uptake varied considerably between oxic and anoxic conditions. Their Figure 4 illustrates how ammonium uptake varies in the

high versus the low marsh, especially as influenced by the concentrations of dissolved oxygen and sulfides in the sediments. Their work contributed to the understanding that nitrogen-limitation alone cannot explain *Spartina* growth dynamics, as other edaphic factors influence how the plant obtains this essential nutrient.

Bradley and Morris (1991a,b) studied the ability of *Spartina alterniflora* to take up nitrogen in the form of ammonium ions. They subjected short form plants taken from the high marsh and potted in sand to a broad range of salinities and later measured their short- and long-term NH_4^+ uptake kinetics following the same methods used by Bradley and Morris (1990b). Following Michelis-Menten kinetics, ammonium uptake was quantified according to V_{max} and K_m, the maximum uptake rate per gram of dry plant tissue and the half-saturation constant, respectively. For salinities less than 50 gL^{-1}, V_{max} did not change. However, increasing salinities caused K_m to decrease, thereby reducing ammonium uptake and decreasing the productivity of the plant. Both short-term increases and long-term exposure to high salinities inhibited ammonium uptake. Bradley and Morris (1992) determined the minimum nitrogen concentration in *Spartina* leaf tissue necessary to sustain growth. This concentration was also a function of salinity. Their study supported many other observations that nitrogen limits both tall and short forms of this saltmarsh plant.

Bacterial transformations of nitrogenous compounds in the sediments are an important source of this limiting nutrient for salt marsh plants. Sundareshwar et al. (2003) found that such bacteria in the salt marsh can be limited by available phosphorus. Differential limitation of salt marsh autotrophs by nitrogen and microbial heterotrophs by phosphorus has important implications for the carbon cycle and for management of coastal habitat in the face of continued anthropogenic inputs of fertilizer and sewage that contain both of these essential nutrients.

Based on earlier work by Yoch and Whiting (1986) mentioned in the following Microbial Communities section, Whiting et al. (1986) examined how tightly coupled nitrogen-fixing bacteria are to the process of photosynthesis by *Spartina alterniflora*. Using field-emplaced and laboratory growth chambers with short *Spartina* from North Inlet, they measured acetylene reduction activity (ARA) under conditions of enhanced carbon dioxide that stimulated the plant's rate of photosynthesis. Data from the hydroponic chambers used established that root-associated bacteria were stimulated under these conditions. The evidence that root microflora utilized photosynthates from *Spartina* suggested tight linkages, but how the fixed nitrogen got utilized by the plant remained unanswered.

Morris and Bradley (1999) addressed the issue of chronic eutrophication by reporting on the carbon balance in plots of the North Inlet salt marsh that had been fertilized monthly since 1984 (see Morris, 1988). This N and P amendment resulted in an increase in mean aboveground dry matter production of *Spartina alterniflora* to 3,280 g m^{-2} y^{-1} from control, unfertilized, plot values of 780 g m^{-2} y^{-1} over the period 1985 – 1996. More importantly, soil respiration in the fertilized plots increased significantly and the amount of carbon belowground decreased, but the amount of C loss in the soil could not account for the amount of respiration increase, suggesting that increased primary production was the cause of the disparity. Incubations of plants in the laboratory produced similar results regarding an increase in soil respiration. Thus fertilization can result in an increase in the rate at which carbon turns over in sediments and can result in a net loss of carbon from the sediment. Such losses add additional carbon dioxide to the atmosphere compared to the normal, non-fertilized conditions.

- **Oil Pollution Effects**

The continuing threat of chronic oil pollution in coastal salt marshes prompted Li et al. (1990) to measure the effects of hydrocarbon exposure to *Spartina alterniflora*. They took healthy plants from the low marsh and moved them to the laboratory where daily additions of oil at 1x and 10x concentrations (= 3.33 and 33.3 gC m^{-2} d^{-1}) were accompanied by measurements of plant growth and respiration for almost two years. They also monitored sediment microbial activity. Compared

to control plants, those exposed to the 1x treatment exhibited a stimulatory response, while those at 10x were inhibited. Both above- and belowground biomass and respiration rates increased over time, as did soil microbe activities (CO_2 production, methanogenesis, N_2 fixation, denitrification), but all of these processes declined greatly in the higher concentration (10x) treatments. The authors suggested that perhaps the microbes were carbon-limited, while plant growth increased as a result of enhanced rates of nitrogen fixation/mineralization.

- **Hydrography and Marsh Elevation**

The influence of hydrography and marsh elevation on the plant community in North Inlet was mentioned by Schwing and Kjerfve (1980) in their studies of circulation in Jones Creek, a waterway that connects North Inlet proper with Winyah Bay. They identified a nodal point (similar to a fall line or a continental divide on land) in Jones Creek that functioned to limit the amount of exchange between the two larger bodies of water. *Spartina alterniflora* dominated the vegetation northward from the node towards North Inlet, while on the southward side of the node towards Winyah Bay a more diverse plant community existed (i.e., *Juncus roemerianus*, *Spartina cynosuroides*), without a dominant species.

- **Models: Light, Nutrients, Marsh Elevation, and Sea Level Rise**

Morris (1989) modeled how *Spartina alterniflora* intercepts incident solar radiation on its leaf surfaces. He found that the highest leaves, being vertically oriented, absorb less sunlight and heat than horizontal leaves. From his model's results, it would appear that this halophyte maximizes light absorption and uses water quite efficiently, all the while minimizing its heat gain from the sun.

A comprehensive examination, done via numerical modeling, of the fates of carbon, sulfur, and oxygen during diagenesis in salt marsh sediments was done by Gardner (1990). Pyrites, sulfur reduction, and organic matter oxidation were followed in a depth profile in the sediment. These processes all have bearing on marsh productivity as will be seen in greater detail below. In another modeling effort, Gardner (2005) examined the marsh's discharge of groundwater through the creek bank into the tidal channel. The model was complex and served to illustrate that there does not seem to be any sort of "underground estuary" in North Inlet that supplies nutrients to creek waters. This underground estuary concept had been proposed by Moore (1999). Rather two-thirds of the seepage occurs mostly near the intersection of the tidal water level with the creek bank (one third comes out in the creek bottom) and reaches volumes of approximately 5-10 liters per longitudinal meter of creek bank per tide. This seepage was proposed as a mechanism by which sulfides are flushed from marsh sediments, thereby resulting in enhanced rates of primary productivity at the creek's edge by *Spartina alterniflora*.

Mean annual sea level changes from year-to-year by an average of almost 3 cm, a variation imposed on the even longer-term rise due to climate change. In addition, mean monthly sea level varies over the solar cycle by 24 cm (about 10 inches) on average. When these changes result in anomalously high or low flooding of the marsh surface, the salt content of the soil can change considerably. Morris (2000) studied long-term relationships between *Spartina* productivity and changes in sea level, noting that net annual aboveground production varies by a factor of two, higher when sea level is higher, lower when less water covers the marsh and soil salinities are higher. Thus hydrography and marsh elevation interact to influence primary production by vascular plants in the coastal ecosystem. This theme and additional work by Morris et al. (2002) on sediment accretion in North Inlet led to development of a model that predicts how stable the plant community will be relative to sea level rise. There is an interesting feedback between plant growth, sediment elevation, and relative sea level rise. A comprehensive review of controls, biotic and abiotic, on the productivity of *Spartina alterniflora* by Mendelssohn and Morris (2002) is a useful resource for those interested in how this plant dominates southeastern salt marsh plant communities.

Researchers examine relationships between *Spartina alterniflora* productivity and sea level.

Because marsh elevation above sea level is such a strong correlate with marsh productivity, Morris et al. (2005), using LIDAR and ADAR imaging data, computed the frequency distribution of this elevation in North Inlet. They found a normal distribution for elevations in which *Spartina* occurred with a median elevation of 0.349 m. *Juncus roemerianus* marsh, however, had a median elevation of 0.519 m above the North American Vertical Datum 1988. Their data suggests that the marsh has not kept up with the slowly accelerating rise of sea level in recent decades. However, an earlier study by Vogel et al. (1996) suggested that the marsh surface is accreting vertically at a rate of 2.7 mm per year, while sea level is rising between 2.2 and 3.4 mm per year, i.e., the marsh is keeping pace with sea level rise and is adding enough sediment to also expand laterally landward. The question about whether *Spartina* and other marsh plants will thrive in the future under continued sea level rise remains to be answered, but additional work on this elevational correlation by Scott (2010) found that marsh surfaces closest to sediment sources (e.g., nearer Winyah Bay) had higher mean elevations than areas at greater distances from sediment sources. The elevational differences, however, were small, and the LIDAR data suggested that none of the North Inlet marsh is presently undergoing submergence from sea level rise.

Mathematical models are a prime tool for predicting the future state of the environment. Because of the extensive work and long-term data that exist for North Inlet's *Spartina alterniflora* population, Mudd et al. (2004) constructed a model of how these plants respond to tidal inundation, sedimentation, submergence time, and changes in its own aboveground biomass. The model relates to how the elevation of the salt marsh platform will evolve under future sea level rise. The model revealed that there is much work still to be done on how water flow and sedimentation rate are affected by emergent vegetation, and how accumulated sediments compact as their accretion rate changes.

Creating a model that incorporated long-term data on belowground biomass of *Spartina* in North Inlet, Mudd et al. (2009) explored additional aspects of how salt marshes might thrive or decline with future increases in sea level. Sedimentation includes both inorganic and organic particles. Incorporation of organic carbon in the model demonstrated that carbon accumulation in the salt marsh is related, non-linearly of course, to supply of inorganic sediment and sea level rise. The model suggests that the response of salt marshes will be greatly dependent on supplies of sediments to estuaries. Because coastal development often alters the sediment supply in rivers leading to estuaries and alongshore on beaches, the carbon budgets of coastal salt marshes could change in significant ways. Mudd et al. (2010) proposed two models that build upon earlier efforts to understand feedbacks between plant growth and sedimentation (of both organic and inorganic particles) as well as the effects of organic particle sedimentation on methods used for dating marsh sediments. These

models of biologically-mediated sedimentation show rather convincingly that most of the rate of sediment accretion in the marsh can be explained by the enhanced particle settling due to reduced turbulence amongst *Spartina alterniflora* stems, particularly in the fertilized plots from which Morris et al. (2002) used data in his model of how the marsh grows under sea level rise. Morris (2004) suggested that the feedback between plant growth and the growth rate of marsh elevation is relevant for coastal areas that are sinking relative to sea level.

Morris (2010) summarized previous work and extends a one-species model for *Spartina alterniflora* in North Inlet to a generalized two-species model that incorporates the various feedbacks between biological and physical factors that affect the competitive abilities of, for instance, invasive plant species. This model examines geomorphological displacement and competition such as occurs when *S. alterniflora* becomes established in new habitats. This coastal macrophyte management issue is currently under intense examination on the west coast of the United States.

Sufficient research has now been done that several investigators have used a compendia of data, all using North Inlet as a core representative piece, to summarize predictions of what will happen as climate change becomes more dramatic (e.g., Day et al, 2008). Data for non-tall forms of *S. alterniflora* along the Gulf and Atlantic coasts of North America incorporate North Inlet measurements that Kirwan et al. (2009) included in a methodologically comparable examination of latitudinal trends in productivity. Kirwan et al. (2010) also utilized North Inlet data to model adaptability in the response of coastal marshes to sea-level rise. It will be interesting to see which of or whether any of the predictions made by Dame et al. (1992) come to fruition.

- **Summary for Vascular Plant Research**

In summary, vascular plant communities, especially those dominated by *Spartina alterniflora*, in North Inlet have been studied more than any other segment of the photosynthetic biota present. Early studies examined plant physiologies and adaptations to changes in soil porewater salinity, and later manipulative studies revealed relationships between plant growth and many environmental variables. Belowground biomass of *Spartina alterniflora* receives oxygen via movement of porewater, from bioturbation activities, and thus tolerates hydrogen sulfide toxicity via actions of sulfate reducing bacteria and these other oxygenation processes. The plant's salinity tolerance results from its osmoregulatory capabilities. Evidence suggests that both tall and short forms of *Spartina* in mid and low marsh levels are regulated by bottom-up forces, primarily nitrogen limitation, with top-down grazing impacts negligible in this regard. High marsh plants are regulated by salinity, not nutrients. The buildup of salt marsh sediments around *Spartina* is a consequence of organic matter accumulation via bioturbation and settling of suspended sediments in the low turbulence zones of the vegetated portions of the marsh. There has been a net increase of sedimentation over time sufficient to match the rate of sea level rise. Annual net dry aboveground productivity of *Spartina* varied by a factor of two during the year and stem density was highly variable, being greater in older portions of the salt marsh. Long-term fertilization of *Spartina* created higher carbon turnover rates and greater loss of carbon dioxide from sediments relative to controls. Flushing of sulfides from porewater at the edges of tidal creeks enhances growth of the plant there. *Spartina* productivity also responds to annual changes in sea level, being higher when sea level is higher and lower when sea level is lower. Edaphic factors (e.g., sediment dynamics, porewater nutrient levels, and the sediment's microbial activities) play important roles in regulating saltmarsh plant communities. Models of plant interactions with and responses to changing stressors, especially sea level, have revealed several phenomena that require additional investigation. Overall the saltmarsh plant community of North Inlet is healthy and productive. However, current research suggests the marsh may not be keeping pace with sea level rise.

» Microbial Communities

The earliest microbial studies in North Inlet concerned how microbes were affected by the twice daily change of the tides. Research evolved afterwards and transitioned from the traditional lab-based studies of microbial communities cultured from the environment to the examination of their abundances and functional characteristics *in situ*, and most recently to an integrated, multidisciplinary approach. Modern molecular methodologies hold great promise for understanding more deeply how diverse microbial communities change over time and influence the type of coastal ecosystem represented by the NI-WB NERR.

Early concerns about water quality in the area centered on human health and the fecal coliform loads that harvestable species (e.g., clams and oysters) might carry. Nelson et al. (2005) reviewed microbiological and water quality data from the years 1967-1990 relevant to land use change at an urbanized site, Murrells Inlet, and at a pristine site, North Inlet. While increasing urbanization had been accompanied by increasing trends in fecal coliforms at Murrells Inlet, the construction of a sewage system decreased these loads starting in 1980. At North Inlet, construction of the Baruch Marine Field Laboratory in 1977 had no measurable impact on water quality above that which existed from natural sources of bacteria in the natural background. North Inlet has thus always been viewed as a relatively pristine, natural site, remaining comparatively uncontaminated by human interventions. This important attribute was critical for its selection as an LTER site and as a National Estuarine Reseaerch Reserve.

Following a rough chronology of research and topical themes, the earliest studies of microbes in North Inlet were conducted by L. Harold Stevenson and his students. Stevenson was also a co-editor with R. Colwell in 1973 of the first volume of the Belle W. Baruch Library in Marine Science entitled "Estuarine Microbial Ecology" dedicated to a pioneer in the study of marine microbiology, Professor Claude E. Zobell.

The earliest studies of microbes themselves, particularly bacteria, in North Inlet emphasized culturable species/taxa and employed classical physiological laboratory assays. Erkenbrecher and Stevenson (1975) examined the influence of tides on the concentrations of microflora in two tidal creeks in North Inlet. They found that aerobic heterotrophic populations in the water column peaked just before low tide due to resuspension and became lowest during high tides due to dilution from the influx of coastal seawater. Average concentrations ranged between 10^4 and 10^5 mL^{-1}, with lower concentrations at the Clambank station where bottom sediments were sandy, hence having less sediment in suspension compared with the muddier Oyster Landing station. They cautioned that microbial populations are quite different from creek to creek and that extrapolations from creek-scale studies to larger areas can be in error. A similar conclusion, though at a much larger spatial scale, was found in a comparison of the microbial communities in two SC marsh systems (ACE Basin and North Inlet) almost 30 years later by Johnson et al. (2006).

Sizemore et al. (1973) sampled sediments and water on the landward side of Debidue Island in North Inlet to measure the abundance and distribution, within the sediment column, of bacteria having proteolytic capabilities. On tests of 204 stock isolates and random isolates from the estuary, 44% of sediment organisms were proteolytic, while 49% of those from the water also exhibited the ability to degrade protein, casein in this study. Seasonal changes in these percentages were slight, and the population of proteolytic bacteria was highest at a depth of between 2 and 8 cm in the sediment. An earlier techniques paper established the protocol for these studies and was followed by a physiological scoping paper on the role of dissolved oxygen in proteolytic activity (Sizemore and Stevenson, 1970, 1974).

Coull (1973) reviewed the extant literature on the role of microbes in the ecology of marine meiobenthos, small metazoans that inhabit marine sediments globally. Coull posited the importance of bacteria and other microbes as food for meiofauna

and in decompositional processes involving these ubiquitous organisms that have been studied extensively in North Inlet. Coull's students later measured meiofaunal grazing rates on sediment microbes and bacteria in North Inlet (Montagna et al., 1983; Montagna, 1984a, b).

In a study of the fungal community, Cowley (1973) sampled soil from 7 stations along an intertidal transect in North Inlet from the tall *Spartina* to the upper edge of the high intertidal *Juncus* zone to quantify fungal species. He found much greater biomass of culturable species in the *Spartina* "debris" between the *Salicornia* and *Juncus* regions but considerably more diverse communities at the other stations.

Pitts and Cowley (1974) sampled fungi and discovered that sediments in and around the burrows of *Uca pugilator* contained a red yeast (*Rhodotorula mucilaginosa*). When crabs were active in October, 94% of the animals examined contained this same yeast in their mid-gut. In winter (February), less than 8% contained the yeast. Because several other mycoflora were found in the sediment, the authors suggested that this red yeast is a selected dietary component of this fiddler crab species. Cowley and Chrzanowski (1980) sampled yeast from the sediment and in the midguts of the fiddler crab, *Uca pugilator*. They found that two species of yeasts were abundant around their burrows at Clambank Landing, North Inlet, as well as in their guts. They suggested that yeast ingestion could supply B-vitamins to crabs that might experience a vitamin-deficient diet.

Physical-chemical factors and the effects of changes in the tide on microbial communities (Erkenbrecher and Stevenson, 1975) and the flux of microbial biomass as it is affected by the tide were studied by Erkenbrecher and Stevenson (1977). The same two investigators also examined changes in ATP (a proxy for microbial biomass), chlorophyll *a*, POC, and suspended materials during four 40-hr time series during the year and found that a high marsh creek was an exporting system for these materials (Erkenbrecher and Stevenson, 1978). They also found a close association between bacteria and suspended matter in that study. Stevenson (1978) suggested that many of the bacteria in aquatic systems must adapt to large changes in their physical environment (e.g., solar insolation, oxygen concentrations, nutrient substrate concentrations, etc.) or else they will die. He proposed that an alternative strategy for survival in the face of a changing environment is for bacteria to become physiologically dormant. At that time, this hypothesis was quite controversial.

A study of microbial communities as they are influenced by freshwater input into North Inlet from Winyah Bay found that salinity had little influence on or relationship with total microbial biomass (as ATP) in the salt marsh creeks of North Inlet (Weiland et al., 1979).

Chrzanowski and Stevenson (1979, 1980) contributed to tests of the Outwelling Study hypotheses by quantifying fluxes of fungi and total microbial biomass (again as ATP) during synoptic sampling events across a 320-m transect in Town Creek near the mouth of North Inlet. They found that fungal biomass fluctuated out of phase with the tide, with low values at high and high values at low tides. Their data also suggested that fungi are mostly associated with particulate organic matter that gets resuspended into the water column by ebbing tides. As part of the Outwelling Study, studies of total microbial biomass (ATP) along three transects across major creeks in North Inlet were coupled with water flow measurements to estimate fluxes of ATP to and from the coastal ocean. Stevenson et al. (1980) found that the ATP density (mg ATP per cubic meter) in the water column was highest during high tides, with a net import of approximately 40 mg ATP per second in the two creeks that connected directly with the ocean, and net export across the transect of a creek that empties into Winyah Bay. The complexities of flow over time both horizontally and vertically and during periods of stratification made these measurements difficult (Chrzanowski et al., 1981; Kjerfve et al., 1981).

The utility of using ATP as a reliable measure of total microbial biomass was called into question by Stevenson et al. (1981) who demonstrated that the luminescence from the luciferin/luciferase reaction for measuring ATP does not come exclusively from

the ATP nucleotide. Additionally, they provided evidence for past overestimation of ATP due to different methods of peak height estimation and water filtration used by different investigators. Wilson et al. (1981) also showed that, on average, bacterial ATP comprised only about 25% of the total ATP measured in high marsh water samples where sediment-associated microbes were abundant.

The study of microbes in North Inlet took a methodological leap in the early 1980s with the introduction of newer analytical techniques and instrumentation, e.g., epifluorescence microscopy and SEM (scanning electron microscopy). These instruments allowed quantification of the "planktobacteria" (= bacterioplankton) and for the first time the actual numbers of bacteria in various types of samples were measured in North Inlet (Wilson and Stevenson, 1980).

Although direct counts of bacteria were not conducted in most studies of microbial biomass in North Inlet, the use of ATP as a surrogate measure served to answer many of the flux questions posed by investigators, especially at smaller spatial and temporal scales. Chrzanowski and Zingmark (1986) sampled water moving across the marsh in a flume constructed in the Bly Creek basin near the field lab synoptically with samples taken from a transect across Bly Creek. Their measurements of ATP suggested that microbial biomass was passively filtered and removed from the water column by the tall form of *Spartina* along the creek bank and that the high marsh was the place where microbial communities separated into different components.

Chrzanowski and Zingmark (1989) measured bacterial abundance, biomass and secondary production in surface water samples collected at three stations in North Inlet: forest, high marsh creek, and low marsh creek. All sites were within a single drainage basin and were sampled bi-weekly for a year. The forested stream had lower abundances, biomass and production rates than the two marsh creek stations. Abundances and growth rates were higher during low tides at these two marsh creek stations as well. Bacterial secondary productivity co-varied with salinity. The results suggested that bacterial dynamics (growth rates) were more closely associated with individual water masses than with any aspect of the landscape.

The activity of nitrogen-fixing bacteria in salt marsh sediments associated with *Spartina* roots was investigated by Yoch and Whiting (1986). They measured the short-term effect of ammonium additions on acetylene reduction activity *in situ* in the short *Spartina* zone of the marsh. Ammonia inhibited nitrogenase activity in sediments and in both dead and live roots. The kinetics of this inhibition and its impact on nitrogen-fixation requires additional study. Gandy and Yoch (1988) determined the relative contribution of sulfate-reducing bacteria (SRB) and fermenting bacteria to nitrogen fixation in salt marsh sediments and on the roots of *Spartina alterniflora*. They collected sediment cores from between *Spartina* culms from the high marsh near Clambank Landing and removed roots while maintaining anoxic conditions. Using amendments and inhibitors, they measured acetylene-reducing activity (ARA) and showed that activation of dormant bacterial cells, not cell growth, accounted for measured ARA. Furthermore, 70% of the ARA in the uppermost 5 cm of the sediment was due to SRB, while ARA between 5 and 10 cm depth in the sediment was due to fermenting bacteria. SRB were found to be abundant on *Spartina* roots.

Other studies were done by time-series sampling of flooding and ebbing tidal waters in portions of the marsh confined in linear flumes (e.g., Chrzanowski and Spurrier, 1987). Microbial biomass was measured as concentrations of ATP normalized to unit areas of marsh surface, with fluxes determined by volume transport of these water concentrations over time. Although these ATP measurements had many methodological sources of error and high variabilities (see Stevenson et al., 1979), they served to illustrate that the marsh surface was neutral with respect to transport of microbial biomass, receiving as much from large tidal creeks within the marsh as they exported to them (Chrzanowski and Spurrier, 1987).

In the aftermath of the Outwelling Study, what was learned there stimulated many other investigations of microbial ecology in North Inlet. Trophic selectivity was the focus of work by Wetz et

al. (2002) who examined changes in the suspended microbial community as it passed over clumps of oysters in a flume. They found that the oysters, *Crassostrea virginica*, removed mostly phototrophic nanoflagellates and diatoms but left heterotrophic nanoflagellates, cyanobacteria, and heterotrophic bacterioplankton largely unaffected.

In the 1990s, new molecular techniques were utilized to examine the ecological roles these ubiquitous microbe-sized organisms play in the coastal ecosystem. These new techniques do not require the organisms to be cultured, hence the >95% of viable but non-culturable species/taxa could now be examined with regard to their biodiversity/relatedness and, in conjunction with classical microbiological methods, their ecological significance in different habitats within the salt marsh ecosystem. For instance, physiological studies of *Spartina alterniflora*, the salt marsh cordgrass, have shown clearly that these plants are nitrogen-limited and that their growth rates are affected by numerous environmental variables, e.g., temperature, salinity, light regime, macronutrient concentrations, etc. (e.g., Bradley and Morris, 1990b). Cordgrass success in the marsh, however, results from interactions with specialized microbial communities associated with their roots (see below).

Particle- or surface-associated bacteria present challenging problems for enumeration and process-related characterization. The study of microbial communities in the sediments and on plants in North Inlet started in the late 1980s and early 1990s with studies by D. Yoch, R. Lovell and others from the Dept. of Biological Sciences at the University of South Carolina in Columbia, SC. For example, Whiting et al. (1986) examined acetylene-reduction activity (ARA) in root-associated bacteria that function in nitrogen fixation in the salt marsh grass, *Spartina alterniflora*. They found that N-fixation was enhanced rapidly when photosynthesis was stimulated, suggesting that ARA was dependent upon plant photosynthate as an energy source. Sediment respiration, ARA, methanogenesis and denitrification were examined in microcosm experiments involving the stimulatory effects of chronic hydrocarbon exposure in *Spartina* by Li et al. (1990). Steward and Lovell (1992) devised an improved method for measuring uptake of radiolabel by sediment bacteria. Ansede and Yoch (1997) investigated sediment bacterial involvement in the production of DMSP (dimethylsulfoniopropionate) lyase using water and sediment samples from North Inlet.

In the 1990s Lovell and his students participated in multidisciplinary investigations with several benthic ecologists interested in the production of secondary compounds made by burrowing invertebrates, particularly infaunal polychaete worms found in the muddy and sandy marine sediments of the NI-WB NERR. Steward et al. (1992) looked at the relationships between bacterial abundance and activity, microalgal biomass, and meiofaunal distribution in sediments containing biogenic bromophenols in North Inlet. An additional examination of how bacteria respond to the presence of bromophenol, a secondary metabolite that is produced by marine polychaete worms, was made in a study by Lovell et al. (1999).

To maintain its high rate of primary productivity, *Spartina* maintains a supply of nitrogen through the nitrogen-fixing capabilities of its associated diazotroph community, the function of which was inferred using molecular microbiological techniques (Bagwell and Lovell, 2000a,b). Spatial and temporal dynamics of the rhizosphere diazotroph assemblage on several species of salt marsh plants has been studied in depth by Bagwell et al. (1998), Piceno et al. (1999), Piceno and Lovell (2000a,b), Lovell et al. (2000), Bagwell et al. (2001), Lovell et al. (2001a,b), Brown et al. (2003), and LaRocque et al. (2004). An overview of these and other such studies is provided in Lovell (2005), but diazotroph studies have continued to the present as well (e.g., Lovell et al., 2008; Gamble et al., 2010; Davis et al., 2011; Lovell and Davis, 2012).

Additional multidisciplinary work was done by Phillips and Lovell (1999) who examined the distributions of total bacteria and active bacteria in biofilms that occur inside the lining of the tubes built by the marine infaunal polychaete worm, *Diopatra cuprea*, a macrobenthic-sized

animal commonly found in tidal creeks in the NI-WB NERR. Matsui et al. (2004) examined sulfate reducing bacteria that occur within this worm's tubes. It should be mentioned that these studies on worm tube microbiology were built upon earlier work on the biogeochemical microenvironments of worm tubes and burrowing crustaceans where significant heterotrophic and chemoautotrophic metabolic activities were measured (Aller et al., 1983). Aller's work continued with microcosm experiments (Aller and Yingst, 1985) in which non-steady state concentrations of ATP and bacteria at the sediment surface were consistent with the concept of "microbial gardening" by macrobenthic bivalves and polychaete worms. Aller and Aller (1998) later confirmed the role of microorganisms in remineralization processes mediated by macrobenthic fauna.

Dang and Lovell (2002a) used hybridization probes and fluorescence techniques to enumerate and characterize the marine Rhodobacter group collected in seasonal, size-fractionated samples from Oyster Landing, North Inlet. Species from this group comprised about 25% of the particle-associated and 18% of the free-living bacterial assemblage and confirmed that the Rhodobacter group is present year-round in the water column of this tidal creek. Dang and Lovell (2000, 2002b) had previously established that members of this group are among the early colonists on clean surfaces and occur throughout the salt marsh, suggesting their prominence in biofilm formation on many types of surfaces in this habitat.

In a complex set of experiments designed to better understand ecological couplings between the microbial food web and primary producers involved in the microbial food web and the "microbial loop", De Lorenzo et al. (2001) utilized a subtraction methodology – elimination of certain functions necessary for metabolic operations – on artificial substrates that had soaked in a tidal creek and accumulated a natural consortium of microorganisms. By incubating these consortia in the presence of metabolically inhibiting substances (an antibiotic mixture, DMSO, a photosynthesis inhibitor, and cyclohexamide, a eukaryotic growth inhibitor) they were able to deduce the existence of an interdependent nexus of interactions between primary producers and protozoan heterotrophs in the water column that also involved the benthic microbial heterotrophic community. Interactions amongst these components of the microbial loop varied seasonally, with a more active microbial loop in summer and a more linear food web structure in the fall. This study is a good example of how researchers have progressively broadened their studies from individual elements of the coastal ecosystem towards an integrative approach.

Molecular examinations of the bacterioplankton communities in the ACE Basin and in North Inlet by Johnson et al. (2006) revealed that there were great differences in their respective community structure. Using denaturing gradient gel electrophoresis (DGGE), they found that the communities under the different salinity regimes in each area were remarkably different. The free-living bacterial community in North Inlet was consistent with that found to develop with the summer phytoplankton bloom there that is associated with a typical microbial loop dynamic in the water column. Characterization of the bacterioplankton in North Inlet by Johnson et al. (2006) was also consistent with that necessary for the dynamic coupling between phytoflagellates and bacteria documented by Lewitus et al. (1998). Such close examination of bacterial dynamics in the waters of the NI-WB NERR serve as a nice complement to ongoing comparative analyses of bacterial production (BP) and phytoplankton biomass (as chl *a*, CHLA) that has been conducted by the NI-WB NERR at the Oyster Landing SWMP station. Changes in the BP:CHLA ratio in North Inlet reveal covariance between heterotrophic and autotrophic processes, but additional sampling of bacterial assemblages as well as direct measure of phytoplankton production rates will be necessary to quantify this linkage more completely (Apple et al., 2008).

Indole-3-acetic acid (IAA) is a plant growth regulator (auxin) that is produced naturally and is well-studied, especially in terrestrial plants. Gutierrez et al. (2009) collected *Spartina* and *Juncus* in North Inlet and grew them in the laboratory

until bacterial outgrowths occurred on their root systems. These outgrowths were then isolated and grown in culture medium and tested for their ability to produce IAA. Eight *Vibrio* strains and five species-level clades containing numerous isolates and presumptively five new species were also found to produce IAA, the first time that estuarine or marine bacteria have been found to do so. This discovery suggests that diazotrophic strains in this genus may be coupled tightly with plant productivity because stimulation of root growth by the auxin results in more nitrogen-fixing capacity for the plant. Such interactions have relevance for carbon cycling but remain largely unexplored in estuarine habitats.

A combination of molecular and physiological methods was used by Gamble and Lovell (2011) to identify strains of Vibrionaceae and *Vibrio parahaemolyticus* in the sediments of North Inlet. Some of these bacterial strains are known pathogens, especially among people who have eaten contaminated shellfish or who have skin wounds. After measuring the abundance of these strains over the seasons in intertidal creek water, interstitial pore water and fiddler crab burrow water, they found highly increased numbers ("hot spots") of these bacterial strains in the burrows. Thus burrows engineered by *Uca* serve as refugia and enrichment zones for Vibrionaceae , particularly in burrows in the *Juncus* zone and also in short- and tall-form *Spartina* zones. Given the short generation times (10-90 minutes) of these bacteria, the burrows act as incubators before the bacteria are flushed out by tidal flow. Based on known fiddler crab burrow densities, tens of trillions of these bacteria enter tidal creeks with each change of the tide. The authors suggest that this finding of high numbers of potentially pathogenic bacteria in a relatively pristine environment deserves additional study.

Several microbiological investigations have been initiated recently but as yet are unpublished. D. Kim and S.H. Jung are listed in the 2011 compendium of "Current Research, Monitoring, and Education Projects", compiled by P. Kenny at the Baruch Marine Field Laboratory, as measuring microbial diversity in soil samples (with a DNA sequencer) along transects in the NI-WB NERR at locations affected by varying degrees of erosional disturbance events. Lovell and Matsui continue their collaboration examining how infaunal burrowing or tube-building marine macrobenthic organisms (polychaete worms) influence sediment microbiota. They will use fluorescent *in situ* hybridization (FISH), microelectrodes, and fluorescent redox potential probes to examine sulfate reducers in these microhabitats. Matsui and Fletcher continue their work examining the distribution of bacteria on the roots of marsh plants (*Spartina* and *Juncus*) and also employ FISH of 16S rRNA and confocal laser scanning microscopy in their work. Lovell is also continuing his earlier studies (with Dang) of man-made surface colonization by microbes and biofilm formation in North Inlet, studies with implications for the possible prevention of marine biofouling.

Microbiological studies in the North Inlet portion of the NI-WB NERR have made great advances, both conceptually and methodologically, over the last four plus decades. Interesting questions about their community dynamics remain, and their role in virtually all biogeochemical processes in the terrestrial and aquatic habitats of the reserve awaits deeper clarification, definition, and understanding. However, much has been learned during this time, and some major findings include that microbial biomass (as ATP) is greatest at high tide, with offshore import to North Inlet and export of ATP to Winyah Bay. About 25% of total ATP in the water column is bacterial in origin. There was some evidence that tall, creekbank *Spartina* passively filters microbes from the water on rising tides and that microbial communities differentiate once in the high marsh. The marsh surface is neither a net source nor a net sink for bacteria, and oyster reefs do not appreciably filter out heterotrophic bacterioplankton. There is an abundant and diverse mycoflora in North Inlet sediments. More recent studies of microbial communities no longer require that microbes be culturable, and direct counts show concentrations of up to 10^5 aerobic heterotrophic cells per ml in the water column. Diazotrophs and other root-associated groups take up photosynthate and stimulate *Spartina* productivity via their nitrogen-fixing capabilities. Microbial loop processes

dominate during summer, with more linear food web interactions in the rest of the year. Linkages between bacterial production and concentrations of chlorophyll-*a* have been found, emphasizing the important role of particulate organic matter in microbial communities of the water column. Rhodobacter is an abundant group in the water column and may contribute to the formation of biofilms on clean surfaces. The stimulatory effects of benthic infauna and even low chronic levels of hydrocarbons have been documented as enhancing microbial activity. *Vibrio* strains (pathogenic) exist in North Inlet's sediments, particularly in fiddler crab burrows where tides regularly flush *Vibrio* populations into the tidal creeks. The diverse community of microbiota is intimately linked with all aspects of biogeochemical cycles studied in this coastal ecosystem.

» Benthos

The benthos of the NI-WB NERR is a highly diverse group of organisms. The benthic community undergoes dynamic changes in abundance and species composition during the year, and one of the greatest research challenges is to understand what factors cause these large temporal changes and how these changes affect the ecosystem. Hundreds of studies on benthos in North Inlet have been published, and standardized monitoring of the benthic fauna continues today, albeit at a somewhat reduced level of effort now compared to earlier years. There are probably very few other sites in the world with such an information-rich dataset on both macrobenthos and meiobenthos available to researchers as exists for the NI-WB NERR. None can match the initial frequency (biweekly) and duration of benthos monitoring information available.

RESEARCH HISTORY OF BENTHIC STUDIES: A BRIEF SUMMARY

Much of the worldwide research done on intertidal and subtidal benthos is conducted on rocky shore, hard-bottom communities existing at higher latitudes. A major attribute of the NI-WB NERR is that it provides relatively easy access to researchers for the study of soft-bottom benthic communities. The area is representative of many other coastlines in the southeastern United States as well as other sub-tropical coastlines dominated by salt marsh plants rather than submerged aquatic vegetation (seagrasses) or mangrove communities.

The benthos of the North Inlet estuary and surrounding environs was not known very well until after 1969 when the Belle W. Baruch Institute for Marine Biology and Coastal Research was created and researchers were allowed access for scientific study of the area. Clams and oysters had been harvested here for centuries, evidenced by the presence of many large Native American shell middens in the marsh. The early 1970s studies concerned ecophysiological adaptations and energetics of intertidal organisms, single species' ecology and pollution biology, quantitative distributional surveys of both macro- and meiobenthos, and taxonomy. Work progressed from there to manipulative studies focused on the role of benthos in the estuarine food web and evolved into long-term monitoring studies in different habitats so that natural changes in abundance and diversity of benthic fauna could be measured and mechanisms causing season-to-season and year-to-year changes might be elucidated. Additional studies on mechanisms promoting site-selection and settlement of the free-swimming larvae of benthic animals were conducted in ensuing decades as more benthic ecologists and scientists from many other disciplines and institutions joined forces with faculty at USC and elsewhere to utilize the relatively pristine NI-WB NERR as a study site. This has broadened the research base considerably.

HABITATS/SETTING

Whether intertidal or subtidal, the benthic community also varies in species composition according to differences in the physical structure of the habitat and the availability of food present. Biotic forces such as competition, predation, parasitism, and the arrival of drifting planktonic larvae to an area also influence the type of benthic community that lives in any particular habitat. Acting together, these physical and biotic forces

create large-scale patterns in the distribution and community structure of benthos, both laterally and vertically with respect to the location of sea level as it changes with the tide.

INTERTIDAL BENTHIC COMMUNITIES

- **Open coast surf zone**

This habitat is physically dominated by wave action/storms and thus harbors a benthic community dominated by organisms that can withstand or escape the rigors of physical wave disturbance. There have been no formal studies of the surf zone meiofauna on South Carolina's beaches, and it is unknown whether beach nourishment has any permanent effects on the community. According to Ruppert and Fox (1988), the macrobenthic animals inhabiting the surf zone are numerically dominated by small, fast-digging, bivalves (in the genus *Donax*) and annelids (worms) that burrow through the sediments at depths of a few centimeters where they are not readily eroded by wave action. Mole crabs in the genus *Emerita* can become very abundant in the spring and summer. Overall, the macrobenthos is much less abundant in the surf zone than elsewhere, with only 10s to 100s of individuals per square meter.

Beaches on the landward side of barrier islands are exposed to less wave energy than the open coast. However, this particular habitat just inside North Inlet's mouth has not been sampled quantitatively.

- **Vegetated marsh**

The most visible portion of the salt marsh is vegetated by several plant species but dominated by the smooth cordgrass, *Spartina alterniflora*. Zonation of the plant community is conspicuously associated with the amount of inundation and exposure to air induced by the semidiurnal tides. The tallest form of cordgrass grows at the edges of tidal creeks in the low marsh. Shorter forms grow in the higher portions of the intertidal area, the high marsh. The highest intertidal areas are covered by sea lavender (*Limonium carolinianum*), glasswort (*Salicornia virginica*), and the rush (*Juncus roemerianus*). Several other plant species occupy the supratidal zone between the high marsh and the forest. Sediments in the vegetated marsh are muddiest in the low marsh and grade into larger grain sizes with increasing elevation into the high marsh which is comprised of sandy muds. The most visible macrobenthic fauna in the vegetated marsh are fiddler crabs, mud snails, and periwinkle snails. Many other less visible taxa are present (e.g., polychaete worms). The subtidal portions of the vegetated marsh host a variety of fauna including crustaceans - particularly grass shrimp, penaeid shrimp (seasonally), crabs, and amphipods – mollusks, annelids, and other taxa. Motile organisms move from subtidal regions into the vegetated portion of the marsh to feed and for protection from predators. Both meiofauna and macrofauna are abundant in the intertidal and subtidal vegetated marsh. Detritus formed from dead stems and leaves of *Spartina* first collects as piles of wrack in the intertidal zone where it later decays and gets mobilized as small particles. These particles get colonized by bacteria and are ingested by a variety of fauna that live in the sediments and water column. Thus the vegetated marsh is essential both for habitat and for the food web it supports.

- **Unvegetated mud and sand flats**

This portion of the salt marsh is home to numerous burrowing worms, clams, and fiddler crabs. The sediment here is contoured by fast-moving tidal currents, and ripple marks are common on the sand surface. Mudflats are pock-marked by shallow pools, many of which are made by stingrays during times of high tide. Several coastal bird species use these flats as foraging and feeding grounds. When the flats are exposed during warm times of year, thousands of fiddler crabs emerge from their burrows and engage in behavioral displays as part of their mating ritual. The surface of the flats is usually covered by a thin film of benthic diatoms and other algae that migrate vertically within the uppermost few millimeters of the sediment in their search for optimal levels of sunlight. Mud-flat fauna, however, are adapted to much less rigorous physical conditions, as evidenced by the accumulation of finer grained (smaller sized) sediments that would otherwise wash away quickly in faster-moving currents at high tide.

The large Debidue sand flat opposite the mouth of North Inlet is more exposed to the elements (wind and waves) than other flats in the area. Samples of macro- and meiobenthos collected biweekly for 4 years at the Debidue sand flat demonstrated the high spatial and temporal variability in abundance that is characteristic of physically-controlled communities. No seasonal trends in abundance were discernable in either the macro- or meiobenthic sizes of the impoverished benthic fauna.

- **Oyster reef**

Intertidal and subtidal oyster reefs are one of the most prominent biological features of southeastern US salt marshes. They are comprised of the eastern oyster, *Crassostrea virginica*, that grows as clusters of individuals cemented together.

Oyster reefs process prodigious amounts of particulate organic matter during feeding and expel equally large amounts of fecal and pseudofecal matter that becomes colonized by free-living microbes. This organic material then serves as food for a host of deposit-feeding invertebrates such as polychaete worms, shrimp, and other smaller crustaceans like ostracods. Thus many studies of oyster reefs have been done in the context of reefs as connected systems whose intake and output of organic matter can be budgeted in energetic terms. Isolated oyster reefs have been "enclosed" for before and after study of the changes that occur in various water constituents (particulates, nutrients, etc.) flowing across and over a reef.

Oyster reefs occur allong many of the creek edges in North Inlet.

Oyster reefs also serve as unique, hard-bottomed living space for a variety of animals restricted to this habitat and seldom found elsewhere. A list of invertebrate organisms found within oyster reefs can be found in Fox and Ruppert (1985) and in **Appendix D**. They include polychaete worms from several different families, several species of small crabs, and a diverse group of snails, sponges, anemones, sea stars, and shrimps, among others. Small fishes can also be found living within oyster reefs, and motile nekton frequent these areas in search of food during high tide. Many locals find the edges of oyster reefs to be especially good places to cast baitfish or shrimp in hopes of catching large red drum and other fishes.

SUB-TIDAL BENTHIC COMMUNITIES

- **Creek bottoms (shell hash) and tidal pools**

The bottoms of subtidal creeks and larger pools of water that do not become empty at low tide are perhaps both the most-studied and the least well-understood habitats in the NI-WB NERR. Their community composition has been monitored extensively through time by examining dredge and epibenthic sled collections made from the bottom of Town Creek.

Animals collected in this manner are most abundant in the warmer months of the year. However, there have been very few studies conducted that examine how this creek bottom habitat is actually utilized by the organisms that reside there or that use the habitat for transit, yet many species are found only here. Currents usually are strong enough to scour the finer sediments away, leaving bits of oyster and other bivalve shell material (shell hash) exposed on the bottom. It is one of the few places within the salt marsh that has hard substrate colonized

with many attached colonial organisms (soft corals, bryozoans, sponges) adapted to life in fast-moving water (tidal currents can exceed 2-3 knots along the bottom).

MACROBENTHOS

There are many different soft-bottom benthic habitats in North Inlet and very few hard-bottoms. To characterize temporal changes of the macrobenthic community, two representative sites were selected for sampling. Both had been sampled for meiofauna on a long-term basis beginning in 1972, so having data for communities of both size-classes from the same sites was attractive. However, macrobenthos at several other locations in North Inlet had been sampled before the start of the LTER program. Among the earliest quantitative collections were those made on intertidal sandbars located in major tidal creeks by Holland and Dean (1977a). These areas were dominated by suspension-feeders in their sandy portions and by deposit-feeders in the muddy-sand areas. Two haustoriid amphipod (Crustacea) species dominated the fringe areas of the sandbars in these tidal creeks. Between 15 and 44 total macrobenthic species were found in their surveys at three sites, each of which had four discretely different habitats for which the macrobenthos was characterized. Seasonal changes in the sandbar community were reported by Holland and Polgar (1976) who found that differences in the reproductive patterns and life histories of the numerically dominant amphipods controlled the dynamics of the community. Both these publications were based on dissertation studies by Holland. Holland and Dean (1977b) also studied razor clam biology in North Inlet in a different area of the marsh.

As part of the National Science Foundation's Long-Term Ecological Research program, the macrobenthos was first sampled on a regular, biweekly, basis in 1981 at two subtidal sites – the Debidue sand flat and the muddy Bread and Butter Creek (Michener et al., 1986). The sandy site sampling effort was discontinued in 1985 because core-to-core variability in abundance was too high to detect anything more than very large, irregular, changes over time. These data are not included here. Since then, long-term sampling has continued only at the Bread and Butter site. Macrobenthos sampling frequency was decreased to quarterly in 1998 due to a lack of funding for the labor-intensive processing and specialized identification of benthic fauna, with sorting currently only to major taxon and total abundances being tabulated at this taxonomic level. Unfortunately, many (4 of 8 replicate cores) of the macrobenthos samples collected quarterly since 1998 remain uncounted, but analysis of prior data suggested that just 4 core samples per date were sufficient to document seasonal changes in abundance. All macrobenthos samples collected are preserved in buffered formalin and have been placed into semi-permanent archival storage on the premises.

Macrobenthos at the subtidal, muddy long-term collection site in Bread and Butter Creek undergo dramatic but regular changes in abundance each year (Service and Feller, 1992; Edwards et al., 1995). The pattern starts with high numbers of organisms (primarily polychaete worms and bivalves) in the coldest months, with densities over 50,000/m^2 (Figure 70). Coincident with the arrival of many transient epibenthic and nektonic predators in late winter and early spring, the macrobenthic community begins a rapid decline in abundance throughout the spring that continues into the early summer. Summertime lows of only a few thousand individuals per square meter persist until fall, at which time recruitment of new individuals into benthic populations begins (Service and Feller, 1992; Feller et al., 1992). This pattern has been

Macrobenthic core sampling.

seen in detail in the early portion of the long-term collections made biweekly for many years and still remains visible as an annual pattern even with the most recent samples that were collected on only a quarterly basis. Although changes in macrobenthic community structure (relative abundances of individuals of each species and numbers of species) are no longer documented in the quarterly samples, based on recent data, there is little reason to believe that major shifts have taken place through time, but this is an unanswered question. The community has always been dominated by polychaetes, mostly in the spionid, capitellid, and cirratulid families, oligochaetes, and a less rich bivalve community. Because they are numerical dominants, all of these taxa show high seasonality signals (Figures 71 and 72), but the seasonal signals are less clear for some other taxa such as shelled gastropods (Figure 73). Individuals from many polychaete families are found each year, and the number of families varies from two to about six (up to 13 in the entire time-series). Many other taxa have been recorded in North Inlet and are listed in the Baruch database along with metadata (information about the sampling protocol) (**www.baruch.sc.edu**).

The long-term record for total macrobenthos abundance (Figure 70) hints at some potentially interesting cyclic phenomena on the order of 14 years. However, with the decrease in sampling frequency and sample size, the resulting loss of precision in seasonal, annual, and inter-annual changes in abundance, suggests many more years of data will have to be collected before such cycles could be substantiated statistically. Likewise, it will take a dramatic change in abundance over time to even suggest that an effect of global climate change could have taken place. There are many other less statistically noisy ways to measure long-term climate change than by monitoring soft-bottom benthic communities. Several biotic and abiotic forces are likely at play in causing these wide seasonal swings in macrobenthos abundance each year, but the only one that has been examined in any quantitative detail is predation by fishes and shrimp (e.g., Service et al., 1992; Beseres and Feller, 2007a,b; Pollack et al., 2009). Predation losses are significant, but this alone cannot account for the seasonal declines in springtime that have been documented on a regular basis. Many questions remain about recruitment, competition, and food webs as drivers of changes in macrobenthic community structure.

As seen in other soft-bottom habitats around the world, certainly competitive interactions among and between species are possible in the macrobenthos, and changes in water temperature or dissolved oxygen concentration must also drive some portion of the observed changes, but none of these abiotic factors has been examined in other than a correlative manner in North Inlet.

A study of oyster recruitment by Michener and Kenny (1991) at three locations in North Inlet using settling plates and tubes showed that variability of recruitment among tubes and plates was as great as between sites and among intertidal elevations. Settlement and recruitment patterns of oysters was affected by both physical and biological factors which operate across several scales, making it difficult to compare studies of settlement conducted at different spatial and temporal scales. Other studies of recruitment (the settling of planktonic larvae of benthic organisms to the bottom) by Luckenbach (1984a, 1987) suggest that post-settlement processes are important in determining the future size of bivalve and other populations in North Inlet. Changes in the salinity regime also have large impacts on recruitment of planktonic larvae to the benthos (Richmond and Woodin, 1996, 1999). Recruitment can also be impacted as a consequence of predation activity (Wethey et al., 2001), and signal cues for settlement come in a variety of ways (Woodin et al., 1995). Many more manipulative and other types of experiments must be done to understand what causes the observed wide seasonality of the macrobenthic community in North Inlet.

The following list provides a brief sense of the diverse benthic research undertaken:

- Oyster reef energetics (for *Crassostrea virginica*, Dame, 1972), filter-feeding (Dame et al., 1980), and macrobenthic fauna inhabiting oyster reefs (Dame, 1979), intertidal versus subtidal growth (Crosby et al., 1991)

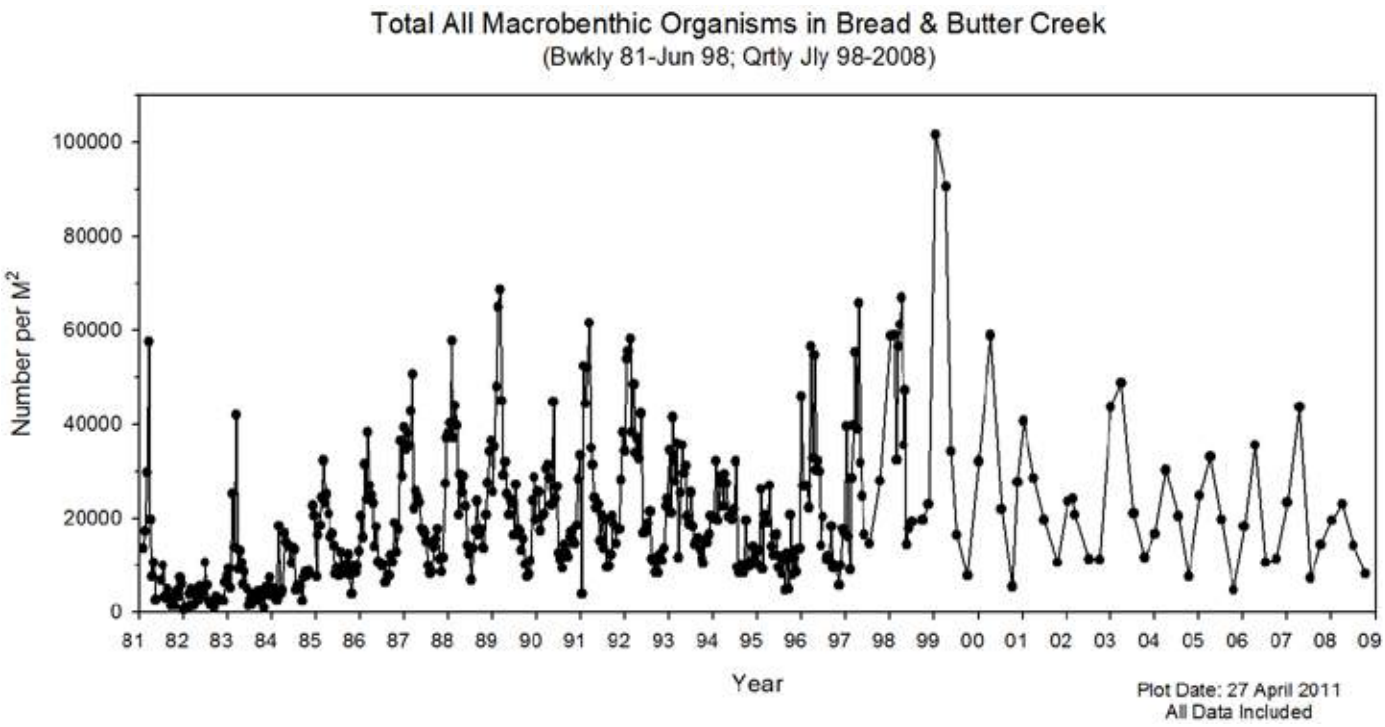


Figure 70. Total macrobenthic organisms in Bread and Butter Creek.

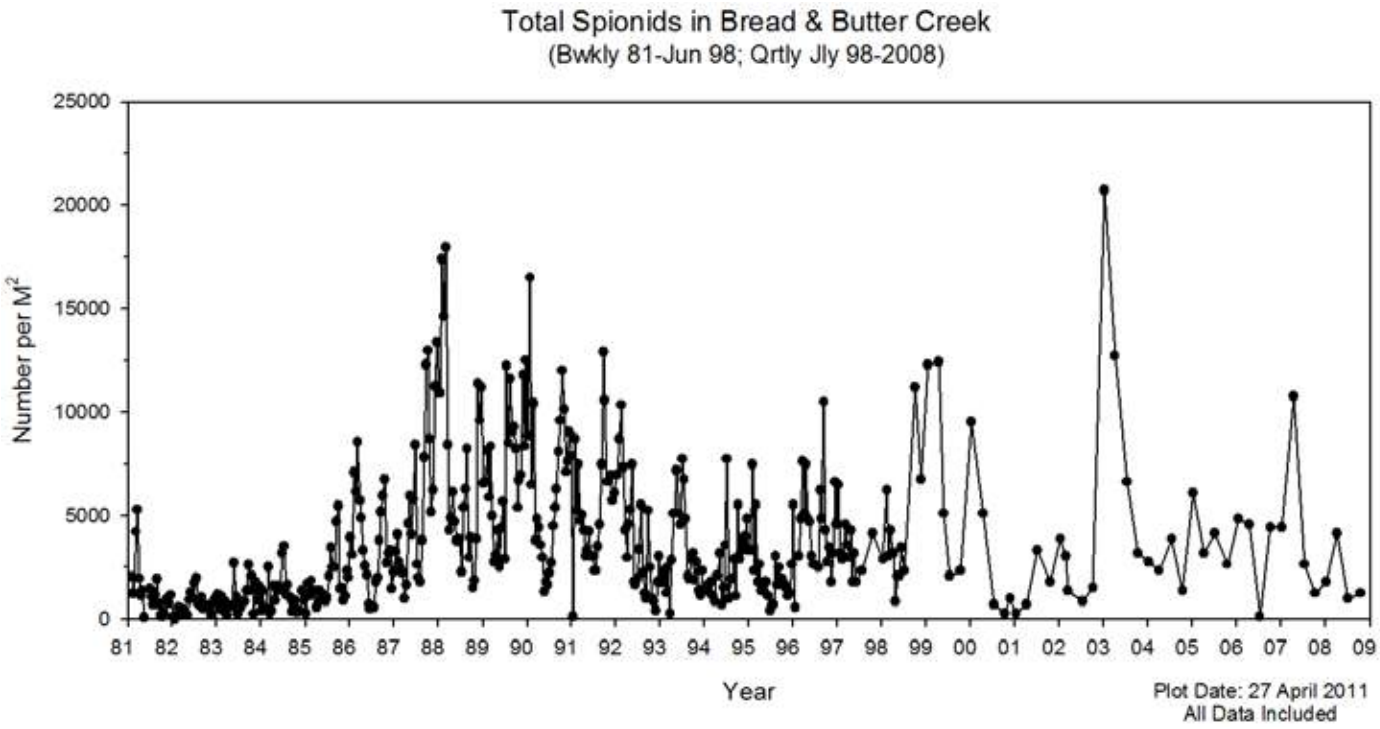


Figure 71. Total spionids in Bread and Butter Creek.

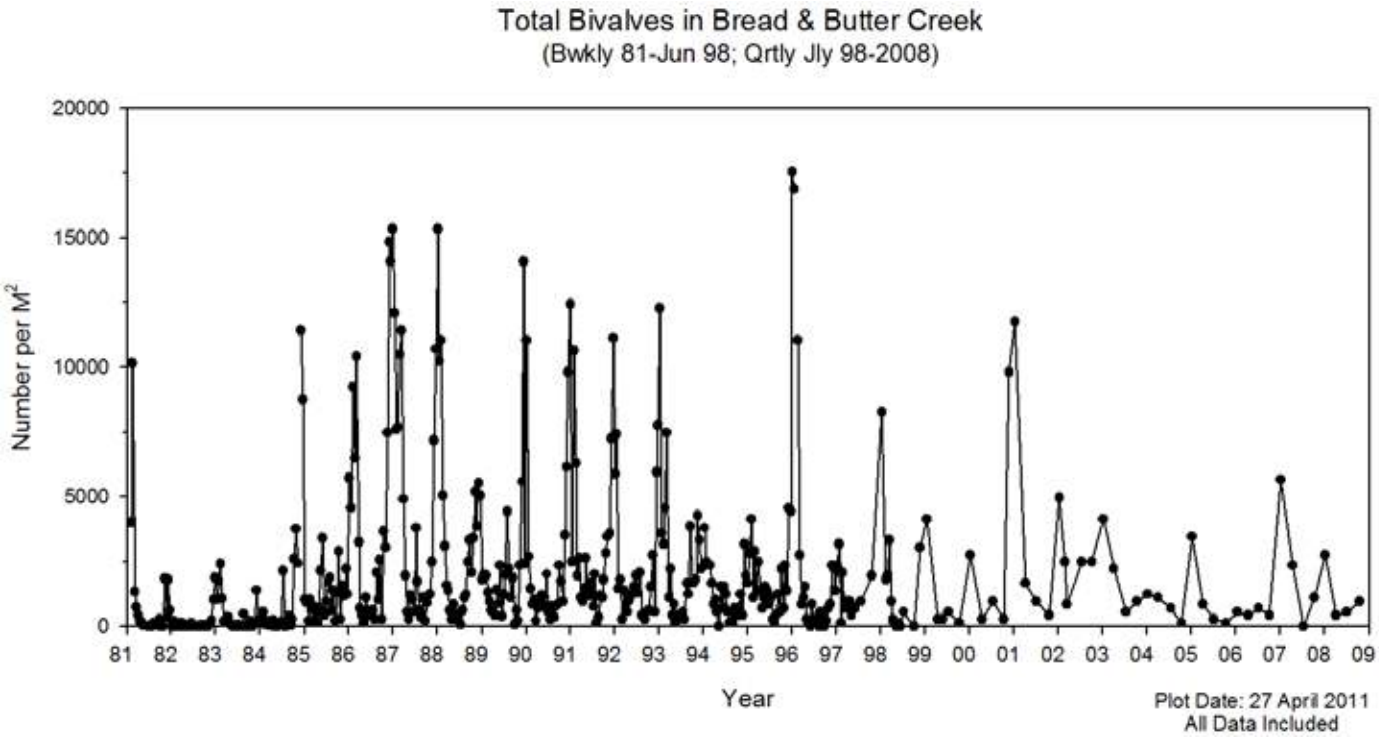


Figure 72. Total bivalves in Bread and Butter Creek.

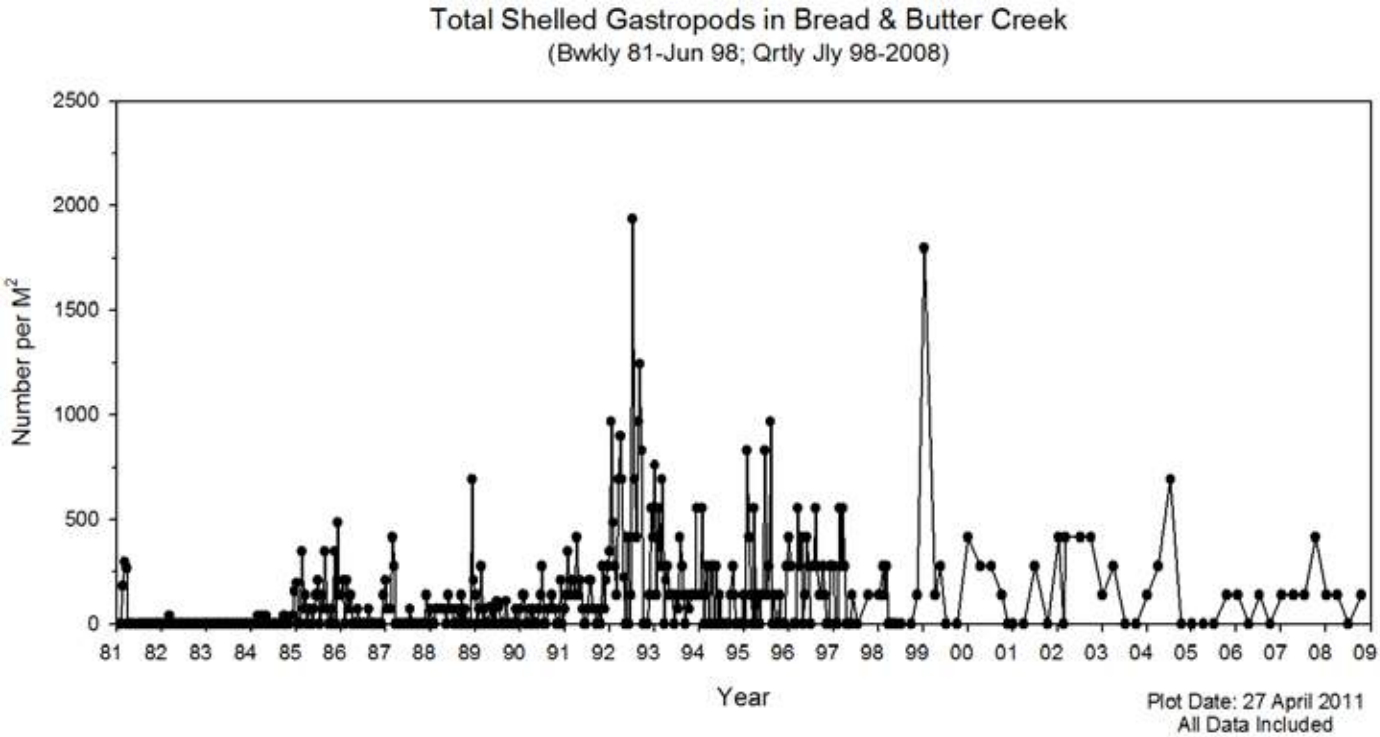


Figure 73. Total shelled gastropods in Bread and Butter Creek.

- Annelids, effects of organic enrichment on assemblages (Kihslinger and Woodin, 2000), ecology of a capitellid (Schaffer, 1979), intraspecific reproductive polymorphism in *Streblospio benedicti* (Pernet and McArthur, 2006)
- Amphipod competition and disturbance in sandflat populations (Grant, 1981a,b)
- Grass shrimp life-history and development patterns (Alon and Stancyk, 1982), production and feeding ecology (Sikora, 1977)
- Nudibranch taxonomy and new species (Shoemaker et al., 1978; Eyster, 1980) and life history and development (Eyster, 1979; Eyster and Stancyk, 1981)
- Mud snail freezing tolerance (Hilbish, 1981)
- Mud crab fatty acid incorporation (Lunetta and Vernberg, 1971), osmoregulation (Boone and Claybrook, 1977), distribution and behavior (McDonald, 1982), genetics and growth (Hilbish and Vernberg, 1987)
- Ribbed mussel reproduction in intertidal populations (Borrero, 1987), temperature effects on metabolic rates (Hilbish, 1987), growth (Borrero and Hilbish, 1988), and energy budget (Wilbur and Hilbish, 1989)
- Hard clam genetics (Rawson and Hilbish, 1991)
- Invasive species, green porcelain crab (Hartman and Stancyk, 2000; Hartman et al., 2002)
- Fiddler crab respiration rate (Dame and Vernberg, 1978), hatching rhythms (Bergin, 1981), sediment reworking (bioturbation, McCraith et al., 2003), and herd behavior (Viscido et al., 2001, 2002; Viscido and Wethey, 2002)
- Barnacle larval settlement patterns and post-settlement mortality (Young, 1991)
- Brittlestars: salinity tolerance (Stancyk and Schaffer, 1977), reproduction and morphology (Heatwole and Stancyk, 1982), regeneration and autotomy (Donachy and Watabe, 1986; Clements et al., 1988, 1993; Dobson et al. 1991), particle selection trophic dynamics (Clements and Stancyk, 1984), habitat preferences (Zimmerman et al., 1987), and browsing activity and partial (sub-lethal) predation (Stancyk et al., 1994; Pape-Lindstrom et al., 1997), subsurface feeding capabilities (Gielazyn et al., 1999), characterization of food resources (Hoskins et al., 2003)
- Odor plumes as signals emanating from the benthos (Moore et al., 1993; Zimmer-Faust et al., 1995; Finelli et al., 1999, 2000)
- Immunochemically-defined taxonomic relationships among soft-bottom benthic fauna (Feller and Gallagher, 1982; Feller, 1984b)
- Habitat modification and ecosystem engineering (McRae and Woodin, 1984; Woodin and Marinelli, 1991; Woodin et al., 2010), and hydrodynamics of animal tubes in the sediment (Luckenbach, 1986)
- Predator-prey interactions involving macrobenthos and penaeid shrimp (Beseres-Pollack et al., 2008), mud snails (Feller, 1984a), hard clams (Feller 1986)
- Crypsis (decorating) behavior and energetics of an onuphid polychaete, *Diopatra cuprea* (Berke, 2006; Berke and Woodin, 2008)
- Parasitic crabs (Bell, 1988; Bell and Stancyk, 1983)
- Gorgonian growth and development (Kingsley and Watabe, 1984)

There have also been several studies of the microbial ecology of sediments containing biogenic bromophenols (Steward and Lovell, 1997; Lovell et al., 1999) and the effects of these organic compounds as deterrents of predation (Woodin et al., 1987). Brominated compounds have also been found to serve as signals of the suitability of sediments for colonization and settlement (Woodin et al., 1993, 1997). Otherwise, recruitment of various benthic species to the substrate has been examined by Woodin (2007) and Woodin et al. (1998). Interestingly, as pointed out by Fielman et al. (1999, 2001), these naturally-occurring brominated compounds could easily interfere with assessments of toxic chemicals found in marine sediments that might be considered anthropogenic in origin rather

than natural. Cowart et al. (2000) found that two types of polychaete larvae, those with and without egg yolk, also contained halogenated compounds that are parentally-derived secondary defense mechanisms, the first report of these compounds in polychaete larvae. Because these compounds have been found in species from a variety of polychaete families, it is possible that chemically-mediated traits themselves may be important for structuring benthic communities in soft-sediments. On the other side of the equation are mechanisms for dealing with the toxic properties of halogenated compounds, and there have been several interdisciplinary biochemical/genetic studies of these detoxifying enzymes in polychaetes in North Inlet (e.g., Chen et al., 1991; Yoon et al., 1994; Zhang et al., 1996; Chen et al., 1996; Roach et al., 1997; Lebioda et al., 1999; Han et al., 2001; LaCount et al.,2000; Lincoln et al., 2005).

There have also been several studies of symbiotic and commensal relationships involving crabs and polychaetes, especially for a rather large burrow-dwelling polychaete (*Chaetopterus*) (Grove and Woodin, 1996; Grove et al., 2000). Many other studies conducted by students doing independent research or senior thesis projects also provide valuable insights into the ecology of benthic animals in North Inlet and often serve as preliminary work that later evolves into full research projects funded by federal, state, and private organizations.

Building on the pioneering studies of how the huge populations of fiddler crabs in North Inlet and Winyah Bay maintain themselves reproductively (Christy, 1982; Christy and Stancyk, 1982; Christy, 1989; Christy and Morgan, 1998), more recent fiddler crab studies concern habitat choice by juveniles using molecular methods to identify which species settles where (Behum et al., 2005) and the survival capacities of their planktonic larval stages in low-salinity waters (Brodie et al., 2007; Godley and Brodie, 2007). With concerns for how organisms might adapt to climate change, Jost and Helmuth (2007) measured the mortality imposed by thermal stresses experienced by ribbed mussels (*Geukensia demissa*) that bury themselves in the salt marsh. Iacarella and Helmuth (2011) performed laboratory experiments on the ubiquitous periwinkle snail, *Littoraria irrorata*, that explored how this species manages to keep from over-heating and suffering from dessication as it inhabits the salt marsh. An interesting interplay between the shading and cooling effects of *Spartina* and how the plant simultaneously reduces cooling around it by impeding air flow and its evaporative cooling effects were at play in both of these studies.

Recently, research on the adaptive value of various types of fiddler crab behavior has been conducted by Decker and Griffen (2012). These investigators measured boldness exhibited by female sand fiddlers (*Uca pugilator*) as certain behaviors are (or are not) influenced by physiological aspects of their feeding biology. The gut morphology of fiddler and other brachyuran crabs was measured by Griffen and Mosblack (2011) to see whether they could predict the types of diets, as percent herbivory, and the relative consumption rates in a suite of 15 species in this group of crustaceans. Another aspect of animal behavior was studied by Griffen et al. (2012) who experimentally demonstrated how foraging behavior by the xanthid mud crab, *Panopeus herbstii*, upon their bivalve prey was influenced (or not) in the presence of a predator, the toadfish *Opsanus tau*, that eats the mud crab. Such indirect effects are difficult to measure, but they have been found to exist among other species in many other habitats besides the oyster reefs where this particular type of indirect trophic interaction is most likely to occur.

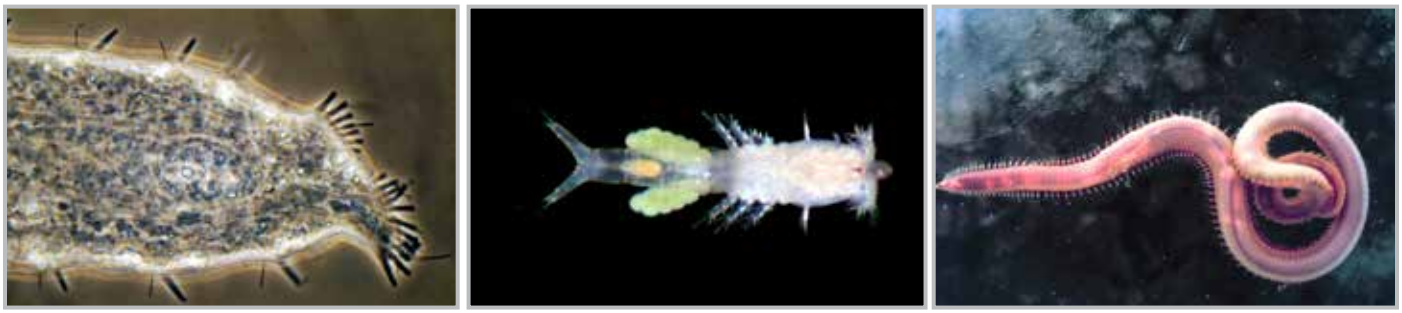
In a manipulative study by Toscano and Griffen (2012), various sizes of the mud crab, *P. herbstii*, were placed into subtidal cages containing bivalve prey that they normally consume in the oyster reefs. They found that large crabs ate the most bivalves, suggesting that oyster harvesting practices that remove living space for larger mud crabs have the potential to greatly alter trophic relationships that normally occur in unharvested reefs. Evidence for such a possible effect was provided by a field study of the sizes of mud crabs present in oyster reefs having a range of harvest pressure. Harvested reefs contained smaller mud crabs than unharvested reefs.

In summary, macrobenthic research has revealed a highly diverse community of organisms in all habitats sampled in North Inlet. Community dynamics have changed regularly each year in Bread and Butter Creek as wintertime high abundances decline rapidly in spring and early summer when numerous epibenthic predators enter the estuary. Although experimental evidence suggests that predators negatively impact macrobenthic populations, predation alone cannot explain the magnitude of the rates of decline and increase measured. Physical factors and biotic interactions like competition likely play a strong role in structuring macrobenthic communities as well. Polychaete and oligochaete worms and bivalves are the most common members of the soft-bottom macrobenthos, and total community abundances reach maximum values of 50,000 individuals m^{-2} in winter most years. Recruitment processes, both pre- and post-settlement, greatly impact the structure of both soft- and hard-bottom communities as well. The macrobenthos of hard substrates like oyster reefs is understudied. Ophiuroid studies have included a wide variety of topics. Burrowing fiddler crabs and worms play an important role in biogeochemical cycles when they are most active in warmer times of year. Macrobenthic fauna attract a variety of avian predators to the salt marsh each year, and numerous species of fish and invertebrates prey upon macrobenthos throughout the year. Studies of physiological and morphological adaptations to temperature in intertidal bivalves have shown that the effects of climate change and sea level rise can have large impacts on the community. Chemical defensive compounds in several taxa also impact community interactions. Studies of macrobenthos in a variety of habitats within North Inlet have encompassed numerous marine ecological subjects and processes (e.g., competition, trophic interactions, food selection, biodiversity, taxonomy, energetics, population dynamics, spatial distribution, recruitment, seasonality, secondary production, bioturbation, physiology, parasitism, autotomy, etc.). Despite this large body of work, many questions remain concerning the relative importance of biotic and abiotic forces that structure the macrobenthic community.

MEIOBENTHOS

Most of the practicing meiobenthologists in the United States and in many foreign countries have academic ties to the University of South Carolina's interdisciplinary Marine Science Program and the Belle W. Baruch Institute for Marine and Coastal Science. Many researchers from all over the world have visited the Baruch Marine Field Laboratory facilities to study the species-rich meiofauna of North Inlet. It is recognized, both nationally and internationally, that probably more is known about the ecology of meiofauna in North Inlet than at any other place in North America.

The long-term meiobenthos sampling program at North Inlet, 1972-1995, has involved core sampling from two subtidal sites: muddy Bread and Butter Creek, and sandy Debidue Creek. The abundant meiofaunal community at both locations is dominated numerically by nematode worms, with harpacticoid copepods, gastrotrichs, and turbellarians also being prominent. Other taxa (e.g., meiobenthic polychaetes) may increase rapidly in abundance at various times of the year, but the same annual decline seen in macrobenthos also takes place in the meiobenthos – high abundances in winter with springtime declines to summer lows and autumnal recovery back to the winter peak. The seasonal signal is more clearly seen in the Bread and Butter data (Figure 74) than at the Debidue Creek site where fluctuations in abundance are less marked (Figure 75). In contrast to the muddy-bottom meiofauna, changes in the meiobenthic community at the more wave-energetic sandy site are probably influenced primarily by physical or abiotic rather than by biotic factors. Hints of cyclical changes in abundance are visible in the record, but sampling would need to take place over a considerably longer period to establish whether they are regular phenomena. As is the case for macrobenthos, the only driver of changes in abundance that has been experimentally and quantitatively investigated on meiofauna is predation, mostly by transient juvenile fishes (the spot) and various shrimps. Several other potential drivers of changes in meiofaunal abundance over time have been examined (see below). Predation



Images of benthos commonly found in North Inlet: gastrotrich *left*, harpacticoid copepod *center*, polychaete *right*.

alone cannot explain the observed regular seasonal peaks and valleys of abundance or their amplitudes.

There are several hundred publications based on meiofauna research in North Inlet. The following review/synthesis papers provide context and have been among the most influential with regard to stimulating new research and leading this field of study forward nationally and internationally:

- Trophic relationships involving meiobenthic organisms (Coull, 1973);
- A call for hypothesis testing in meiofaunal studies (Coull and Bell, 1979);
- Harpacticoid copepods and their ecology, a review (Hicks and Coull, 1983);
- Field experimentation (Coull and Palmer, 1984);
- General meiofauna ecology (Coull, 1988); and
- Pollution and toxicology (Coull and Chandler, 1992).

Most of the North Inlet meiofaunal publications can be grouped into several rather broad categories (Table 6). There is considerable overlap among categories within many of the references listed in this generalized manner. Topical highlights include taxonomy of nematodes and harpacticoid copepods, centimeter-to-meter scale spatial distribution patterns, tidal transport and dispersion mechanisms, feeding of meiofauna upon bacteria and dead organic matter (detritus), their trophic role as prey in marsh/estuarine food webs involving predatory juvenile fishes, shrimps, and crabs, long-term changes in abundance and species diversity, their utility as sentinels of changes in water quality and/or presence of toxic substances, their numerical response to the impacts of human development in surrounding watersheds, their effect on juvenile members of the macrobenthos, and, most recently, the stability of their genetic make-up under various environmental stressors such as persistent pesticides and petroleum-based residues. Toxicological tests using meiofauna, particularly harpacticoid copepods, as sentinels or indicators of degraded habitat are currently under evaluation by the international Organization for Economic Cooperation and Development for eventual adoption as a mandatory screen for potential endocrine-disrupting chemicals.

Results of the meiofauna sampling effort in North Inlet have revealed a productive community dominated numerically by nematodes (70%) and harpacticoid copepods (20%) in both intertidal and subtidal sites. Taxonomy of harpacticoid copepods is well-documented, but many other taxa require additional work. Total meiofaunal abundances are somewhat higher intertidally than subtidally, always with more in muddy than in sandy sediments, and range seasonally from hundreds of animals per 10 cm^2 in mid-to-late summer to several thousands per 10 cm^2 in winter. A majority of the meiofaunal animals are usually found within the uppermost few centimeters of the sediment where dissolved oxygen concentrations remain sufficiently high above the deeper redox potential discontinuity layer. Their abundances in the sediment do not vary significantly with changes in tidal levels nor from day to night in any of the habitats. Meiofauna are patchily distributed – their abundances may vary by an order of magnitude between replicate cores taken within an area of one square meter. Therefore, high ($n > 3$) numbers of core samples must be collected

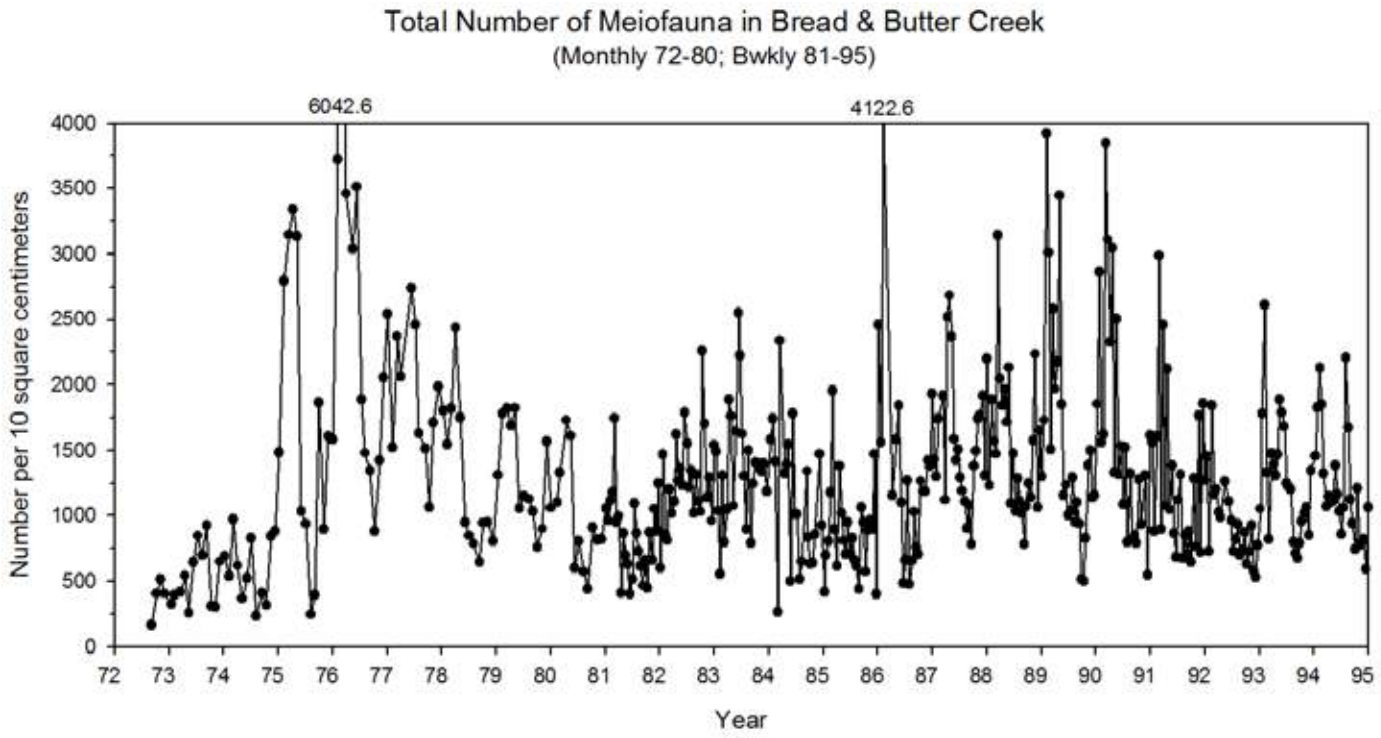


Figure 74. Total meiofauna in Bread and Butter Creek.

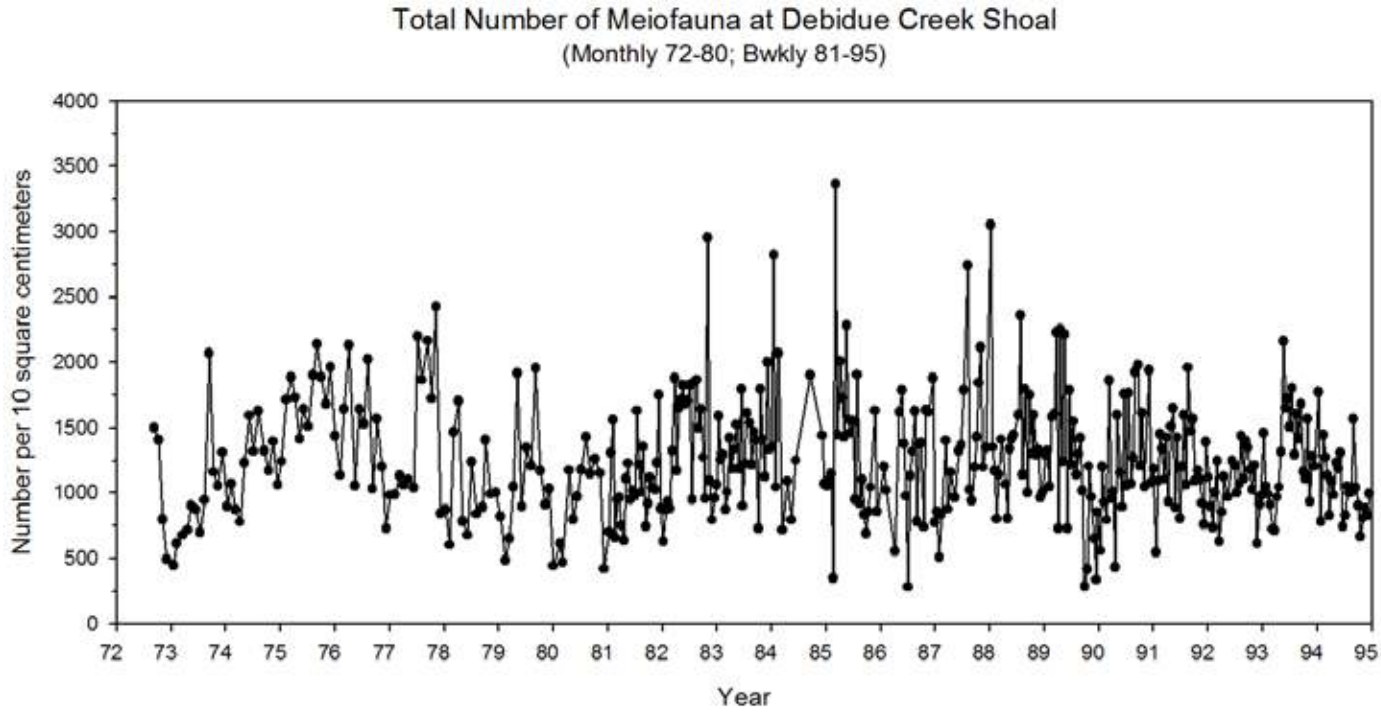


Figure 75. Total meiofauna at Debidue Creek Shoal.

Table 6. A categorized list of representative studies on North Inlet meiofauna.

Community Dynamics/ Demographics	Coull and Fleeger (1977), Hogue (1978), Bell (1979), Fleeger (1979, 1980), Montagna et al. (1983), Coull and Palmer (1984), Coull (1985a,b), Coull and Dudley (1985), Eskin and Coull (1987), Edwards and Coull (1987), Richmond et al. (2007)
Development/ Life-History	Coull and Vernberg (1975), Coull and Dudley (1976), Palmer (1980), Palmer and Coull (1980), Coull and Grant (1981), Bell (1982), Williams-Howze and Coull (1992), Williams-Howze (1996), Green et al. (1995, 1996)
Dispersal	Bell and Sherman (1980), Palmer and Brandt (1981), Eskin and Palmer (1982), Palmer (1984, 1986), Palmer and Gust (1985), Palmer and Malloy (1986), Coull et al. (1989)
Disturbance	Sherman and Coull (1980), Billheimer and Coull (1988)
Distribution/ Abundance	Bell et al. (1978), Coull et al (1979), Ivester (1980), Findlay (1981, 1982), Osenga and Coull (1983), Montagna (1982), Montagna et al. (1983), Eskin and Coull (1984), Eskin and Coull (1987), Coull and Feller (1988), Steward et al. (1992), Schizas et al. (1999)
Encystment (copepod)	Coull and Grant (1981)
Feeding By	Levy and Coull (1977), Montagna (1983, 1984a,b), Feller (1984a, b), Couch (1989), Feller et al. (1990)
Feeding On	Bell and Coull (1978), Smith and Coull (1987), Marinelli and Coull (1987), Palmer (1988), Nelson and Coull (1989), Ellis and Coull (1989), Coull (1990), Scholz et al. (1991), Feller and Coull (1995), Marshall and Coull (1996), DiPinto and Coull (1997),
Genetics	Staton et al. (2001, 2002, 2005)
Interactions	Ivester and Coull (1977), Bell (1980), Bell and Coull (1980), Creed and Coull (1984), Zobrist and Coull (1992, 1994)
Metabolism/ Physiology/ Energetics	Coull and Vernberg (1970), Vernberg and Coull (1974, 1975, 1981), Sellner (1976), Vernberg et al. (1977), Fleeger and Palmer (1982), Feller and Warwick (1988), Morris and Coull (1992)
Minor Taxa	Gastrotrichs: Hogue (1978); Kinorhynchs: Horn (1979), Higgins and Fleeger (1980); Platyhelminth flatworms: (Ax, 1995)
Models	Bell and Coull (1980), Coull (1986)
Pollution/ Toxicology	Coull et al. (1981), Strawbridge et al. (1992), Green et al. (1993), Green and Chandler (1994), Chandler et al. (1994, 1997a, b), Schizas et al. (2001, 2002), Staton et al. (2002), Klosterhaus et al. (2003)
Taxonomy	Coull (1975, 1976, 1977)

for an accurate census of the community whenever or wherever they are sampled. It is likely that nearly every juvenile form of the diverse array of estuarine fauna, both vertebrate and invertebrate, with a portion of their life cycle spent in contact with the sediment ingests meiofauna. Noted predators of meiofauna include epibenthic fauna such as bottom-feeding fishes, shrimps, and crabs. As for the macrobenthos, seasonal changes in abundance of meiobenthos cannot be explained by predation alone. Tidal current-aided dispersion of meiofaunal taxa is rapid and widespread. Meiofauna also play a prominent role in breaking down detrital products of intertidal plant growth so that these materials become available to members of the detritus-based food web in salt marsh and estuarine ecosystems. Because meiofaunal organisms reproduce so rapidly and have such short life cycles, they have been used as model organisms to document the population-level effects of several different types of pollutants, especially pesticides and herbicides, commonly used in farming in the southeastern U.S.

Benthic core sampling technique.

Researchers sample meiofauna on Debidue Creek Shoal.

» Zooplankton

Multicellular organisms collectively known as the zooplankton comprise a diverse, dynamic, and abundant component of the estuarine fauna. Most of the hundreds of zooplankton types that occur in the North Inlet waterways are microscopic, less than 5 mm in overall length. Zooplankton play important roles in aquatic food webs as they consume microscopic algae (phytoplankton), microbes, and organic material and, in turn, are eaten by larger animals.

Zooplanktonic taxa for which all developmental and adult stages occur as planktonic forms are known as holoplankton. Those with only some stages that have a planktonic existence are known as meroplankton. The majority of large invertebrates and fishes that live in North Inlet produce larvae that are planktonic for days to weeks before changing into a more recognizable juvenile form. Because the shape, size, color, and behavior of a larva changes quickly and often radically during their time in the plankton, and because many related species look very similar, their visual identification is difficult. Even the larval forms of some our most common shellfishes and worms cannot be easily identified in zooplankton samples.

A more complete introduction and description of the zooplankton of the Atlantic and Gulf of Mexico coasts, including detailed illustrations and ecological information to facilitate identifications, can be found in Johnson and Allen (2012).

Zooplankton sampling in North Inlet with a surface net (top) and an epibenthic sled (lower).

HISTORY OF ZOOPLANKTON RESEARCH IN THE NORTH INLET AREA

The earliest published study of local zooplankton was by Lonsdale and Coull (1977) who used 153-micron nets to characterize the composition and seasonality of the copepod size fraction of the zooplankton at several stations in North Inlet from January 1974 to August 1975. Other early studies were on the vertical distribution of fiddler crab larvae (DeCoursey,1977), physiology of fiddler crab larvae (Vernberg, W. and Jorgensen, 1977) and energetics of various North Inlet zooplankters (Vernberg, W., 1977). Numerous other field and laboratory studies that focused on larval crustaceans and fishes were published as theses, dissertations, or as articles in the primary literature. Christy and Stancyk (1982) studied the flux of invertebrate larvae between the estuary and coastal ocean with significant imports of six of 20 taxa and a significant export of fiddler crab larvae due to the timing of larval release during spring tides. Tidal, lunar, and seasonal fluxes of small mesozooplankton were determined in the Outwelling Study in the early 1980's (Dame et al.,

1986). Moore and Reis (1983) examined the spatial and temporal patterns of some large zooplankters. Tidal and diel (Johnson et al., 1990) and seasonal patterns (Allen et al., 1995) were described for both small and large mesozooplankton and their zooplanktivorous predators. Houser and Allen (1996) analyzed tidal and diurnal patterns of a full range of zooplankton in an intertidal creek basin. Interannual patterns of small (0.2-1.5 mm, caught in 153 micron mesh net) and large mesozooplankton (1.6-15 mm, caught in a 365 micron net) were interpreted by Allen et al. (1996). Long-term changes and responses of this size fraction to climate change from 1981-2003 were discussed in Allen et al. (2008). The most comprehensive set of data for both size fractions is in the long-term time series study which began in January 1981 and continues still. More than thirty years of biweekly collections from Town Creek probably represents the longest time series for these two size fractions of zooplankton in any ocean-dominated estuary. Results from this study, combined with information from other local studies, have been used to form the descriptions of the composition and dynamics of the assemblages below.

MAJOR TAXONOMIC GROUPS

Table 7 lists the small animals that were sampled by the 153-micron nets, and Table 8 identifies the larger taxa collected in the 365-micron epibenthic sled tows. Between the two net types, more than 50 taxonomic categories representing more than 200 species of invertebrates and fishes have been enumerated in the mesozooplankton samples. Mean densities, periods of seasonal occurrences, peak periods of abundance, and numerically dominant taxa are provided for all categories. Partial processing of collections made after 2010 indicates that there have not been many changes in the composition and relative abundances of major contributors to the two assemblages, so the information in these tables is still very relevant in 2014.

• Small Mesozooplankton: 153-µm mesh

Copepods are small crustaceans (generally 0.5 – 2 mm length) that account for most of the organisms in 153-micron mesh collections. They are permanent members of the zooplankton (holoplankton), and they often occur in densities of thousands per cubic meter, especially in the summer season. The highest density of total copepods collected in North Inlet was greater than 119,000 individuals m^{-3} in June 1981. At least 10 copepod species regularly occur in the water column in North Inlet, with the calanoid copepod, *Acartia tonsa* (Figure 76), being especially abundant all year. From May through September, *A. tonsa* comprises about 50% (on average) of all copepod numbers. *Parvocalanus crassirostris*, *Pseudodiaptomus pelagicus*, *Oithona* spp., and *Euterpina acutifrons* are also found year-round. *Temora turbinata* is a fall-occurring species, while both *Centropages hamatus* and *Eurytemora affinis* are primarily present in winter and spring. All copepod occurrences and peak abundances are shown in Table 7.

Most copepods reproduce sexually with females either shedding or carrying eggs that hatch into the early developmental stage, the nauplius (plural = nauplii). These minute planktonic forms have five stages of development and usually give rise to five copepodid (juvenile or pre-adult) stages, the last of which closely resembles the adult. The sixth copepodite is the adult stage. Due to high fecundity and mortality rates, the naupliar and copepodid stages always outnumber the adults. Because it is difficult to identify nauplii or copepodid stages to species, they are often counted together in mixed species categories (Table 7). Copepods feed by harvesting small suspended particles, both living (as phytoplankton and microzooplankton) and dead (organic aggregates). In turn, copepods are major sources of food for larger zooplankton (e.g., larval shrimps, chaetognaths, jellyfishes) and fishes (e.g., larval fishes, adult anchovies, herrings, and silversides).

Barnacle nauplii are among the most common of the local zooplankton types. These early developmental stages originate from the adults of several species of barnacles that grow on oyster

Table 7. Composition of small mesozooplankton in North Inlet, SC, 1981-2003 collected in 153-µm mesh nets. Taxonomic category name (A = Adult, C = Copepodid life stage), primary annual period of occurrence (POC), average density for the POC based on biweekly 1981-1992, quarterly 1993-2003 samples, maximum density during the study (same data as previous), months of peak abundance, and the primary taxa comprising the counting category.

Taxon or Category	POC	Mean (No./m³)	Max (No./m³)	Peak Month	Primary Taxa
hydromedusae	Jan 1 - Dec 31	37.6	448.8	May - Oct	mostly *Clytia*, *Bougainvillia*, *Nemopsis* spp.
gastropod veligers	Mar 1 - Sep 30	281.6	2,042.4	Mar - Sep	*Nassarius* spp., *Boonea* spp., *Melampus pominate*
bivalve larvae	Jan 1 - Dec 31	199.9	6,146.1	Jun - Sep	*Mercenaria* spp., *Crassostrea* spp. dominate in summer
polychaete larvae	Jan 1 - Dec 31	479.5	12,044.5	May - Dec	dozens of contributors; see macrobenthos list
cladocerans	Jan 1 - Dec 31	14.8	432.6	May, Oct - Nov	unidentified taxa
ostracods	Jan 1 - Oct 31	4.5	72.0	Mar - May	unidentified taxa
total copepods (A & C)	Jan 1 - Dec 31	9,086.8	119,404.4	May - Sep	All copepod taxa below plus unidentified Adults and Copepodids
Acartia tonsa (A)	Jan 1 - Dec 31	1,104.7	24,560.8	May - Sep	
(C)	Jan 1 - Dec 31	3,128.4	48,616.0	Apr - Sep	
Centropages hamatus (A)	Dec 1 - May 15	55.0	642.8	Dec - May	
(C)	Nov 1 - Apr 30	361.8	4,966.6	Dec - Apr	
Eurytemora affinis (A)	Jan 1 - May 31	11.8	918.5	Feb - Apr	
(C)	Jan 1 - May 31	61.4	3,074.9	Feb - May	
Labidocera aestiva (A)	May 16 - Sep 30	5.4	376.6	June	
(C)	Apr 1 - Nov 30	102.2	1,412.1	May - Nov	
Parvocalanus crassirostris (A)	Jan 1 - Dec 31	1,981.3	30,428.9	May - Oct	
Paracalanus spp. (A)	Jan 16 - Dec 31	7.7	232.9	Apr - May, Oct - Nov	
(C)	Jan 16 - Dec 31	42.0	1,516.5	Apr, Jul	
Temora turbinata (A)	Jun 16 - Nov 15	17.9	419.8	Jun, Oct	
(C)	Jly 1 - Dec	80.6	1,278.4	Oct - Nov	
Pseudodiaptomus pelagicus (A)	Apr 1 - Nov 15	97.2	2,226.6	Apr - Sep	Originally named:
(C)	Apr 1 - Sep 30	1,443.6	11,540.1	May - Aug	*P. cornatus*

Table 7 continued.

Taxon or Category	POC	Mean (No./m³)	Max (No./m³)	Peak Month	Primary Taxa
unidentified calanoid copepods (A & C)	Jan 1 - Nov 15	299.3	8,670.2	Feb, Jun	*Temora* spp., *Tortanus* spp. Primarily copepodid life stages
Euterpina acutifrons (A)	Apr 16 - Dec 15	339.4	3,065.7	May - Nov	
unidentified harpacticoid copepods (A)	Feb 1 - Nov 15	66.5	1,888.8	Apr - Jun	*Coullana* spp.
Oithona spp. (A)	Jan 1 - Dec 31	933.3	8,951.7	Apr, Dec	*Oithona colcarva* and other species
unidentified cyclopoid copepods (A)	Jan 1 - Dec 31	77.1	1,880.2	Apr, Jul, Sep	*Corycaeus* spp., *Saphirella* spp., *Oncaea venusta*
unidentified copepod nauplii	Jan 1 - Dec 31	1,014.8	16,741.6	May – Sep Nov - Feb	
barnacle nauplii	Apr 16 - Sep 30	5,327.9	44,113.8	May - Aug	
cyprids	Apr 16 - Aug 31	172.3	4,114.4	May - Jun	*Balanus eburneus, Chthamalus fragilis*
crab zoeae	Apr 16 - Oct 15	1,208.4	9,058.2	May - Sep	*Uca* spp., *Panopeus* spp., *Callinectes* spp.,& many others
bryozoan (cyphonautes) larvae	Jan 1 - Dec 31	56.6	1,049.2	May - Jul	Unidentified bryozoan taxa
bipinnaria/brachiolaria larvae	Jun 16 - Sep 15	7.5	188.3	Jun	*Luidia* spp., *Astropecten* spp., *Astarias* spp.
salps & doliolids larvae	Jun 16 - Nov 30	2.2	46.2	Sep	Unidentified salp taxa
Ophio- and echino-pluteii larvae	May 1 - Nov 15	107.6	1,858.2	Jun, Aug - Oct	*Ophiothrix* spp., *Microphiopholis* spp., *Arabacia mellita* & other brittlestars & urchins
ascidian “tadpole” larvae	Jun 1 - Nov 15	5.1	149.9	Jul	*Mogula* spp., *Stylla* spp., & other tunicates
larvacean (appendicularian) larvae	Apr 16 - Nov 15	304.3	2,655.6	Jun, Sep	*Oikopleura* spp.
other mesozooplankton	May 1 - Dec 15	150.7	1,165.2	May - Sep	Larval fish, amphipods, shrimp larvae, mysids, chaetognaths
total small mesoplankton	Jan 1 - Dec 31	15,069.1	143,383.9	May - Sep	all taxa above

reefs and other hard surfaces in the estuary. Pairs of horns on the heads of barnacle nauplii (Figure 76) distinguish them from the otherwise similar-looking copepod nauplii. Later stages can be very abundant especially from May through August. The last naupliar stage transforms into a small clam-like larva known as the cyprid (Figure 76). The cyprid attaches to a suitable hard surface and metamorphoses, becoming a more familiar looking barnacle.

From spring through fall, crab zoeae occur in almost all zooplankton collections, sometimes numbering in the thousands per cubic meter from pulsed releases during spring ebbing tides. This timing facilitates their transport to the coastal ocean for further growth and development. These larvae have unusually large heads with helmets that are usually spiked (Figure 76). Zoeae hatch from eggs carried by female crabs representing more than 15 local species. In most summer collections, fiddler crab (*Uca* spp.) zoeae are by far the most abundant, but zoeae from several species of mud crabs (e.g. *Panopeus herbstii*) and swimming crabs (e.g. *Callinectes sapidus*) also occur. After hatching, early stage fiddler crab zoeae pass through several advanced zoeal stages before transformation to the megalopa stage (Figure 77). Megalopae move with flooding tides into the marsh creeks and become small crabs in the adult habitat.

Due to different spawning times for polychaete worms (there are dozens of species), polychaete larvae are found throughout the year. Unlike crustacean larvae that grow in stages by shedding their old exoskeletons, polychaete larvae add segments and bristles and begin to resemble small adults before leaving the plankton and settling on to benthic habitats (Figure 76).

Uca pugilator. Crab zoeae occur in almost all zooplankton collections in North Inlet, sometimes numbering in the thousands per cubic meter.

Lots of other familiar estuarine invertebrates produce large numbers of zooplanktonic larvae. Bivalves (including clams and oysters) and gastropods (snails) start out as round ciliated forms known as veligers (Figure 76) that eventually develop thin shells as they settle to the bottom. Bryozoan larvae called cyphonautes are less common but uniquely triangular-shaped members of the zooplankton. Bipinnaria and brachiolaria larvae of seastars, ophiopluteii larvae of brittlestars, and echinopluteii larvae of sea urchins and sand dollars are found during the warmest period of the year. Ascidian "tadpole" larvae of tunicates are also found in summer.

Cladocerans (Figure 76), related to the common freshwater *Daphnia* spp., are ocean-based crustaceans that sometimes occur in the estuary during summer. The larvae of other ocean-dwelling forms including salps, doliolids, and larvaceans (appendicularians) can sometimes occur at densities exceeding 1000 per cubic meter (Costello and Stancyk, 1983). Another clam-like swimming crustacean that appears in the zooplankton is the ostracod. These small adult forms live on or in the bottom but are sometimes re-suspended and/or swim into the water column, but they are never very abundant. However, other small, bottom-dwelling meiobenthic ostracods are quite abundant in the sediment.

Hydromedusae (Figure 76) are very small jellyfishes. Most originate from soft bodied, branched colonies of animals that grow on hard surfaces. Like larger, more familiar jellyfishes, hydromedusae use tentacles to collect food. If in large enough numbers, they can have a substantial impact by grazing on copepod populations and other small planktonic types. Hydromedusae are found in both sizes of collection nets, but with an order of magnitude greater abundance in 153-µm mesh samples.

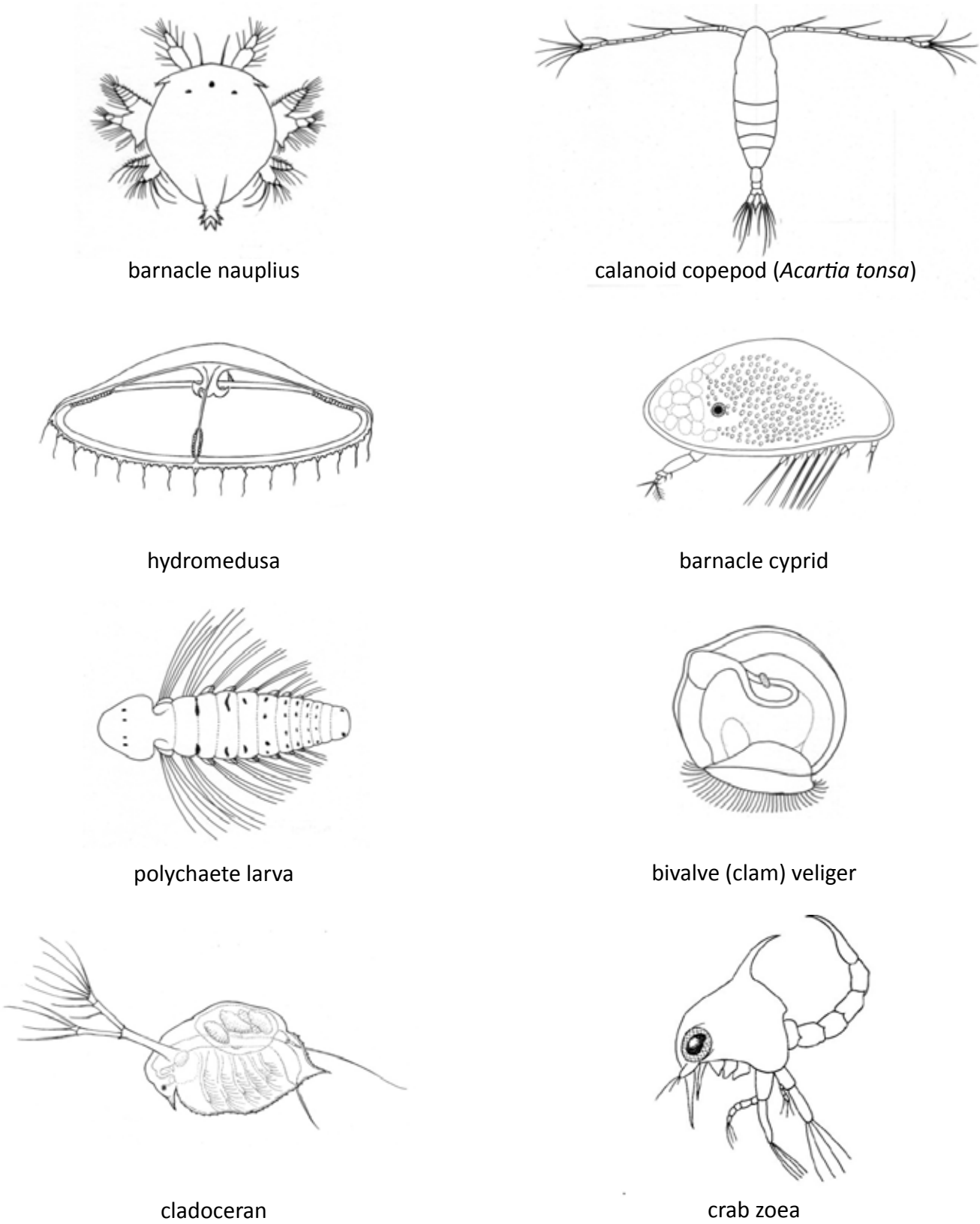


Figure 76. Common small mesozooplankton taxa found in North Inlet : *Acartia tonsa* adult, crab zoea, barnacle nauplius, hydromedusa, cladoceran, polychaete larva, bivalve veliger and barnacle cyprid (illustrations by Marni Fylling; from Johnson and Allen, 2012, with permission). All are typically less than 2 mm in length except hydromedusae which range from about 2 mm to more than15 mm in diameter.

- **Large Mesozooplankton: 365-µm mesh**

The large size fraction of the mesozooplankton represents a diverse assemblage of invertebrates and larval fishes, some of which are permanent and others only temporary members. Animals comprising this assemblage are collected by both the 153 and 365 micron meshes; however, most of the animals listed as large zooplankton are not enumerated in the 153 micron samples. Larger, faster swimming zooplankton can sense the pressure wave of the small mesh net and avoid being captured by small mesh nets. Animals listed as small zooplankton are generally not well retained by the 365 micron mesh and are not enumerated in these collections. Accordingly, quantitative data for each taxonomic category comes from only one of the mesh sizes with the exception of the hydromedusae which span a wide range of sizes.

The constituents counted in the 365-micron epibenthic sled collections in North Inlet are characterized in Table 8 (Allen et al., 2008). These summary data are based on the first 22 years of biweekly collections, ending in 2003. Since then, only samples taken on certain quarterly dates have been processed; however, no major changes have been observed in the composition or relative abundances of these taxa, so the following information is applicable through 2014.

Chaetognaths (arrow worms) are among the largest of the holoplanktonic forms (Figure 77). These very abundant coastal ocean species occur in the high salinity creeks of North Inlet where they consume smaller zooplankton including copepods and larval fishes.

Larval shrimps are among the more conspicuous members of the large mesozooplankton. Grass shrimp (*Palaemonetes* spp.) larvae (Figure 77) are typically the most abundant from spring through fall, but snapping shrimp (*Alpheus* spp.), mud shrimp (*Upogebia affinis*), and penaeid shrimp (*Litopenaeus setiferus*, *Farfantepenaeus aztecus*, *Farfantepenaeus duorarum*, *Rimapenaeus constrictus*) larvae are also present during the warmest months (Table 8). Larvae of several species of ghost or callianassid shrimps occur in the estuary. Each shrimp species passes through a series of larval stages before transforming into a postlarva which precedes settlement into the adult habitat on the bottom. The adults of some shrimps are very small (typically < 20 mm) and can only be collected with plankton nets. *Lucifer faxoni* is a thin, unusual-looking shrimp of oceanic origin that swims high in the water column. The related sergestid shrimp, *Acetes americanus carolinae*, is slightly larger and more oriented to the lower or deeper levels of the water column. *Urocaris longicaudata* (formerly *Periclimenes longicaudatus*), *Latreutes*, and several other small adult shrimps found in North Inlet are closely associated with the bottom.

The late larval stages of crabs, known as megalopae, are also common constituents of the large mesozooplankton. Fiddler crab (*Uca* spp.) far outnumber all others in North Inlet, but xanthid (mud), portunid (swimming), and hermit crabs are also present during the warmest period of the year. Large porcellanid crab zoeae (including *Petrolisthes armatus*) are counted among the 365 micron-caught crab larvae. Less common mantis (stomatopod) shrimp larvae are also included in the 365 micron sample counts.

A common group of small crustaceans that brood their young are collectively known as the peracaridians. Mysid shrimps, also known as opossum shrimps (Figure 77), generally resemble some of the small adults of the true (decapod) shrimps, but incubate their young in ventral pouches. *Neomysis americana* is the most abundant mysid shrimp during the cold season when decapod shrimps are uncommon. Mysids sometimes move together in large schools or shoals, and densities of many hundreds per cubic meter are common in these aggregations. During summer, at least six other species become more numerous in collections made close to the bottom (Heard et al., 2006). Two distinct groups of amphipods, the gammarids (Figure 77) and caprellids, are year-round residents that live mostly near the bottom, especially on structure such as soft corals, sponges, and bryozoans. Cumaceans and isopods also occur near the bottom, but many species of all of these groups move into the water column to mate and feed.

Table 8. Composition of large mesozooplankton in North Inlet, SC, 1981-2003 collected in the 365 µm mesh sled net. Taxonomic category name, primary annual period of occurrence (POC), mean density for the POC based on biweekly 1981-2003 collections, maximum density during the study (based on same data as previous), months of peak occurrence, and primary taxa and/or life stages comprising the counting category (Allen et al., 2008).

Taxon or Category	POC	Mean (No./m³)	Max (No./m³)	Peak Month	Primary Taxa
chaetognaths	Jan 1 – Dec 31	8.02	167.44	Jun - Aug	mostly *Sagitta hispida*, *S. tenuis*
hydromedusae	Jan 1 – Dec 31	1.36	49.43	May - Jul	mostly *Clytia*, *Bougainvillia*, *Nemopsis*
mysids	Jan 1 – Dec 31	8.84	986.74	Jan - Jun	mostly *Neomysis americana* juveniles and adults
gammarid amphipods	Jan 1 – Dec 31	3.63	131.83	May - Aug	*Gammarus*, *Ampelisca*, *Cerapus* juveniles and adults
caprellid amphipods	Jan 1 – Dec 31	0.95	20.86	Feb - Aug	*Caprella* juveniles and adults
cumaceans	Jan 1 – Dec 31	0.46	37.29	Mar - May	*Diastylis*, *Oxyurostylis*, *Leucon* juveniles and adults
isopods	Jan 1 – Dec 31	0.11	3.94	May - Jly	*Edotia*, *Livoneca* juveniles and adults
others	Jan 1 – Dec 31	0.60	20.55	May - Sep	polychaete larvae, porcellanid crab zoeae, pagurid crab megalopae, pychnogonids, leeches, nudibranchs
adult shrimps	Jan 1 – Dec 31	0.56	16.18	May - Aug	*Palaemonetes*, *Hippolyte*, *Neopontonides*, *Rimapenaeus* and other adult shrimps, except the four taxa listed below
Urocaris	Jan 1 – Dec 31	0.44	10.29	Sep - Oct	*U. longicaudata*
Acetes	May 16 – Nov 15	1.90	206.70	Jly - Aug	*A. americanus* juveniles and adults
Lucifer	Apr 16 – Dec 15	0.58	9.77	Jun - Oct	*L. faxoni* juveniles and adults
Latreutes	Apr 1 – Sept 30	0.12	4.05	May - Aug	*L. parvulus* juveniles and adults

Table 8 continued.

Taxon or Category	POC	Mean (No./m³)	Max (No./m³)	Peak Month	Primary Taxa
total shrimp larvae	Jan 1 – Dec 31	3.97	65.64	Apr - Oct	All shrimp larvae, including the taxa below
Palaemonetes	Apr 1 – Nov 30	3.30	29.77	May – Sep	*P. pugio* and *P. vulgaris*
Alpheus	Apr 16 – Nov 15	1.72	31.41	May – Sep	mostly *A. heterochaelis*
callianassids	Apr 16 – Oct 31	0.29	8.49	May – Sep	*Callichirus*, *Biffarius*, *Gilvossius*
Upogebia	Apr 1 – Nov 15	0.34	7.33	May– Sep	*U. affinis*
penaeid shrimps	Jan 16 – Oct 31	0.28	4.82	Mar - Sep	*Farfantepenaeus aztecus*, mostly *Litopenaeus setiferus*, some *F. duorarum*
total fish larvae	Jan 1 – Dec 31	6.20	214.34	Feb - Sep	All fish larvae, including the taxa below
Gobiosoma	Apr 16 – Sept 30	11.49	206.48	May – Sep	mostly *G. bosc*
Anchoa	Apr 16 – Sept 15	0.59	9.33	May –Jul	*A. mitchilli* and *A. hepsetus*
Leiostomus	Dec 1 – May 15	0.49	12.27	Jan – Apr	*L. xanthurus*
Lagodon	Dec 1 – May 15	0.22	6.94	Jan - Mar	*L. rhomboides*
pinnotherid crab	May 16 – Oct 31	1.59	39.93	Jun – Aug	mostly *Zaops* (Pinnotheres) ostreum first crab
crab megalopae & juvenile	Feb 1 – Nov 30	3.83	145.74	May – Sep	mostly *Uca pugnax* and *U. pugilator,* some *Callinectes* and xanthids
stomatopod larvae	May 16 – Sep 30	0.08	1.45	Jun – Aug	*Squilla empusa*
fish eggs	Apr 1 – Oct 31	0.63	10.82	Apr - Jun	mostly *Anchoa*
total large mesoplankton	Jan 1 – Dec 31	40.84	1054.36	May - Sep	all taxa above

Hydromedusae are collected in both the 153 and 365 micron collections. Because there is such a wide range in size among hydromedusae only large individuals are counted in the 365 micron collections.

Larval fishes can be very abundant in summer samples (Table 8). More than 45 species have been identified in North Inlet zooplankton collections. During summer, diversity is highest with goby (*Gobiosoma* spp.) (Figure 76) and anchovy (*Anchoa* spp.) dominating most larval fish collections. During the coldest part of the year, larval spot (*Leiostomus*) (Figure 76), pinfish (*Lagodon*), southern/summer flounder, Atlantic menhaden, speckled worm eel, and American eel larvae dominate.

Dozens of wormlike animals such as oligochaetes and nematodes that usually live on the bottom can be found in both small- and large-mesh mesoplankton collections. Sediment-dwelling copepods can also become resuspended and are captured by nets. Free swimming leeches, crawling sea spiders (pycnogonids), mites, branchiurans (fish lice), and sea slugs (nudibranchs and pteropods) are among the many unusual small invertebrates that are occasionally collected.

SPATIAL PATTERNS

Comparisons of small mesozooplankton (153-µm mesh) densities at four locations within the North Inlet system were conducted by Lonsdale and Coull (1977). They showed, based on 20-month means, that total zooplankton and most taxa densities were highest in the mouth of the inlet and at the Town Creek/Old Man Creek confluence. Densities near the middle of Bly Creek were somewhat lower, and they were lowest in the southern end of South Jones Creek. Allen et al. (1982) found that densities and the diversity of small and large zooplankton in South Jones and No Man's Friend Creeks were more similar to those in North Inlet and lower Winyah Bay than to the upper portion of Winyah Bay during most of the year. In a study of larval fishes in North Inlet, Allen and Barker (1990) found very similar seasonal and interannual patterns between two sampling sites (near the inlet mouth and at the confluence of Town Creek/Clambank Creek). Moore and Reis (1983) did not observe significant differences in large zooplankton collected from a bank-to-bank transect across Town Creek. Occasional collections outside of the inlet have shown higher densities of chaetognaths, cladocerans, sergestid shrimps, and intermediate developmental stages of estuarine shrimps and crabs than those within the estuary. Especially high densities of larval decapods, fishes, and mysids have been found in summertime collections in the surf zone within hundreds of meters of the beach.

TIDAL AND DIEL PATTERNS

Several short-term studies at the long-term site in Town Creek indicate that although the composition of the small and large zooplankton assemblages does not change much between tidal stages, the highest densities of most taxa occur near high tide and lowest densities occur near low tide. Time-of-day also affects densities of many taxa; densities of the larger, more motile forms tend to be higher at night than in daytime, probably because of a lower ability to detect and avoid nets than during the day. Vertical stratification of zooplankton is not commonly observed in the shallow creeks, especially with the small mesozooplankton. However, in a summertime 48-hr study in Town Creek, surface – bottom comparisons of large zooplankton revealed several taxa that vertically segregate; hydromedusae, *Upogebia* larvae, and fish eggs were more abundant in surface collections, whereas callianassid shrimp larvae and crab megalopae preferred the bottom. Some small zooplankton, including *Acartia tonsa*, showed a tendency to remain near the bottom during the day and dispersed throughout the water column at night.

SEASONAL PATTERNS

The abundances of both small (Figure 78) and large (Figure 79) zooplankton indicated similar patterns with minimum densities during the coldest months, sharp increases in spring, high but irregular patterns in summer, and sharp drops in the fall. Water temperature and day-length are often mentioned as the primary determining factors for seasonal fluctuations in abundance and composition of zooplankton.

Seasonal changes in the composition of each of the two size fractions of North Inlet zooplankton follow a regular pattern with the highest diversity occurring during the warmest period. In the small mesozooplankton assemblage, copepods dominated during every season, comprising 64-73% of the average catch. Figure 80 shows the proportions of the non-copepod categories each season, and barnacles were by far the most abundant taxon all four seasons. Polychaete larvae, larvaceans, bivalve veligers, and gastropod veligers accounted for smaller proportions year round, and crab zoeae accounted for less than 10% in spring and summer. The periods of occurrence for all small taxa are found in Table 7. In 2012, the general patterns of seasonal occurrence for dominant taxa shown in

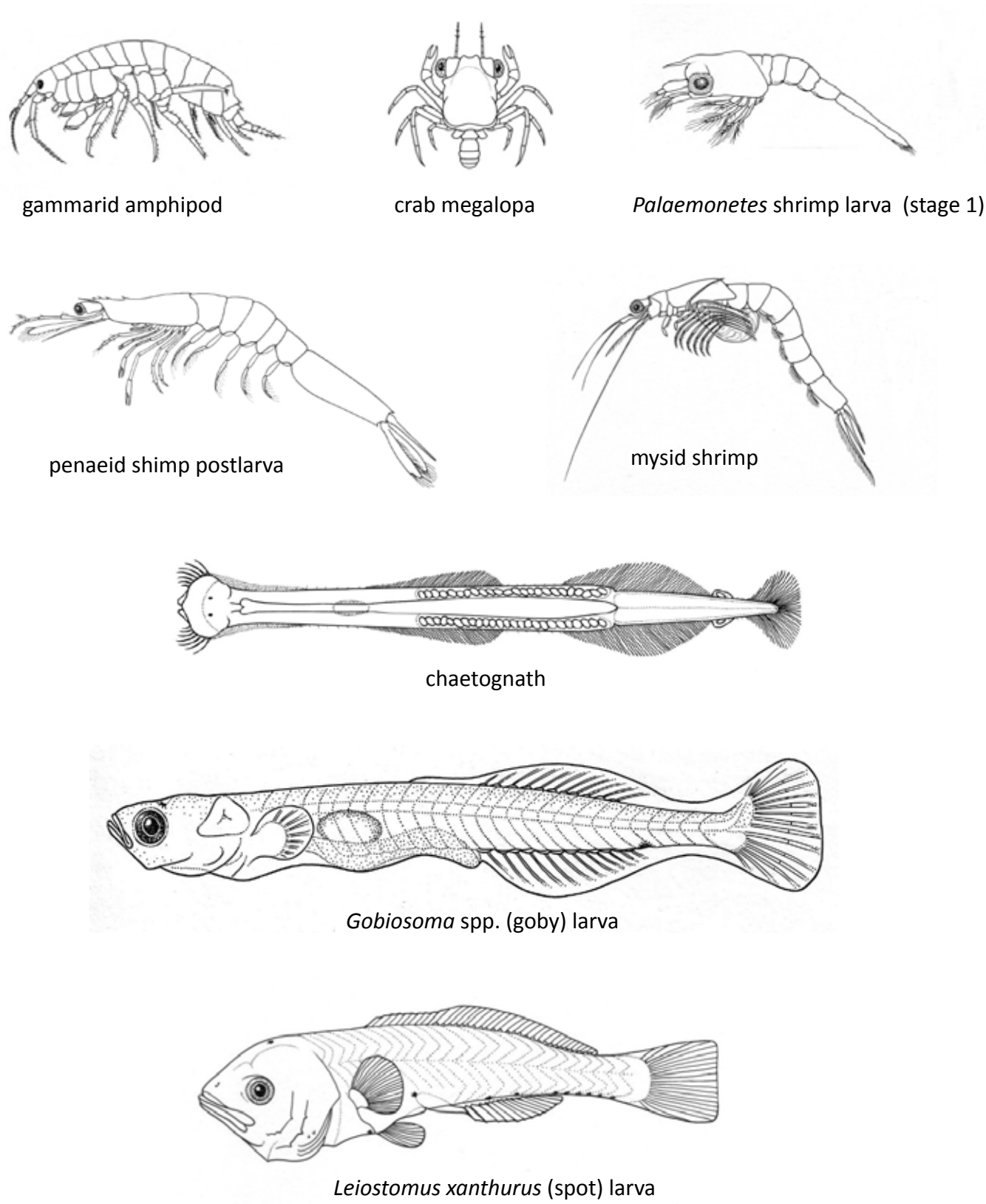


Figure 77. Common large mesozooplankton taxa found in North Inlet: mysid, *Palaemonetes* spp. shrimp larva, penaeid shrimp postlarva, crab megalopae, chaetognath, goby larva, *Leiostomus xanthurus* larva, gammarid amphipod. (illustrations by Marni Fylling; from Johnson and Allen, 2012, with permission). These animals may reach sizes of up to almost 10 mm length.

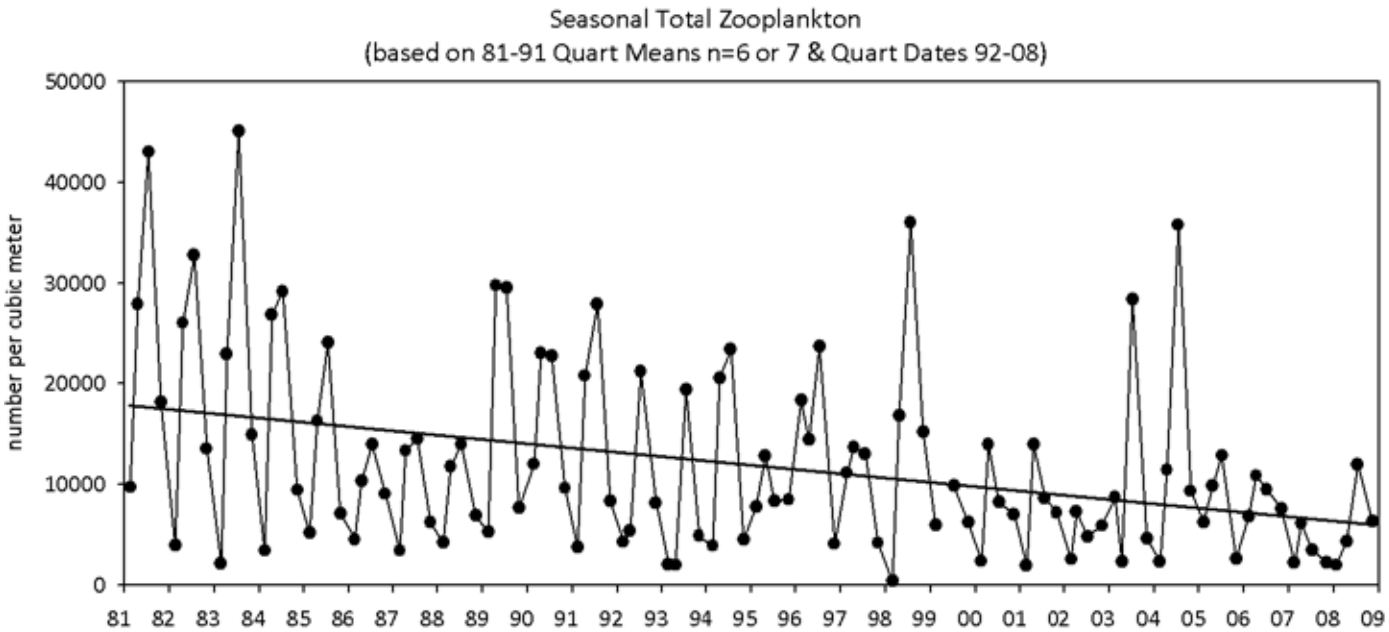


Figure 78. Abundance of total small mesozooplankton in North Inlet. Quarterly mean densities are shown for January 1981 – January 1992 and quarterly values from April 1992 – December 2008. A quarterly trend line, determined with linear regression analysis, showed a significant long-term decrease in abundance.

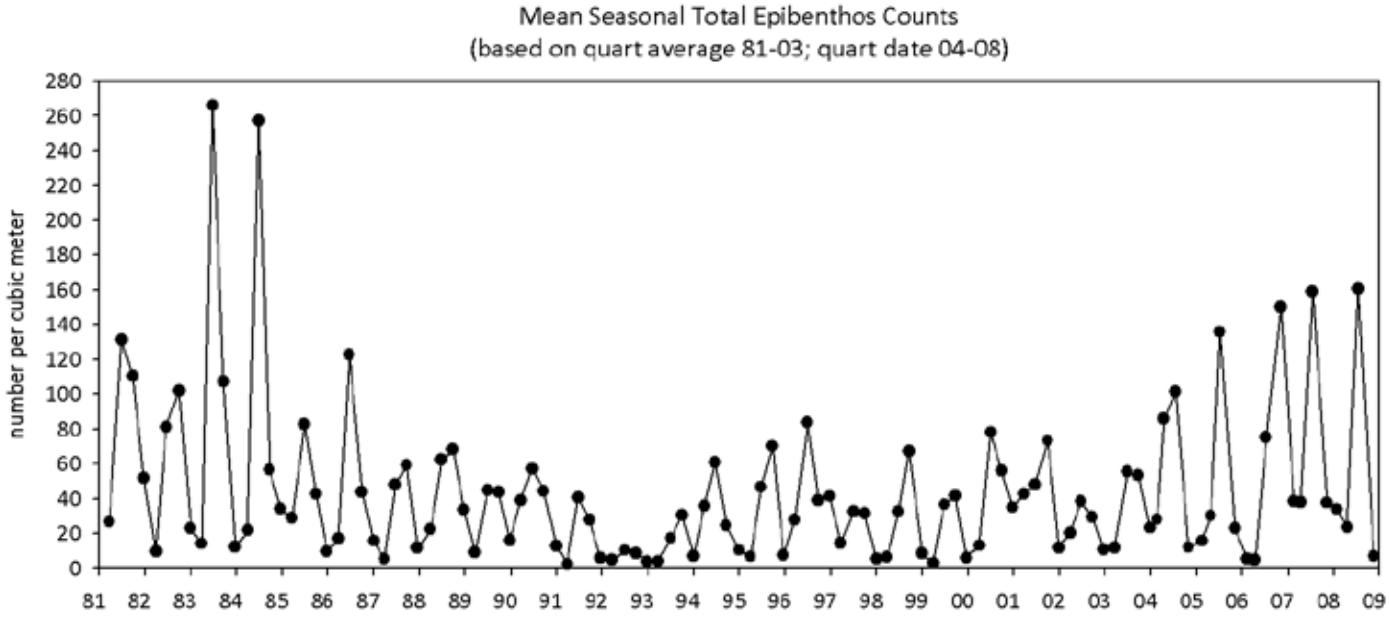


Figure 79. Abundance of total large mesozooplankton in North Inlet. Mean densities are shown from January 1981 - December 2008 (based on quarterly means 1981-2003, quarterly values 2004-2008).

this table were very similar.

The average seasonal proportions of large mesozooplankton taxa from 1981-2003 are shown in Figure 81. Mysids and amphipods were the major groups in the winter and spring, making up ~65% and ~45%, collectively and respectively. Fish larvae and chaetognaths also contributed in spring, when densities of large mesozooplankton were the highest for the year. These two groups, plus adult and larval shrimps and crab megalopae, dominated in summer. Seasonal changes in the composition of larval fishes were large with the highest proportions occurring in the spring and summer. In the fall chaetognaths numerically accounted for over 50% of the total catch.

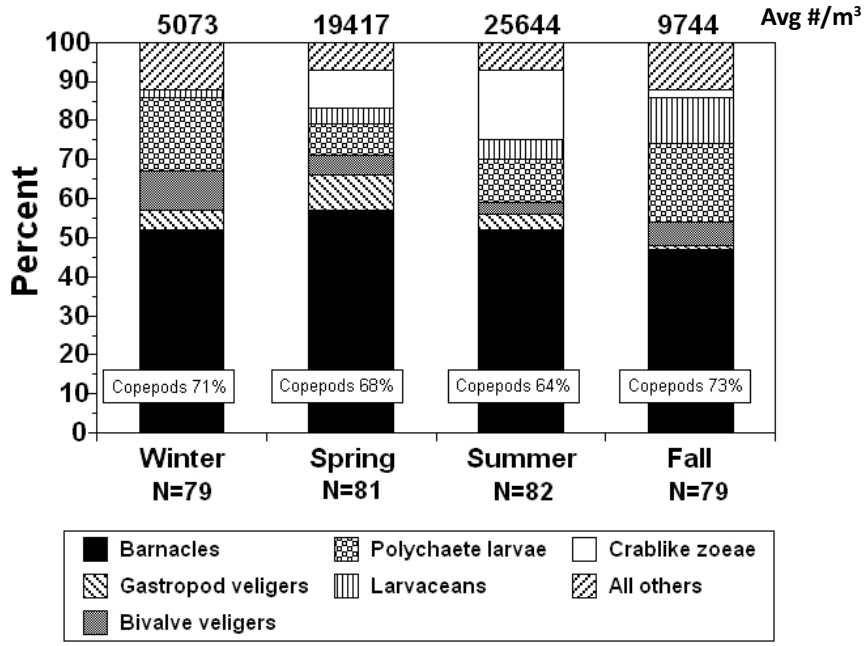


Figure 80. Seasonal composition of small zooplankton in North Inlet. Proportions of the total catch are based on the biweekly and quarterly long-term average density for each season (n = 23 years). Seasonal average numbers (per cubic meter) of total small mesozooplankton from the biweekly and quarterly database are denoted above each seasonal bar; sample size (N) is listed below. Bars represent percent of total catch for each category comprised AFTER removing copepods from the database.

YEAR-TO-YEAR PATTERNS AND LONG-TERM TRENDS

Large variations in zooplankton abundance have been observed between years. Seasonal mean densities from 1981-2008 are shown for the small and large size fractions of the zooplankton in Figure 78 and Figure 79, respectively. Three- to ten-fold differences in mean abundances for the same season are not unusual between consecutive years. Peak summer abundances of the small zooplankton were in excess of 50,000 individuals m^{-3}, and the long-term average for all seasons combined was about 15,000 m^{-3}. Highest abundances of large mesozooplankton were 100-300 m^{-3}, and the overall average was about 41 m^{-3}.

Long-term trend analysis for the small mesozooplankton

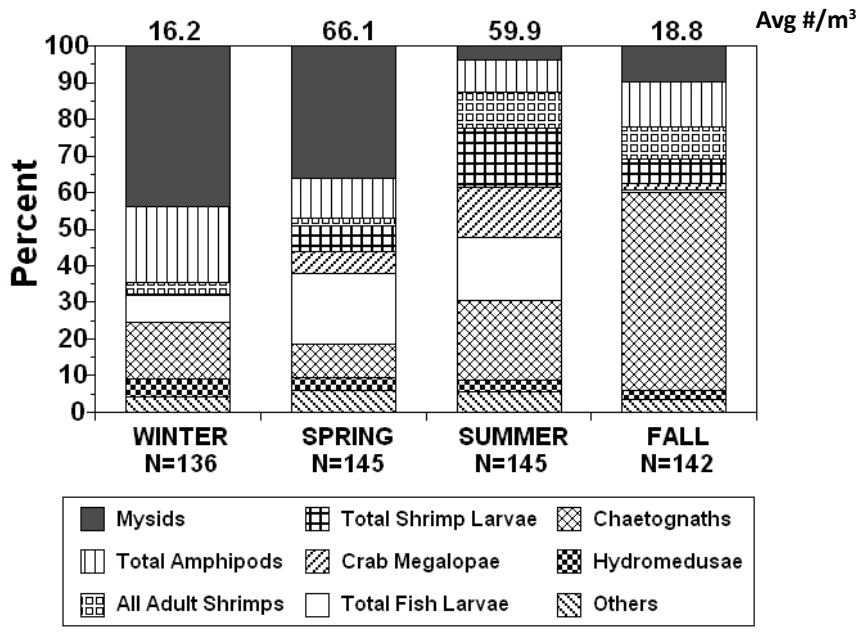


Figure 81. Seasonal composition of large mesozooplankton in North Inlet. Proportions of the total catch are based on the biweekly long-term average density for each season (n = 23 years). The average seasonal total catch is denoted above each bar in numbers per cubic meter; sample size (N) is listed below.

indicated a significant decrease in the densities of total organisms between 1981 and 2008 (Figure 78). No long term-trend was observed for the large mesozooplankton which went from high levels in the 1980s to very low densities in the 1990s, then increased through 2010 (Figure 79). Although abundance varied widely among years, the composition of these assemblages did not change much over the period. Understanding how the many interacting environmental and biological factors influence zooplankton abundances is a difficult challenge.

Salinity is thought to be a major factor influencing the abundance of zooplankton within estuaries. Figure 82 shows the long-term biweekly pattern for salinity at the Town Creek sampling site over the 32-year time series. The long-term mean salinity is 32, not much less than typical ocean salinities of 35. Long-term trend analysis did not show an overall change in salinity. The most depressed salinities in North Inlet almost always occurred in winter and spring and usually coincided with the incursion of brackish water from Winyah Bay into North Inlet during periods of high Pee Dee River discharge and winter rains. High winter rainfall in South Carolina and in North Inlet corresponded well with the occurrences of El Niño climatic events (Allen et al., 2008). Salinity directly affects the zooplankton with lower densities of oceanic forms such as chaetognaths occurring during these periods. The long-term decrease in small zooplankton may be related to a significant long-term decrease in river discharge into Winyah Bay and the associated reduction in nutrients and phytoplankton in this section of the coast. Check for recent publications for updated analyses of trends and factors affecting zooplankton abundances in North Inlet.

Changes in water temperature can be expected to affect zooplankton abundances. Although water temperature and total large zooplankton abundances were not correlated, the overall increase of 1.0 °C and winter increase of 1.7 °C from 1979 - 2011 could be expected to affect the population dynamics of estuarine zooplankton. Other factors including tidal and ocean current patterns, dissolved oxygen, incident light and penetration, food availability, predation pressure, and human activities in the watersheds also affect zooplankton dynamics. We have begun to identify relationships between changes in the local, regional, and global climate change/variability and zooplankton community structure. Continued collections, measurements, and data analyses in the years to come will enable important insights into possible relationships between estuarine zooplankton and climate change.

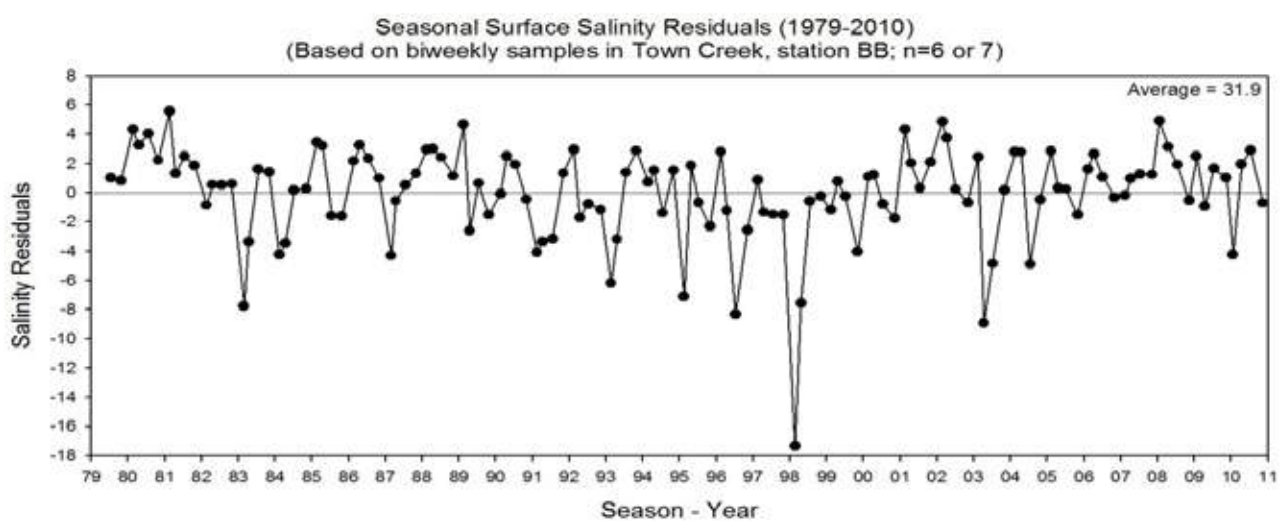


Figure 82. Salinity measured at the surface of Town Creek (near the confluence of Town and Clambank Creeks) at the time of the biweekly zooplankton collections near mid ebb tide, 1981-2011. The extended periods of winter-spring low salinities corresponds well to the occurrence of moderate or strong El Niño (EL) events. Salinity values are represented on the plot as residuals, or deviations from the long-term means for each season.

» Nekton

Fishes, shrimps, crabs, squids, and other macroscopic invertebrates abound in the waters of North Inlet and Winyah Bay. Collectively these motile animals are known as the nekton. Unlike zooplankton (an assemblage of weakly swimming forms or drifters) and benthos (an assemblage of sedentary or slow moving animals that live on or in the sediment), the nektonic organisms are generally capable of directed movements in tidal systems. This diverse and dynamic group includes many species which play key roles in coastal ecosystems and fisheries. More than 180 species of fishes and about 30 shrimps, swimming crabs, and squids have been identified within North Inlet. In this section, the focus is on the patterns of distribution for the 15 or 20 species that account for more than 90% of the individuals collected. More than 95% of all of the fish species known from North Inlet are represented by larval or juvenile life stages, which is why estuaries are often characterized as nurseries.

Because so many fishes are referred to by different common names in different locations, scientists and fishery managers have had to agree on the use of single common names for each species of fish. Throughout this document, we use the common names accepted by the American Fisheries Society. Scientific (Latin) names and additional information about all species known from both estuaries are provided in **Appendix E**.

NEKTON RESEARCH IN THE NORTH INLET AREA

Researchers working in local estuaries over the past 30 years have generated a lot of information about the distribution, life cycles, physiology, and behavior of fishes, shrimps, and crabs. The characterization of the nekton that we present here is based primarily on results from several long-term surveys, but information from other studies was used to provide additional facts and perspectives. The first surveys of fishes in North Inlet were conducted by scientists in the 1960s as part of the Belle W. Baruch Foundation's effort to establish a baseline understanding of the fauna associated with the tidal waters of Hobcaw Barony (Freeman 1970). Since the early 1970s, much of the research on North Inlet fishes has been focused on their distribution and behavior in intertidal creeks. Burns (1974) characterized the larval fish assemblages and Cain and Dean (1976) conducted a comprehensive study on seasonal changes in the abundances of resident and transient fishes in an intertidal creek. Information on the uses of shallow creeks by early life stages of fishes were contributed by Shenker and Dean (1979), Bozeman and Dean (1980), Reis and Dean (1981), and Crabtree and Middaugh (1982).

Moore and Reis (1983) characterized the nekton in the tidally dominated channel inside of the inlet. Ogburn and Allen (1993) studied relationships among shore-zone species adjacent to subtidal channels. Lehnert and Allen (2002) demonstrated the diversity and abundance of fishes using shelly bottoms adjacent to intertidal oyster reefs. Bretsch and Allen (2006) described patterns of tidal migrations of nekton into and out of intertidal creeks. Allen et al. (2007) demonstrated considerable spatial variations in the extent of nekton use among neighboring intertidal creeks and showed that these could be attributed to differences in hydrogeomorphological features of the habitat. Christian and Allen (2014) followed up on that study by developing an ecological network analysis of food web structure using data from the eight creeks; the model indicated differences in food web attributes with wide creeks having greater carbon cycling, higher trophic efficiency, and greater export in the form of nekton than narrow creeks. In another study, Allen et al. (2013) demonstrated that nekton feeding and excreting in intertidal creeks contributed dissolved nutrients to the water, potentially nourishing benthic microalgae that provide food for the small invertebrates that the fish consume while using the creeks. In 2010 and 2012, collaborating visiting scientists used new multibeam sonar technology to study the behavior of fishes moving between subtidal channels and intertidal creeks.

Some researchers have focused on single species. Middaugh (1981) studied the reproductive ecology of the Atlantic silverside. Chestnut (1983) studied the feeding behavior of spot. Potthoff and Allen (2003) demonstrated high site fidelity for young-of-

the-year pinfish. Johnson et al. (1990) showed tidal and diel patterns in the feeding of the bay anchovy on zooplankton, and a companion study showed spatial and seasonal partitioning of the zooplankton prey field by the two species of anchovies and two species of silversides in subtidal channels (Allen et al. 1995). Smith (2012) conducted a one year study of the occurrences of large, trammel-net susceptible nekton in North Inlet creeks. Moore (2012) characterized the distributions of sharks and rays in subtidal creeks, and Maxwell (2008) studied the movements of the young-of-the-year Atlantic sharpnose sharks in the estuary.

With the establishment of the North Inlet Long-Term Ecological Research (LTER) site in 1980, scientists were able to initiate a four-year seine and trawl study to investigate seasonal, interannual, and spatial patterns of nekton occurrence in the lower estuary (Ogburn et al., 1988). In 1984, the nekton research program shifted emphasis to understand the shallow intertidal habitats where diversity and densities are highest. The Oyster Landing nekton study was initiated to document interannual and interdecadal changes in nekton use of an intertidal creek basin and to relate them to changes in environmental conditions. Analyses of data collected from 1984-2011 were used to develop the descriptions of nekton distributions presented below. Another study of fishes conducted in the early 1980s in creeks connecting North Inlet and Winyah Bay added to our understanding of the nursery function of the estuary (Allen et al., 1982). Information about larval fishes has been generated by the long-term zooplankton program (see section on North Inlet zooplankton) and other studies (Beckman and Dean, 1984; Allen and Barker, 1990, Allen et al., 2008; Able, et al., 2011). The NI-WB NERR began supporting the long-term monitoring programs for nekton and zooplankton in 1994, continuing the effort that began with NSF-LTER support in 1981.

This rich history of studies on the nekton of North Inlet forms the basis for the general descriptions that follow.

COMMON FISHES, SHRIMPS, AND CRABS

Of the more than 180 species of fishes and dozens of motile macroinvertebrates known from the area, few are very abundant, widely distributed, and regularly observed. Studies have shown that <10% of the species account for >90% of the individuals. Most species can be classified as either residents or transients of the estuary. Resident species reproduce, grow and die within the estuary. Examples of common residents are mummichog, striped killifish, sheepshead minnow, gobies, blennies, and grass shrimps. Transient nekton species occur only during certain periods of the year. They spawn in the ocean or in rivers and rely on the estuary during at least some stage of their life cycle. Examples of common transients are spot, pinfish, striped mullet, white mullet, brown shrimp, white shrimp, Atlantic menhaden, silver perch, and the mojarras. Many more transient than resident species occur in North Inlet, but most transient species are represented by young of tropical species that appear in low numbers during summer. Some species are difficult to classify as residents or transients. For example, juvenile red drum, black drum, and southern flounder occur year-round for one to several years before leaving the estuary to spawn in other places. Some other fish species, such as sheepshead and bay anchovy, leave only for short periods during the coldest part of the year. General distributions and life history patterns are described for some of the most common fishes and macroinvertebrates below.

'Fishes of North Inlet: an Identification Guide' by Simpson et al. (2006) provides more detailed information about the identification, life cycles, spatial and temporal distributions, and behavior of about 100 of the most commonly encountered species in the estuary.

The mummichog, *Fundulus heteroclitus*, is probably the most conspicuous and familiar of the resident fishes. It occupies flooded intertidal salt marshes and flats and retreats to adjacent creek edges and pools around low tide. The mummichog lays eggs at the bases of *Spartina* plants during spring tides. This small predator of

marsh invertebrates plays an important ecological step in the transfer of energy to larger fishes and birds. Because mummichogs are hardy and readily trapped, 'mud minnows' are favored baits used by flounder fisherman. Other resident salt marsh killifishes have similar distributions and life cycles.

The mummichog, *Fundulus heteroclitus*, is probably the most conspicuous and familiar of the resident fishes.

The grass shrimps, *Palaemonetes pugio* and *P. vulgaris*, are very abundant in flooded intertidal areas and adjacent shallows. Adults of these almost transparent and very active crustaceans are about one half inch in size and often form large groups in water less than a few inches deep. During the warmest six months, females release microscopic larvae from eggs that they carry. After about two weeks of development in the plankton, miniature shrimp settle into adult habitats. Grass shrimps consume small benthic animals, algae, and decomposing plant material and in turn serve as an important food source for many fishes and birds.

Atlantic silverside (*Menidia menidia*) is a common year-round resident that inhabits shorelines and shallow creeks where it often occurs in schools of similarly-sized individuals. Adults 2-3 inches in length demonstrate lunar periodicity in their spawning and small silversides of three species are common throughout the summer and fall. The rough silverside (*Membras martinica*) remains near the surface of major creeks, and the inland silverside (*Menidia beryllina*) is mostly found in shallow fringing habitats where salinities are somewhat lower. Atlantic silversides are most conspicuous from fall to spring when similar-sized anchovies and mullets are absent. Silversides consume zooplankton, but larger individuals also prey on epibenthic invertebrates and large larval fishes.

There are probably more anchovies (bay anchovy, *Anchoa mitchilli*, and striped anchovy, *Anchoa hepsetus*) in local estuaries during the warmest months than any other kind of fish. Schools are found in subtidal creeks, open waterways, and along shorelines, with many moving into intertidal creeks at high tide. Small mesh nets are necessary to demonstrate the presence of what are usually enormous numbers of juvenile anchovies. Larvae, juveniles, and adults all consume zooplankton, including the developmental stages of other fishes, shrimps, and crabs. Fast swimming predators such as bluefish, mackerels, seatrouts, and ladyfish often scatter anchovy schools at the surface and terns dive on them from above. The bay anchovy spawns near inlets, especially in early summer. The striped anchovy appears to be mostly a coastal ocean spawner, but juveniles are abundant in the estuary. Anchovies overwinter in the ocean, and they are one of the first fishes to repopulate the creeks once temperatures reach about 15° C.

The commercial (penaeid) shrimps (the brown, white, and pink shrimps) are not residents of the estuary. Juvenile penaeid shrimps found in the creeks originate from larvae produced in the ocean. The smallest juvenile penaeids resemble grass shrimps, and they co-occur in the same marsh fringe habitat from late spring through fall. However, most juvenile penaeids are much larger than the largest grass shrimps. The brown shrimp, *Farfantepenaeus aztecus*, arrives in early spring and grows to sub-adult size (3-4 inches) before leaving the estuary in mid-summer. White shrimp, *Litopenaeus setiferus*, juveniles arrive starting in early summer and move to coastal waters as they reach pre-harvestable size in late summer and fall. White shrimp continue to recruit to the estuary throughout the warm months, and some juveniles overwinter in deeper portions of the system. Penaeid shrimps consume small benthos while foraging in the creeks and also during excursions across the flooded marsh. The pink shrimp (*Farfantepenaeus duorarum*) is much less abundant, but, together, these three penaeid shrimps play a major role in estuaries by exporting

locally produced biomass to the ocean. Penaeid shrimps comprise the most valuable fishery in SC.

Spot, *Leiostomus xanthurus*, is by far the most abundant demersal (bottom dwelling/feeding) fish occupying the estuary from March through November. Adults produce larvae in deep coastal waters, and planktonic postlarvae settle into the creeks from December through March. Spot consume meiobenthos and increasingly larger macrobenthos through the summer. They leave for more thermally stable and warm waters when they are 3-4 inches long in the fall. Some second year juveniles return, and adults (2+ years) comprise a short-lived fall fishery in the deeper channels and beaches before migrating to offshore spawning areas. Juvenile spot are one of the most widely distributed and abundant of the small silvery fish, and schools in intertidal creeks and open waters can be very large. Silver perch (*Bairdiella chrysoura*) is a less common drum which varies greatly in abundance between years. Silver perch feed on shrimps and fishes, with juveniles occurring in intertidal creeks and larger individuals (up to about 8 inches) in subtidal channels. The Atlantic croaker (*Micropogonias undulatus*) is another small local member of the drum family. It is more abundant along the salinity gradient of Winyah Bay but juveniles are present in North Inlet creeks throughout the warm season.

Pinfish, *Lagodon rhomboides*, juveniles are common in the creeks of North Inlet. Like spot, they recruit as postlarvae from the ocean in the winter-spring and grow to a few inches in size before leaving in the fall. Second and third year pinfish also occur in the deeper channels, especially near oyster reefs and other structure during the warm seasons. Pinfish of all sizes consume small swimming and crawling epibenthic invertebrates but, unlike spot, do not generally gulp sediment to obtain food. They are perhaps the most aggressive of the common fishes and annoy recreational anglers by stealing bait from their fish hooks.

Spotfin mojarra, *Eucinostomus argenteus*, juveniles are regularly collected in creeks, shore zones, and channels from mid-summer through fall. Small juveniles of this common sub-tropical fish arrive from the coastal ocean and grow rapidly during their stay in the estuary. The bright silvery spotfin mojarra is readily distinguished from the spot, pinfish and silver perch by having a small mouth located on an extendible base, but these four small silvery fishes are often confused with one another. This unique mouth of the mojarras presumably facilitates feeding on small invertebrates near or in the bottom. Several other very closely related species include the silver jenny and Irish pompano, which also occur during the warmest months.

Striped mullet, *Mugil cephalus*, is especially conspicuous in the estuary during the warm seasons when schools of juveniles travel close to the surface, both in flooded intertidal areas and open waters. Several year classes of these cylindrical, fast-swimming fishes can be observed during the summer and fall, but only mid-age and older individuals occur through the winter. Adults spawn in the ocean in the fall, and half-inch young-of-the- year move into the creeks in winter. Juveniles grow to 4 or 5 inches before leaving with cooling temperatures in the fall. White mullet, *Mugil curema*, juveniles co-occupy the estuary during the summer, but adults do not occur inside the inlet. Both species consume living and decomposing plant material and small benthos. Small mullets are consumed by many fish predators, but, locally, adults also constitute important food sources for

Common fishes found in North Inlet (top to bottom): juvenile white mullet , flounder, and spot

bottlenose dolphins and osprey. Another abundant but unrelated schooling fish in summer, is the flat-sided Atlantic menhaden (*Brevoortia tyrannus*). Like the striped mullet, ocean-spawned juveniles recruit to the creeks and grow before leaving in the fall. Menhaden feed by filtering plankton from the water column.

The blennies and gobies, especially the naked goby (*Gobiosoma bosc*), are small, abundant demersal fishes that are largely unnoticed by anybody but fishery scientists who recognize them as playing key roles in the ecology of tidal creeks. Blennies and gobies are year-round residents and cryptic occupants of bottoms with shell or other structure. Most live in permanently flooded channels, but some make excursions into the intertidal. They produce large eggs which adhere to bottom material, and an adult usually tends the nest until hatching occurs. Gobies are by far the most abundant larval fish in early summer, an indication that we greatly underestimate their abundance in the estuary. Juveniles and adults of about eight species of gobies and blennies occur incidentally in nets and other standard collection gear. They consume a variety of small motile invertebrates. Other cryptic residents with similar life cycles and habits include the oyster toadfish and skilletfish.

The southern flounder (*Paralichthys lethostigma*) is the largest of the ten or more local flatfish species. The closely related and generally smaller summer flounder (*Paralichthys dentatus*) has a similar life cycle. Adults of both species reproduce offshore in the late fall, and postlarvae recruit to estuaries in winter. Juveniles occupy creeks and flats and many appear to remain in or close to the estuary for their first two years of life. Reproductive age adults return to estuaries in the spring and spend their summers feeding in estuaries. The southern flounder prefers muddy areas in the creeks, whereas the summer flounder is more likely to be found near inlets and beaches. Both are ambush predators on other nekton. Other species of flounders are also transients, but adults are much smaller than flounders targeted by anglers. The bay whiff (*Citharichthys spilopterus*) and fringed flounder (*Etropus crossotus*) are especially common small flatfishes in North Inlet during summer.

Blue crab, *Callinectes sapidus*, is the most familiar of the large crabs. It is considered a resident species with all life stages occurring within the estuary except the intermediate larval stages. Female blue crabs typically mate with males in lower salinity areas and then move to inlets to release early stage planktonic larvae (zoeae) which are transported offshore by coastal currents. Development occurs on the continental shelf and planktonic megalopa larvae enter the estuary weeks later. Blue crabs from a fraction of an inch to the largest adults may be found in any intertidal or subtidal habitat during all but the coldest months during which they become inactive and less conspicuous. Juveniles are particularly abundant on flooded marshes in summer. All stages are voracious predators on slow-swimming fishes, benthic invertebrates, and carrion. After at least two years of age, the blue crab becomes an important commercial and recreational resource. Blue crab comprises the second most valuable fishery in SC.

Red drum (*Sciaenops ocellatus*), Atlantic croaker (*Micropogonias undulatus*) and the kingfishes (mostly *Menticirrhus saxatilis*) are bottom-feeding members of the drum family that, like the spot, are sought by recreational anglers in North Inlet. Spotted seatrout (*Cynoscion nebulosus*) and weakfish (*Cynoscion regalis*) are also drums but tend to feed on shrimps and fishes in the water column. Small juvenile stages of these members of the drum family are not frequently collected in nets. Red drum spawns around inlets and beaches in August- September. Very small juveniles settle into shallow salt marsh areas and most red drum

Red drum *Sciaenops ocellatus* are sought by recreational anglers in North Inlet.

spend their first 3 to 4 years living in the same system. They grow to about 12 inches at age one year, 22 inches at age two, 27 inches at age three, and 31 inches at age four. After about 4 years of age, most red drum leave the estuary and live in the coastal ocean. Females do not spawn until they are 33 inches long (about 5 years old), and they may live more than 40 years. Anglers should consult state regulations regarding size and catch limits and should also use careful catch-and-release techniques to preserve viable populations of these recreational fishing favorites.

Other large fishes that anglers target in North Inlet include the sheepshead (*Archosargus probatocephalus*) and black drum (*Pogonias cromis*). Both have vertical bands but very different mouths. The sheepshead has a prominent terminal mouth with conspicuous teeth for scraping and biting, whereas the black drum has a subterminal (under-slung) mouth with whiskers and no large teeth. Bluefish (*Pomatomus saltatrix*) is another favorite of local anglers. Juvenile (to 2 or 3 lbs) bluefishes are voracious, toothy, fast swimming predators that chase schools of small bait fishes in open waters, including inlets, sandbars, and beaches.

Tarpon, permit, Florida pompano, ladyfish, planehead filefish, striped burrfish, and lookdown are among the regular and sometimes abundant warm-water species that are represented by juveniles during the summer. Adults of most of these species spawn in warmer southern waters, and larvae or small juveniles sometimes find their way into the estuary from spring to fall. Several species of jacks, groupers, snappers, puffers, butterflyfishes, and others known from the tropics have been found in North Inlet creeks, especially in late summer and fall. More information on the less common species of bony fishes appears in **Appendix E**. Twelve species of sharks and eight species of rays and skates have been documented in North Inlet. Juvenile Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks are commonly encountered by anglers in the creeks especially from May to August. Most species of sharks including the large and sometimes free-jumping blacktip shark (*Carcharinus limbatus*) are found during the summer. The fairly small, reddish, long-tailed Atlantic stingray (*Dasyatis sabina*) is the most common of the rays known from North Inlet. The Southern stingray (*Dasyatis americana*), weighing up to 100 lbs or more, and the somewhat smaller but increasingly abundant bluntnose ray (*Dasyatis sayi*) are found in the estuary during summer and early fall.

SEASONAL PATTERNS

Dynamic and predictable are good words to describe the seasonal occurrences of nekton in North Inlet. The patterns documented in our long-term study at Oyster Landing Basin (OLB) are representative of the timing and movements of fishes, large shrimps and crabs throughout the estuary. Figure 83 shows the Oyster Landing Basin and the location of collections in the intertidal pool (OL) and at the enclosure on the intertidal marsh (OI).

The Oyster Landing nekton study documented interannual and interdecadal changes in nekton use of an intertidal creek basin.

Nekton abundance peaks from April to October, with much lower abundances occurring during the colder months. Patterns for three different nekton categories are shown in Figure 84. The "primary transient" category includes a group of nine common transient taxa represented by first year juveniles that recruited from ocean spawning areas. This group of fishes and shrimps accounted for the majority of individuals caught at OLB each year, averaging about 84% of the total catch from April through October. The "other" category includes dozens of much less common transients plus later life stages of those taxa identified in the transient category; they never accounted for more than a few percent of the total catch each year. The "resident" category includes species that occur year round. Residents accounted for 5 – 30% of the total catch each year; their average contribution to the total catch was 13%. Taxa comprising all three categories are identified in Table 9, and their relative abundances are discussed below. For the primary transients, abrupt increases in abundance in the spring were followed by irregular levels through the summer and rapid declines in the fall each year. Other transients exhibited similar patterns. For residents, seasonal patterns were less regular from year to year, but residents were often more abundant than transients and even dominated the catch during the coolest period.

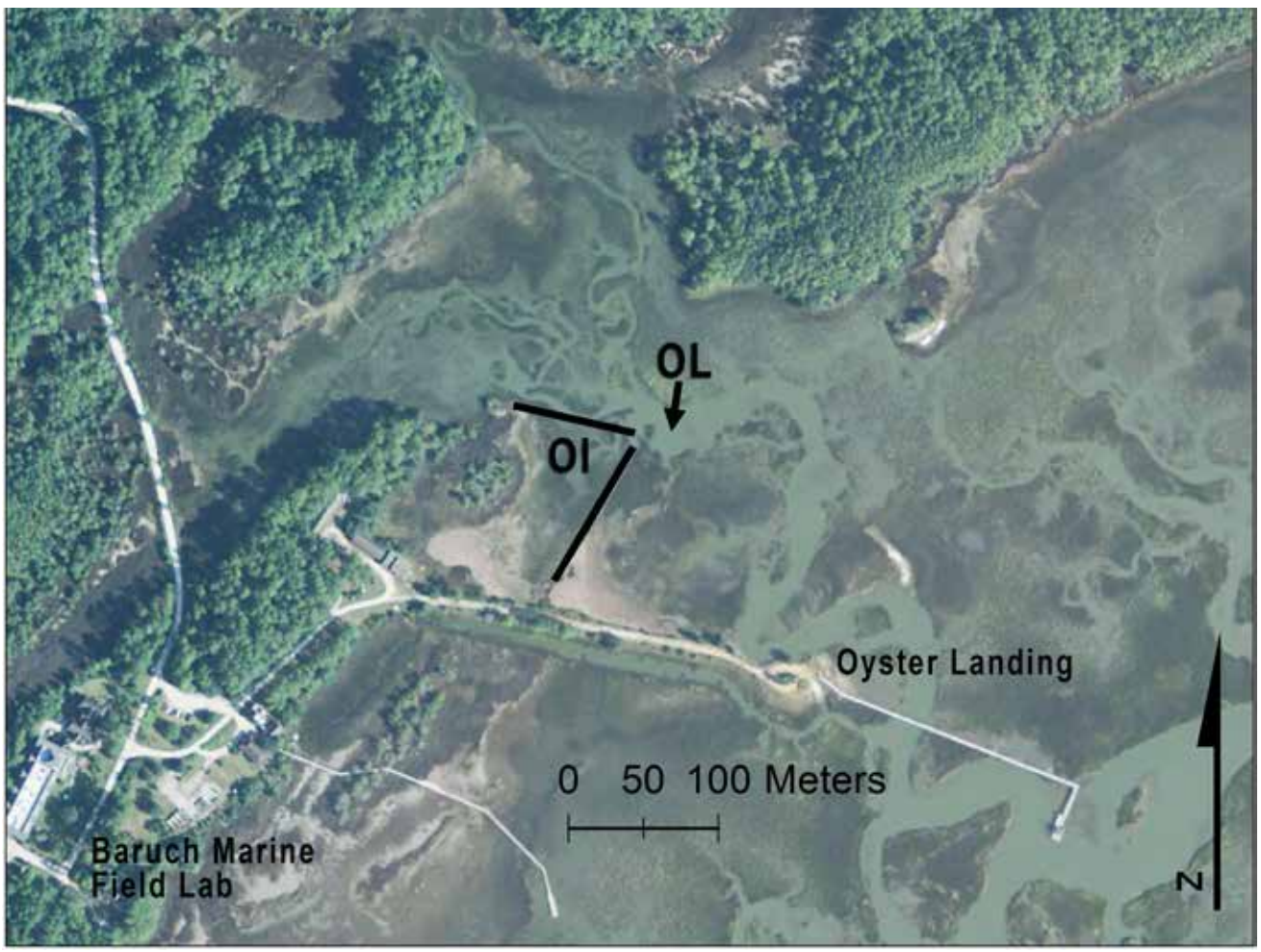


Figure 83. Map of Oyster Landing nekton study area, North Inlet, SC. Seine collections were made from an intertidal pool (OL) isolated within the creek bed at low tide every two weeks from Spring 1984 to Fall 2007. In 1995, collections were also made from the marsh at high tide by enclosing an area (OI) of about one acre with removable panels (black bars); nekton were collected in a block net as they retreated with the ebbing tide.

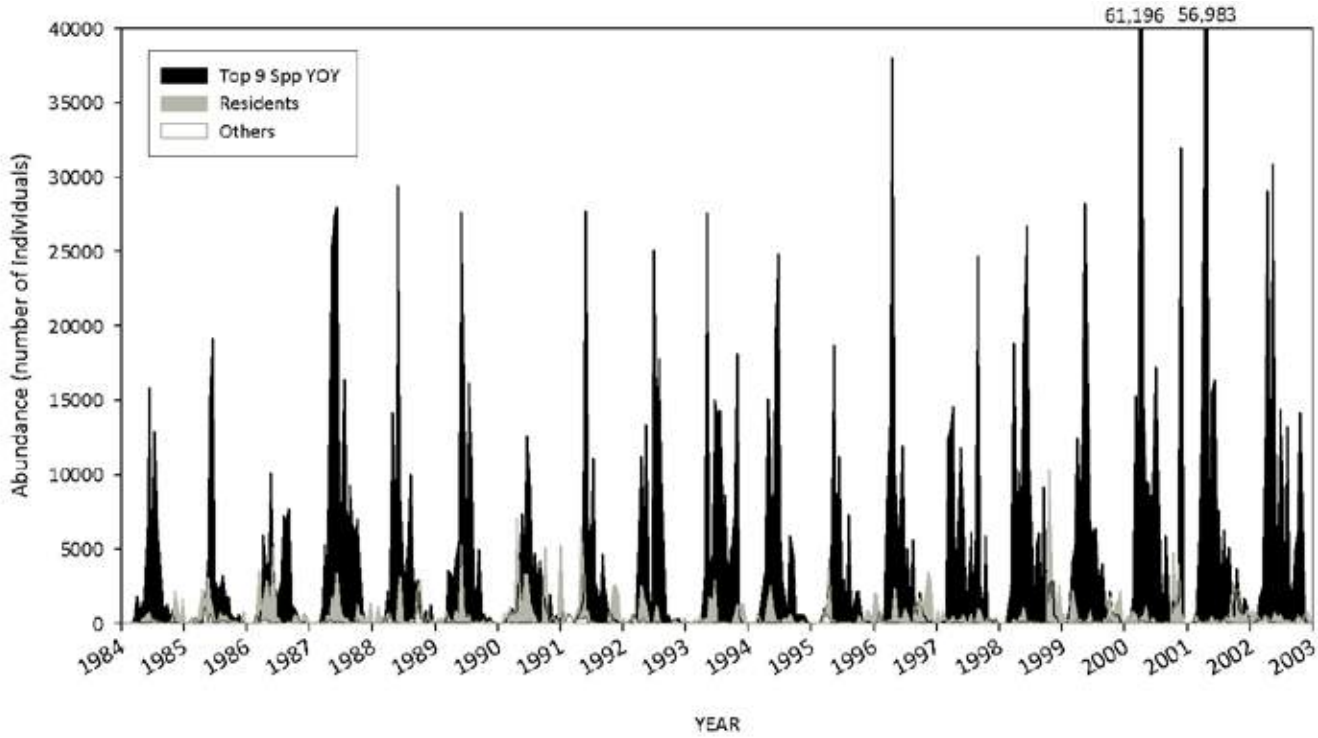


Figure 84. Biweekly abundance of nekton at the long-term monitoring site at Oyster Landing Basin, North Inlet, SC, from January 1984 – December 2003. Catches were made with a single seine haul at low tide in an isolated pool within the intertidal creek bed. Three nekton categories are shown. 'Transients' represent young-of-the-year of the 9 taxa that consistently dominated the catch. 'Residents' represent the assemblage of small fishes that occurred year round. 'Others' is composed of all other transients plus later life stages of the taxa clumped in the Transient category. The taxonomic composition of each group is given in Table 9.

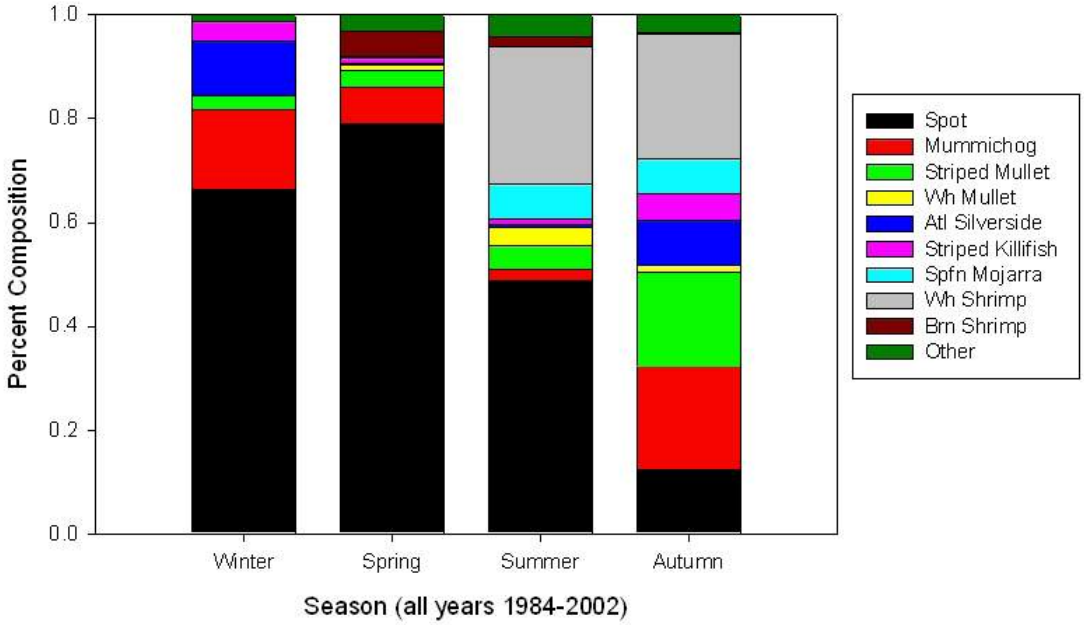


Figure 85. Proportions of the total catch that each of the most abundant taxa comprise during each season. The values are averages based on biweekly collections made from 1984- 2002 at the Oyster Landing Basin (OL).

Table 9. Species composition of the three nekton categories comprising the biweekly seine catch at Oyster Landing Basin from 1984 – 2003. Within each list, the taxa (common names) are ranked from most to least abundant according to total catches over the 20 year period. See **Appendix E** for other species. Note that grass shrimps were not included in these analyses.

Primary transients	Other transients	Residents
spot	treadfin shad	mummichog
white shrimp	ladyfish	striped killifish
striped mullet	crevalle jack	Atlantic silverside
brown shrimp	pink shrimp	sheepshead minnow
mojarras	bay anchovy	inland silverside
white mullet	gizzard shad	blue crab
Atlantic menhaden	Irish pomano	blackcheek tonguefish
pinfish	Atlantic croaker	red drum
silver perch	southern flounder	mosquitofish
	other jacks, flounders, seatrouts	black drum
	1+ age mullets, spot, pinfish	American eel
		all gobies and blennies

Very large increases in the abundance and diversity of nekton from winter to summer can be attributed to the immigration of fishes and shrimps from the ocean. As indicated in Figure 85, one species, spot, is by far the most abundant of the transients that arrive in the salt marsh as advanced larval stages every winter. Young-of-the-year pinfish, southern and summer flounder, Atlantic menhaden, striped mullet, and brown shrimp also arrive during the coldest months. In the late spring and early summer, white mullet, white shrimp, and mojarras recruit to the shallows of North Inlet. The arrival of anchovies and other year classes of spot, mullets, flounders, rays and sharks add to the diversity and abundance of transients during the summer. Water temperature and day length are thought to control the timing of seasonal migrations of many taxa. Peak migrations into and out of the estuary can be influenced by changes in weather patterns, especially in fall when the first cold fronts trigger large migrations to the more thermally stable and warmer coastal ocean areas.

HABITATS AND DISTRIBUTIONS

Even though it is possible to encounter any species of fish in any habitat or location within the estuary, the composition of nekton in specific habitats is fairly predictable. Information from the literature and from supplemental collections with seines, trawls, gill, nets, and hook and line fishing has provided a general understanding of the occurrences of common species in the primary aquatic habitats in the North Inlet area.

- **Surf zone on the beachfronts:** Striped killifish and Atlantic silversides occur year- round. Striped mullet, white mullet, and Atlantic menhaden account for major increases in fish abundance during the summer. Southern kingfish, northern kingfish, red drum, Florida pompano, pinfish, spot, bluefish, southern stingrays, and Atlantic sharpnose sharks, blacktip sharks, blacknose sharks, bonnetheads, and, more rarely, tarpon, Spanish mackerel, and king mackerel are caught by anglers in the surf.

- **Shore zone along major creeks and sounds near the inlet:** In addition to the striped killifish and Atlantic silverside, pipefish, searobins, flounders, and puffers can be found through most of the year. With warming temperatures, anchovies, mullets, and Atlantic menhaden become abundant. Juvenile spot, pinfish, mojarras, jacks (especially crevalle), planehead filefish, stargazers, inshore lizardfish, tonguefish, penaeid shimps, and a variety of crabs also add to the biomass and diversity during summer. Except for southern and bluntnose stingrays, most of the large fishes that frequent the beachfront surf do not commonly occur along lower wave energy shorelines. The composition of nekton in shore zones changes from the barrier islands to the forest edge with an increasing presence of mummichogs, grass shrimps, blue crabs, and penaeid shrimps.
- **Channel bottoms:** Larger fishes tend to occur in deeper water, so the largest spot, pinfish, Atlantic croaker, black drum, flounders, and sharks may be found in subtidal creeks. Some fishes occur almost exclusively in association with structure (e.g., shell accumulations, pilings) in permanently flooded waters. These include oyster toadfish, black seabass, snappers, groupers, Atlantic spadefish, sheepshead, and American eels. Numerous species of gobies and blennies and the skilletfish are found more in shallow subtidal than in intertidal habitats, though they occur in flooded oyster reefs. Other large fish that are caught by anglers in deeper waterways include spotted seatrout, bluefish, weakfish, Atlantic cutlassfish, and hardhead catfish. During winter and spring, the spotted hake, southern hake, clearnose skate, smooth dogfish, ocellated flounder, and windowpane can be found in deeper channels. Even accounting for differences in the sampling techniques, major differences exist between the nekton occupying subtidal channels and shore zones/intertidal creeks.
- **Open waters of large creeks and sounds:** Anchovies (bay anchovy and striped anchovy), silversides (Atlantic silverside, rough silverside), mullets (striped mullet, white mullet), squids, and Atlantic menhaden are especially common in the water column during the warm months. Other herrings (and shads), Atlantic needlefish, bluefish, ladyfish, sharks, halfbeaks and mackerels also occur here during warm periods. Atlantic silversides are by far the most commonly encountered open water fishes during winter. In studies comparing nekton catches near the bottom to those near the surface, patterns of separation in depth and diet were apparent for the various zooplanktivorous fishes (anchovies and silversides) (Johnson et al. 1990; Allen et al. 1995).
- **Intertidal creeks and mudflats:** More than 60 species of nekton regularly migrate through flooded intertidal creeks. Many, but not all, of the fishes and shrimps that move into flooding intertidal creeks and edges of channels also move onto the flooded marsh surface. Mummichog, striped killifish, sheepshead minnows, and grass shrimps move up and down the long axes of intertidal creeks with the tide, but most seek refuge in pools during low tide. Striped mullet, white mullet, spot, pinfish, mojarras, Atlantic silverside, brown shrimp, white shrimp, blue crab and anchovies move in with the flooding tide and back to adjacent subtidal areas with the ebb; however, some individuals remain in intertidal pools (Bretsch and Allen, 2006). Large southern flounders, stingrays, and red drum use well-flooded, large intertidal creeks. Although there is a general relationship with larger fish occurring at deeper depths, some large fishes including striped mullet and red drum routinely move into water only slightly deeper than their body height. Almost all of the species found in intertidal creeks also occur on flooded flats, with higher abundances and diversity occurring on muddy than on sandy flats.
- **Flooded marsh:** Mummichogs and grass shrimps account for most of the small nekton that occur in the flooded grass year round, but

other residents include the striped killifish, sheepshead minnow, silversides, and blue crabs. Large striped mullet and red drum also occur all year. Juvenile striped mullet and white mullet rove in large schools from spring to fall. Spot, penaeid shrimps, and ladyfish forage on the marsh surface during the warm period. Less commonly encountered on the marsh are the sailfin molly, mosquitofish, spotfin killifish, sleepers, lyre goby, and rainwater killifish which appear to favor low salinity areas near the forest edge.

Community members assist with sorting the catch from the Oyster Landing survey.

TIDAL MOVEMENTS OF NEKTON

The use of several sampling strategies has provided insights into movements of common fishes, shrimps, and crabs during different stages of the tide. In general, ebbing tides force animals off the intertidal marsh, flats, and creeks into the deeper channels. During summer low tides, shallow subtidal channels often appear to be boiling with fishes and shrimps as schools of small, active nekton become concentrated there. Many of these tidal migrants remain close to the water's edge, perhaps maximizing their avoidance of predators and placing them in the best position to occupy intertidal areas as they become covered with the rising or advancing flood tide.

From 1995 – 2002, collections were made from the flooded marsh surface at high tide (OI) on the same date that collections were made from the adjacent pool at low tide (OL) (Figure 83). Posts were set around a section of marsh (approximately one acre) located adjacent to the pool. On dates scheduled for sampling the flooded marsh, the area was enclosed by setting fiberglass panels between the posts at high tide. A ¼ inch mesh stop net was set at the lower end to collect animals retreating with the ebbing tide. At low tide, the stop net was emptied and then a nearby pool was seined with a ¼ inch mesh net before the tide started to re-flood the area.

Comparison of the two catches (high tide flooded marsh surface vs low tide pool) showed that the same species used the marsh at high tide and remained in the pool at low tide. The same resident and transient ranked highest in both the high and low tide collections. Mummichog was clearly the most abundant resident taxon in both the high and low tide catches, and spot was by far the most common transient in both areas. But there were important differences in relative abundances of some common taxa as well as in the occurrence of some less common taxa. Young-of-the-year transients accounted for the largest proportion of the catches in both the pool and flooded marsh, but residents tended to be more abundant on the marsh than in the pool.

Mummichogs, spot, and striped mullet caught retreating from the marsh were significantly smaller that those seined from the low tide pool. White shrimp, brown shrimp, white mullet, and blue crab were larger on the marsh. Differences in the collection efficiencies of the stop net and seine could account for some of these size differences, but these results in large part reflected ontogenetic differences in patterns of tidal movement within and among life stages of the species. For instance, large white shrimp move onto the flooded marsh and then leave the intertidal creek basin rather than remaining in the pool at low tide. Higher species richness in the high tide collections also indicates that many species leave the basin with the ebbing tide.

Because small adult grass shrimps are not retained by ¼ inch mesh nets, they were not quantified in the OLB study. Field observations have revealed

Nekton caught in the Oyster Landing surveys were measured using an electronic system.

that grass shrimps are among the first to move into the intertidal and last to leave it. This "first in – last out" pattern was demonstrated in a supplemental study that employed an array of lift nets located across an elevation gradient extending from the edge of a shallow subtidal creek to the high marsh. Predictable and sequential movements of different species and life stages of nekton into intertidal creeks were also demonstrated in a study by Bretsch and Allen (2006) using sweep flumes. Together these studies have revealed patterns of habitat use by nekton that probably reflect behavioral adaptations that minimize competition for space and food while maximizing use of the available resources.

FACTORS INFLUENCING THE DISTRIBUTION OF NEKTON

One of the most difficult challenges for scientists interested in the distributions and biology of nekton is identifying factors that influence changes in these parameters. The description above of nekton distributions among habitats indicates that physical structure is important, with some species preferring shallow over deep areas, or the sandy surf over muddy creeks. Within subtidal channels, gobies and blennies are abundant in areas with accumulations of shell and almost absent in flat sandy areas nearby. In one study comparing the use of eight intertidal creeks by nekton, large differences were related to the geomorphology of the creeks with more nekton using shallow, gently sloped creeks with slow rates of flooding and ebbing. This preferential use of creeks with certain characteristics continued season after season (Allen et al., 2007).

Seasonal patterns of nekton occurrence in the estuary, and even in certain habitats, are generally related to varying physical conditions in the water. Measurements of environmental conditions made at the time nekton are sampled are useful in establishing such relationships, especially when made over weeks, months, and years. Water temperature is clearly a primary factor in the timing of migrations, metabolism, growth, reproduction, and other aspects of the biology and behavior of both fishes and motile macroinvertebrates. Total abundance and total number of species (often referred to as species richness or diversity) were highest during the warm months. Other physical (e.g., dissolved oxygen concentration, water clarity) and biological (e.g., availability of food, predators) factors which are closely related to water temperature cannot be easily separated and thus confound our understanding of which factors most strongly influence nekton behavior.

Salinity is another important controlling factor for estuarine nekton, but it too was significantly related to water temperature in the Oyster Landing Basin. Increased rainfall during the spring and summer reduces characteristically high salinities in North Inlet creeks, especially near the edge of the forest. There were no significant relationships between the abundances of common nekton species in OLB and salinity, but major and extended depressions in salinity at OLB resulted in temporary reductions. During wet winters, brackish water from Winyah Bay can move into North Inlet via Town and South Jones Creeks. Some fishes typical of low salinity including Atlantic sturgeon, American shad and longnose gar have been captured in the system, but these are uncommon and occur over short periods of time. Major tropical disturbances have temporarily affected fish distributions in OLB. The retreat of the

surge of Hurricane Hugo (September 1989) scoured accumulated organic materials off the marsh and out of the creek beds near the forest. Displaced fish returned after several weeks that fall, but the altered habitat might have been responsible for the low level of transient production observed in 1990. The introduction of some unusual tropical fishes, invertebrates, and sargassum weed occurs after periods of sustained winds from the east.

Biotic factors also play important roles in the distribution and biology of nekton. Studies have shown that fish move into intertidal areas to consume prey and that some species and life stages have fairly specific diets. For instance, adult red drum forage for fiddler crabs on the marsh surface, the only habitat in which this crab occurs. The availability and quality of food resources influences the behavior and movement of nekton and can affect growth rates and other physiological functions. Competition among individuals of the same and different species affects their distributions and growth, while predation affects survival. Fish are responsive both to changing biotic and physical conditions.

LONG-TERM TRENDS

The large week-to-week variations in total nekton abundance shown in Figure 84 are typical as different age groups of different species occupy the basin on different tides, months, and seasons. On any given tide during spring, a large school of young-of-the-year spot might remain in the pool, only to spend the next tide somewhere else. Accordingly, we tend to use seasonal averages in interpreting trends over years and decades. In Figure 86, seasonal means for the entire OL (low tide seine) and OI (high tide block net) time series are shown. Long-term trend analyses have shown that there was a significant increase in nekton abundance in the OL Basin from 1984 to 2002. This could have been influenced by the generally lower salinity during the 1990s when a series of El Niño events created increased rainfall and runoff into the OL Basin and area in general. From 1995 to 2010, the trend indicated a significant decrease in total nekton with only about half as many fishes and shrimps occurring in recent years compared to the mid-1990s. A series of extended droughts and high salinity started in about 2001. No doubt, other factors influenced the trends and additional analyses are being conducted to better

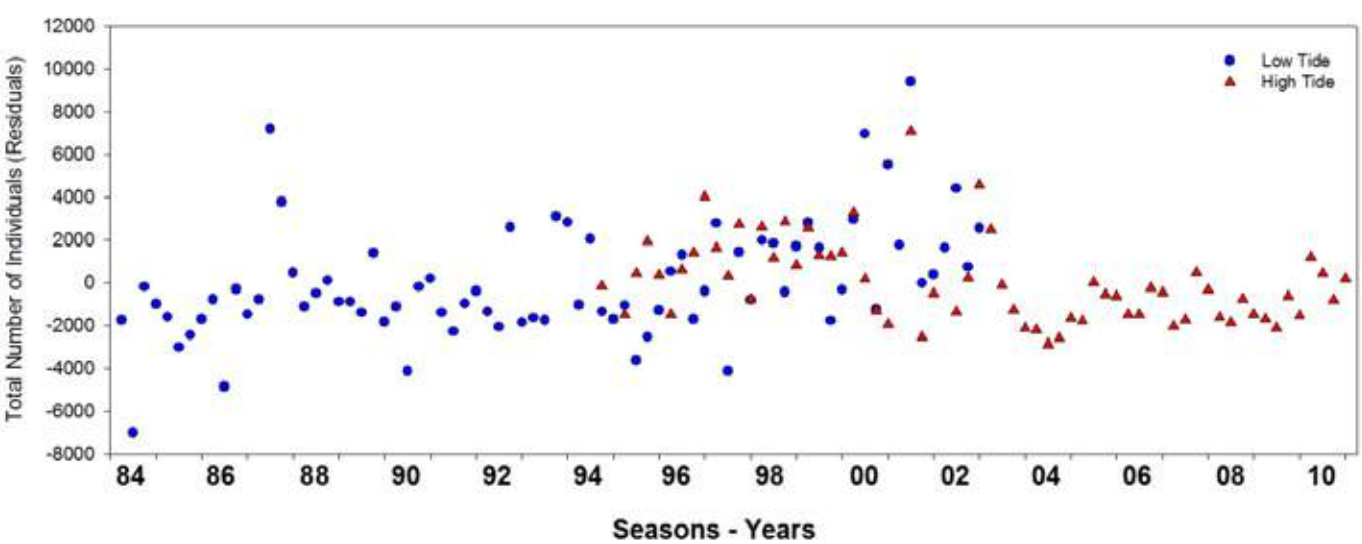


Figure 86. Total numbers of nekton caught in the low tide pool (circles, seine, 1984-2002) and on high tide flooded marsh (triangles, enclosure-blocknet, 1994-2010). These are seasonal values shown as residuals or deviations from the long-term means for each season in each of the time series. The two series overlapped from 1995-2007 with the high and low tide samples being collected on the same day.

understand the effects of long-term changes in environmental conditions on the composition, abundance and growth rates of nekton in the nursery habitats of the estuary.

During the 7 year period when collections were made from both the flooded marsh and low tide pool (total of 64 paired collection dates), there was a strong correlation between the catches. For the total catch, the numbers of nekton using the basin when flooded was a good predictor of how many would be in the pool at low tide. This demonstrated relationship enabled us to compare the trends for the independent time series over the decades.

FISHERIES

South Carolina's largest inshore fisheries, the penaeid shrimps and blue crab, are absolutely dependent on estuaries. White, brown, and pink shrimps require marshes to complete their life cycles, and there are relationships between the amount of habitat (and perhaps the quality of that habitat) and the amount of adult shrimps that are available to the ocean-based fishery. Blue crabs are harvested with baited traps within the estuaries, and this is the only commercial fishery that is allowed in the North Inlet system. This small traditional trap fishery occurs mostly during the winter season.

The vast majority of fishes known from North Inlet are not recognized as commercially or recreationally important species. In fact, since red drum and spotted seatrout were designated gamefish in the 1980s and because gill nets were banned from inshore waters, estuarine finfish species are not allowed to be harvested for commercial markets. However, incidental catches of flounders, whitings, spot, Atlantic croakers and a few other species in shrimp fishery trawls in the ocean are sold in small quantities. The recreational harvest of red drum, southern/summer flounder, seatrouts, sheepshead, bluefish, sharks, and some additional species comprises a valuable economic asset to the coastal counties. The other more than 100 species of small fishes that occur in SC estuaries are not of any direct economic value but they play critical roles in the ecology of these productive systems, often serving as food sources of larger and more familiar local fishes.

A nekton sampling crew heading out to the Oyster Landing site.

» Reptiles, Amphibians, and Mammals

Herpetofauna (reptiles and amphibians) occur in a wide-variety of habitats across the North Inlet–Winyah Bay area. Their distribution and abundance are determined by water regime, salinity, and vegetative community (Sandifer et al., 1980) which vary greatly from the upland pine-forest to the marshes and tidal creeks. Reptiles and amphibians are not abundant in saltwater environments and adjacent areas. Their distribution is patchy in space and time. Compared to other animal assemblages in the North Inlet area, research on the herpetofauna has been sparse; however, observations made over the long-term and a few limited, directed surveys, especially in the uplands, have revealed the presence of over 65 species and detailed information on some of the more widely-distributed species.

Among the most abundant and conspicuous reptiles within the NERR boundaries are turtles found in the marine environment, on barrier islands, in tidal creeks, and at the marsh–upland interface. A different group of reptiles and amphibians occurs in the adjacent watershed including non-tidal, forested wetlands.

Turtles are the most widely-distributed and well-studied of the herpetofauna in the NI-WB NERR. Of these, loggerhead (*Caretta caretta*) and green sea turtles (*Chelonia mydas*) occur in the coastal marine habitat and are considered mostly transient. The loggerhead, the most abundant of the sea turtle species in South Carolina, is often observed in tidal creeks and open waters in North Inlet. It is listed as Threatened under the U.S. Endangered Species Act. Small green turtles, usually with a carapace width around 30 cm, have been fairly commonly observed in shallow tidal creeks. The leatherback sea turtle (*Dermochelys coriacea*) has not been recorded within North Inlet, but adults are frequently reported from the ocean during their northern migration up the coast.

Loggerhead and green turtles are typically not residents of local waters during the coldest months. Both species live exclusively in the water except when they come on shore to lay eggs. Loggerheads and rarely green sea turtles nest on area beaches from mid-May through August, with individual females returning to nest 3-7 times over the course of a season. Loggerhead sea turtles are primarily carnivorous and feed mostly on shellfish that live on the ocean floor and in the tidal creeks of the estuary.

Populations of loggerhead sea turtles have declined over the past decades. Loss of nesting habitat, incidental capture in recreational and commercial fisheries, and predation pressure from nest raiders including raccoons, foxes, coyotes, and feral hogs are some of the threats to sea turtles. The South Carolina Department of Natural Resources (SCDNR) oversees a very successful network of sea turtle volunteers who monitor and protect nests on several of the state's beaches during the nesting season. Members of a local volunteer organization (South Carolina United Turtle Enthusiasts) are part of this network and have been monitoring sea turtle nesting on Debidue Island for more than 20 years. The southern two mile (3.2 km) undeveloped stretch of Debidue Island (Hobcaw Beach) is within the NI-WB NERR boundary and provides important nesting habitat for the loggerhead sea turtle. Additional information about the status of sea turtles in South Carolina can be found on the SCDNR website: www.dnr.sc.gov/seaturtle/.

The loggerhead, the most abundant of the sea turtle species in South Carolina, is often observed in tidal creeks and open waters in North Inlet. It is listed as Threatened under the U.S. Endangered Species Act.

The diamondback terrapin (*Malaclemys terrapin*) is a small, long-lived estuarine turtle that is relatively common in salt marsh creeks. This is the only turtle species in North America endemic to brackish coastal marshes and it is an important component of the salt marsh ecosystem where it feeds on mollusks and crustaceans. The diamondback is considered a commercial species in South Carolina. The South Carolina Department of Natural Resources has the authority to issue collection permits, but has not done so recently given the unknown population status of this species across the state and elsewhere (Gibbons et al., 2001).

Genetic studies on diamondbacks have revealed that populations in South Carolina are not distinct from each other or from those in North Carolina. Intentional transplants of terrapin for the commercial industry have disrupted the natural population's genetic structure, and some populations in South Carolina are genetically more like those found in Texas (Hauswaldt and Glenn, 2005).

Diamondback terrapins are present in the intertidal creeks of North Inlet throughout the year.

Terrapins are present in the intertidal creeks throughout the year, but are most often observed during the summer months between May and August when nesting in the dry soft sand/soil above mean high tide levels. During the winter months, they dig into the soft bottoms and banks of intertidal creeks where they remain relatively dormant until spring. The habitat needs of juvenile terrapins are poorly understood. Investigators from Francis Marion University and Coastal Carolina University have been radio-tagging adult terrapins to determine site fidelity, home ranges, and nesting sites in the North Inlet system.

Major terrestrial threats to terrapins include loss of nesting habitat from coastal development and predation by raccoons and fire ants. In the marine environment, threats include abandoned crab pots. Other threats include boat and propeller mortality and habitat and water quality degradation. High site fidelity of this species indicates that once a population is extirpated, it is unlikely to return naturally.

Several other turtles have been observed in the watershed surrounding North Inlet, especially the eastern mud turtle (*Kinosternon subrubrum*) and the eastern box turtle (*Terrapene carolina*). Also found in the swamps adjacent to North Inlet salt marshes are snapping turtles (*Chelydra serpentina*), yellowbelly slider (*Chrysemys scripta*), and spotted turtle (*Clemmys guttata*).

American alligators (*Alligator mississippiensis*) are relatively common in the North Inlet area. They are generally limited to freshwater areas but can be seen in estuarine waters especially close to the edge of the forest after major periods of rainfall. These tend to be small and medium sized individuals and they rarely stay in salty waters for very long. Occasionally, alligators are seen in the surf on the barrier islands.

American alligators, such as this small one in a drainage ditch near the BMFL, visit the estuarine waters in North Inlet, but must return to fresh water.

Twenty-two species of snakes can be found in the Hobcaw Barony uplands, but none frequents the salt marsh or tidal creeks. Occasionally, canebrake rattlesnakes (*Crotalis horridus*) and cottonmouths (*Agkistrodon piscivorous*) have been observed on the upper reaches of the salt marsh, but most local snakes have specific upland habitat requirements. Among the more commonly seen snakes in the pine forests are the corn snake (*Elaphe guttata*), rat snake (*Elaphe obsoleta*), and king snakes (*Lampropeltis* spp.). The black racer (*Coluber constrictor*) is likely to reside in open areas and wetland margins. Water snakes (e.g., *Nerodia* spp.) are found in freshwater marshes and ponds. Venomous snakes such as the copperhead (*Agkistrodon contortrix*) are more likely seen in drier habitats, whereas the pygmy rattlesnake (*Sistrurus milliarius*) is likely to be found from upland forest to wetland and swamp habitat. The Eastern coral snake (*Micrurus fulvius*) is seen only rarely. This elusive species, found in the pine forest and on sandy soil, is a SC State Species of Concern.

Frogs and toads comprise the majority of the amphibian species. These are all freshwater dwelling animals, and none occurs in the salt marsh or tidal creeks of North Inlet. Thirteen species are distributed across habitats ranging from relatively dry regions with brushy undergrowth, including the Eastern spadefoot (*Scaphiopus holbrooki*) and oak (*Bufo quercicus*) toads. Freshwater wetlands are preferred by the tree frogs including spring peeper (*Pseudacris crucifer*) and the southern cricket frog (*Acris gryllus*). Among the several species of frogs of the genus *Rana* in local wetlands, only the southern leopard frog (*Rana spenocephala*) is sometimes observed in low-salinity tidal marshes.

Sirens, skinks, newts, lizards, salamanders and freshwater turtles constitute the remainder of the amphibians and reptiles. These too occupy a variety of freshwater habitats, well away from the edge of the salt marsh (Martof et al. 1980). A list of amphibians and reptiles for Hobcaw Barony and adjacent estuaries is provided in **Appendix F**.

Reptiles and amphibians occur in a wide-variety of habitats across the North Inlet–Winyah Bay area. Occasionally, canebrake rattlesnakes (top left) and cornsnakes (top right) are observed on the upper reaches of the salt marsh. Green anoles (bottom left) are commonly seen, but glass lizards (bottom right) are more secretive.

In the NI-WB NERR, mammals include both aquatic and terrestrial species and are distributed across a variety of habitats including salt marsh, cypress-tupelo wetlands, pine-hardwood forest, and mixed and longleaf pine forest (**Appendix G**). Small terrestrial mammals dominate the local species distribution. Most are in the Family Muridae which includes the marsh rice rat (*Oryzomys palustris*), eastern harvest mouse (*Reithrodontomys humulis*), cotton mouse (*Peromyscus gossypinus*), and southern red-backed vole (*Clethrionomys gapperi*). Cotton mice and voles are typically woodland dwellers and occur along water courses where stumps, down logs, and tangles of brush and vines offer suitable retreats; they also occur frequently in woodland areas bordering open fields. Marsh rice rats typically inhabit marshy, including upper salt marsh, areas,but they may be found in almost any place where grasses and sedges offer an adequate food supply and protective cover (Webster et al., 1985).

The marsh rabbit (*Sylvilagus palustris*) is present in the forest, fields, and lawns around the North Inlet salt marsh. Although known to be an excellent swimmer, it has not been observed in the intertidal marsh or tidal creeks.

Three species of squirrel can be found here and include the gray (*Sciurus carolinensis*), southern fox (*Sciurus niger*), and the southern flying squirrel (*Glaucomys volans*). All eat nuts, acorns and insects. These species overlap in their distribution but have some differences in preferred habitat. The gray squirrel prefers hardwood forests and forested wetlands, whereas fox squirrels are more abundant in mature oak-hickory forests. The southern flying squirrel is the only carnivorous member of the squirrel family. It is also almost completely arboreal. Its omnivorous diet includes acorns, nuts, berries, fruits, seeds, buds, blossoms, insects, birds, nestlings, eggs and, occasionally, carrion.

The only bat species commonly observed in the area is the little brown bat (*Myotis lucifugus*). This species is one of the most common bats in the U.S. and Canada. It feeds primarily on aquatic insects and can be found foraging along forest edges, streams and small cultivated areas. Bats can be found during the day in hollow trees or under the bark of dead trees. Standing dead trees may also be used as maternity colonies.

The southern fox squirrel occurs in the upland forests adjacent to North Inlet.

Larger semi-aquatic species include river otter (*Lontra canidensis*), beaver (*Castor canidensis*), and mink (*Mustela vison*). River otters are occasionally observed in salt marsh creeks as well as in freshwater streams around the border of North Inlet. They occur throughout the year and are usually seen in small groups. Historical statewide data are limited for mink, but they are known to be susceptible to threats including harvest, loss of habitat, and contaminants (Baker, 1999). Minks were extirpated by hunters in the 1800s and re-introduced by the SC Dept. of Natural Resources in recent decades. Individuals are occasionally seen in salt marsh creeks in North Inlet.

The beaver is a freshwater species that occurs throughout the watershed adjacent to North Inlet, but it occasionally wanders to the edge of salt marsh creeks. Because of its habit of damming drainage ditches and culverts, the beaver is often considered a nuisance to forest managers.

Mink were re-introduced to the area in recent decades after being extirpated by hunters in the 1800s.

Historically, there have been sightings of black bear in the Hobcaw Barony forest and at least a few reports have been made over the past several decades; however, no fully documented occurrences are available. Their occasional occurrence should not be a surprise because they are well established in the local river basins and individuals show up in neighborhoods in Georgetown and the Waccamaw Neck.

Some uplands mammals including white-tailed deer and feral hog are actively managed. Although Bernard Baruch and guests actively hunted the property for deer in the early 1900s, harvest restrictions limited hunting in the 1960s. Unrestricted growth in the deer population has affected deer health. An outbreak of Hemorrhagic Disease occurred around 1980, resulting in a major die-off.

Feral hogs may have been on the Hobcaw Barony since the arrival of the European settlers. Clemson University wildlife researchers conducted many studies from 1970-1990. Trapping initiated in the 1970s resulted in the capture of about 1000 hogs, leaving an estimated 300 to 400 animals. A total of 1,672 hogs were harvested in 2000, and several hundred were harvested additionally as a part of a USDA Brucellosis study. Feral hogs cause extensive damage when rooting, an activity that alters sensitive sand dunes and wetland habitats. Hogs may also impede longleaf pine regeneration and provide an opening in habitat for invasive plant species such as *Phragmites*.

Many years without harvesting of deer and feral hogs on the property led the Baruch Foundation to suggest that populations of both white-tailed deer and feral hogs are over-abundant. To this end, the Hobcaw Barony Wildlife Management Plan (Bruce 2003) was developed. The purpose of this plan was to estimate population size of white-tailed deer and feral hogs along with eastern wild turkey (*Meleagris gallopavo silvestris*) and bobwhite quail (*Colinus virginianus*), and to subsequently develop appropriate management recommendations. Estimates of 95 deer per square mile and a total of 600-1500 feral hogs were determined. Management recommendations for these species included a 50 percent reduction in deer and an intensive trapping/shooting schedule for feral hogs in an attempt to eliminate as much of the population as possible.

Little predator control has been practiced on the property. Raccoons (*Procyon lotor*) are considered in high abundance on the property. Sightings of opossums (*Didelphis virginiana*) are numerous. Bobcats (*Lynx rufus*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), and coyotes (*Canis latrans*) occur but little is known about their ecology and behavior.

The only completely aquatic mammal in the North Inlet estuary is the bottlenose dolphin (*Tursiops truncatus*). They feed on fish, including mullet, sea trout, red drum, and flounder. Bottlenose dolphins are both a coastal and an oceanic species, with the coastal ecotype preferring waters less than 30

White-tailed deer (left) and feral hogs (right) are actively managed under the Hobcaw Barony Wildlife Management Plan.

meters (~98 feet) in depth. The habitats they occupy range from rocky reefs to calm lagoons and open waters. The coastal ecotype is adapted for shallow waters. Its smaller body and larger flippers suggest increased maneuverability and heat dissipation. These dolphins occur along the outer coastline and in bays, sounds, inlets, estuaries and other inland waters (Hersh and Duffield, 1990).

Although the bottlenose dolphin is the most common marine mammal along the southeastern coast, certain coastal stocks appear to be depleted based on the most recent stock assessments (Waring et al., 2002; MMC 2004). Threats to this species include natural predation, disease, parasites and natural biotoxins and human-caused factors such as incompatible coastal development practices, pollutants, vessel strikes, and debris entanglement.

A dozen or so dolphins are residents of North Inlet. Local surveys by Coastal Carolina University researchers have recognized some of the same individuals for more than 15 years, with at least one female, "Eve", producing young in the estuary multiple times. Calculations have shown that these resident dolphins consume a significant proportion of the large fish population in North Inlet (Young and Phillips, 2002). Ongoing studies of this species will provide more detailed information on their bioenergetics, social structure and behavior.

SPECIAL STATUS SPECIES

The eastern woodrat or "packrat" is a SC State Species of Concern. It can be found in wooded areas with dense understories and its dens are often occupied by a succession of individuals, each one adding more sticks and other material to the collection. Dens average 61-91 cm (24-36 inches) in height and offer protection from many predators. Woodrats store edible and non-edible material in their dens, and it is not known why the inedible materials are kept. Threats to this species likely include loss of habitat. However, only limited information is available on their status and additional potential threats.

A dozen or so dolphins are residents of North Inlet each year, including this female, Eve, and her calf.

Bobcats are documented in the uplands and marshes surrounding North Inlet, but no conclusive evidence of a jaguarundi or mountain lion has been found.

The Gulf Coast jaguarundi (*Puma yagouaroundi cacomitli*) is currently designated as endangered in its entire range. It is a native of Mexico and Texas. The presence of this ever-elusive species continues to be the catalyst for many animated debates throughout the Southeast. Many reports of a medium-sized, long-tailed cat that resembles this species have been made on Hobcaw Barony over the years , especially along roads close to the salt marsh, but except for footprints photographed at the locations of observations, the presence of this cat has yet to be fully documented. The jaguarundi is also found in Florida, although these are descendants of a small population introduced to that area in the 1940s.

Despite reports of the occurrence of the large, long-tailed Eastern mountain lion (also known as cougar or panther) throughout coastal South Carolina, its presence remains debated and denied by the SC Dept. of Natural Resources. Carcasses of cougars examined by wildlife officials have been clawless indicating the animal was likely an escapee or released by a private pet owner.

» Birds

It could be argued that the 16,000 acre Hobcaw Barony property is protected in perpetuity and that there is a National Estuarine Research Reserve here today because of birds – namely the ducks that attracted Bernard Baruch to the area and resulted in his purchasing the property in 1905 as a hunting retreat. Baruch in his autobiography (Baruch, 1957) writes:

"…I naturally grasped the opportunity that came to me in 1905 to acquire a veritable Shangri-La in my native South Carolina – famed Hobcaw Barony, whose sandy beaches and salt marshes once offered the finest duck hunting in the United States…"

Later in the chapter on Hobcaw Barony, Baruch describes a typical duck hunting experience:

"To the eastward, as the sun rose, one could see tens of thousands of ducks. At times they appeared like bees pouring out of a huge bottle. Their numbers were so great that you had to blink your eyes to be sure that you were not suffering from some illusion. As the sun mounted above the horizon, flock after flock would break away from the swamps and rice fields and come down to the marshes, flying in V formation. Nearing the marsh or hearing the call of the hunter, they would circle around and come down to the decoys. I have seen outlined in the sky the patterns of the very creeks from which the ducks rose."

Birds thus hold a special place in Hobcaw's history and have been subjects of study since the creation of the Belle W. Baruch Foundation in 1964.

Some of the first bird work conducted on the property was informal in nature – day counts, modeled a bit like Audubon Christmas Bird Counts, but much smaller in geographic scope, focusing just on the Hobcaw Barony property. Birders from around the state looked forward to the "Bellefield Annual Bird Count" where they spent the morning birding in different regions of the property and gathered for lunch and refreshments at Bellefield House at the invitation of host Ella Severin, Belle Baruch's trusted friend and resident trustee of the Belle W. Baruch Foundation. These counts, initiated in the late 60s by Dr. Harry Freeman, Professor of Biology at the College of Charleston and later picked up for a few years by the Waccamaw Audubon Society, continued into the 1980s. These once a year efforts provided snapshots of what birds were present on Hobcaw in the fall. However, to our knowledge, no attempt was made to organize and analyze the information systematically, and the count was discontinued in the late 1980s. Based on these counts, breeding bird surveys, Winyah Bay Christmas Bird Counts, and other surveys and observations made by individuals over the years, 276 species of birds have been observed in or adjacent to the boundaries of the North Inlet – Winyah Bay NERR (**Appendix H**). Rare and unusual avian visitors to North Inlet have also been documented including Sabine's Gull (Sutton et al., 1986) and Snowy Plover (Pulliam et al., 1996.)

Birds classified as endangered or threatened that breed and/or feed in or near the reserve include Wood Stork, Red-cockaded Woodpecker,

Bernard Baruch purchased the Hobcaw Barony property as a duck hunting retreat in 1905. Photo courtesy of the B.W. Baruch Foundation.

Piping Plover, Least Tern, and Bald Eagle. The entire Hobcaw Barony property is designated an "Important Bird Area" by the National Audubon Society. In addition to providing important habitat to several endangered and threatened species, Hobcaw Barony and the reserve serve as breeding habitat for many species of neotropical migratory birds, including warblers, painted buntings and shorebirds.

The first effort to systematically record bird species utilizing North Inlet occurred during the NSF-funded Outwelling Study, covered in greater detail in the water quality section for North Inlet. In the bird sub-study of the Outwelling Study, investigators designed a plan to identify and quantify birds in the estuary and calculate their contributions to energy flow in the system. Christy et al. (1981) used four methods to census bird populations in the North Inlet study area: aerial surveys twice a month along eight transects; twice a month high tide counts of communally resting shorebirds; nearly daily spot checks to monitor arrival and departure of low-density transient species; and airboat surveys to estimate clapper rail numbers. A total of 94 species of birds were recorded feeding on or over the North Inlet marsh during the period October 15, 1978 – October 15, 1979. Species numbers and numbers of individuals were greatest in spring (March-early May) and fall (July-early September.) Wading birds (Ciconiiforms) comprised more than 25% of the population in spring and made up over 60% of the spring avian biomass. In terms of energy flow, wading birds were calculated to contribute more than half of the avian-based flow in spring and summer, with the White Ibis population responsible for most of this. The contribution of wading birds to energy flow in the fall and winter was considerably less (15%) and was attributed to fewer wading birds present in the marsh in fall and greater numbers of non-wading birds, particularly shorebirds (Charadriiformes) and passerines, including migrating swallows. The authors also noted that the impact of waders on the North Inlet marsh is greatest during the breeding season when several species, including White Ibis, nest on the nearby Pumpkinseed Island in Winyah Bay.

Airboat surveys were used to estimate numbers of clapper rails as part of the Outwelling Study.

Clapper rails are one of the most abundant bird species in North Inlet marshes.

Bird surveys were continued through a second year of the Outwelling Study and yielded additional insights into the avian communities in North Inlet. Bildstein et al. (1982a) recorded 95 species of birds foraging on or over the North Inlet marsh over the two year period, October 15, 1978 – October 15, 1980. Three species, Clapper Rail, Short-billed Dowitcher, and White Ibis, comprised over half of the birds sighted on an annual basis. Species richness was greatest in the spring (March – early April) and lowest in early summer (June - early July) and late autumn (October). Clapper Rail, White Ibis and Great Egret comprised over half the avian biomass. Clapper Rails were the most abundant species in all four seasons and the largest component of the avian biomass for all seasons

except spring when White Ibis contributed more. The authors indicated that these results point to the need to concentrate future efforts on the primary contributors to the North Inlet avian community, particularly Clapper Rails and White Ibis. One question presented was whether the observed 100% increase in the rail population between April and late September is due to reproductive success of breeding birds in the region, an influx of birds from the north, or both. Another future area for research identified by the authors is the role of large breeding colonies in structuring salt marsh bird communities. They concluded by saying that although they documented the size and structure of the North Inlet marsh avian community, their study does not provide structural mechanisms. In other words, how is the community affected by neighboring avian communities and how might disturbances of these neighboring populations impact the North Inlet community? These were insightful questions that led to additional research on many aspects of the avian populations in and surrounding the reserve, particularly feeding and breeding behavior of wading birds, especially White Ibis, in future years.

Additional analysis of the shorebird component of the North Inlet avian community censused during the two-year period, 1978-1980, was conducted (Bildstein et al., 1982b.) Twenty-one species of shorebirds were sighted during the period. Seventeen of the 21 species were observed during all four seasons and five species bred on or near the study site including American Oystercatchers and Willets. Most of the species were more abundant in spring and only Sanderling and Lesser Yellowlegs were most common in winter. Dowitchers, primarily Short-billed Dowitchers, comprised 43% of all shorebirds sighted. Calculated average energy flow for the entire avian community was 9.9 kcal $m^{-2}yr^{-1}$. Shorebird calorie consumption averaged 1.3 kcal $m^{-2}yr^{-1}$ with dowitchers accounting for 41% of all shorebird caloric consumption.

These early avian community studies were incorporated into an analysis and synthesis of all parameters examined during the Outwelling Study in order to assess net material and water fluxes for North Inlet (Dame et al., 1986.) Bird census data were used to estimate density at 2.6 birds ha^{-1} and a biomass of 0.7 kg ha^{-1} dry weight. The avian community was also estimated to consume 8.1 x 10^5 kcal of food annually. It was noted that although the bird contribution to carbon export in the system (estimated at 0.05 g m^{-2} yr^{-1}) was comparatively lower than other biological components examined, birds removed quantities of material and coupled the marsh-estuarine system to other environments where they can increase nutrients around breeding and roosting colonies. They may also play a role in regulating the distribution and abundance of benthic and fish populations in the marsh-estuarine system.

Shorebird foraging and predation on benthic communities has been explored by graduate students working in North Inlet. Grant (1981c) used a bioenergetic model to examine the potential effects of predation by shorebirds (Charadrii) on a population of the burrowing amphipod *Acathohaustorius millsi* on an intertidal flat on Debidue Beach near the mouth of North Inlet. Predator and prey abundances were determined August – November 1977. Amphipods were collected in 12 cores taken monthly. Shorebirds were censused bi-weekly in a defined area on Debidue Flat where the cores were taken. Recorded species included Dowitcher, Sanderling/Peep, Semipalmated Plover, Dunlin, Black-bellied Plover, Knot and Willet. Results of the model indicated that *A. millsi* accounted for 10.4% of the caloric intake of the shorebirds at the location studied. Grant suggested that the small contribution of the amphipod to shorebird diets was related to the availability of its prey, including burrow depth, and shorebird behavior. He suggested that further prey availability studies are needed to better understand predator-prey interactions. In another study, Grant (1984) examined the relationship between sediment microtopography and shorebird predation. Dowitchers, which are tactile feeders that use their bills to probe for prey, were observed foraging on Debidue Flat on a low tide in September 1980. Dowitcher probe holes were randomly sampled on ripple crests and troughs and the depths of the probes were measured. Sediment penetrability was measured at a later date in both

ripple crests and troughs. The number of dowitcher probe marks on crests was found to be significantly higher than in adjacent troughs. Semipalmated Sandpipers which spent most of their time pecking versus probing were also observed foraging in these areas and showed no preference for crests or troughs. Penetrability tests showed that ripple troughs were significantly less penetrable than crests. Grant suggested that tactile foraging birds respond to microscale foraging cues.

Luckenbach (1984b) investigated the foraging behavior of five species of shorebirds in relation to tubes of the polychaete worm *Diopatra cuprea* on Debidue Flat in North Inlet during the summer of 1982. Benthic macrofauna composition and abundance around tubes and in tube-free areas were also determined. Of 102 foraging episodes noted, only 4 were in the vicinity of high densities of worm tubes, even though the greatest densities of prey items were around the tubes. These results supported the hypothesis that worm tubes serve as a refuge to infauna from shorebird foraging, at least for the species observed that included Willet, Least Sandpiper, Lesser Yellowlegs and two species of Dowitchers.

As mentioned earlier, Clapper Rails and waders, particularly White Ibis, were identified in the early census work to be significant avian components of the North Inlet system in terms of numbers, biomass and energy flow (Christy et al., 1981, Bildstein et al., 1982a.) Additional investigations were subsequently conducted to learn more about age and sex-related differences in foraging and flight patterns of White Ibis as well as mechanisms controlling the seasonal periods when ibises were observed feeding in the North Inlet marsh. A similar set of protocols was used in a variety of studies of White Ibis conducted in the 1980's, with observations made from a 18.5 m tower that overlooks the North Inlet marsh. Bildstein (1983) investigated age-related differences in both flocking and foraging behavior of White Ibises in North Inlet during July and August, 1980-1982. Most ibises fed in flocks and 95% of the juveniles fed in the company of adults. Juveniles hunting near adults were 47% as successful as adults on a per probe basis and caught prey at 40% of the adult rate. The author noted that even though considerable age-related differences in the feeding ecology of ibises were observed, they did not explain why the differences exist. Bildstein continued to explore these relationships in June and July of 1983 (Bildstein, 1984). Paired sequential 4-minute observations of two age classes of White Ibises (2nd year and > 2nd year birds) feeding within 5 m of each other in mixed-age flocks were made from the 18.5 m tower. Number of times a bird stepped, looked up, probed into a crab burrow or captured prey was recorded. Second-year ibises were only 50% as successful on a per-probe basis as older birds and caught prey 67% as frequently. The author compared these results to an earlier study of foraging behavior of first-year ibises which were observed to only capture prey at 40% the adult rate, thus showing a gradual improvement in foraging success of 2nd year birds. Further investigations into the foraging behavior of White Ibises feeding

The foraging behavior of White Ibis adults (left) and juveniles (right) was investigated by observation from a tower that overlooks North Inlet.

in flocks was conducted June – August in 1983 and 1984 (Petit and Bildstein, 1987.) Sequential 4 minute paired observations of adult White Ibises feeding in North Inlet marsh in four different social situations were made with spotting scopes from the 18.5 tower: central adults in large flocks (≥ 15 birds); peripheral birds in large flocks; adults in small flocks (5 or fewer birds); and solitary adults. Similar to previous studies, behaviors recorded included number of steps, number of probes into burrows or at surface crabs, number of fiddler crabs captured, number of times and total amount of time bird looked up and scanned its surroundings. In large flocks, the only significant differences in foraging behavior were that peripheral ibises looked up more often and for longer periods of time than central birds. Ibises in small flocks, single birds, and to some extent, ibises on the edges of large flocks stepped quickly to capture fiddler crabs before they could get into burrows. Even though central birds spent less time being vigilant in large flocks, they did not realize any advantage in terms of greater prey capture rates, likely as a result of depressed availability of surface crabs due to the activity of surrounding birds that caused crabs to remain in their burrows.

Petit and Bildstein (1986) examined the development of formation flying in recently fledged White Ibises in a study conducted in North Inlet June 25-September 1, 1984. Over the study period, juvenile ibises showed an increased tendency to fly in formation, from 17.8% in late June up to 88.0% in late August. Foraging differences between male and female White Ibises and energetic consequences were explored in a study by Bildstein (1987) conducted in North Inlet marsh May-July 1985 and May-August 1986. As with previous ibis behavior studies, paired 4-minute observations were made, this time of males and females foraging together in mixed flocks. To control for flock effects demonstrated in previous studies, pairs of birds feeding in larger flock peripheries or small flocks were analyzed separately from pairs feeding in the centers of large flocks. Even though male ibises have significantly longer bills (27%) than female ibises, males captured prey at similar rates to females. No significant differences were observed between males and females for any of the measured foraging parameters.

Several additional investigations and discoveries on different aspects of White Ibises and other wading birds have been made, primarily through work conducted on or in connection with what was historically a large wading bird colony on Pumpkinseed Island in Winyah Bay. These studies are treated separately in the bird section of the chapter covering Winyah Bay.

Although birds were not shown to be a significant direct contributor to nutrient exchange or energy flow relative to other measured biological components (Christy et al. 1981), they can serve to link ecosystems. In order to explore this idea, Bildstein et al. (1992) compared the annual inputs of nitrogen, phosphorus, potassium and calcium from atmospheric, stream flow, and ibis sources at the colony site in Winyah Bay to North Inlet over a two year period. Total amounts of nutrients contributed by ibises varied considerably between years, largely as a result of significantly lower numbers of nesting ibises in 1985 versus 1984. Results also showed that nutrient inputs to estuaries from colonial nesting birds can be substantial compared to atmospheric sources.

Marsh harrier behavior, specifically inter- and intra-specific aggressive interaction of Northern Harriers was studied over four winters between 1979 and 1984 (Bildstein and Collopy, 1985.) Northern Harriers escort flight behavior was observed in two different locations and habitats during these winters: North Inlet salt marsh in South Carolina and the Paynes Prairie, a freshwater marsh prairie in Florida. “Escorting flight” was defined as two birds flying in tandem within 50 m of one another with the trailing bird turning at least once to follow the leading bird. The sizes of the hunting ranges were also determined for five individuals. In both SC and FL, most individuals maintained areas of exclusive use for several hours up to 15 days (maximum period of continual observations.) In SC, exclusive areas averaged 70 ha. Harriers in the North Inlet marsh spent 4.3% of their time engaged in escorting flight behavior with other harriers

compared to 4.1% in the Florida freshwater prairie system. South Carolina harriers were also observed to attack Red-tailed Hawks 13 times, Peregrine Falcons twice and a Cooper's Hawk once. High-speed chasing and stooping were much more common in inter-specific interactions than intra-specific interactions. During these five winters, the same investigators also examined the foraging behavior of Northern Harriers (Collopy and Bildstein, 1987). They compared foraging behavior, hunting success and diet of harriers. They recorded the time birds spent perching, hunting in flight, soaring, carrying prey, and feeding. The method of hunting, number of pounces and prey species were also recorded. Five types of pounces were observed. Harriers in the North Inlet marsh spent 33.8% of their time hunting compared to 27.2% for the Florida birds. North Inlet harriers captured prey on 15.1% of their pounces while Paynes Prairie harriers were successful on 5.8% of their attempts. The difference in hunting success between the two populations of overwintering harriers was explained by differences in prey. Harriers in North Inlet captured small and medium sized birds exclusively (rails and sparrows) while harriers in the Paynes Prairie were observed catching cotton rats. The authors concluded that habitat and prey base influence the foraging behavior and hunting success of harriers.

Comparatively little bird research has occurred in North Inlet in the last two decades compared to the activity that occurred in the 1980s, largely as a result of principal investigators moving to other regions of the country and the lack of others filling this niche. However, the North Inlet – Winyah Bay NERR has been involved in regular surveys of some species, including annual censuses of Piping Plovers that overwinter in South Carolina and Wilson Plovers that nest on area beaches in the spring. The south end of Debidue Beach and all of North Island are within the reserve boundaries. The South Carolina Department of Natural Resources (SCDNR) coordinated state-wide surveys of Wilson's Plovers in 2009 and 2010. Three breeding pairs of Wilson Plovers were reported to nest on Debidue Beach in 2009 and zero in 2010 while 26 and 23 pairs nested on North Island in 2009 and 2010, respectively (F. Sanders, personal communication.)

The American Oystercatcher, *Haematopus palliatus*, is classified by SCDNR as a Species of Concern (SCDNR, 2005) and has been the focus of recent monitoring and conservation efforts by the agency. SCDNR conducted surveys of wintering American Oystercatchers in South Carolina (Sanders et al., 2004) and assessed breeding season abundance and distributions of American Oystercatchers in the state (Sanders et al. 2008.) Surveys conducted over three winters, 1999-2002, found oystercatcher numbers to be relatively stable ranging from 3,327-3,734. The greatest concentrations of oystercatchers were observed between the Cape Romain National Wildlife Refuge and Dewees Inlet (Cape Romain Region) and accounted for 51-57% of the state totals over the three years. North Inlet oystercatcher numbers ranged between 100 and 200 each year. Breeding season surveys of oystercatchers were conducted by SCDNR, 2001-2003. A mean of 1,105 oystercatchers were recorded each year. Breeding pairs numbered 407 and 397 in 2002 and 2003, respectively, with 57% of the birds nesting in the Cape Romain Region. Oystercatchers in North Inlet totaled 22, 41 and 63 in 2001, 2002 and 2003, respectively, with 14 nesting pairs recorded in both 2002 and 2003. Nesting areas traditionally used by American Oystercatchers and other beach nesting birds in North Inlet are posted and roped off each nesting season to discourage people (and their dogs) from walking through the area. SCDNR scientists and NERR staff also record sightings of banded, color-marked individuals. To date, observations of marked oystercatchers have demonstrated that North Inlet is used by birds banded as nestlings in Virginia, North Carolina and Georgia. American Oystercatchers with colored bands have been observed and recorded with a webcam mounted at the Oyster Landing pier near the Baruch Marine Field Laboratory.

The NI-WB NERR initiated a secretive marsh bird monitoring effort in spring 2009 to assess distribution and relative abundances of Clapper Rails, *Rallus longirostris*, in the marshes of North Inlet. Reserve staff and volunteers counted Clapper Rails along routes using a standardized call broadcast method developed by the U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit

Bird nesting areas in the reserve are roped off by the SCDNR each nesting season.

Volunteers help to monitor secretive marsh birds by listening for their calls following a standardized procedure.

(Figure 87). The Reserve also serves as a banding location for Painted Buntings. This is part of a citizen science project coordinated by a researcher at the University of North Carolina-Wilmington.

Marsh sparrows have also been the focus of recent studies initiated by investigators from the University of Connecticut and Coastal Carolina University. One study is designed to examine the migration patterns, survival and condition of tidal marsh sparrows. Another is looking at the relationship of marsh sparrow abundances at different sites in the North Inlet-Winyah Bay NERR to marsh characteristics. All recently initiated bird studies that have not yet resulted in publications are more fully described in the Current Research, Monitoring, and Education Projects 2012. This publication is updated annually by the Baruch Marine Field Laboratory in cooperation with the NI-WB NERR and is available electronically on the Baruch Institute website: www.baruch.sc.edu.

Although a great deal of avian research and monitoring has occurred in North Inlet in the past, especially in the 1980s, there are many opportunities for additional studies. The North Inlet – Winyah Bay NERR provides an excellent location for survey work and investigations on birds and their roles in coastal ecosystems.

Seaside sparrows inhabit the marshes of North Inlet.

Figure 87. Secretive marsh bird census locations in the North Inlet-Winyah Bay NERR

A webcam mounted at the Oyster Landing pier provides a peek at a popular roosting spot for birds during high tide and has been used to document the appearance of banded birds, including the American Oystercatchers, L1 and M7 (right).

» Insects

Although ubiquitous, seasonally abundant, and also annoying at times, the insect population in the NI-WB NERR is poorly understood. No comprehensive surveys and only a few scientific studies have been conducted. It is likely that many of the species found in similar estuarine habitats in North Carolina and Georgia as reported by Luckett Davis in *An Annotated Checklist of the Biota of the Coastal Zone of South Carolina* (Zingmark, 1978) also occur here. Davis's species list could provide a foundation for future insect survey work in the North Inlet-Winyah Bay region.

A field entomology class from the University of Guelph in Canada visited the Hobcaw Barony property in spring of 2004. A list of species that they collected and identified during this field course is included as **Appendix I**. Most of their collections were made on the upland portions of the property, with an emphasis on acalyptrate Dipterans (a subset of flies), Hymenoptera (bugs), and certain beetles of the order Coleoptera. They reported state records of the following species: *Panagagaeus crucigerus* (Carabidae), *Dirrhagofarsus lewisi* (Eucnemidae); *Abedus immaculatus* (Belostomatidae), *Proxius gypsatus* (Aradidae), *Otiocerus degeeri* (Derbidae), *Otiocerus stolli* (Derbidae), and *Cyarda melichari* (Flatidae) found in relatively large numbers in high marsh shrubs and *Juncus*. They also reported state records for the following reduviids: *Apiomerus crassipes*, *Melanolestes picipes*, *Phirontis modesta*, *Pselliopus cinctus* and *Repipta taurus*.

North American Butterfly Association Butterfly Counts have been conducted on the Hobcaw Barony property, including the North Inlet and Winyah Bay portions of the NERR, every year since 1993. More than eighty-five species of butterflies have been observed on Hobcaw Barony during these counts and at other times (**Appendix J**). Some of these species are salt marsh dependent, laying their eggs on marsh host plants. For example, the Eastern Pygmy-Blue, the smallest butterfly in North America, uses salt marsh glasswort, *Salicornia* spp., as its host plant. Saltgrass, *Distichlis spicata,* is the caterpillar host plant for the Salt Marsh Skipper.

More than 85 species of butterflies have been documented on the Hobcaw Barony property, including the Juniper Hair-streak (top), Eastern Pygmy-Blue (bottom).

Phaon Crescents are another special coastal species and have been observed necturing on *Lippia* plants near salt marsh and beach habitats in the Reserve.

Signficant herbivory of *Juncus roemerianus*, *Iva frutescens*, and *Spartina alterniflora* was observed in summer 2003 and also summer 2004 in several areas of the North Inlet salt marsh (W. Allen, pers. ob). At least three different species of grasshoppers were very abundant and were observed grazing on the marsh vegetation. Some *Iva* plants were completed stripped of their leaves and did not recover by the next year.

Several NERR sites, including the NI-WB NERR, have served as platforms for research on the latitudinal variation of herbivores and plant-herbivore interactions in salt marshes. Wason and Pennings (2008) examined the latitudinal variation in composition of tettigoniid grasshoppers in salt marshes along the Atlantic coast. Two sites in the North Inlet-Winyah Bay NERR were sampled in this study that spanned from Florida to Maine. Eight species of grasshoppers were collected and identified from the *Spartina alterniflora* zone, with *Orchelimum fidicinium* dominating the community at low latitudes and *Conocephalus spartinae* dominating at high latitudes. In another study, Pennings et al. (2009) examined latitudinal variation in herbivore pressure in Atlantic Coast salt marshes using three different approaches: herbivore counts, leaf damage assessments and transplant experiments. Herbivores were sampled in different salt marsh vegetations zones and included several species of insects, gastropods, a mite and a decapod crab. Results of herbivore counts showed that chewing herbivores and gall makers were more abundant at lower latitudes. Chewing herbivore damage to plants was also greater at low versus high latitudes. In transplant experiments, plants transplanted to low latitude sites experienced two orders of magnitude more herbivore damage than plants transplanted to high latitude sites. Although distinct latitudinal differences in herbivory were observed, results varied with herbivore feeding guild. The authors suggested that future studies would benefit from comparisons of herbivores from different feeding guilds.

Significant insect herbivory of salt marsh plants has been observed in North Inlet marshes, but research is needed to better understand the role of insects in marsh food webs.

Areas for future work on insects are wide open, given the limited extent of our knowledge not only on species composition, but on the role insects are playing in the North Inlet and Winyah Bay systems. Insects can be significant consumers of marsh primary productivity and are important links in marsh food webs. Additional research is needed to better understand these interactions.

» Invasive Species

Approximately 42% of Threatened or Endangered species are at risk due to invasive species (Pimentel et al., 2005). The National Invasive Species Management Plan defines invasive species as, "an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health" (National Invasive Species Management Council, 2008). Many non-native species are non-invasive and can even be beneficial to the ecosystem and humans. This section will briefly describe species considered to be invasive, as defined above, which have either been documented as occurring in North Inlet or are considered a future threat to the area. Table 10 contains a list of invasive animal species and Table 11 lists invasive plant species that have been documented in the South Carolina coastal region.

MARINE INVERTEBRATES

There are an estimated 500 alien marine species within the coastal waters of the US. Marine species are spread beyond their native ranges though shipping related causes, such as ballast water transfer and hull fouling, and also through the transport of fishing and diving gear and recreational boat traffic. In some cases, invasions have occurred as a result of both intentional and unintentional releases of species from mariculture, aquariums, and live seafood and fish bait trades. The environmental impacts of invasive marine invertebrates include

the loss of biodiversity due to preying upon native species, decreased habitat availability and increased competition for native species, the introduction of parasites and disease, and in some cases, through smothering and overgrowth of natives. Economic impacts of marine invasive species are well documented, and include the interference with fisheries through fouling or tearing of nets, damage to infrastructure through fouling of pipes, wharves, buoys etc., disruption to tourism, and the costs of clean up, control, and treatment or quarantine. To date, there has been no successful eradication of invasive marine invertebrates in the United States (Benson, 2014).

Although no major shipping or commercial fishing occurs within North Inlet, the introduction of marine invasive species is a concern due to water exchange with Winyah Bay where these activities do occur, as well as the potential for introductions through recreational uses of North Inlet. No long-term monitoring directly targeting marine invasive species has occurred within North Inlet. Settlement substrates were placed at Oyster Landing and Clambank Creek in 2007 for a DNR study of green mussel (*Perna viridis*) recruitment. Most records of marine aquatic invasive species in the area are the result of incidental catch.

The Asian tiger shrimp, *Penaeus monodon*, was reported in North Inlet in 2013 (NAS …[cited 2014]). Mature tiger shrimp can be distinguished from native penaeid shrimp by their overall rusty brown color and the distinctive black and white banding across the back and on the tail. This species, native to the Indo-West Pacific oceans, has a rapid growth rate and broad tolerance to salinity (2-30) that have contributed to the success of this species in aquaculture, however, these are also characteristics that enable it to invade new areas. (FAO, 2014; McCann et al., 1996). Tiger shrimp are currently found from North Carolina to Texas, and nearly 300 tiger shrimp were collected off the coast of South Carolina, Georgia and Florida in 1988 over three months after an accidental release of roughly 2,000 animals from an aquaculture facility in South Carolina (NAS …[cited 2014]). The impacts of this invasive shrimp on the native fauna in areas where it has been introduced are uncertain. The tiger shrimp has been shown to be a more aggressive predator on soft-bodied invertebrate benthic organisms than native shrimp, feeding primarily on small crabs, shrimp, bivalves and gastropods (Marte, 1980).

The titan acorn barnacle, *Megabalanus coccopoma*, was first collected from South Carolina waters in the Folly River, near Charleston Harbor, in the fall of 2006, and was found in a seawater intake pipe at Oyster Landing in 2011. This large, pink barnacle, native to the eastern Pacific, grows to around 5 cm in height and can attain a body mass 100 times greater than that of native species (Tibbetts, 2007). Water temperatures may prevent its permanent establishment in South Carolina, and population die offs in the winter of 2009-10 are suspected to be the result of low water temperatures. (SC DNR, 2014).

The green porcelain crab, *Petrolisthes armatus*, was first observed in South Carolina in low densities in the spring of 1995 and has been reported as far north as Murrells Inlet in 2000. Hartman (2003) found fluctuations in the population of *P. armatus* from 300 to 0 individuals/m^2 in North Inlet over a three-year study. Seasonal temperature changes appeared to be the major reason for population changes.

The Indo-Pacific Swimming Crab, also known as the spiny hands crab, *Charybdis hellerii*, was discovered by staff of the Southeastern Regional Taxonomic Center at the Marine Resources Research Institute in Charleston, SC in 2001. It was collected in 2002 in Town Creek in North Inlet (SERTC, 2014).

The green porcelain crab, *Petrolisthes armatus.*

The Asian green mussel, *Perna viridis*, has not been documented in North Inlet, but was discovered in South Carolina in 2006 on a settlement panel in the Folly River. Subsequent surveys in 2007 and 2008 by SC DNR of four sites from Murrells Inlet to Port Royal Sound only found 9 live mussels in Folly River. Mussels have been found incidentally in seawater intake pipes and vessel hulls in the Charleston area, suggesting that a much greater source of propagules is available along the South Carolina coast. The northern expansion of this tropical species is constrained by low water temperatures, although there is no consensus on where this thermal tolerance will be reached along the east coast of the United States. Initial predictions suggested it would not survive north of Georgia (Baker et al., 2002), however, Knott et al. (2008) found a population that persisted for two years in the Folly River. In addition to hull fowling and clogging intake pipes, *P. viridis* may out-compete the commercially important native eastern oyster, *Crassostrea virginica*, and little is known about the biodiversity associated with *P. viridis* patches compared to *C. virginica* (Firth et al., 2011).

INSECTS AND DISEASES

The redbay ambrosia beetle, *Xyleborus glabratus*, bores through the bark of trees and introduces a fungus that causes laurel wilt, a disease that can kill several tree species in the Lauraceae family, including the redbay, *Persea borbonia*. Redbay is the primary food source for the Palamedes Swallowtail caterpillar, and a large component of the coastal forest understory. The fungus is extremely fast-acting and trees typically die within a month after being infected. In the areas where the beetle has been found, there can be a loss of up to 90% of redbay (SCFC, 2012). The beetle is believed to have been introduced into Georgia in 2002 by infested packing materials, such as wooden crates and pallets (Thomas, 2007). In 2003, significant redbay mortality on Hilton Head Island, South Carolina, was reported to the South Carolina Forestry Commission, and by 2011 redbay mortality was confirmed in 11 South Carolina Counties (SCFC, 2012). Laurel wilt was confirmed in Georgetown County and on the Hobcaw Barony property in 2012.

The kudzu bug, *Megacopta cribraria*, a close relative of the stink bug, was first seen in Georgia in October of 2009 and has now spread throughout Georgia, South Carolina, and other southern states. Kudzu bugs feed on kudzu and on many other legumes such as wisteria and soybeans. The large number of kudzu bugs and the foul odor attributed to their secretions make them a nuisance around buildings and other structures. Kudzu bugs were observed in large numbers adjacent to the Reserve headquarters in 2012

The kudzu bug is considered a nuisance around buildings and structures due to its fowl odor. It is unknown what impact this species may have on agriculture.

VERTEBRATE ANIMALS

Feral swine may be the most destructive of the invasive species found on Hobcaw Barony. Introduced by European settles in as early as the 1600s, escaped and free ranged swine were documented to be one of the primary causes for longleaf pine regeneration failures as early as the 1930s. Swine compete with native species for forage, as well as causing extensive damage to understory plants through their rooting and feeding activity. The disturbance caused by this rooting activity may contribute to the spread of invasive plant species such as *Phragmites* and chinese tallow tree that can quickly colonize disturbed sites. Swine are also a major predator of native wildlife including ground nesting birds, amphibians, and even sea turtles through nest predation.

Coyotes first appeared in South Carolina about 30 years ago and continue to expand greatly in numbers and are currently found in every county in the state. Sea turtle nest depredation by coyote has become a concern on North Island and neighboring beaches.

AQUATIC PLANTS

The red alga, *Gracilaria vermiculophylla*, is an invasive alga native to Southeast Asia that has invaded many estuaries in North America and Europe. The presence of *G. vermiculophylla* on the east coast of the USA from Massachusetts to South Carolina has been confirmed using molecular techniques (Gulbransen et al., 2012). In North Inlet, *G. vermiculophylla* blooms and declines seasonally. *G. vermiculophylla* reaches its peak abundance in the early summer and declines in abundance through the fall. By winter, it is absent from the intertidal mudflat. During this time and into the spring, the diversity of other seaweed species increases in North Inlet. By mid spring, *G. vermiculophylla* is once again present and other seaweed species decline in abundance. By the summer, *G. vermiculophylla* is the dominant, greatly abundant seaweed in North Inlet, where it can be found covering the lower mudflat. Though negative relationships between *G. vermiculophylla* abundance and the abundance of other seaweed species has been found in seaweed communities elsewhere in the world, there has not been sufficient research at this time to suggest that the patterns of abundance observed in North Inlet are the result of direct competition between the non-native *G. vermiculophylla* and other seaweed species (Lindsay Haram, personal communication).

The common reed, *Phagmites australis*, occurs in tidal salt and fresh, non-tidal and upland habitats throughout large parts of Canada and the entire continental US. Although it has been a minor component of North American wetland plant communities for thousands of years, it has become a dominant species in the past century and both genetic and environmental arguments have been made to explain the recent range expansion. The loss of biodiversity and habitat as native plants are replaced by monotypic stands of *Phragmites* is of concern. No formal mapping effort of *Phragmites* in North Inlet has been completed, but it is known to occur in the ditches near the Reserve headquarters at the Baruch Marine Field Laboratory. In July 2012, Mozdzer and Neubauer investigated how methane emissions and net ecosystem exchange are altered with *Phragmites australis* invasion in tidal fresh and brackish marshes of North Inlet (Mozdzer, personal communication). Mozdzer worked in *Phragmites* invaded brackish marshes by Marsh Rd and in an oligohaline marsh near Barnyard Village on Hobcaw Barony. At these sites, Mozdzer and Neubauer found that methane emissions were three fold higher than adjacent native vegetation. These changes in methane emissions have important implications with respect to the carbon balance of tidal wetlands. While tidal wetlands have been described as "blue carbon" pools due to their ability to sequester disproportionately more carbon than terrestrial ecosystems, changes in species composition, like *Phragmites* invasion, can result in increased methane emissions which can potentially change the radiative forcing of the ecosystem.

VASCULAR PLANTS

In the early 1990s, the woody shrub beach vitex, *Vitex rotundifolia*, was planted for erosion control on South Carolina beaches, but by the mid-1990s plant specialists began to notice beach vitex spreading on state beaches where it was crowding out native species like sea oats. A workshop was hosted by the North Inlet-Winyah Bay National Estuarine Research Reserve in 2003 to address concerns about the spread and possible impacts of the plant on loggerhead sea turtle nesting. This workshop brought together private citizens, personnel from state and Federal agencies, and representatives from non-profit organizations, resulting in the formation of the South Carolina Beach Vitex Task Force, which later became simply the Beach Vitex Task Force after North Carolina and Virginia joined the effort. In 2004, the Task Force received a National Fish and

Beach vitex can rapidly colonize dunes, reducing plant diversity and adversly impacting sea turtle nests.

Wildlife Foundation grant to begin removal of the plants. Clemson University researchers performed experiments to determine the best herbicide and application method, and personnel began removing *Vitex* and replanting dunes with native vegetation. From 2003 to 2011, the Task Force received over $800,000 in grants from a diverse group of stakeholders including the National Fish and Wildlife Foundation, US Fish and Wildlife Service, Natural Resources Conservation Service (NRCS), Town of Pawleys Island, the Donnelley Foundation and the Bunnelle Foundation. Through the Task Force's education and outreach efforts, ordinances banning beach vitex have been passed in a number of NC and SC beach communities. A GIS data base of occurrences, reported by volunteers through a web site maintained the Reserve, and through SCDNR and NRCS survey efforts, is currently maintained by NRCS.

Chinese tallow tree, *Triadica sebifera*, was initially introduced to South Carolina in the 1700s. It commonly occurs on disturbed sites such as spoil banks, roadsides, agricultural lands, urban areas, and storm-damaged forests. It is considered a severe threat in the piedmont and coastal plain regions of South Carolina due to its displacement of native species through vigorous growth and spread. No formal mapping or eradication effort of tallow has been done adjacent to North Inlet, but tallow trees are found throughout the uplands surrounding the Reserve.

RESEARCH AND EDUCATION EFFORTS

No formal survey or mapping efforts of invasive species within the NI-WB NERR have been conducted to date. This remains an important research and management need, especially as climate change is predicted to increase the distribution and impact of many invasive species. The reserve partnered with the North Carolina, ACE Basin, and Sapelo Island NERRs on a project to work with the nursery industry to prevent the sale of invasive landscape plants. The project began in 2012 with a series of interviews with growers and nursery owners to better understand the barriers to preventing the sale of invasive plants and promoting the use of native plants in landscaping. The next step of the project will be to develop an outreach plan to educate homeowners about invasive landscape plant species and native alternatives.

Table 10. Invasive invertebrate and vertebrate animal species occurring in the South Carolina coastal region. Species that are known to occur in North Inlet, Winyah Bay, or the adjacent Hobcaw Barony uplands are in **bold**.

Marine Invertebrates			
Charybdis hellerii	**spiny hands crab**	*Perna viridis*	Asian green mussel
Haplosporidium nelson	**MSX, an oyster disease**	***Petrolisthes armatus***	**green porcelain crab**
Megabalanus coccopoma	**titan acorn barnacle**	*Phyllorhiza punctata*	Aust. spotted jellyfish
Molgula manhattensis	**sea grape**	*Styela plicata*	rough sea squirt
Mytella charruana	charrua mussel	*Synidotea laevidorsalis*	Isopod
Penaeus monodon	**Asian tiger shrimp**		
Insects			
Aedes albopictus	Asian tiger mosquito	*Ochlerotatus japonicus*	Asian mosquito
Megacopta cribraria	**Kudzu bug**	***Xyleborus glabratus***	**Redbay ambrosia beetle**
Vertebrate Animals			
Canis latrans	**coyote**	*Pterois volitans*	Red Lionfish
Dasypus novemcinctus	Nine-banded armadillo	***Sus scrofa (feral type)***	**Feral pig**
Myocastor coypus	Nutria	*Trachemys scripta elegans*	Red-eared slider

Table 11. Invasive plant species occurring in the South Carolina coastal region. Species that are known to occur in North Inlet, Winyah Bay, or the adjacent Hobcaw Barony uplands are in **bold**.

Aquatic Plants			
Alternanthera philoxeroides	**Alligatorweed**	*Ludwigia uruguayensis*	Water primrose
Gracilaria vermiculophylla	**Red algae**	***Phagmites australis***	**Common reed**
Egeria densa	Brazilian elodea	*Pistia stratiodes*	Water lettuce
Eichhornia crassipes	Water hyacinth	*Salvinia molesta*	Giant salvinia
Hydrilla verticillata	Hydrilla		

Vascular Plants			
Ailanthus altissima	Tree of heaven	*Lespedeza bicolor*	Two Color Bush Clover
Albizia julibrissin	**Mimosa, Silktree**	*Lespedeza cuneata*	Sericea
Arundo donax	**Giant Reed**	***Ligustrum* spp.**	**Privet**
Broussonetia papyrifera	Paper Mulberry	*Lonicera fragrantissima*	Sweet Breath of Spring
Carduus nutans	Nodding Thistle	***Lonicera japonica***	**Japanese Honeysuckle**
Celastrus orbiculatus	Asian/Oriental Bittersweet	*Lygodium japonicum*	Japanese Climbing Fern
Cinnamomum camphora	**Camphortree**	***Melia azedarach***	**Chinaberry**
Cirsium vulgare	Bull Thistle	*Microstegium vimineum*	Japanese Stilt Grass
Clematis terniflora	Yam-leaved clematis	*Miscanthus sinensis*	Chinese Silvergrass
Crotalaria spectabilis	**Showy Rattlebox**	*Morus alba*	White Mulberry
Cytisus scoparius	Scotch Broom	*Murdannia keisak*	Wart Removing Herb
Daucus carota	Queen Anne's Lace	*Panicum repens*	Torpedo Grass
Dioscorea polystachya	Chinese yam, Air potato	*Paspalum dilatatum*	Dallis Grass
Elaeagnus pungens	**Thorny-olive**	***Paspalum notatum***	**Bahia Grass**
Elaeagnus umbellata	Autumn-olive	*Paspalum urvillei*	Vasey's Grass
Eragrostis curvula	Weeping Love Grass	*Paulownia tomentosa*	Princess Tree
Festuca arundinacea	Tall Fescue	*Phyllostachys aurea*	Golden Bamboo
Firmiana simplex	Chinese Parasol Tree	*Polygonum cuspidatum*	Japanese Knotweed
Hedera helix	**English Ivy**	*Poncirus trifoliate*	Trifoliate Orange
Imperata cylindrical	Cogongrass	*Populus alba*	White Poplar
Pueraria montana	**Kudzu**	*Sorghum halepense*	Johnson Grass
Rosa bracteata	Macartney Rose	*Spiraea japonica*	Meadowsweet
Rosa laevigata	Cherokee Rose	*Tamarix ramosissima*	Saltcedar
Rosa multiflora	Multiflora Rose	***Triadica sebifera***	**Chinese Tallow Tree**
Securigera varia	Purple Crownvetch	*Vinca major*	Bigleaf Periwinkle
Sesbania punicea	Rattlebox	*Vinca minor*	Common Periwinkle
Solanum pseudocapsicum	Jerusalem Cherry	***Vitex rotundifolia***	**Beach Vitex**
Solanum viarum	Tropical Soda Apple	***Wisteria sinensis***	**Chinese Wisteria**

Winyah Bay's Major Biota

» Primary Producers

Few studies pertaining to primary producers in Winyah Bay have been conducted, especially in comparison to North Inlet. Those that have been done involve phytoplankton and vascular plants and are summarized below. No studies on benthic microalgae or macroalgae were found for Winyah Bay in the literature search for this summary document.

PHYTOPLANKTON

Chlorophyll *a* has been measured in the NI-WB NERR 20 day water chemistry program at the SWMP sites since 1994. At the Thousand Acre Marsh location in Winyah Bay, chlorophyll *a* concentrations during July 3-4, 2010 were lowest during low tide and highest at high tide (Figure 88). This tidal pattern did not vary much between day and night.

Short-term variability was greatest during summer when there were up to 8-fold differences in the minimum and maximum values during single 26-hour collection periods (Figure 89). The June and August peak values of 80 to more than 100 mg L^{-1} are very high concentrations for the brackish portion of an estuary. In general, chlorophyll *a* was highest during summer and lowest from December to April, but low summer values were equivalent to high winter values.

No long-term trend was evident for chlorophyll *a* at the Thousand Acre Marsh site; however, summer and fall levels from 1994-96 and 2004-10 were generally higher than those from 1997-2003 (Figure 90). Interannual variations in chlorophyll *a* at this site did not correspond to patterns of salinity or river runoff, perhaps because of the alternating influence of the adjacent shallow marsh and creeks during ebbing tides and the exchange with the Mud Bay section of the larger estuary during flooding tides.

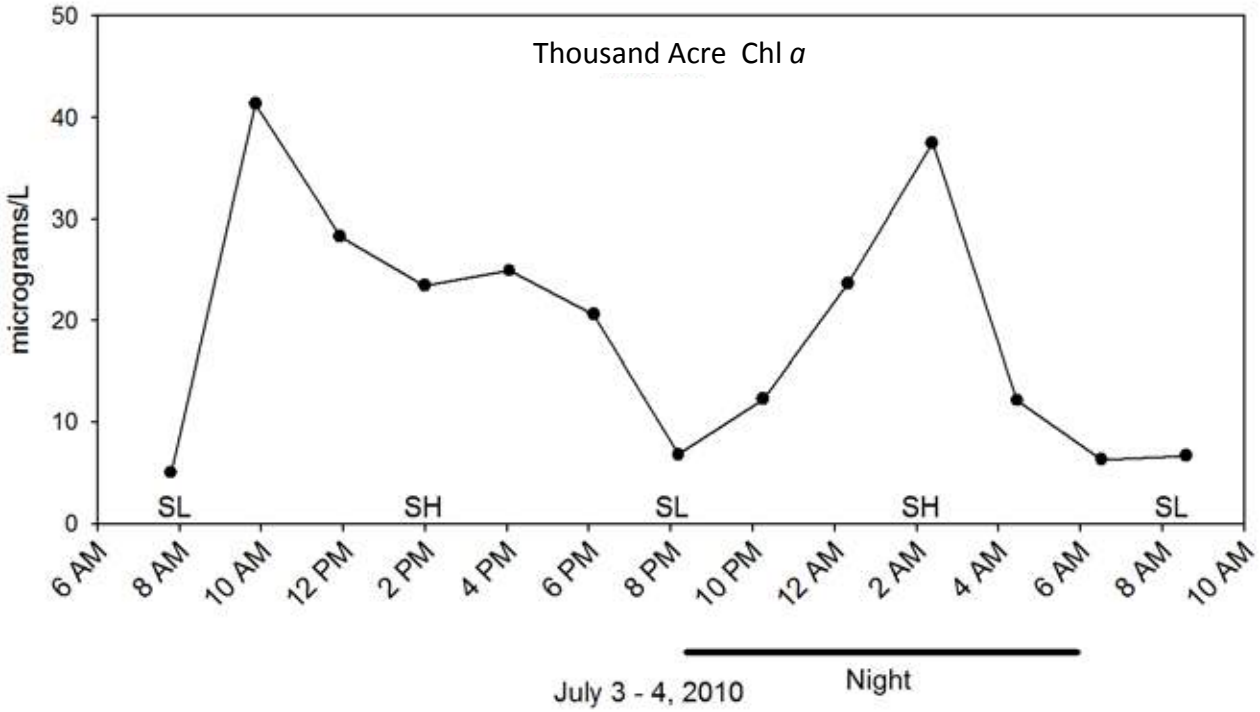


Figure 88. Chlorophyll *a* concentrations in water samples collected every hour July 3-4, 2010 at the NI-WB NERR SWMP Thousand Acre Marsh monitoring site.

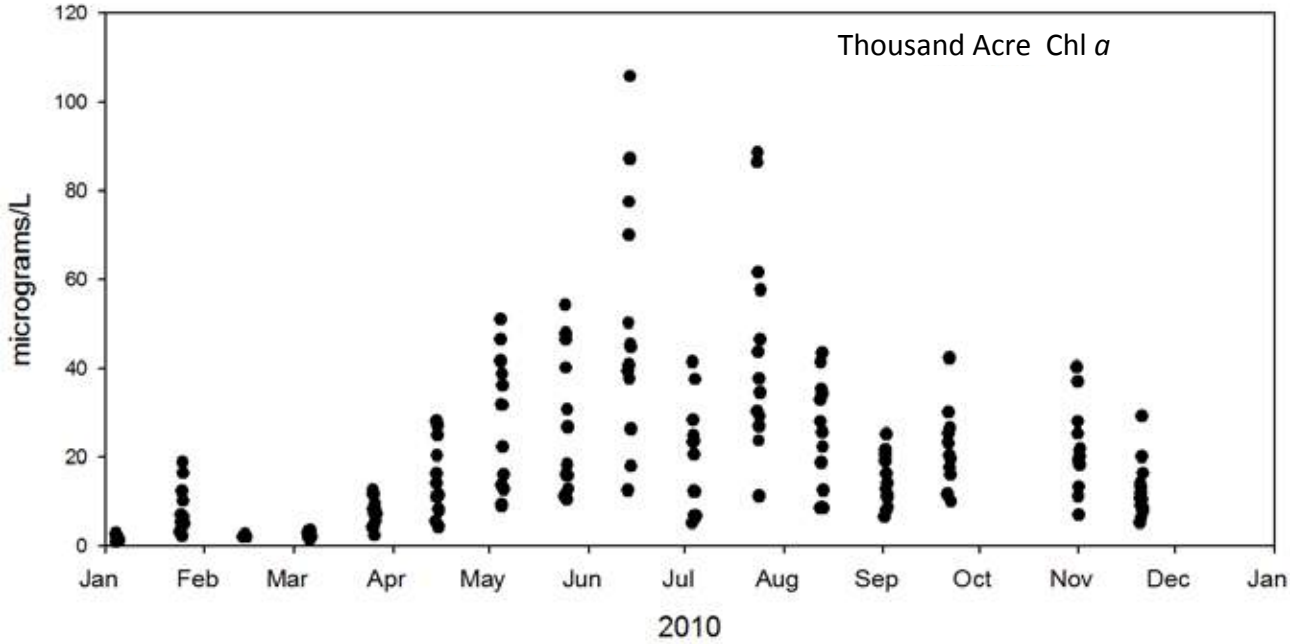


Figure 89. Chlorophyll *a* concentrations in water samples collected every hour during the 20 day samplings in 2010 at the NI-WB NERR SWMP Thousand Acre Marsh monitoring site.

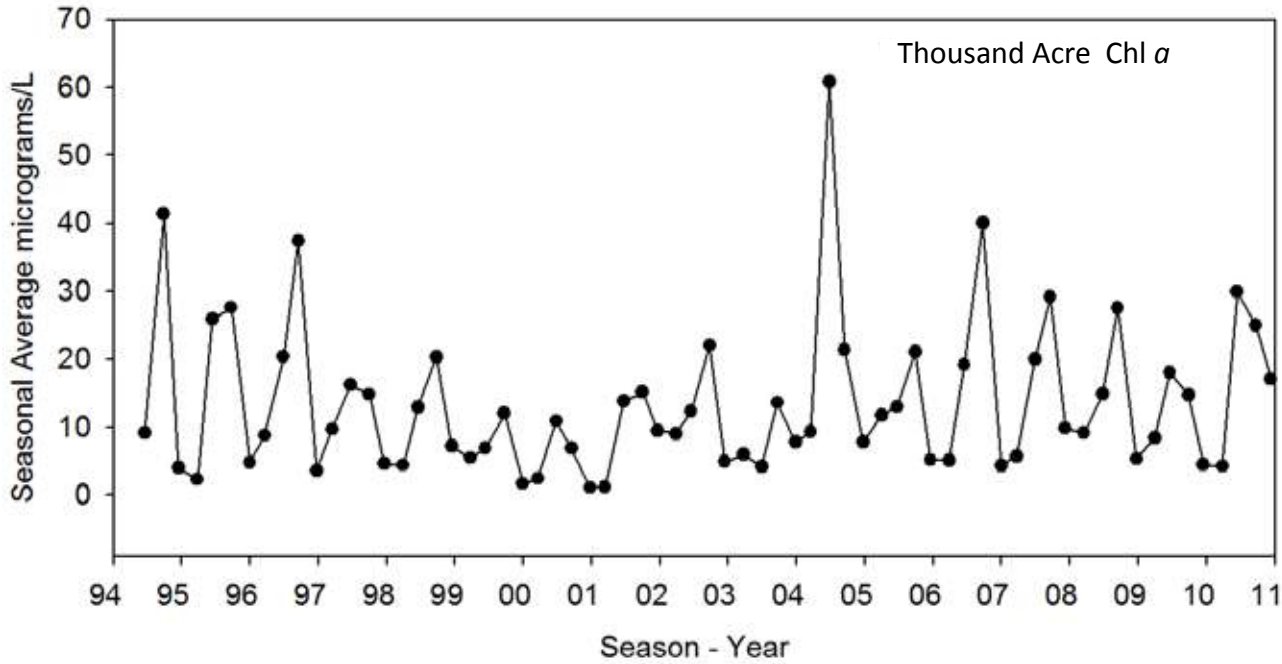


Figure 90. Mean seasonal chlorophyll *a* concentrations in water samples collected from 1994-2010 at the NI-WB NERR SWMP Thousand Acre Marsh monitoring site.

SUMMARY OF OTHER STUDIES ON PHYTOPLANKTON IN WINYAH BAY

Compared to North Inlet, the phytoplankton community in Winyah Bay is considerably less studied. As part of a state-wide study, the SCECAP program (Dept. of Natural Resources) occasionally measures chl-*a* concentrations at various stations in the bay. A volunteer water sampling effort associated with the Winyah Rivers Foundation measures chlorophyll and other water quality parameters at river parks in the upper Bay. Ranhofer (2009) and Ranhofer et al. (2009) studied the role of nutrient limitation. Lawrenz et al. (2010) and Lawrenz (2011) investigated the role of light as a control on community composition.

Ranhofer's (2009) dissertation research involved the phytoplankton's utilization of dissolved organic phosphorus via expression of alkaline phosphatase, a hydrolyzing extracellular enzyme, using a cell-specific enzyme-labeled fluorescence assay. These investigations were run using *in situ* nutrient-addition bioassays and laboratory time-series experiments with cultures representing five different taxa. Lastly, she investigated how the presence of humic acids affects the ability of the phytoplankton to utilize phosphomonoesters as a source of phosphorus.

Ranhofer et al. (2009) found that diatoms dominated both the riverine site (at the confluence of the Pee Dee, Waccamaw, and Black Rivers) and the coastal site just between the jetties at the entrance to Winyah Bay. Nitrogen limitation existed at each site: in May at the coastal station, and in August at the riverine station. Phosphate limitation was not demonstrated at either site. The expression of the enzyme occurred in a range between 30% and 1% of the cells and only in cells with low abundance. The general lack of either N or P limitation suggested that riverine input of these elements was high. Their work pointed to the need for more study of the role of the dissolved organic phosphorus pool and its utilization in Winyah Bay. Those interested in the topic of nutrient supply and pollution in Winyah Bay should consult Kucklick and Bidleman (1994a, b), Krest et al. (2000), Eddins (2001), Goni et al. (2003), Buzelli et al. (2004), and the SCECAP website.

Lawrenz's dissertation (2011) involved the study of CDOM, chromophoric or colored dissolved organic matter's effects on water color and hence on phytoplankton community composition in Winyah Bay. She found that cryptophytes dominated in upstream portions of the bay when wind-mixing was low; otherwise, diatoms dominated. Cryptophytes and cyanobacteria harvested light more efficiently than diatoms or chlorophytes in blackwaters containing high amounts of CDOM. Their earlier paper (Lawrence et al., 2010) is basically the text from Chapter 3 of her dissertation. The other chapters relate to species-specific studies of fluorescence (Lawrenz and Richardson, 2011) using natural phytoplankton populations from Winyah Bay, extraction protocols for phycobilins, underwater light fields and phytoplankton community composition in North Inlet, with a model of spectral irradiance, light absorption, and vertical mixing.

VASCULAR PLANTS

The baseline habitat map developed for the North Inlet-Winyah Bay NERR (Figure 65), presented at the beginning of this Ecological/Biological Setting chapter, indicates that much of the Winyah Bay portion of the NERR is comprised of high marsh and maritime forest vegetation in contrast to North Inlet where low marsh vegetation dominates. The description of Winyah Bay's macrophyte community provided by Blood and Vernberg (1992) is the most recent summary of what types of vascular plants can be found there. The diverse (species-rich) plant community exists because there is such a wide range of salinities occurring in Winyah Bay. Thus freshwater, brackish water, and salt marshes all exist, with freshwater marshes covering the greatest area and salt marshes the least. Nearly all of the marsh area in Winyah Bay is affected by tidal changes in water level. Tiner (1977) provided the species inventory presented by Blood and Vernberg (1992).

Unfortunately, there have been no studies of vascular plant productivity or biomass in Winyah

Bay. By all outward appearances, the *Spartina* surrounding Mud Bay looks the same as in North Inlet. It is unknown whether the more brackish environment in this part of the NERR significantly alters the growth rate and productivity of cordgrass relative to the same species growing in North Inlet. Such a difference would be very difficult to detect given the wide range of vascular plant production values reported for North Inlet.

Much of the Winyah Bay portion of the NERR is comprised of high marsh and maritime forest vegetation in contrast to North Inlet where low marsh vegetation dominates.

» Microbial Communities

The Winyah Bay portion of the NI-WB NERR has received considerably less microbiological study than North Inlet over the last four decades. It was not until the 1990s that any close examination of water quality was made on a regular basis in Winyah Bay. Earlier studies were directed at assessing human health issues that arise from industrial pollutants and agricultural runoff entering the bay from the surrounding watershed, primarily through the Pee Dee, Waccamaw, and Sampit rivers. The focus then was on fecal coliform bacteria, heavy metals, organic compounds (pesticides) and anything potentially harmful that might enter harvestable species of fish and shellfish. These data were compiled and reviewed by Blood and Vernberg (1992) who summarized what was known in the period 1970 to 1985. At that time, however, no regular, standardized sampling programs existed from which any trends in the health of the Winyah Bay estuary could be inferred. Most of the microbiological studies have been conducted by state agencies specifically to measure fecal coliforms as they relate to water quality and the need to close public shellfish beds after particularly high runoff events. Such precaution is necessary because the receiving waters of Winyah Bay likely contain more human-derived (from rural septic tank overflow) and larger quantities of animal-derived (e.g., cattle, swine, poultry) coliforms than occur in North Inlet.

The most coordinated and comprehensive coastal monitoring program to have taken place in Winyah Bay is called the South Carolina Estuarine and Coastal Assessment Program (SCECAP) that began in 1999. This program's goal is to monitor the condition of the state's estuarine habitats and associated living resources on a biannual basis. It is a collaboration between the SC Department of Natural Resources and the SC Department of Health and Environmental Control. The SCECAP samples water and sediments at 6 sites in North Inlet and 24 sites in Winyah Bay, though not all are sampled every year because they use a random, probability-based sampling regimen. The program issues a summary update covering two-year periods that compares data from many other locations in the state and by virtue of the sampling design is able to make some trend assessments of habitat and resource quality changes over time. These reports are available online (**www.dnr.sc.gov/marine/scecap/**). Van Dolah et al. (2008) provide comparative analyses of estuarine habitat quality that include fecal coliform measurements in 29 different watersheds in South Carolina, including Winyah Bay.

Ullman and Aller (1979) studied the biogeochemistry of sediments in Mud Bay, including the anaerobic decomposition of organic matter that leads to the production of iodine. Ullman and Aller (1983) found that about 90% of the dissolved iodine flux comes from the top 10 cm of the sediment in Mud Bay.

Fungal infections in fish, particularly menhaden, have been assessed by Dykstra et al. (1989) on specimens captured in Winyah Bay. Long et al. (1996) and Long (2000) utilized a 5-min microbial

bioluminescence test on organic extracts from sediments in Winyah Bay as part of a larger NOAA program examining sediment toxicity in U.S. estuaries. Guentzel and Tsukamoto (2001) examined the role of microorganisms in the speciation of mercury compounds as they influence the bioaccumulation and bioconcentration of this heavy metal in the marine food web leading to fishes.

Heterotrophic bacteria release dissolved organic matter (DOM) as they grow and multiply, get grazed by microplanktonic protozoans, or die from viral lysis. The origin and composition of DOM produced by bacterioplankton in water samples from Winyah Bay was studied by Kawasaki and Benner (2006). They incubated water samples in artificial media containing glucose as the sole carbon source for several months and found that extracellular release of dissolved organic matter (e.g., amino acids and amino sugars) can result in the underestimation of bacterial carbon production rates unless these releases are taken into account.

Microbiological investigations typically require quantification of microbe abundance. Most methods for doing this are expensive and time consuming, particularly for particle surface-associated bacteria. Swenson et al. (2012) developed a fluorometric method that is relatively rapid and inexpensive using cultures of sediment bacteria collected from Winyah Bay. This high throughput method may be useful for the examination of antibiotic resistance.

Based upon the low number of studies conducted on microbial communities from or in Winyah Bay, this portion of the NI-WB NERR is severely understudied.

» Benthos

MACROBENTHOS IN WINYAH BAY

The earliest studies of macrobenthos beneath the open waters of Winyah Bay were reported by Hinde et al. (1981). The impetus for these efforts was a proposed ship channel-deepening project. Their three replicate samplings per station were collected in October 1980 along the main axis of the Bay towards the southwestern shoreline in the high-salinity portion of the estuary. They also collected some samples offshore near the mouth, but none of their study was done inside the NI-WB NERR boundary. Benthos in the collections from the 12 total sampling stations were dominated by pelecypods and polychaete worms. Amphipods and gastropods were also prominent in the collections. Some 154 taxa were identified in the collections. Species diversity was highest in the offshore stations and lowest near South Island where sediment conditions and high currents afforded habitat suitable for high densities of the mussel *Brachidontes exustus*.

Biogeochemical studies in the sediments of Mud Bay, inside the present NI-WB NERR boundary, have been done by Aller and Ullman reported earlier in the Water Quality chapter. Unfortunately, none of these particular studies was designed to assess benthic community structure there. Mud Bay is extremely shallow during low tides and many investigators have inadvertently been trapped there when their boats became grounded in soft sediments that resist walking efforts. Anecdotal observations of the Mud Bay area during such times has revealed the presence of numerous deposit- and suspension-feeding bivalves (e.g., *Mya arenaria*, *Macoma balthica*), but the sediments can be muddy one year and have a muddy-sand or sandy-mud consistency the next, making these bivalve communities ephemeral.

The soft sediment of the South Carolina coast, referred to and celebrated by locals as 'pluff mud', can make research difficult in shallow systems such as Mud Bay.

Van Dolah et al. (1984) collected benthos in the same area offshore as Hinde et al. (1981) near the mouth of Winyah Bay but focused on the dredge disposal site. The macrobenthic fauna consisted, species-wise, mostly of polychaete worms, amphipod crustaceans, pelecypod bivalves, gastropod snails, and decapod crustaceans. Numerically the community was dominated by pelecypods with polychaetes being second most abundant, then amphipods and bryozoans. Over 357 invertebrate species or taxa were found in the survey. Neither spatial (station-to-station) nor seasonal differences in abundance were significant.

Aller and Yingst (1985) studied the distribution of solutes around a capitellid polychaete and two bivalve species in Mud Bay and found that these organisms irrigate the sediments in which they live. The resultant transport of dissolved oxygen into reducing sediments makes the habitat suitable for these organisms.

The transport of the planktonic larvae of many benthic species is strongly affected by currents and tides. Stancyk and Feller (1986) provided a mini-review of what is known about larval transport mechanisms for non-decapod invertebrate larvae in estuaries such as Winyah Bay.

The South Carolina Estuarine and Coastal Assessment Program (SCECAP) was started in 1999 by the SC Department of Natural Resources in conjunction with the Department of Health and Environmental Control. It is designed to monitor the health status of the state's estuaries and other tidal waters by periodically (about every 2 years) sampling a variety of related water quality parameters, including macrobenthic fauna, at locations all along the South Carolina coastline. The most recent report by Bergquist et al. (2009) covers the period 2005-2006 and includes coarse results from benthic samples taken in the open water region near the mouth of Winyah Bay. The macrobenthic fauna were dominated by polychaetes, mollusks, and amphipods. Based on the number of species found (species richness), total faunal density (number of individuals), and mathematical measures of species diversity (H') and evenness (J'), the data were assigned a score according to the Benthic Index of Biotic Integrity (B-IBI, Van Dolah et al., 1999). The samples collected in the Bay near the mouth were assessed as Fair, while those collected just outside the Bay were Good. Samples taken in North Inlet were also scored as Good according to the B-IBI. An interesting aspect of the SCECAP is that the same stations are not sampled each time. Rather a probabilistic statistical methodology is used to determine which among the thousands of possible regionalized stations in SC will be sampled each time. For all years between 1999 and 2006 in which different open water stations were sampled farther up the Bay, upper Winyah Bay was among the locations having the most numbers of degraded (Poor) stations in the state. However, the SCECAP's benthos samples are collected outside the NERR boundary in Winyah Bay.

LaSalle et al. (1991) inventoried the flora and fauna of the low intertidal salt marsh that developed on a dredge spoil island area in Winyah Bay. Oligochaetes and polychaetes dominated the assemblages there, one that developed 8 years after unconfined sediments were placed and the other that was only 4 years old. Macrobenthos densities were high in both.

Kamermans et al. (1999) examined shell length and weight relationships for a bivalve (*Macoma balthica*) in the Mud Bay region of Winyah and compared them with those for shells from several other locations on both sides of the Atlantic Ocean. Shells from Winyah Bay were among the largest collected, suggesting that recruitment had not occurred in Mud Bay in recent years, as no small individuals were found.

MEIOBENTHOS IN WINYAH BAY

A collection of benthic foraminifera was made in Winyah Bay by Collins et al. (1995). Using a Van Veen grab sampler and taking subsamples from the 11 collections made along Winyah Bay's main axis, no live specimens were found. Upstream in the Intracoastal Waterway, outside the Bay in the nearshore, and in North Inlet, many living forams were collected. The authors ascribed the absence of living specimens in Winyah Bay to pollution there.

In summary, the benthos of Winyah Bay is undersampled, and no data on benthic communities exist within the NERR boundaries in the Bay. Given the very different hydrographic regime in Winyah Bay compared to that in North Inlet, there are many opportunities to characterize and compare the community structure of macrobenthos, meiobenthos, and microbenthos in a stressed environment (Winyah Bay) with that in an unstressed environment (North Inlet).

» Zooplankton

The spatial and temporal distributions of mesozooplankton in Winyah Bay estuary are more complex than in North Inlet. The taxonomic composition, seasonal patterns, and relative abundance of constituents of both the small- and large-mesh size fractions are largely the same in the high salinity areas of both estuaries during most seasons and years. However, when freshwater discharge from one or more of the rivers increases and the salinity gradient is shortened along the axis of Winyah Bay, there is a net seaward displacement of the typical high salinity inhabitants of the lower Bay toward the ocean with replacement by a less abundant and diverse assemblage of low-salinity forms. Even during average runoff conditions, the salinity at the jetties can vary by 20 or more between high and low tides. During periods of relatively moderate and steady riverine discharge, zooplankton with different salinity preferences vary along the axis of the Bay. General information about zooplankton composition, distribution, and behavior in river-dominated estuaries can be found in Johnson and Allen (2012).

Most of what we know about Winyah Bay zooplankton comes from studies in the early 1980s. In a one-year study (August 1980 – July 1981), collections were made at South Jones and No Man's Friends Creeks (at the connecting points between North Inlet and Winyah Bay) every three weeks. Every other cruise that year was an intensive 24-hour series of bihourly collections at each site. This was known as the Coastal Energy Impact Program (CEIP) Phase I study (Allen et al., 1982). In addition to a focused effort to characterize the zooplankton at those creeks, a companion series of collections was made at six locations extending from the jetties to the lower river every six weeks. Starting in August 1981 (CEIP Phases II & III), a more intensive sampling program provided collections from the original six stations (plus five others) along the axis of Winyah Bay (Allen et al., 1984). Towed 153-micron mesh ring nets and a 365-micron mesh epibenthic sled were used to collect samples about once each month for one year. Collections from this series of stations characterized assemblages throughout the Bay on a single day. In another series (tidal series of CEIP II & III), opening and closing nets (both 153- and 365-micron) were deployed to determine vertical distributions in the lower, middle, and upper Bay once per month. Other CEIP II & III sampling efforts included a 48-hour series which examined tidal and diel changes in abundance, composition, and vertical distributions in the lower Bay in September 1982. Below is a summary of the spatial and seasonal patterns determined in these studies. More details and results from the short-term studies are available in the cited reports.

OVERALL PATTERNS

Zooplankton concentrations varied considerably throughout Winyah Bay, both temporally and spatially. With the small mesozooplankton, the upper bay had fewer and different species present in lower numbers. Relatively few species occurred in both the upper and lower bay regions, and the lower bay more closely resembled nearshore coastal and North Inlet environments (Allen et al., 1982). Seasonal changes occurred throughout the bay, but patterns were not always similar among the upper, middle, and lower bay. Like in North Inlet, copepods dominated the small mesozooplankton community, with the calanoid copepod, *Acartia tonsa*, being the most abundant overall. *Parvocalanus crassisrostris*, *Eurytemora affinis* and *Pseudodiaptomus cornatus* were also common calanoids in Winyah Bay. Among the cyclopoid copepods, only *Oithona colcarva* and *Halicyclops* spp. were common. *Euterpina acutifrons* was the only planktonic harpacticoid copepod which was found regularly in the bay. Other holoplankton which comprised a large percentage

of the total number of small mesozooplankton included medusae, rotifers, appendicularians and chaetognaths.

The temporary or meroplanktonic forms consisted mostly of the eggs and larval stages of fish and benthic invertebrates. The most common larvae found were barnacles (nauplii and cyprids), crab zoeae, polychaetes, and mollusk larvae (gastropod and bivalve veligers) (Allen et al., 1984). Many of the less abundant holoplankton and meroplankton were the same taxa found in North Inlet collections.

Mysid shrimps were perhaps the single most important group of large mesozooplankton in Winyah Bay, by comprising over half, and up to 80%, of all organisms collected overall (Allen et al., 1984). Like the North Inlet large zooplankton community, mysids along with amphipods, shrimp and fish larvae, chaetognaths, and hydromedusae were the dominant groups in Winyah Bay. However, the numbers and species of mysids and larval fishes and shrimps can be quite different. For example, a few clupeids, sciaenids, and soles which were abundant in Winyah Bay were rare or absent in North Inlet.

SEASONAL PATTERNS

Small and large zooplankton densities in Winyah Bay peaked in summer and were lowest (typically about 10 times lower) during the coldest months, in large part due to the absence or very low densities of invertebrate larvae from November to March. Copepods comprised at least 60% of the small zooplankton catch from May to November and more than 80% in January and March (Figure 91). *Acartia tonsa* was the dominant copepod throughout the Bay during the warm season.

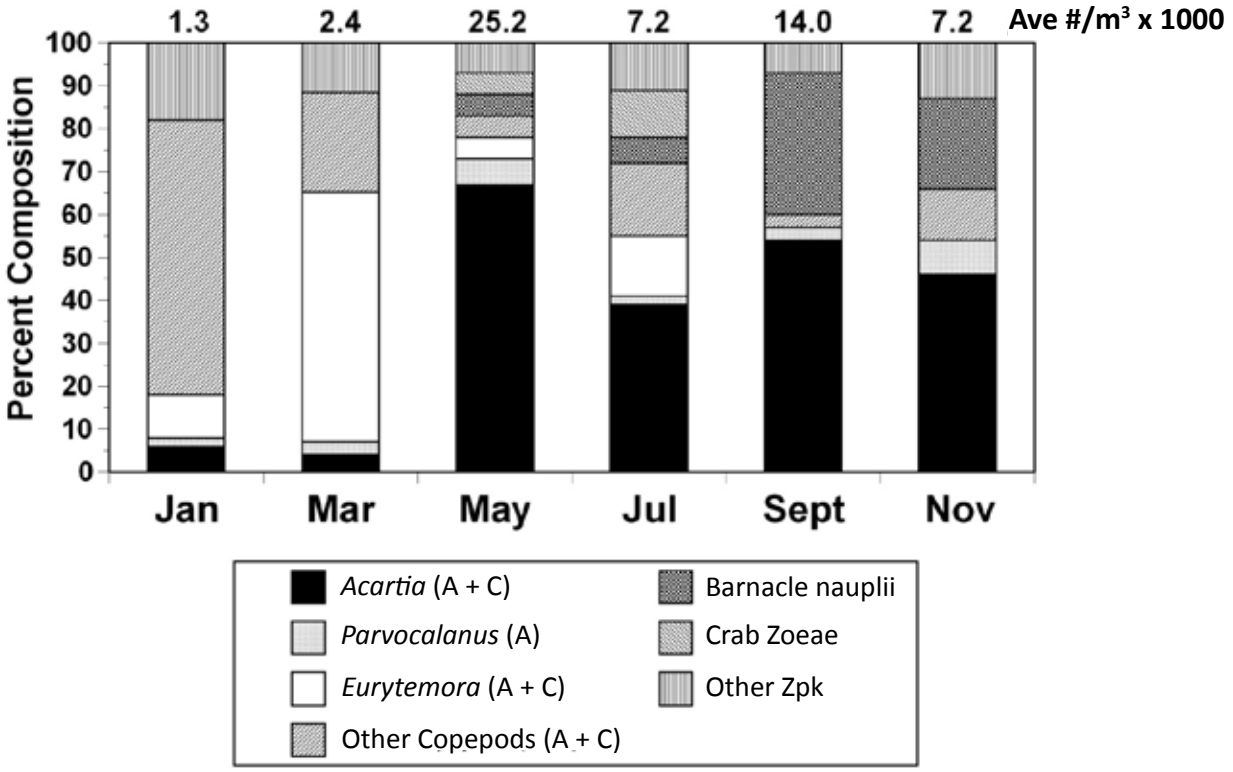


Figure 91. Mean bimonthly composition of small mesozooplankton (153-micron mesh) collected in Winyah Bay on a single date each month (November 1981 – September 1982). Each value is a mean of all 11 stations sampled on that date. Mean abundance of total organisms is located above each bar. Adapted from Fig. 5-8 in Allen et al., 1984.

Parvocalanus crassirostris was abundant in the lower Bay year round, but especially from spring to fall. Other copepods collected near the ocean included *Centropages hamatus* during winter and *Oithona colcarva*, *Pseudodiaptomus pelagicus*, *Labidocera aestiva*, and *Paracalanus parvus* during the warmest months. Other copepods were more important during the winter and spring, especially in the upper Bay where *Eurytemora affinis*, a species that favors low salinity waters, often exceeded *A. tonsa* in abundance. Crab zoeae represented the largest meroplanktonic group during summer, and barnacle nauplii comprised the most important larval group in the fall; neither taxon was collected in January or March (Figure 91).

For large mesozooplankton, mysids (almost entirely *Neomysis americana*) and gammarid amphipods accounted for about 35-95% of the catches during the year, with especially large proportions occurring from September to March (Figure 92). Shrimp larvae, crab megalopae, and fish larvae were the major meroplankters from spring to fall. 'Others' including *Lucifer*, *Acetes*, isopods, and cumaceans comprised a particularly large proportion of the catch in May. Although chaetognaths were common especially during summer in the lower bay, they were not enumerated in the CEIP studies. Hydromedusae were not enumerated, but their densities during spring and summer, particularly in channels in the mid bay, were very high, with more than one liter of jellyfish occurring in some tows.

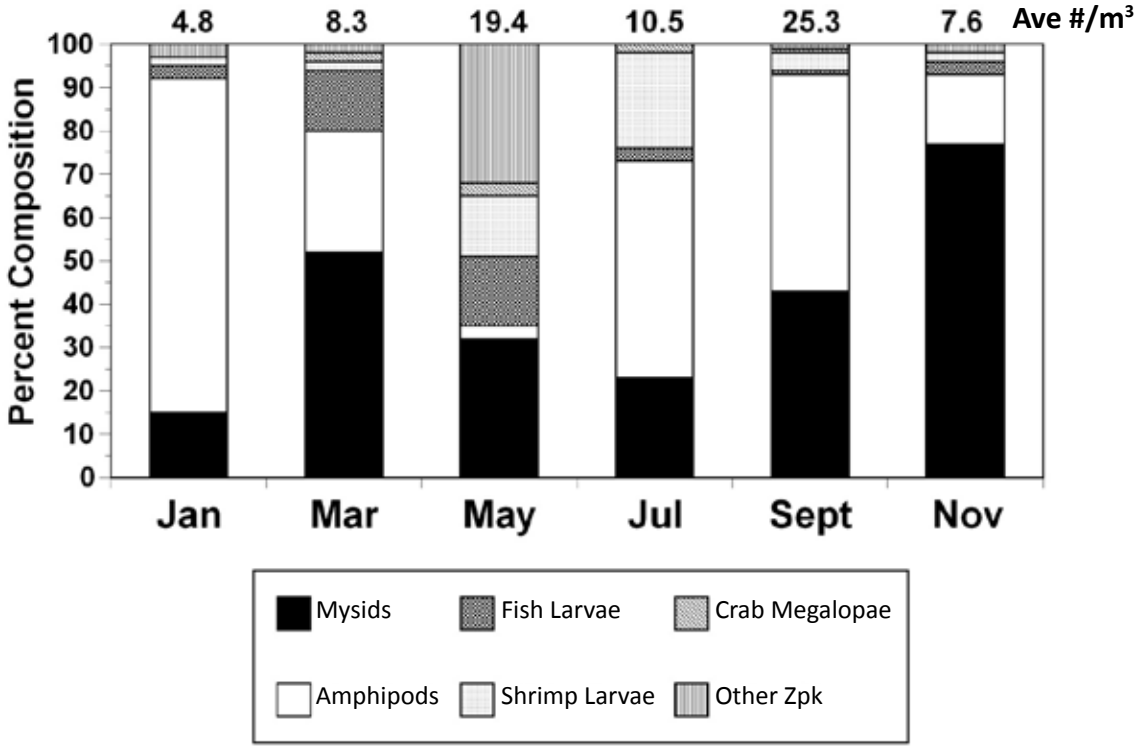


Figure 92. Bimonthly mean composition of large mesozooplankton (365-micron mesh) collected in Winyah Bay on a single date each month (November 1981 – September 1982). Each value is a mean of all 11 stations sampled on that date. Mean abundance of total organisms is located above each bar. Adapted from Fig. 6-1 in Allen et al., 1984.

SPATIAL PATTERNS IN TAXON DENSITY AND DIVERSITY

Small mesozooplankton diversity was greatest in the lower bay where 15-31 taxa occurred throughout the year. The middle bay taxon diversity was most variable with 8-28 categories, and the upper bay had the least on almost every cruise with 8-20 taxa. Total small zooplankton densities were lower in the upper bay with annual means of 6,000-9,700 m^{-3} compared to 8,000-13,000 m^{-3} for the lower bay (Figure 93). Diversity of large zooplankton was also highest near the ocean. However, total densities of large animals did not show the same decreasing pattern toward the riverine end of the gradient exhibited by total small zooplankton. Instead, rather consistent differences in density occurred among sites, with some stations in all three zones being much lower than other nearby stations (Figure 94). Based on the less complete list of enumerated taxa, most Winyah Bay densities were 2-15 m^{-3}, and the peak was 147 m^{-3}. Data in the CEIP II & III report for individual taxonomic categories makes it possible to make density comparisons for them between the estuaries.

Comparisons of average proportions of the major taxa showed that most were widely distributed throughout the Bay. *Acartia tonsa* accounted for ~ 10% at the most oceanic site and reached highest densities in the intermediate salinity areas of the middle bay, but this species often accounted for 30-70% of the total in the upper bay (Figure 93). *Parvocalanus crassirostris* was generally restricted to the lower half of the bay and *Eurytemora affinis* to the upper half during their periods of occurrence.

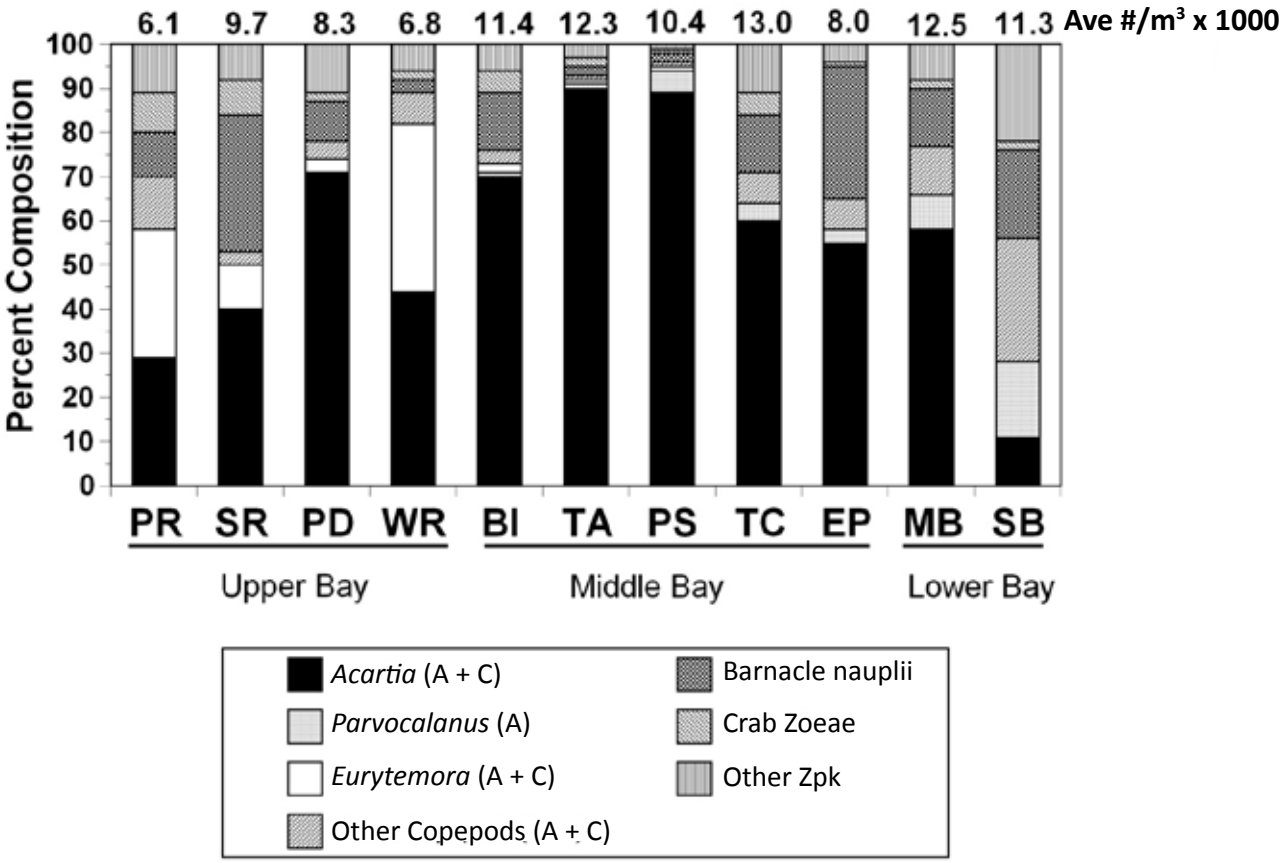


Figure 93. Mean sampling station taxon composition of small mesozooplankton (153-micron mesh) collected at 11 sites in Winyah Bay. Each value is a mean of collections made on all dates (November 1981 – September 1982). Mean abundance of total organisms for each station for all dates is located above each bar. Adapted from Fig. 5-7 in Allen et al., 1984.

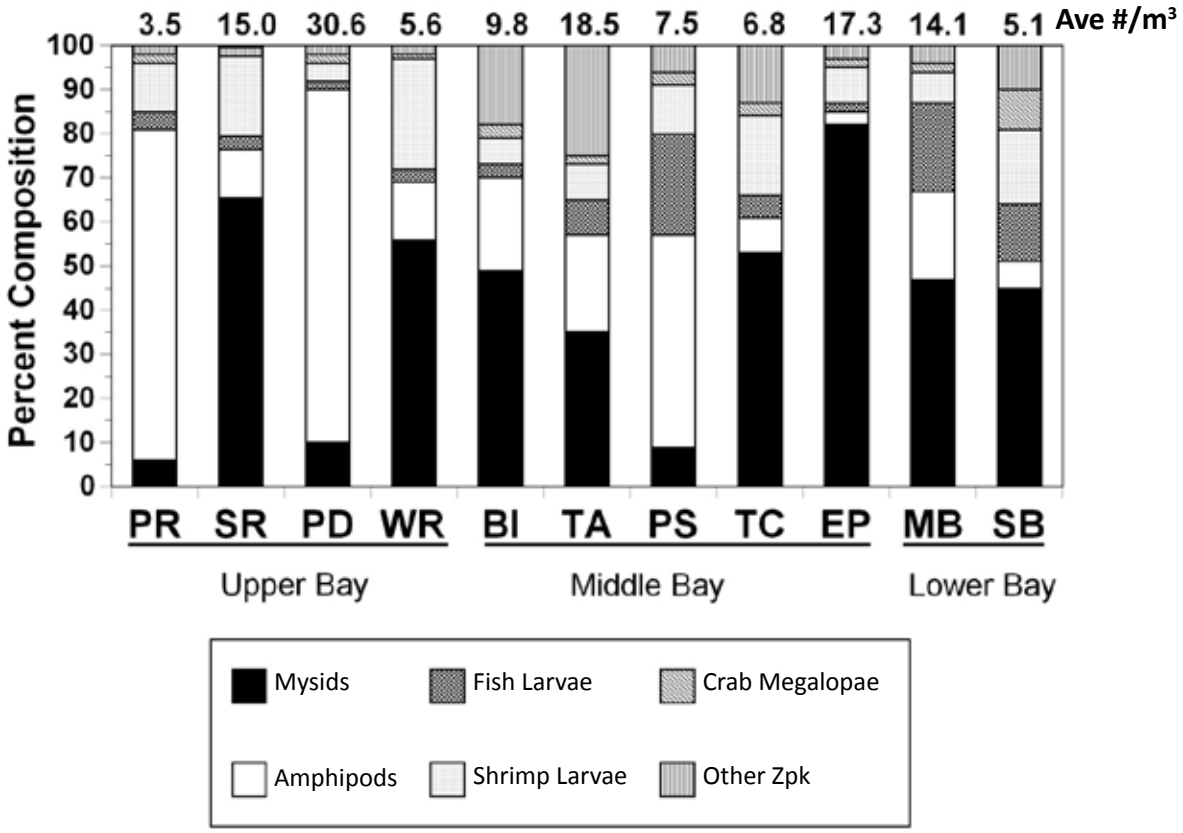


Figure 94. Mean sampling station taxon composition of large mesozooplankton (365-micron mesh) collected at 11 sites in Winyah Bay. Each station value is a mean of collections made on all dates (November 1981 – September 1982). Mean abundance of total organisms for each station for all dates is located above each bar. Adapted from Fig. 6-2 in Allen et al., 1984.

Barnacle nauplii and crab zoeae were widely distributed in the Bay. For the large zooplankton, high salinity types including chaetognaths, *Lucifer*, *Acetes*, isopods, and cumaceans did not occur in the upper bay. Many types of shrimp larvae, fish larvae, and crab megalopae were collected along the salinity gradient as various stages followed recruitment patterns into and out of the estuary (Figure 94). Recent studies by R. Brodie, R. Tankersley, R. Styles, and S. Borgianini and their students have examined behavioral and hydrographic mechanisms that enable fiddler crab megalopae to recruit in an upstream direction to upriver settling sites.

WATER COLUMN AND TIDAL PATTERNS

Bimonthly surface-bottom mesozooplankton collections were made at 3 stations, representing the 3 regions (upper, mid, and lower) of Winyah Bay in 1981-1982. In addition, one day-night 48-hr study was made at the mouth of the bay in September 1982. These studies indicated that there were no significant differences between surface and bottom densities (number per cubic meter) of total small zooplankton; however, there were significant taxon-specific differences observed in both short-term studies. During their peak abundances in the warm months, both adult and copepodid stages of *Acartia tonsa* had higher bottom densities than the surface waters during the day (Allen et al., 1984). *Pseudodiaptomus coronatus* had higher densities in bottom waters but barnacle nauplii were more abundant in surface waters. No vertical differences were observed for *Parvocalanus crassirostris*, but they were most abundant at high tide. As for the large zooplankters, higher densities for most categories occurred on the bottom, especially during strong current velocity conditions. Fish larvae were the most important group in surface collections, especially at slack tide (Allen et al., 1984).

LONG-TERM PATTERNS AND ISSUES

Because there are neither recent nor continuing studies of zooplankton in Winyah Bay, we cannot address the potential impacts of human activities or climate change in one of the nation's largest estuaries. If the global pattern of increasing ENSO events continues, and local rainfall and runoff patterns change, we could expect a compression of the salinity gradient (the zone between freshwater and oceanic water) within Winyah Bay, because higher river discharges would push and shift much of the mixing zone outside of the jetties. The effect of this water mass displacement on larval recruitment processes could be significant if current and salinity patterns are not favorable for species that require marsh habitats to complete development. Because many economically and ecologically important estuarine invertebrates (e.g., penaeid shrimps, blue crabs, clams) and fishes (e.g., red drum, spotted seatrout, flounder, mullets) use shallow marsh nursery areas in the middle bay, major alterations in salinity and temperature regimes could affect the abundance, growth, distribution, and other characteristics of these populations in Winyah Bay.

» Nekton

The nekton community in Winyah Bay is abundant, diverse, and dynamic, more so than in North Inlet. Differences are mostly related to the strong effects of the rivers on freshwater inflow and salinity. With a long axial salinity gradient, deeper channels, more expansive shallow subtidal bottoms, and a greater variety of wetland types, Winyah Bay provides habitat for many species that are uncommon or absent in North Inlet.

Much of what is known about the nekton in Winyah Bay comes from two studies. Wenner et al. (1981) conducted a bay-wide trawl study that included 5 stations along the main stem of the estuary and one additional station in each of the four rivers; a complete range of salinities was represented on each sampling date. In another study, the large creeks connecting the Mud Bay section of Winyah Bay and North Inlet (Allen et al., 1982) were sampled. This study used trawls, epibenthic sleds, and gill nets to collect nekton in No Man's Friend and South Jones Creeks; salinities here were typically brackish to high (24 – 32). Other information provided in this section comes from occasional scientific collections and observations from local recreational and commercial landings.

COMMON FISHES, SHRIMPS, AND CRABS

The majority of nekton taxa that occur in the high salinity, salt marsh-dominated North Inlet system also occur in the southern portion of Winyah Bay closest to the ocean. Comparisons between the lists of species collected in surveys of both estuaries indicate a high degree of overlap (**Appendix E**). Direct comparisons of relative abundances and size distributions cannot be made because of differences in the types of sampling gear and the timing of the collections in the two estuaries. Nevertheless, seasonal patterns of occurrence and associations with particular habitats (e.g., marsh, shoreline, and subtidal channels near the inlet) are similar for those species that favor high salinities. Species diversity is higher in lower Winyah Bay than in the middle and upper regions of Winyah Bay. Table 12 lists species which were collected in Winyah Bay but were absent from or uncommon in North Inlet and lower Winyah Bay. As is the case in North Inlet, most species found in lower Winyah Bay were represented by larval or juvenile life stages (Wenner et al., 1981).

DOMINANT SPECIES

Star drum *(Stellifer lanceolatus*) was the most abundant of 77 species of fishes and motile macro-invertebrates collected in the two-year trawl study of the bay (Wenner et al. 1981). It was especially abundant during the fall at locations between the lower and middle regions of the Bay. Curiously, the star drum is a rare fish in North Inlet, occurring in less than one percent of all of the collections made with various gear types during the past 30 years. Only a few small juvenile star drum were caught in trawls in the creeks, especially in the southern part of the system. The star drum is known to spawn from spring to fall along the Atlantic coast. Large star drum are found in the Bay in the spring, and much higher numbers of juveniles occur in the same area in the fall. Star drum appears to be more

Table 12. Partial list of fish species that occur in Winyah Bay but are uncommon or absent from North Inlet. Most of these were documented in the DNR trawl study conducted in 1977-78 (Wenner et al., 1981). Salinity ranges are defined as high (30-35), brackish (15-29), low (3-14) and freshwater (<2).

Common Name	Scientific Name	Salinity Range
star drum	*Stellifer lanceolatus*	high to low
white perch	*Morone americana*	brackish to fresh
striped bass	*Morone saxatilis*	brackish to fresh
white bass	*Morone chrysops*	brackish to fresh
longnose gar	*Lepisosteus osseus*	brackish to fresh
white catfish	*Ameiurus catus*	brackish to fresh
channel catfish	*Ictalurus punctatus*	fresh
blue catfish	*Ictalurus furcatus*	brackish to fresh
flat bullhead	*Ameiurus platycephalus*	fresh
brown bullhead	*Ameiurus nebulosus*	fresh
American shad	*Alosa sapidssima*	high to fresh
blueback herring	*Alosa aestivalis*	brackish to fresh
Atlantic sturgeon	*Acipenser oxyrhynchus*	brackish to fresh
shortnose sturgeon	*Acipenser brevirostrum*	brackish to fresh
redear sunfish	*Lepomis microlophus*	fresh
warmouth	*Lepomis gulosus*	low to fresh
redbreast sunfish	*Lepomis auritus*	fresh
largemouth bass	*Micropterus salmoides*	low to fresh
common carp	*Cyprinus carpio*	fresh
hogchoker	*Trinectes maculatus*	high to fresh

of an open water fish than the spot (which is also very common); it tends to be collected in deeper water such as channels rather than along the edges of marshes.

Atlantic croaker (*Micropogonias undulatus*) is common throughout the Winyah Bay estuary, and can be considered a resident species. It is especially abundant in early and mid-summer when small croaker that recruited as larvae the previous fall occur across a wide range of salinities and regions of Winyah Bay. In general, Atlantic croaker appears to be more common in the middle than in the lower bay, and juveniles can be found in very low salinities. Steady growth of young-of-the-year Atlantic croakers is evident from winter through fall. One-year-old-plus Atlantic croakers are also found in Winyah Bay during all seasons. This drum has a strong affinity for the bottom, but occurs from the deepest channels to the shallowest subtidal creeks and flats. Unlike the spot which is also very abundant (especially in shallow water in the mid and lower bay), the Atlantic croaker does not make excursions into the high intertidal flats and marshes at high tide. Atlantic croaker was much

more abundant than spot in the channels sampled in the trawl study, but spot was the most abundant demersal fish in the creeks connecting the two estuaries. Spot was the most abundant demersal fish in North Inlet.

Hogchoker (*Trinectes maculatus*) is probably the most abundant and widely dispersed flatfish in Winyah Bay. However, its distribution is skewed toward the low salinity end of the system. The hogchoker is a year round resident. During summer, adults occur in the high salinity areas where they spawn and then move up the bay to freshwater.

Blue catfish (*Ictalurus furcatus*), an introduced species to the rivers of Winyah Bay, commonly occurs in salinities up to 10 in the upper and middle bay. White catfish (*Ictalurus catus*) favors the lower salinity areas of the upper bay. Catches of both catfishes in Winyah Bay tend to be highest in winter and spring following high river discharge; the distribution of these and other freshwater fishes shifts up the rivers in summer.

Atlantic menhaden (*Brevoortia tyrannus*) is also a year-long resident in Winyah Bay. This pelagic filter feeder is most abundant in the lower bay, but schools of juveniles occur far up the salinity gradient during the warmest seasons. Densely packed schools of medium and large menhaden are common and conspicuous features in the lower bay in all but the coldest months. Adults move into the coastal ocean to spawn in the fall, and larvae recruit during winter. Large schools of juvenile menhaden are often observed in shallow subtidal areas such as Mud Bay throughout the summer.

Blue crab (*Callinectes sapidus*) occurs from the shallow fringes to the deepest channels during all seasons. Adult blue crabs mate in the upper bay and egg-bearing females migrate toward the ocean where they release larvae. Females with egg masses have been collected from early spring to late fall. Once they have mated and moved to high salinity areas, they stay there. Males remain in the brackish and lower salinity reaches of the bay where they are sought by commercial trappers as the largest and most valuable members of the species. Most blue crabs live less than three years. Young blue crabs tend to favor the shallowest areas and occur across a wide range of salinities and habitat types.

A female blue crab, *Callinectes sapidus*

Penaeid shrimps constitute the most valuable fishery in the Winyah Bay area. White shrimp (*Litopenaeus setiferus*) larvae arrive from coastal ocean spawning grounds starting in May. The production of larvae continues until early summer. Juveniles grow quickly in the productive shallow expanses of the middle and upper bay. The first subadults move into the ocean in mid-summer, signalling the beginning of a directed commercial fishery that continues until early winter. This movement of white shrimp from the estuarine nursery to the ocean continues until mid-fall. Upon reaching adulthood in the ocean, white shrimp produce larvae that move into the estuary, thus completing the cycle. Young white shrimp overwinter in the deeper parts of the estuary and ocean where they grow slowly until spring, then they produce the next summer generation. Major freshwater inflow events such as those associated with tropical storms in the summer and fall are known to move small shrimp out of Winyah Bay prematurely.

The brown shrimp (*Farfantepenaeus aztecus*) also recruits from the ocean, but larvae arrive during winter. Juveniles favor higher salinity areas than the white shrimp and most juveniles leave the estuary as subadults by mid-summer. Brown shrimp

comprise the early season penaeid fishery harvest, and the more numerous white shrimp comprises the mid-summer and fall crop. The pink shrimp (*Farfantepenaeus duoarum*) is generally the least common of the three species and often comprises <5% of the commercial catch. The occurrence of relatively high numbers in the DNR trawl study might indicate a tendency for them to remain in the deeper portion of estuaries. White and brown shrimp are much more common in shallow subtidal bottoms. The pink shrimp's seasonal distribution is similar to that of the white shrimp.

American shad (*Alosa sapidissima*) adults arrive from over-summering areas in New England waters every winter. They traverse the salinity gradient *en route* to spawning areas far up the rivers. After spawning, most adults return to the ocean. In spring, juvenile American shad move downstream and occur in brackish areas for the first year or two before joining the adult population in its migration up the Atlantic coast. There is evidence that, like salmon, American shad return to the estuaries/rivers from which they originated. The commercial fishery usually begins in January. Gill netters favor female shad with ripe ovaries (roe). American shad has comprised an important local fishery in Winyah Bay for more than a century, and it is the only finfish that is commercially harvested from the estuary.

Atlantic sturgeon (*Acipenser oxyrinchus*) also uses Winyah Bay as a nursery. Adults move long distances from the coastal ocean to freshwater streams where they spawn in the spring. Juveniles produced far into the river systems spend several years in the estuary. Individuals up to six feet in length have a curious habit of sky rocketing out of the water from time to time and reports of leaping sturgeons are common in Winyah Bay. These bony-plated fish are bottom feeders. Adults were intensively harvested to produce caviar until the 1970s. With individuals capable of reaching more than 50 years of age and females not reaching maturity until about age 15, recovery of the population has been slow. Harvesting has been prohibited since the late 1970s. The shortnose sturgeon (*Acipenser brevirostrum*), which is less common in Winyah Bay, is also listed as an endangered species.

Striped bass (*Morone saxatilis*) is a year-round resident of the Winyah Bay system, but remains in the rivers from spring to fall. Spawning takes place in freshwater and juveniles develop there. Older juveniles and adults move into the upper and middle reaches of the estuary, including Mud Bay and the Western Channel, in the late fall, but only during years when freshwater inflow is high. They can remain in low salinity waters throughout the winter months before moving upstream. Unlike striped bass populations from NC and northward, SC striped bass do not migrate to the ocean and almost no exchange is thought to occur among estuaries. White perch (*Morone americana*), a close relative of the striped bass, is common along low-salinity and riverine shorelines, especially at the mouths of creeks and old rice field canals. They are year-round residents that do not occur in the middle or lower bay.

Bay anchovy (*Anchoa mitchilli*) appears to be widely distributed along the salinity gradient and is likely one of the most abundant fishes occupying the open waters of Winyah Bay in all except the coldest months. Striped mullet (*Mugil cephalus*) is ubiquitous and conspicuous in the estuary, and multiple year-classes occur in the shallow waters, especially during the warmest seasons.

SEASONAL PATTERNS

Species diversity and abundance of nekton is highest during summer and early fall and lowest during the coldest months. Patterns of seasonal change described for the salt marsh and shallow-water nekton in North Inlet are similar for the same species in Winyah Bay. Catfishes, hogchoker, Atlantic croaker, and blue crab are among the most abundant of the channel-dwelling nekton throughout the Bay from spring through fall. Anchovies, Atlantic menhaden, and striped mullet account for much of the sharp increase in fish abundance in the water column and shallow portions of the Bay in summer and fall. During summer, penaeid shrimps, star drum, and blue crabs can be among the most numerous nekton in the main channels. Sharp decreases in transient species mark the beginning of winter when Atlantic menhaden, Atlantic croaker, and white catfish are among the most common

inhabitants especially in the deeper channels. Except for species represented by early life stages that recruit from offshore, transient species diversity and abundance remains low in spring.

HABITATS AND FACTORS INFLUENCING DISTRIBUTION

Habitat types in Winyah Bay include the same kinds of salt marshes, intertidal creeks, and low energy shorelines found in North Inlet. However, this much larger system is dominated by open water rather than the large subtidal creeks that occur in the marsh-dominated North Inlet system. A wider range of habitats including deep (>8 m) channels, wider expanses of shallow subtidal habitats, steeper marsh edge shorelines, and a variety of marsh types along the long salinity gradient account for a greater diversity in the nekton in Winyah Bay.

Occasional collections with seines, trawls, and gill nets as well as angling experiences and reports from other anglers, indicate that many of the species familiar in higher salinity areas also occur well up the bay. Red drum, southern flounder, and striped mullet are sometimes caught in very low salinity waters far up the rivers. Black drum and sheepshead are regularly caught in low salinity waters in the upper bay during summer. Studies in other river-influenced estuaries indicate that small juvenile spot, southern flounder, Atlantic croaker, and Atlantic menhaden move far up the salinity gradient in the spring. American eels are much more abundant in Winyah Bay than in North Inlet, and adults spend several years in the rivers before migrating to mid-ocean spawning areas.

The DNR trawl study showed that high salinity areas of the bay yielded more nekton and were richer in species than locations further up the bay. The lowest values occurred in the tidal freshwater sections of the Black, Pee Dee and Waccamaw Rivers. The up-estuary sites had the lowest and least variable salinities. Rapid and major changes in salinity occur in the middle and lower bay after extended periods of rainfall and freshwater runs off the watershed into the rivers. Brown-stained, low-salinity water can extend into the lower bay and brackish conditions can occur outside of the jetties for days or weeks at a time. Such conditions displace high-salinity species to the ocean until more typical conditions are re-established.

Of course, other environmental conditions can influence nekton distribution in the area. Water clarity, dissolved oxygen, concentrations of dissolved and particulate materials, current velocities, availability of food, and presence of predators are among the many factors known to affect nekton distributions. Effects of pollutants and habitat modification, including the frequent dredging of navigation channels, are largely unknown but health advisories based on mercury content in some tidal freshwater species persist. Due to the complex and dynamic nature of aquatic environments and the difficult challenges associated with detecting movements and abundances of motile nekton, our knowledge of the effects of changing environmental conditions on nekton in Winyah Bay is insufficient.

» Reptiles, Amphibians and Mammals

A greater diversity of reptilian and mammalian species occur in and around Winyah Bay than in the North Inlet area. Of course, we might expect differences in the distributions and relative abundances of many of the species to occur due to the greater variety of habitat types along the Bay's salinity gradient. In addition, some species seen in the open waters and brackish marshes of Winyah Bay have not been sighted in the high-salinity, marsh-dominated North Inlet system. More complete information about the ecology and distributions of many of the following species can be found in Sandifer et al. (1980).

Loggerhead sea turtles, and less frequently juvenile green sea turtles, have been spotted from the jetties to the low-salinity waters of the Sampit River. Diamondback terrapins appear to be less abundant in Winyah Bay marshes and waterways than in North Inlet. Several turtles typical of freshwater are sometimes sighted in low-salinity marshes and waterways; these include the common snapping turtle (*Chelydra serpentina*), Florida cooter (*Chrysemys floridana*), yellowbelly slider (*Chrysemys scripta*), and chicken turtle (*Deirochelys*

reticularia). The eastern mud turtle (*Kinosternon subrubrum*) and eastern box turtle (*Terrapene carolina*) are often observed on the uplands around old ricefields and low salinity marshes on the western and southern margins of Hobcaw Barony. Several other turtle species more typical of ponds are occasionally found around Winyah Bay.

Snakes commonly found in and around low-salinity marshes of Winyah Bay include the cottonmouth, banded water snake, eastern mud snake, rainbow snake, and yellow rat snake. The distributions and habits of these and other more terrestrial species including the canebrake rattlesnake, black racer, corn snake and green snake are described in more detail in the section on North Inlet reptiles and amphibians.

The American alligator is the most conspicuous reptile inhabiting the marshes, shorelines, canals, creeks, and open waters of Winyah Bay. Although they stray toward the ocean end of the estuary, alligators are most likely to be found in the low-salinity and freshwater areas of the upper bay. Under protection from hunters since the 1970s, alligators have become common in some areas. Individuals up to about 10 ft (3 m) live in tidally-influenced rice field canals and impoundments, and it is not unusual to see large individuals swimming across Winyah Bay.

Few amphibians are found outside of freshwater habitats, but the southern leopard frog (*Rana sphenocephala*) is sometimes observed in low-salinity marsh areas (Martof et al., 1980). The two-toed amphiuma (*Amphiuma means*) has been collected in traps in low-salinity rice field canals associated with Winyah Bay.

Among the aquatic mammals, the bottlenose dolphin is the most abundant, with groups of a few to ten or more moving throughout the bay especially during the summer months. Dolphins are most likely to be seen around the jetties and sometimes many dozens can be observed feeding on by-catch behind active shrimp trawlers outside the jetties. In most years a West Indian manatee is spotted in the Sampit River, but these are stray individuals which only remain in the area for days to weeks during coast-wide migrations. River otters occur near marshes from near the ocean to the tidal freshwater reaches of the Bay. Beavers are found almost exclusively around freshwater streams draining into tidal freshwater marshes. It is noteworthy that neither the muskrat nor the nutria, small mammals that are common in more southern and northern marshes, occurs in the Winyah Bay area.

Terrestrial mammals sighted on the barrier islands include raccoon, feral hog, white-tailed deer, gray fox, red fox, bobcat, raccoon, Virginia opossum, beaver, marsh rabbit, cottontail rabbit, gray squirrel, southern fox squirrel, southern flying squirrel, red bat, eastern wood rat, marsh rice rat, and cotton rat. These and several species of moles, voles, and shrews also occur in upland areas adjacent to marshes along brackish and freshwater marshes farther up the Bay. Although the following species are known to occur in coastal South Carolina, we are not aware of records of striped skunk, long-tailed weasel, and various other rats, mice, and voles (Webster et al., 1985). A survey using capture techniques in preferred habitats would likely document the occurrences of other mammals in the terrestrial systems around Winyah Bay.

» Birds

Much of the bird work directly tied to Winyah Bay was conducted on Pumpkinseed Island. This small 9-ha low elevation, tidally inundated island is situated in the shallow Mud Bay portion of Winyah Bay and historically hosted one of the largest wading bird colonies in the South Carolina. It was used by wading birds from at least the late 1960s through the 2002 breeding season. White Ibises, *Eudocimus albus*, were among the most numerous of the nesting waders during most years with over 20,000 nests counted in 1987 (Shepherd et al. 1991.) Other waders that utilized the island included Great Egrets, Snowy Egrets, Tri-colored Herons, and Glossy Ibises. Nest counts were conducted annually by Baruch investigators by ground surveys and/or aerial flights during the breeding season from 1979-1991. Aerial censuses of the wading bird colony were conducted

by the South Carolina Department of Natural Resources Department (SCDNR) in the early 1990s through 2011. No wading bird nesting activity was noted on Pumpkinseed Island on any of the annual surveys conducted by SCDNR 2003-2011, indicating that the site was not used after the 2002 nesting season (C. Hand, personal communication). Figure 95 shows the number of breeding pairs of White Ibises on Pumpkinseed Island over the survey years, 1979-2003.

During the heyday of wading bird nesting on Pumpkinseed Island, ornithologists and graduate students flocked to the site to carry out research. Peter Frederick, a student in pursuit of a doctorate, spent long hours over five breeding seasons (1979-1983) on the island investigating various aspects of the mating behavior and mating strategies of White Ibis (Frederick, 1985). Frederick observed ibises from a portable 1x1x4 m tall burlap – covered blind camouflaged with needlerush. He was able to recognize individual ibises by distinct facial features, particularly the outline of the border between facial skin and feathers. In his dissertation and in a subsequent publication, Frederick described extrapair copulations (EPC) in this otherwise monogamous species and presented potential costs and benefits of this strategy (Frederick, 1985 and 1987a). EPCs were found to be a frequent and regular occurrence in White Ibises, with one-third to one-half of all observed copulation attempts between members of different pairs. Almost 93 % of all males and 96% of all females were involved in EPCs at least once. Frederick estimated that EPCs could result in fertilization of about 6% of the eggs. Responses of male White Ibises to their mate's EPCs were also observed and recorded (Frederick, 1987b.) In this study, no evidence of physical attacks by males on their mates, abandonment, or reduction of parental care as a result of EPCs was observed.

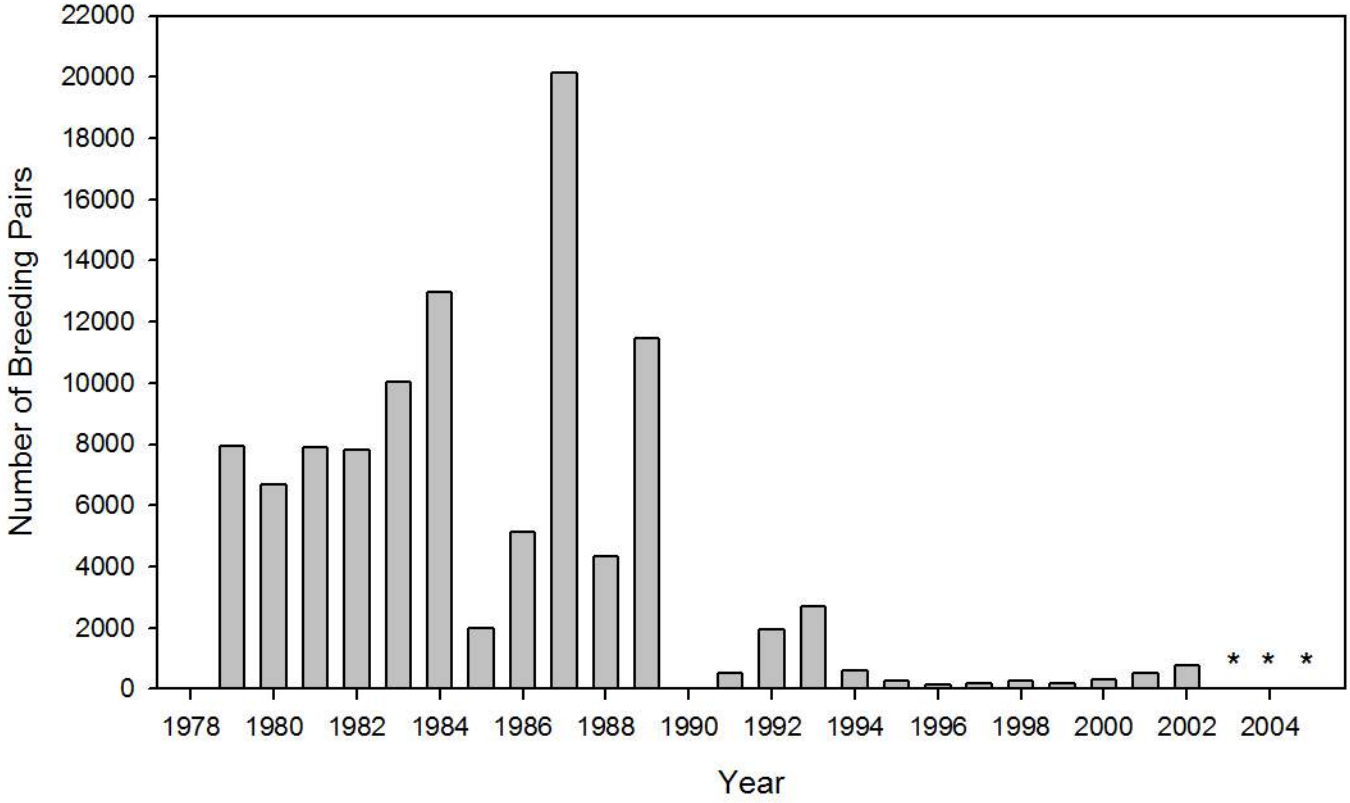


Figure 95. White Ibis nesting pairs on Pumpkinseed Island. None were observed during surveys conducted in 2003, 2004, 2005 or in subsequent years.

In a study of White Ibis mating behavior, individual ibis could be recognized by distinct facial features, particularly the outline of the border between facial skin and feathers.

Frederick (1987c) also investigated the impacts of tidal washovers on nesting White Ibises over five breeding seasons, 1980-1984. Aerial nest surveys were conducted before and after destructive tide events during each breeding season. Sixty-one percent of the nest starts were abandoned during or immediately following extremely high tides during this five year period. Tides high enough to wash over nests occurred at least once each season. Based on ground observations of the reactions of ibises to tidal inundations, eggs often floated out of nests or were washed out by wave action. Marked eggs known to have been covered with water for more than an hour during early incubation later hatched. Frederick pointed out that despite a history of destructive washovers, Pumpkinseed Island continued to support a stable population of White Ibises. Frederick suggested that other factors such as food abundance and low predator densities may be more important in determining site fidelity than breeding failure caused by tidal inundation.

Factors affecting the breeding success of White Ibises were further investigated by Bildstein et al. (1990). Breeding numbers of ibises, reproductive success, adult foraging behavior, nestling diets and rainfall were analyzed for two major White Ibis colonies in the state. White Ibis nesting pairs on Pumpkinseed Island were relatively constant with 6,000-8,000 pairs during the first four years of the study, 1979-1982. They increased in 1983 and 1984 to 12,973 and 13,763 pairs respectively and then declined to less than 2,000 pairs in 1985. This decline occurred even though similar numbers of ibises returned to the North Inlet – Winyah Bay area in late March and early April of 1985 and 1984. In 1986, more than 5,000 pairs bred on Pumpkinseed Island. Over 13,000 pairs of ibises bred on Drum Island near Charleston, SC in 1984, while fewer than 1,000 pairs nested in 1985. At Pumpkinseed Island, the peak number of ibises flying inland to feed in freshwater swamps was higher in 1984 than in 1985 or 1986. Nestlings were still being fed large numbers of crayfish into late June – early July in 1984 while in 1985 and 1986, crayfish were not a significant portion of the diet late in the breeding season. Ibises switched from feeding their nestlings crayfishes to feeding them mainly fiddler crabs in 1985. Starved, desiccated and seemingly abandoned nestlings were also observed in the Pumpkinseed colony during 1985 while none were seen in this condition in 1984. A regression analysis comparing rainfall to colony size showed that more ibises nested in wet years than in dry years and that variation in rainfall six months preceding hatching explained 71% of the annual variation in the maximum number of ibises nesting at the site. The authors suggested that declines in the nesting numbers and reproductive success at the two colony sites resulted from reduced availability of crayfishes during dry periods. These findings demonstrated the importance of freshwater wetlands and prey for breeding White Ibises.

Aerial surveys were used to investigate the impacts of tidal washovers on nesting White Ibises.

Johnston and Bildstein (1990) conducted a controlled experiment in summer 1985 designed to examine the hypothesis that ibis parents fly long distances (as observed with ibises nesting on Pumpkinseed Island) to secure freshwater prey for their young because nestlings cannot develop normally on brackish water prey. Nestlings from Pumpkinseed Island were collected and brought to the Baruch Marine Field Laboratory for the experiment. They were provided one of three different diets: unaltered crayfish, fiddler crabs, or crawfish soaked in brine to the approximate salt level found in fiddler crabs. During the first seven days of the feeding experiment, nestlings fed the unaltered crayfish diet gained significantly more mass than nestlings fed one of the saltier diets. Nestlings on the fiddler crab and salty crayfish diet lost approximately 3% of their body mass per day until freshwater instead of brackish water was made available to them at day 7 of the experiment. The authors concluded that nestling ibises can only tolerate high salt diets if freshwater is made available to them. The results also supported the hypothesis that ibises fly long distances inland to obtain freshwater prey for their young.

The movements of individual adult White Ibises were tracked over three breeding seasons, 1987-1989 (DeSanto et al. 1997). Adults captured on the Pumpkinseed nesting colony were equipped with backpack radiotelemetry units and were monitored from the ground and from fixed-wing aircraft. Individuals caring for pre-fledged young travelled to freshwater swamps, abandoned rice fields, impoundments and ponds, with distances ranging from 4-32 km from the colony site. Regurgitant and fecal samples collected at the colony site from the young of radiotelemetered adults contained bony fish, crayfish and insects. Salt marshes 2-5 km from the colony were visited less often. After the young fledged or nests failed, ibises decreased visits to freshwater habitats and doubled their relative use of salt marshes for foraging. DeSanto et al. (1990) also investigated the behavioral development of nesting White Ibises. DeSanto observed a total of 17 hand-reared White Ibis nestlings in 1986 and 1987 and also observed 400 parent-reared nestlings on Pumpkinseed Island 1985-1988, focusing on their physical characteristics and behavioral development. Radiotelemetry units were also placed on eight 25-31 day-old juveniles to determine when they leave the colony site to forage on their own. These birds left between 47-56 days of age. Similar plumage and behavior development was observed in hand-reared and parent-reared nestlings. In both cases, individual variation in bill markings and also begging calls was noted. The authors suggested that these individual differences may enable parent birds to locate and preferentially care for their young that leave the nests after about 15 days and live in groups or “crèches” of at least 30 similar aged birds.

Hurricane Hugo, a category 4 storm, ravaged the South Carolina coast in September 1989. Shepherd et al. (1991) examined the impact of Hurricane Hugo on the breeding ecology of wading birds at Pumpkinseed Island. They reported that damage to the vegetation on the island was slight overall, with the greatest damage to shrubs used by nesting Great Egrets and Snowy Egrets versus grasses and needlerush used by Tri-colored Herons, Glossy Ibises and White Ibises. The number of nesting pairs of Great Egrets and to a lesser extent Tri-colored Herons decreased after the storm while Snowy Egrets increased. Most dramatically, however, zero White Ibis nested on Pumpkinseed Island in 1990 when over 10,000 pairs had nested there in spring 1989. The authors suggested that Hurricane Hugo disturbed local freshwater feeding sites and reduced the availability of crayfish that the adults need to feed their young.

In the years following Hurricane Hugo, wading birds continued to use Pumpkinseed Island to varying degrees before abandoning the island completely after the breeding season of 2002. At least 35 years of use by wading birds is a long time for colonies that are reported to be nomadic. Why Pumpkinseed was abandoned after all those years remains a mystery but it is not unusual in the world of wading bird ecology. Pumpkinseed Island holds a special place in the history of wading birds in recent decades and in the hearts of so many who built their careers on studies carried out there.

» Insects

The insect discussion presented in the North Inlet section of the document also applies to Winyah Bay due to the very motile nature of most insect species. This said, some of the butterfly species that utilize specific host plants in marshes may be more abundant in brackish and freshwater marshes found along Winyah Bay versus the salt marshes of North Inlet. One example is the Palatka Skipper, *Euphyes pilatka* that uses Sawgrass, *Cladium jamaicense*, as its host plant. Sawgrass occurs in the brackish marshes within the Winyah Bay portion of the NERR. As mentioned in the North Inlet section, few studies have been conducted on insect dynamics and ecology within the NERR.

The Palatka Skipper occurs in the brackish marshes of Winyah Bay

» Invasive Species

Most of the invasive species described in the North Inlet section are also present or of concern in Winyah Bay. The Asian tiger shrimp, *Penaeus monodon*, has been collected in Winyah Bay and directly offshore, and the most documented infestation of the spiny hands crab, *Charybdis hellerii*, in South Carolina is in Winyah Bay (SERTC, 2014).

The first infection of the invasive swimbladder parasite *Anguillicoloides crassus* in the wild in the United States was reported in Winyah Bay in 1995. This nematode is endemic to East Asia, and is considered one potential reason for the decline in American eel, *Anguilla rostrata*. A recent study found that 46% of the American eels in Winyah Bay were infected with adult and 31% with larval *A. crassus*, and approximately 20% of eels examined in Winyah Bay showed severe swimbladder damage (Hein, 2012).

Similar to North Inlet, the common reed, *Phagmites australis*, is found throughout the area adjacent to the waters of Winyah Bay. The Winyah Bay Invasive Species Cost-share Program is a partnership of the Winyah Bay Task Force and the South Carolina Department of Natural Resources, National Fish and Wildlife Foundation, US Fish and Wildlife Service, Natural Resource Conservation Service, The Nature Conservancy, Clemson University, Historic Ricefields Association, Ducks Unlimited and other organizations. Funding is provided to assist in the treatment and control of *Phragmites* on private properties in Winyah Bay and the surrounding watershed.

Large rafts of hydrilla, *Hydrilla verticillata*, are periodically washed into Winyah Bay following upriver floods. These rafts may temporarily persist and become a nuisance where they accumulate around docks and other structures, but the salinity of the bay is too high for *Hydrilla* to become established.

In 2006 a red-bellied pacu, a fish closely related to piranha and native to South American rivers, was caught in the upper Sampit River. This individual was likely a pet release as this species is a popular aquarium pet fish that can grow up to 33 inches. While this single individual did not pose a threat to the Winyah Bay system, it did draw attention to the issue of invasions through intentional release.